Morphological and molecular identification of four new resupinate species of *Lyomyces* (Hymenochaetales) from southern China

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Abstract

Four new wood-inhabiting fungal species, *Lyomyces bambusinus*, *L. cremeus*, *L. macrosporus* and *L. wuliangshanensis*, are proposed based on a combination of morphological and molecular evidence. *Lyomyces bambusinus* is characterized by resupinate basidiomata with colliculose to tuberculate hymenial surface and broadly ellipsoid, hyaline, slightly thick-walled, smooth basidiospores. *Lyomyces cremeus* is characterised by resupinate basidiomata with smooth, cream hymenial surface and ellipsoid, hyaline, thin-walled to slightly thick-walled basidiospores. *Lyomyces macrosporus* is characterized by pruinose basidiomata with reticulate hymenial surface, presence of three kinds of cystidia and larger basidiospores (6.7–8.9 × 4.4–5.4 µm). *Lyomyces wuliangshanensis* is characterized by coriaceous basidiomata and ellipsoid, hyaline, slightly thick-walled, smooth basidiospores. The phylogenetic analyses based on molecular data of the internal transcribed spacer (ITS) region sequences revealed that the four new species belonged to *Lyomyces*. *Lyomyces bambusinus* grouped with *L. sambuci*. *Lyomyces cremeus* clade was sister to a clade comprised of *L. microfasciculatus*. *Lyomyces macrosporus* was sister to *L. allantosporus*. *Lyomyces wuliangshanensis* was closely related to *L. mascarensis*.

Keywords

Phylogeny, Schizoporeaceae, taxonomy, wood-inhabiting fungi, Yunnan Province
Introduction

Lyomyces P. Karst. typified by L. sambuci (Pers.) P. Karst., is a small corticioid genus characterized by resupinate to effused basidiomata with smooth to granular or odontioid 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, cyanophilous basidiospores (Karsten 1881; Bernicchia and Gorjón 2010). The members of Lyomyces grow on dead, still-attached or fallen branches of angiosperms, on dead wooden and herbaceous stems, or occasionally on gymnosperm wood (Yurchenko et al. 2017). Twenty-three species are currently known in Lyomyces worldwide (Rabenhorst 1851; Karsten 1881, 1882; Peck 1903; Bourdot and Galzin 1911; Cunningham 1959, 1963; Wu 1990; Hjortstam and Ryvarden 2009; Yurchenko et al. 2013, 2017; Gafforov et al. 2017; Riebesehl and Langer 2017) and five species were recorded in China (Xiong et al. 2009; Gafforov et al. 2017; Riebesehl and Langer 2017).

Molecular studies on Lyomyces and related genera have been carried out recently (Riebesehl and Langer 2017; Yurchenko et al. 2017; Viner et al. 2018; Riebesehl et al. 2019). Riebesehl and Langer (2017) indicated that Hyphodontia s.l. should be divided into several genera: Hastodontia (Parmasto) Hjortstam & Ryvarden, Hyphodontia J. Erikss, Kneiffiella (Pers.) Gray, Lagarobasidium Jülich, Lyomyces and Xyloodon (Pers.) Gray and thus 35 new combinations were proposed, including fourteen Lyomyces species. The clarification of Lyomyces sambuci complex was conducted based on ITS and 28S sequences analyses and four new species of Lyomyces were described (Yurchenko et al. 2017). Viner et al. (2018) studied the taxonomy of Lagarobasidium and Xyloodon, and showed that twelve species clustered into Lyomyces clade and then grouped with Xyloodon clade. Phylogenetic and morphological studies on Xyloodon showed that Xyloodon was distinct from Hastodontia, Hyphodontia, Kneiffiella and Lyomyces and the Lyomyces generic species L. sambuci was sister to L. crustosus (Pers.) P. Karst. formed a single lineage with a high support (Riebesehl et al. 2019).

During investigations on wood-inhabiting fungi in southern China, four additional taxa were found, which could not be assigned to any described species in Lyomyces. In this study, the authors expand samplings from previous studies (Gafforov et al. 2017; Riebesehl and Langer 2017) to examine taxonomy and phylogeny of them within Lyomyces, based on the internal transcribed spacer (ITS) regions sequences.

