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A novel species of *Blackwellomyces* in Guizhou, China

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Abstract

A new species, *Blackwellomyces larvatus*, is described and illustrated from Guizhou, representing the first record of *Blackwellomyces* in this region. This species belongs to the family *Cordycipitaceae* and was discovered parasitizing a lepidopteran larva. It is characterized by orange stromata and the production of a light purple pigment that diffuses into the medium when cultured on potato dextrose agar. Phylogenetic analyses based on a multi-gene dataset indicate that *B. larvatus* is phylogenetically close to *B. kaihuaensis* but forms a distinct lineage, providing support for its recognition as a novel species.

Key words: 1 new species, *Cordycipitaceae*, morphology, phylogenetic analyses

Introduction

Blackwellomyces is a genus of entomopathogenic fungi placed in *Cordycipitaceae*, *Hypocreales*, *Sordariomycetidae, Sordariomycetes* (Hyde *et al*. 2024) that primarily infects arthropod larvae, particularly lepidoptera (Hyde *et al.* 2019, Chuang *et al.* 2024). Since *Blackwellomyces* was segregated from *Cordyceps*, ten species have been accommodated, including six taxa recorded from Thailand (*B. aurantiacus*, *B. calendulinus*, *B. lateris*, *B. minutus*, *B. pseudomilitaris*, *B. roseostromatus*) (Hywel-Jones 1994, Schoch *et al.* 2012, Kepler *et al.* 2017, Hyde *et al.* 2019, Mongkolsamrit *et al.* 2020); and one each from Taiwan (*B. taiwanensis*), Yunnan (*B. changningensis*) and Zhejiang (*B. kaihuaensis*) in China (Li *et al.* 2023, Chuang *et al.* 2024, Ma *et al.* 2024); and *B. cardinalis* (type), which has been recorded in USA, Japan, Republic of Korea and Sichuan Province in China (Kepler *et al.* 2017). *Blackwellomyces* typically produces yellow or orange ascostromata and filiform multi-septate ascospores that do not break into part-spores upon maturity, distinguishing it from other members of *Cordycipitaceae* (Kepler *et al.* 2017). The asexual morph of this genus is usually acremonium-like, evlachovaea-like or mariannaea-like (Mongkolsamrit *et al.* 2020) and their colonies form dense white mycelia on potato dextrose agar (PDA) (Ma *et al.* 2024). Some colonies (e.g., of *B. roseostromatus*)

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produce reddish pigments, which typically readily diffuse into the medium (Sung & Spatafora 2004, Mongkolsamrit *et al.* 2020, Li *et al.* 2023, Ma *et al.* 2024).

Guizhou is a major vegetable-producing region in China, known for its large-scale cultivation of peppers and beans, which are often affected by lepidopteran pests. In this study, we report the first collection of a *Blackwellomyces* species from lepidopteran larvae in Guizhou. We provide a comprehensive description of this species and infer its phylogeny using Bayesian inference (BI) and maximum likelihood (ML) analyses, based on a concatenated dataset of ITS, LSU, SSU, *rpb1*, *rpb2*, and *tef1-α* sequences. The results indicate that following the guidelines of Jayawardena *et al*. (2021), the collected specimen represents a new member of *Blackwellomyces*, which we have named *B. larvatus*.

Materials & methods

Sample collection, morphological studies and isolation

The samples were collected from soil of a mixed forest in Dabanshui Mountain, Zunyi, Guizhou, China, on 21 July 2024, and brought to the laboratory in sealed plastic boxes. The specimens were examined using a Nikon SMZ800N stereomicroscope, and images were taken with a DS-2000 camera, while ImageView was applied to record and measure data. Micromorphological features were examined using a Nikon ECLIPSE Ni compound microscope, and images were taken with a Nikon Digital Sight 10 camera. Measurements were performed using the NIS Elements program version 5.42.02. The photoplates were processed with Adobe Photoshop 2021 software (Adobe Systems, USA). The specimens were deposited in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (HKAS). To obtain a pure culture, a portion of the fruiting body was excised, immersed in 30% hydrogen peroxide for 10–20 seconds, gently rinsed with sterile water, and divided into 3–5 segments using a sterile scalpel. These segments were then inoculated onto PDA medium and incubated at room temperature (28 ± 5 °C) for 7–14 days (Wei *et al.* 2022). The cultures were deposited at Kunming Institute of Botany Culture Collection (KUNCC). Facesoffungi and Index Fungorum numbers were obtained following the methods of Jayasiri *et al.* (2015) and Index Fungorum (2025).

DNA extraction, PCR amplification and sequencing

A small amount of mycelium was scraped from the pure culture into a 1.5 mL centrifuge tube, and DNA was extracted using Ezup Column Fungi Genomic DNA Purification Kit (Sangon Biotech) following the instructions of the manufacturer. To amplify the ribosomal internal transcribed spacer (ITS) region, the primer pair ITS4 and ITS5 was used (White *et al.* 1990). The ribosomal small (18S) and large (28S) subunits were amplified using primer pairs NS4 and NS1 (White *et al.* 1990) and LR5 and LR0R (Vilgalys & Hester 1990), respectively. The largest and second-largest subunit sequences of RNA polymerase II (*rpb1* and *rpb2*) were amplified using primer pairs RPB1-Af and RPB1-Cr (Matheny 2005) and RPB2-5f and RPB2-7cR (Liu *et al.* 1999), respectively. The translation elongation factor 1-α (*tef1-α*) was amplified using primer pairs EF1-983 and EF1-2218 (Sung *et al.* 2007b). The PCR profiles were as follows: an initial denaturation at 98 °C for 2 min, followed by 35 cycles of denaturation at 98 °C for 10 sec, annealing at 56 °C (ITS) or 55 °C (LSU/SSU/*rpb2*/*tef1-α*) or 50 °C (*rpb1*) for 1 min and extension at 72 °C for 10 sec, with a final extension at 72 °C for 2 min. The PCR products were sent to a commercial sequencing provider (Tsingke Company, Beijing, P.R. China) and sequenced using the primers mentioned above.

Phylogenetic analysis

DNA sequences were first analyzed using BioEdit v. 7.7.1 software to assess sequence quality and subsequently submitted to BLASTn on the NCBI website (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Relevant species and outgroup sequences were selected based on previous studies (Mongkolsamrit *et al.* 2020, Huang *et al.* 2021, Li *et al.* 2023, Ma *et al.* 2024, Phutthacharoen *et al.* 2024) and downloaded from GenBank for constructing multiple sequence alignments (Table 1). Multiple sequence alignments were performed using MAFFT v. 7.409 (http://mafft.cbrc.jp/) with default settings and manually refined using BioEdit v. 7.2.5 software.

Phylogenetic analyses were conducted using maximum likelihood (ML) for all individual and combined loci (results of individual gene analyses are not presented), while Bayesian inference (BI) was used only for combined gene analyses. For ML analysis, the optimal substitution model for each gene region was determined using the

model selection criteria available in IQ-TREE v. 1.6.12, based on the Akaike information criterion (AIC) (ITS/*tef1-α*: TN+F+G4; LSU: TN+F+I+G4; SSU: TNe+I; *rpb1*: TN+F+I+G4; *rpb2*: TIMe+I+G4). The ML tree was inferred using the ultrafast bootstrap algorithm in IQ-TREE with concatenated datasets, and 1,000 bootstrap replicates were performed. Maximum likelihood bootstrap (BS) values ≥ 70% are indicated at each node (Nguyen *et al.* 2015).

For BI analysis, the optimal evolutionary model was determined under AIC using MrModeltest v. 2.3 (ITS/LSU/*tef1-α*: GTR+I+G; *rpb1*/*rpb2*/SSU: SYM+I+G) (Nylander 2004). BI trees were generated using MrBayes v. 3.2.7 (Ronquist & Huelsenbeck 2003) based on the optimal criteria for each partition. As part of the burn-in procedure, all sampled topologies below the asymptote (25%) were discarded. The computation stopped when the 'average standard deviation of split frequencies' reached 0.01, and the remaining trees were used to calculate posterior probabilities (PP) in a majority-rule consensus tree. PP values ≥ 0.90 are indicated below or above each node (Fig. 1). Phylogenetic trees and data files were visualized using FigTree v. 1.4.4. (http://tree.bio.ed.ac.uk/software/figtree/) and processed by Adobe Illustrator 2020 (Adobe Systems, USA).

Results

Phylogeny

This study applied a six-gene concatenated dataset for the phylogenetic reconstruction of the genus *Blackwellomyces* in *Cordycipitaceae*, comprising 48 taxa and a total of 4642 nucleotide positions (ITS: 461 bp; LSU: 792 bp; SSU: 944 bp; *rpb1*: 573 bp; *rpb2*: 1017 bp; *tef1-α*: 855 bp). Two strains of *Purpureocillium lilacinum* (CBS 284.36 and CBS 431.87) in the family *Ophiocordycipitaceae* were chosen as the outgroup. Despite slight differences in statistical support for certain branches, the topologies revealed by ML and BI were almost identical (Fig. 1). The monophyly of the genus *Blackwellomyces* is strongly supported (BS = 100%, PP = 1.00). In the phylogenetic tree (Fig. 1), the new collections from Guizhou (KUNCC 25-19105 and KUNCC 25-19106) are grouped together with *B. kaihuaensis* Yi Li, X.C. Zhao, A. Xu & W.F. Lin, collected from Zhejiang province, China.