Materials and methods

Morphological studies

The specimens studied have been deposited in the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Special color terms fol-
Four new resupinate species of *Lyomyces* low Petersen (1996). Macromorphological descriptions are based on field notes. Micromorphological data were obtained from the dried specimens and observed under a light microscope following Dai (2010) and Cui et al. (2019). The following abbreviations are used: KOH = 5% potassium hydroxide; CB = cotton blue; CB+ = cyanophilous; IKI = Melzer’s reagent; IKI− = non-amyloid and non-dextrinoid; L = mean spore length (arithmetic average of all spores); W = mean spore width (arithmetic average of all spores); Q = L/W ratio; n (a/b) = number of spores (a) measured from given number (b) of specimens.

**DNA extraction and sequencing**

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 (Han et al. 2016; Song and Cui 2017). The ITS region was amplified with the primer pair ITS5 and ITS4 (White et al. 1990). 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 followed Shen et al. (2019). The PCR products were purified and directly sequenced at Kunming Tsingke Biological Technology Limited Company, Yunnan Province, P.R.China. All newly generated sequences were deposited in GenBank (Table 1).

**Phylogenetic analyses**

Sequencher 4.6 (GeneCodes, Ann Arbor, MI, USA) was used to assemble and edit the DNA sequence. Sequences were aligned in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/) using the “G-INS-I” strategy and manually adjusted in BioEdit (Hall 1999). The sequence alignment was deposited in TreeBase (submission ID 25382). Sequences of *Palifer verecundus* (G. Cunn.) Stalpers & P.K. Buchanan and *Xylodon asperus* (Fr.) Hjortstam & Ryvarden obtained from GenBank were used as outgroups to root trees following Yurchenko et al. (2017) in Fig. 1.

Maximum parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were applied to the ITS dataset sequences. Approaches to phylogenetic analyses followed Wu et al. (2018) and Zhu et al. (2019) 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 most-parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive
### Table 1. List of species, specimens and GenBank accession numbers of sequences used in this study.

| Species name               | Sample no.       | GenBank accession no. | References                                |
|----------------------------|------------------|-----------------------|-------------------------------------------|
| Lyomyces allantosporus     | KAS-GEL 4933     | KY800401              | Yurchenko et al. 2017                    |
|                            | FR 0249548       | KY800397              | Yurchenko et al. 2017                    |
| Lyomyces bambusinus        | CLZhao 3675      | MN945969              | Present study                            |
|                            | CLZhao 4808      | MN945970              | Present study                            |
|                            | CLZhao 4831      | MN945968              | Present study                            |
|                            | CLZhao 4840      | MN945971              | Present study                            |
| Lyomyces crenus            | CLZhao 2812      | MN945973              | Present study                            |
|                            | CLZhao 4138      | MN945974              | Present study                            |
|                            | CLZhao 8295      | MN945972              | Present study                            |
| Lyomyces crustus           | YG-G 39          | MF382993              | Gafforov et al. 2017                     |
|                            | UC 2022841       | KP814310              | Rosenthal et al. 2017                    |
| Lyomyces erastii           | MA-Fungi 34336   | JX857800              | Gafforov et al. 2017                     |
|                            | YG 022           | MF382992              | Gafforov et al. 2017                     |
| Lyomyces griseliniae       | KHL 12971        | DQ873651              | Larsson et al. 2006                      |
| Lyomyces juniperi          | KAS-GEL 4940     | DQ340316              | Yurchenko et al. 2017                    |
|                            | FR 0261086       | KY081799              | Riebesel and Langer 2017                 |
| Lyomyces macrosporus       | CLZhao 4516      | MN945977              | Present study                            |
|                            | CLZhao 4531      | MN945978              | Present study                            |
|                            | CLZhao 8605      | MN945975              | Present study                            |
|                            | CLZhao 3951      | MN945976              | Present study                            |
| Lyomyces mascarensis       | KAS-GEL 4833     | KY800399              | Yurchenko et al. 2017                    |
|                            | KAS-GEL 4908     | KY800400              | Yurchenko et al. 2017                    |
| Lyomyces microfasciculatus | CLZhao 4626      | MK343568              | Present study                            |
|                            | CLZhao 5109      | MN954311              | Present study                            |
|                            | TNM F 24757      | JN129976              | Yurchenko and Wu 2014                    |
| Lyomyces organensis        | MSK 7247         | KY800403              | Yurchenko et al. 2017                    |
| Lyomyces orientalis        | KAS-GEL 3376     | DQ340325              | Yurchenko et al. 2017                    |
|                            | KAS-GEL 3400     | DQ340326              | Yurchenko et al. 2017                    |
| Lyomyces pruni             | Ryberg 021018    | DQ873624              | Larsson et al. 2006                      |
| Lyomyces sambuci           | 80 SAMHYP        | JX857721              | Yurchenko et al. 2017                    |
|                            | 83 SAMHYP        | JX857720              | Yurchenko et al. 2017                    |
| Lyomyces vietnamensis      | TNM F 9073       | JX175044              | Yurchenko and Wu 2014                    |
| Lyomyces wuliangshanensis  | CLZhao 4108      | MN945980              | Present study                            |
|                            | CLZhao 4144      | MN945981              | Present study                            |
|                            | CLZhao 4167      | MN945979              | Present study                            |
|                            | CLZhao 4206      | MN945982              | Present study                            |
|                            | CLZhao 4475      | MN945983              | Present study                            |
| Palifer verecundus         | KHL 12261        | DQ873642              | Larsson et al. 2006                      |
| Xylodon asperus            | UC 2023169       | KP814365              | Yurchenko et al. 2017                    |

tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for each most-parsimonious tree generated.
Sequences were also analyzed using Maximum Likelihood (ML). ML analysis was conducted 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 2.3 (Nylander 2004) was used to determine the best-fit evolution model for the data set for Bayesian Inference (BI). Bayesian Inference was performed with MrBayes 3.1.2 with a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist and Huelsenbeck 2003). Four Markov chains were used in each of 2 runs from random starting trees for 600,000 generations, 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 that received bootstrap support for maximum likelihood (BS) ≥75%, maximum parsimony (BP) ≥75%, and Bayesian posterior probabilities (BPP) ≥0.95 were considered significantly supported.

Phylogeny results

The ITS dataset (Fig. 1) included sequences from 39 fungal specimens representing 18 species. The dataset had an aligned length of 608 characters, of which 277 characters were constant and 242 parsimony-informative. MP analysis yielded 8 equally parsimonious trees (TL = 978, CI = 0.523, HI = 0.478, RI = 0.738, RC = 0.385). The best-fit model for 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 0.008676. The tree topology obtained by BI and ML was similar to the MP one.

The phylogenetic tree (Fig. 1) demonstrated that all samples grouped into the Lyomyces in the present study. Lyomyces bambusinus grouped with L. sambuci. Lyomyces cremeus formed a monophyletic lineage and then grouped with L. microfasciculatus (Yurchenko & Sheng H. Wu) Riebesehl & Langer. Lyomyces macrosporus was sister to L. allantosporus Riebesehl, Yurchenko & Langer. Lyomyces wuliangshanensis was closely related to L. mascarensis Riebesehl, Yurchenko & Langer.

Taxonomy

Lyomyces bambusinus C.L. Zhao, sp. nov.
Figs 2, 6
MycoBank No: 834036

Holotype. China. Yunnan Province: Puer, Zhenyuan County, Heping Town, Ailaooshan National Nature Reserve, on dead bamboo, 11 January 2018, CLZhao 4831 (SWFC).

Etymology. The epithet bambusinus (Lat.): refers to the occurrence on bamboo.
Basidiomata. Annual, resupinate, ceraceous when fresh, becoming brittle and cracking upon drying, up to 20 cm long and 8 cm wide, 100–200 µm thick. Hymenial surface colliculose to tuberculate, white to cream when fresh, turning cream to buff upon drying. Margin narrow, concolorous with hymenial surface.