TABLE 1. Strains and GenBank accession numbers of the isolates used in this study. Isolates from this study are in bold. Ex-type cultures are indicated by ^{T} while − indicates absent.

Species	Voucher/Culture	GenBank accession number						References
		ITS	nrLSU	nrSSU	*rpb1*	*rpb2*	*tef1-α*	
Akanthomyces aculeatus	TS772	KC519371	KC519370	KC519368	−	−	KC519366	Sanjuan *et al.* (2014)
Aka. aculeatus	HUA 186145 ^{T}	−	MF416520	MF416572	−	−	MF416465	Kepler *et al.* (2017)
Ascopolyporus polychrous	P.C. 546	−	DQ118737	−	DQ127236	−	DQ118745	Chaverri *et al.* (2005)
Asc. villosus	ARSEF 6355	−	AY886544	−	DQ127241	−	DQ118750	Chaverri *et al.* (2005) Bischoff *et al.* (2005)
Beauveria bassiana	ARSEF 1564 ^{T}	HQ880761	−	−	HQ880833	HQ880905	HQ880974	Rehner *et al.* (2011)
Bea. bassiana	ARSEF 7518	HQ880762	−	−	HQ880834	HQ880906	HQ880975	Rehner *et al.* (2011)
Blackwellomyces aurantiacus	BCC 85060 ^{T}	MT000692	MT003028	−	MK411600	MT017819	MK411598	Mongkolsamrit *et al.* (2020)
Bla. aurantiacus	BCC 85061	MT000693	MT003029	−	MK411601	MT017820	MK411599	Mongkolsamrit *et al.* (2020)
Bla. calendulinus	BCC 68500	MT000694	MT003030	−	MT017802	MT017821	MT017842	Mongkolsamrit *et al.* (2020)
Bla. calendulinus	BCC 68502 ^{T}	MT000695	MT003031	−	MT017803	MT017822	MT017843	Mongkolsamrit *et al.* (2020)
Bla. cardinalis	OSC 93610	JN049843	AY184963	AY184974	EF469088	EF469106	EF469059	Sung & Spatafora (2004), Sung *et al.* (2007a) Kepler *et al.* (2012)
Bla. cardinalis	CBS 113411	MH862928	MH874496	NG_013131	−	−	−	Vu *et al.* (2019)
Bla. cardinalis	OSC 93609 ^{T}	−	AY184962	AY184973	DQ522370	DQ522422	DQ522325	Sung & Spatafora (2004) Spatafora *et al.* (2007)

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TABLE 1. (Continued)