Hyphal system. Monomitic; generative hyphae with clamp connections, hyaline, thick-walled, branched, 2.5–3.9 µm in diameter, IKI–, cyanophilous; tissues unchanged in KOH. Numerous crystals present among hyphae.

Hymenium. Two kinds of cystidia: 1) capitate, hyaline, thin-walled, 35–55 × 4–7 µm, smooth or slightly encrusted; 2) tapering, hyaline, thin-walled, 40–65 × 4–5.5 µm, smooth or slightly encrusted; cystidioles present, hyaline, thin-walled, 12–17 × 2–3 µm. Basidia clavate, constricted, thin-walled, with four sterigmata and a basal clamp connection, 16.5–35 × 3.5–7 µm.

Spores. Basidiospores broadly ellipsoid, hyaline, slightly thick-walled, smooth, IKI–, cyanophilous, guttulate, (4.5–)4.7–5.9 (–6.2) × (3.4–)3.7–4.6(–4.8) µm, L = 5.31 µm, W = 4.19 µm, Q = 1.23–1.3 (n = 120/4).

Ecology and distribution. On dead bamboo, causing a white rot. China.

Additional specimens examined. China. Yunnan Province: Puer, Jingdong County, Wuliangshan National Nature Reserve, on dead bamboo, 3 October 2017, CLZhao 3675; Zhenyuan County, Heping Town, Ailaoshan National Nature Reserve, on dead bamboo, 11 January 2018, CLZhao 4808, CLZhao 4840 (SWFC).
Four new resupinate species of *Lyomyces*

Figure 2. Basidiomata of *Lyomyces bambusinus* (holotype). Scale bars: 1 cm (A); 5 mm (B).
**Lyomyces cremeus** C.L. Zhao, sp. nov.
Figs 3, 7
MycoBank No: 834037

**Holotype.** China. Yunnan Province: Jingdong County, Taizhong Town, Ailaoshan Ecological Station, on fallen branch of angiosperm, 23 August 2018, CLZhao 8295 (SWFC).

**Etymology.** The epithet *cremeus* (Lat.): refers to the cream hymenial surface.

**Basidiomata.** Annual, resupinate, ceraceous when fresh, becoming membranaceous upon drying, up to 13 cm long and 5 cm wide, 50–100 µm thick. Hymenial surface smooth, pale cream when fresh, turn cream upon drying. Margin narrow, white to cream.

**Hyphal system.** Monomitic; generative hyphae with clamp connections, hyaline, thick-walled, branched, 3–5 µm in diameter, IKI–, cyanophilous; tissues unchanged in KOH. Numerous crystals present among hyphae.

**Hymenium.** Two kinds of cystidia: 1) capitate, hyaline, thin-walled, 20–40 × 3–5 µm, smooth or slightly encrusted; 2) tapering, hyaline, thin-walled, 18–35 × 3–4.5 µm, smooth or slightly encrusted; cystidioles present, hyaline, thin-walled, 15–20 × 2.5–4 µm. Basidia clavate, with four sterigmata and a basal clamp connection, 9–18.5 × 3–6 µm.

**Spores.** Basidiospores ellipsoid, hyaline, thin-walled to slightly thick-walled, smooth, IKI–, cyanophilous, guttulate, 4.5–5.6(–5.8) × 3.3–4.3(–4.5) µm, L = 5.01 µm, W = 3.94 µm, Q = 1.25–1.3 (n = 90/3).

**Ecology and distribution.** Lignicolous, causing a white rot. China.

**Additional specimens examined.** China. Yunnan Province: Yuxi, Xinping County, Shimenxia Forestry Park, on fallen branch of angiosperm, 21 August 2017, CLZhao 2812; Puer, Jingdong County, Wuliangshan National Nature Reserve, on fallen branch of angiosperm, 5 October 2017, CLZhao 4138 (SWFC).

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**Lyomyces macrosporus** C.L. Zhao, sp. nov.
Figs 4, 8
MycoBank No: 834038

**Holotype.** China. Yunnan Province: Puer, Jingdong County, Taizhong Town, Ailaoshan National Nature Reserve, on fallen branch of angiosperm, 24 August 2018, CLZhao 8605 (holotype in SWFC).

**Etymology.** The epithet *macrosporus* (Lat.): refers to the larger basidiospores.

**Basidiomata.** Annual, resupinate, subceraceous when fresh, becoming pruinose upon drying, up to 22 cm long and 3 cm wide, 100–200 µm thick. Hymenial surface reticulate, cream when fresh, turning cream to buff upon drying. Margin narrow, white to buff.
Figure 3. Basidiomata of *Lyomyces cremeus* (holotype). Scale bars: 1 cm (A); 5 mm (B).
Figure 4. Basidiomata of *Lyomyces macrosporus* (holotype). Scale bars: 1 cm (A); 5 mm (B).

**Hyphal system.** Monomitic; generative hyphae with clamp connections, hyaline, thick-walled, branched, 2.5–4 μm in diameter, IKI−, cyanophilous; tissues unchanged in KOH. Numerous crystals present among hyphae.
Four new resupinate species of *Lyomyces*

**Hymenium.** Three kinds of cystidia: 1) capitate, hyaline, thin-walled, 19–35 × 3–7 µm; 2) tapering, hyaline, thin-walled, 13–20 × 2.5–4 µm; 3) moniliform, hyaline, thin-walled, 15–22 × 4.5–6 µm; fusoid cystidioles present, hyaline, thin-walled, 15–20 × 2.5–4 µm. Basidia subclavate to clavate, constricted, hyaline, thin-walled, with four sterigmata and a basal clamp connection, 22.2–38 × 4.5–7 µm.

**Spores.** Basidiospores ellipsoid, hyaline, slightly thick-walled, smooth, IKI–, cyanophilous, guttulate, (6.4–)6.7–8.9(–9.1) × 4.4–5.4(–5.7) µm, L = 7.84 µm, W = 4.93 µm, Q = 1.48–1.8 (n = 120/4).

**Ecology and distribution.** Lignicolous, causing a white rot. China.

**Additional specimens examined.** China. Yunnan Province: Puer, Jingdong County, Taizhong Town, Ailaoshan National Nature Reserve, on fallen branch of angiosperm, 4 October 2017, CLZhao 3951; Wuliangshan National Nature Reserve, on fallen branch of angiosperm, 6 October 2017, CLZhao 4516, CLZhao 4531 (SWFC).

*Lyomyces wuliangshanensis* C.L. Zhao, sp. nov.

Figs 5, 9
MycoBank No: 834039

**Holotype.** China. Yunnan Province: Puer, Jingdong County, Wuliangshan National Nature Reserve, on fallen branch of angiosperm, 5 October 2017, CLZhao 4167 (SWFC).

**Etymology.** The epithet *wuliangshanensis* (Lat.): refers to the locality (Wuliangshan) of the type specimens.

**Basidiomata.** Annual, resupinate, subcoriaceous when fresh, becoming coriaceous upon drying, up to 15 cm long and 5 cm wide, 50–150 µm thick. Hymenial surface smooth to more or less tuberculate, white to cream when fresh, turning cream to buff upon drying. Margin narrow, concolorous with hymenial surface.

**Hyphal system.** Monomitic; generative hyphae with clamp connections, hyaline, thick-walled, branched, 2–3 µm in diameter, IKI–, cyanophilous; tissues unchanged in KOH. Numerous crystals present among hyphae.

**Hymenium.** Two kinds of cystidia: 1) capitate, hyaline, thin-walled, 22–37 × 3–6 µm; 2) tapering, hyaline, thin-walled, 21–35 × 4–6.5 µm; fusoid cystidioles present, hyaline, thin-walled, 16–21 × 2.5–3.5 µm. Basidia clavate, hyaline, thin-walled, with four sterigmata and a basal clamp connection, 12–20 × 3–4.3 µm.

**Spores.** Basidiospores ellipsoid, hyaline, slightly thick-walled, smooth, IKI–, cyanophilous, guttulate, (3.3–)3.5–5.3(–5.5) × 2.8–4(–4.2) µm, L = 4.3 µm, W = 3.56 µm, Q = 1.22–1.31 (n = 120/4).