Species	Voucher/Culture	GenBank accession number						References
		ITS	nrLSU	nrSSU	*rpb1*	*rpb2*	*tef1-α*	
Bla. changningensis	YFCC 9250 T	PP568073	OR492316	OR492002	OR588131	OR637359	OR608508	Ma *et al.* (2024)
Bla. changningensis	YFCC 9251	PP568074	OR492314	OR492000	OR588132	–	OR608509	Ma *et al.* (2024)
Bla. changningensis	YFCC 9252	PP568075	OR492315	OR492001	OR588133	OR637358	OR608510	Ma *et al.* (2024)
Bla. kaihuaensis	HMAS 285455 T	OQ981961	OQ981968	OQ981975	OQ980409	OQ980408	OQ980401	Li *et al.* (2023)
Bla. kaihuaensis	HMAS 285456	OQ981962	OQ981969	OQ981976	OQ980410	–	OQ980402	Li *et al.* (2023)
Bla. larvatus	**H002-1**	**PQ816945**	**PQ826422**	**PQ826406**	**PQ868080**	**PQ868082**	**PQ868078**	this study
Bla. larvatus	**H002-2**	**PQ826404**	**PQ826423**	**PQ826407**	**PQ868081**	**PQ868083**	**PQ868079**	**this study**
Bla. lateris	MFLU 18-0663 T	MK086059	MK086061	MK086057	MK084615	MK079354	MK069471	Hyde *et al.* (2019)
Bla. minutus	BCC 88269 T	MT000696	MT003032	–	MT017804	MT017823	MT017844	Mongkolsamrit *et al.* (2020)
Bla. pseudomilitaris	BCC 1919 T	–	MF416534	MF416588	–	MF416440	MF416478	Kepler *et al.* (2017)
Bla. pseudomilitaris	BCC 2091	–	MF416535	MF416589	–	MF416441	MF416479	Kepler *et al.* (2017) Hywel-Jones (1994)
Bla. pseudomilitaris	NBRC 101409	JN943305	JN941393	JN941748	JN992482	–	–	Schoch *et al.* (2012)
Bla. pseudomilitaris	NBRC 101410	JN943307	JN941394	JN941747	JN992481	–	–	Schoch *et al.* (2012)
Bla. roseostromatus	BCC 91358 T	MT000697	MT003033	–	MT017805	MT017824	MT017845	Mongkolsamrit *et al.* (2020)
Bla. roseostromatus	BCC 91359	MT000698	MT003034	–	MT017806	MT017825	MT017846	Mongkolsamrit *et al.* (2020)
Bla. roseostromatus	BCC 91360	MT000699	MT003035	–	MT017807	MT017826	MT017847	Mongkolsamrit *et al.* (2020)
Bla. taiwanensis	NTUPPMCC 20-068	MT974227	MT974411	–	–	MW200251	–	Chuang *et al.* (2024)
Bla. taiwanensis	NTUPPMCC 20-071 T	MT974225	MT974409	–	MW200246	MW200250	MW200242	Chuang *et al.* (2024)
Bla. taiwanensis	NTUPPMCC 20-072	MT974226	MT974410	–	–	–	–	Chuang *et al.* (2024)
Cordyceps jakajanicola	BCC 79816 T	–	MN275696	–	MN338484	MN338489	MN338479	Mongkolsamrit *et al.* (2020)
C. jakajanicola	BCC 79817	–	MN275697	–	MN338485	MN338490	MN338480	Mongkolsamrit *et al.* (2020)
C. lepidopterorum	TBRC 7263 T	MF140765	MF140699	–	MF140768	MF140792	MF140819	Mongkolsamrit *et al.* (2018)
C. lepidopterorum	TBRC 7264	MF140766	MF140700	–	MF140769	MF140793	MF140820	Mongkolsamrit *et al.* (2018)
C. militaris	YFCC 6587	–	MN576818	MN576762	MN576878	MN576932	MN576988	Wang *et al.* (2020)
C. militaris	YFCC 5840	–	MN576819	MN576763	MN576879	MN576933	MN576989	Wang *et al.* (2020)
C. neopruinosa	BCC 91361 T	MT000711	MT003047	–	–	MT017838	MT017858	Mongkolsamrit *et al.* (2020)
C. neopruinosa	BCC 91362	MT000712	MT003048	–	MT017818	MT017839	MT017859	Mongkolsamrit *et al.* (2020)
Lecanicillium psalliotae	CBS 532.81	MH861374	AF339560	AF339609	EF469096	EF469112	EF469067	Sung *et al.* (2001), (2007a)
L. psalliotae	CBS 101270	–	AF339558	AF339607	EF469095	EF469113	EF469066	Sung *et al.* (2001), (2007a)
Neotorrubiella chinghridicola	BCC 39684	–	MK632096	MK632122	MK632181	MK632148	MK632071	Thanakitpipattana *et al.* (2020)
N. chinghridicola	BCC 80733	–	MK632097	MK632121	MK632176	MK632149	MK632072	Thanakitpipattana *et al.* (2020)
Purpureocillium lilacinum	CBS 431.87	HQ842812	EF468844	–	EF468897	EF468940	EF468791	Sung *et al.* (2007a) Luangsa-ard *et al.* (2011)
P. lilacinum	CBS 284.36 T	MH855800	FR775484	–	EF468898	EF468941	EF468792	Sung *et al.* (2007a) Vu *et al.* (2019)
Samsoniella aurantia	TBRC 7271 T	MF140764	MF140728	–	MF140791	MF140818	MF140846	Mongkolsamrit *et al.* (2018)
Sam. aurantia	TBRC 7272	MF140763	MF140727	–	–	MF140817	MF140845	Mongkolsamrit *et al.* (2018)
Simplicillium lanosoniveum	CBS 101267	–	–	AF339603	DQ522405	DQ522463	DQ522357	Sung *et al.* (2001) Spatafora *et al.* (2007)
Sim. lanosoniveum	CBS 704.86	AJ292396	AF339553	AF339602	DQ522406	DQ522464	DQ522358	Sung *et al.* (2001) Spatafora *et al.* (2007)