**Ecology and distribution.** Lignicolous, causing a white rot. China.

**Additional specimens examined.** China. Yunnan Province: Puer, Jingdong County, Wuliangshan National Nature Reserve, on angiosperm trunk, 5 October 2017, CLZhao 4108, CLZhao 4144; on angiosperm stump, 5 October 2017, CLZhao 4206; on fallen branch of angiosperm, 6 October 2017, CLZhao 4475 (SWFC).
Figure 5. Basidiomata of *Lyomyces wuliangshanensis* (holotype). Scale bars: 1 cm (A); 5 mm (B).
Four new resupinate species of *Lyomyces*

**Figure 6.** Microscopic structures of *Lyomyces bambusinus* (drawn from the holotype) **A** basidiospores **B** basidia and basidioles **C** cystidia **D** cystidioles **E** a cross section of basidiomata. Scale bars: 5 µm (A); 10 µm (B–E).

**Figure 7.** Microscopic structures of *Lyomyces cremeus* (drawn from the holotype) **A** basidiospores **B** basidia and basidioles **C** cystidia **D** cystidioles **E** a cross section of basidiomata. Scale bars: 5 µm (A); 10 µm (B–E).
Figure 8. Microscopic structures of *Lyomyces macrosporus* (drawn from the holotype) A basidiospores B basidia and basidioles C cystidia D cystidioles E a cross section of basidiomata. Scale bars: 10 µm (A–E).

Figure 9. Microscopic structures of *Lyomyces wuliangshanensis* (drawn from the holotype) A basidiospores B basidia and basidioles C cystidia D cystidioles E a cross section of basidiomata. Scale bars: 5 µm (A); 10 µm (B–E).
Discussion

Miettinen et al. (2016) analyzed a phylogenetic classification in Phanerochaetaceae (Polyporales, Basidiomycota) and showed that the macromorphology of basidiomata and hymenophore construction did not reflect monophyletic groups. The phylogeny we obtained (Fig. 1) shows that the macromorphological and micromorphological characters are not consistent with monophyletic groups.

In our phylogeny, *Lyomyces bambusinus* was sister to *L. sambuci*, but morphologically *L. sambuci* differs from *L. bambusinus* by having ellipsoid to oblong, narrower basidiospores (4.5–6 × 3–3.5 µm, Yurchenko et al. 2017). *Lyomyces cremeus* formed a monophyletic lineage with strong supports (100% BS, 100% BP, 1.00 BPP; Fig. 1) and then was sister to a clade comprised of *L. microfasciculatus*, *L. mascarensis*, and *L. wuliangshanensis*. However *L. microfasciculatus* differs in odontoid hymenophore and presence of minute peg-like fascicles of hyphae (Yurchenko and Wu 2014). *Lyomyces macrosporus* was sister to *L. allantosporus*, but morphologically *L. allantosporus* differs in having porulose hymenophore and suballantoid to allantoid, narrower basidiospores (7–9 × 3–3.8 µm, Yurchenko et al. 2017). *Lyomyces wuliangshanensis* grouped closely with *L. mascarensis*, but *L. mascarensis* differs from *L. wuliangshanensis* by having thin-walled generative hyphae and presence of capitate cystidia (17–38 × 3.5–6 µm, Yurchenko et al. 2017).

Five *Lyomyces* species were reported from China prior to this study, *Lyomyces albus* (Sheng H. Wu) Riebesehl & Langer, *L. capitatocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & Langer, *L. microfasciculatus*, *L. sambuci* and *L. tenuissimus* (Yurchenko & Sheng H. Wu) Riebesehl & Langer. *Lyomyces albus* differs from four new species by its odontoid hymenophore (Riebesehl and Langer 2017); *L. capitatocystidiatus* by grandinoid hymenophore with arachnoid-farinaceous hymenial surface (Xiong et al. 2009); *L. microfasciculatus* by minutely odontoid hymenial surface and small emerging fascicles of flexuous hyphae (Yurchenko and Wu 2014); *L. tenuissimus* by much thinner basidiomata and non-encrusted, subicular hyphae, shorter cystidia and shorter basidia (Yurchenko et al. 2013).

*Hyphodontia* s.l. is an extensively studied group of Hymenochaetales (Dai 2012; Viner et al. 2018; Riebesehl et al. 2019), but the Chinese species diversity is still not well known, especially in subtropical and tropical areas. The four new *Lyomyces* species here described are from the subtropics.

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References

Bernicchia A, Gorjón SP (2010) Fungi Europaei 12: Corticiaceae l. Edizioni Candusso, Lomazzo, 1–1007.

Bourdot H, Galzin A (1911) Hyménomycètes de France: III. Corticiées: Corticium, Epitbele, Asterostromella. Bulletin de la Société Mycologique de France 27: 223–266.

Cui BK, Li HJ, Ji X, Zhou JL, Song J, Si J, Yang ZL, Dai YC (2019) Species diversity, taxonomy and phylogeny of Polyporaceae (Basidiomycota) in China. Fungal Diversity 97: 137–392. https://doi.org/10.1007/s13225-019-00427-4

Cunningham GH (1959) Hydnaceae of New Zealand. Part II. The genus Odontia. In Transactions of the Royal Society of New Zealand 86: 65–103.

Cunningham GH (1963) The Thelephoraceae of Australia and New Zealand. Bulletin of the New Zealand Department of Scientific and Industrial Research 145: 1–359.

Dai YC (2012) Polypore diversity in China with an annotated checklist of Chinese polypores. Mycoscience 53: 49–80. https://doi.org/10.1007/s10267-011-0134-3

Felsenstein J (1985) Confidence intervals on phylogenetics: an approach using bootstrap. Evolution 39: 783–791. https://doi.org/10.2307/2408678

Gafforov Y, Riebesehl J, Ordynets A, Langer E, Ghabad-Nejad M, Zhou LW, Wang XW, Gugliotta ADM (2017) Hyphodontia (Hymenochaetales, Basidiomycota) and similar taxa from Central Asia. Botany 95: 1041–1056. https://doi.org/10.1139/cjb-2017-0115

Hall TA (1999) Bioedit: A user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Han ML, Chen YY, Shen LL, Song J, Vlasák J, Dai YC, Cui BK (2016) Taxonomy and phylogeny of the brown-rot fungi: Fomitopsis and its related genera. Fungal Diversity 80: 343–373. https://doi.org/10.1007/s13225-016-0364-y

Hjortstam K, Ryvarden L (2009) A checklist of names in Hyphodontia sensu stricto - sensu lato and Schizopora with new combinations in Lagarobasidium, Lyomyces, Kneiffiella, Schizopora, and Xylodon. Synopsis Fungorum 26: 33–55.

Karsten PA (1881) Enumeratio Thelephorearum Fr. et Clavariearum Fr. Fennicarum, systemate novo dispositarum. Revue Mycologique Toulouse 3: 21–23.

Karsten PA (1882) Rysslands, Finlands och den Skandinaviska halvöns Hattsvampar. Sednare Delen: Pip-, Tagg-, Hud-, Klubb- och Gelésvampar. Bidrag till Kännedom av Finlands Natur och Folk 37: 1–257.

Larsson KH, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. Mycologia 98: 926–936. https://doi.org/10.1080/15572536.2006.11832622

Miettinen O, Spirin V, Vlasák J, Rivoire B, Stenroos S, Hibbett D (2016) Polypores and genus concepts in Phanerochaetaeaceae (Polyporales, Basidiomycota). MycoKeys 17: 1–46. https://doi.org/10.3897/mycokeys.17.10153

Miller MA, Holder MT, Vos R, Midford PE, Liebowitz T, Chan L, Hoover P, Warnow T (2009) The CIPRES Portals. CIPRES. http://www.phylo.org/sub_sections/portal [2009-08-04. (Archived by WebCite(r) at http://www.webcitation.org/5imQlJeQa)
Four new resupinate species of *Lyomyces*

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Peck CH (1903) Report of the state botanist. Bulletin of the New York State Museum 67: 1–194.

Petersen JH (1996) Farvekort. The Danish Mycological Society's colour-chart. Foreningen til Svampekundskabens Fremme, Greve, 6.

Rabenhorst GL (1851) Klotzschii herbarium vivum mycologicum sistens fungorum per totam *Germaniam crescentium* collectionem perfectam. Editio prima. Centuria 8: 1501–1600.

Riebesehl J, Langer E (2017) *Hyphodontia* s.l. (Hymenochaetales, Basidiomycota) – 35 new combinations and new keys to currently all 120 species. Mycological Progress 16: 637–666. https://doi.org/10.1007/s11557-017-1299-8

Riebesehl J, Yurchenko E, Nakasone KK, Langer E (2019) Phylogenetic and morphological studies in *Xylodon* (Hymenochaetales, Basidiomycota) with the addition of four new species. MycoKeys 47: 97–137. https://doi.org/10.3897/mycokeys.47.31130

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. https://doi.org/10.1093/bioinformatics/ btg180

Rosenthal LM, Larsson KH, Branco S, Chung JA, Glassman SI, Liao HL, Liao HL, Peay KG, Smith DP, Talbot JM, Taylor JW, Vellinga EC, Vilgalys R, Bruns TD (2017) Survey of corticioid fungi in North American pinaceous forests reveals hyperdiversity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. Mycologia 109: 115–127. https://doi.org/10.1080/00275514.2017.1281677

Shen LL, Wang M, Zhou JL, Xing JH, Cui BK, Dai YC (2019) Taxonomy and phylogeny of *Postia*. Multi-gene phylogeny and taxonomy of the brown-rot fungi: *Postia* and its related genera. Persoonia 42: 101–126. https://doi.org/10.3767/persoonia.2019.42.05

Song J, Cui BK (2017) Phylogeny, divergence time and historical biogeography of *Laeetiporus* (Basidiomycota, Polyporales). BMC Evolutionary Biology 17: 102. https://doi.org/10.1186/s12862-017-0948-5

Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4.0b10. Sinauer Associates, Massachusetts.

Viner I, Spirin V, Zibarová L, Larsson KH (2018) Additions to the taxonomy of *Lagarobasidium* and *Xylodon* (Hymenochaetales, Basidiomycota). MycoKeys 41: 65–90. https://doi.org/10.3897/mycokeys.41.28987

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: a guide to methods and applications. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wu SH (1990) The Corticiaceae (Basidiomycetes) subfamilies Phlebiaeidae, Phanerochaetoidae and Hyphodermoideae in Taiwan. Acta Botanica Fennica 142: 1–123.

Wu ZQ, Xu TM, Shen S, Liu XF, Luo KY, Zhao CL (2018) *Elaphroporia ailaoshanensis* gen. et sp. nov. in Polyporales (Basidiomycota). MycoKeys 29: 81–95. https://doi.org/10.3897/mycokeys.29.22086

Xiong HX, Dai YC, Wu SH (2009) Three new species of *Hyphodontia* from Taiwan. Mycological Progress 8: 165–169. https://doi.org/10.1007/s11557-009-0587-3

Yurchenko E, Wu SH (2014) Three new species of *Hyphodontia* with peg-like hyphal aggregations. Mycological Progress 13: 533–545. https://doi.org/10.1007/s11557-013-0935-1
Yurchenko E, Riebesehl J, Langer E (2017) Clarification of *Lyomyces sambuci* complex with the descriptions of four new species. Mycological Progress 16: 865–876. https://doi.org/10.1007/s11557-017-1321-1

Yurchenko E, Xiong HX, Wu SH (2013) Four new species of *Hyphodontia* (*Xylodon* Hjortstam & Ryvarden, Basidiomycota) from Taiwan. Nova Hedwigia 96: 545–558. https://doi.org/10.1127/0029-5035/2013/0092

Zhu L, Song J, Zhou JL, Si J, Cui BK (2019) Species diversity, phylogeny, divergence time and biogeography of the genus *Sanghuangporus* (Basidiomycota). Frontiers in Microbiology 10: 812. https://doi.org/10.3389/fmicb.2019.00812