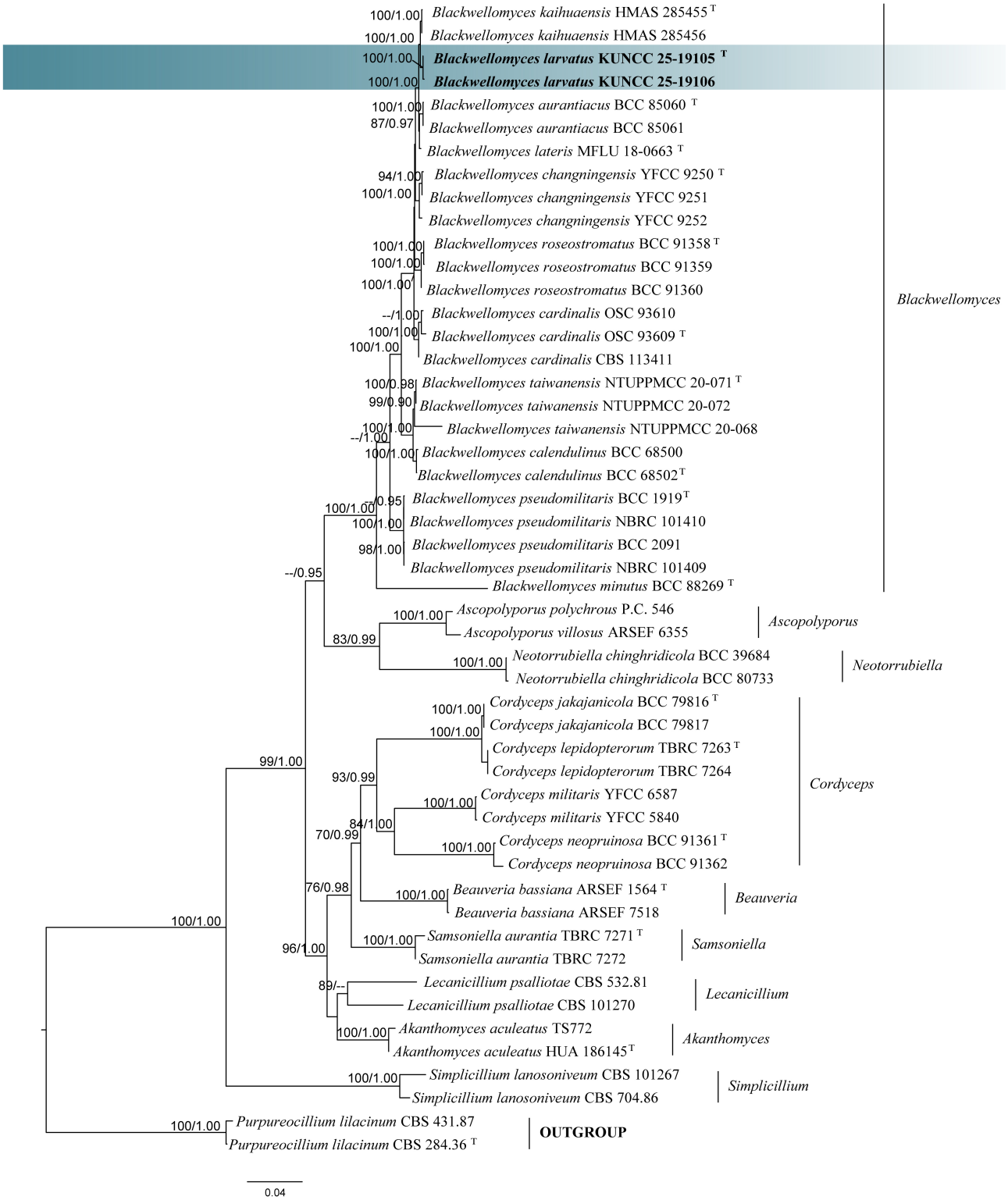

FIGURE 1. Maximum likelihood phylogenetic tree generated from analysis of a combined ITS, LSU, SSU, *rpb1*, *rpb2* and *tef1-α* sequences dataset. ML support values greater than 70% (BS, left) and Bayesian posterior probabilities greater than 0.90 (PP, right) are indicated near the nodes. The strain numbers are noted after the species names. Isolates from this study are indicated in bold. [T]: type strains.

Taxonomy

Blackwellomyces larvatus S.K. Huang & K.D. Hyde *sp. nov.* (Fig. 2)
Index Fungorum IF 903426 , *Facesoffungi* FoF 17341

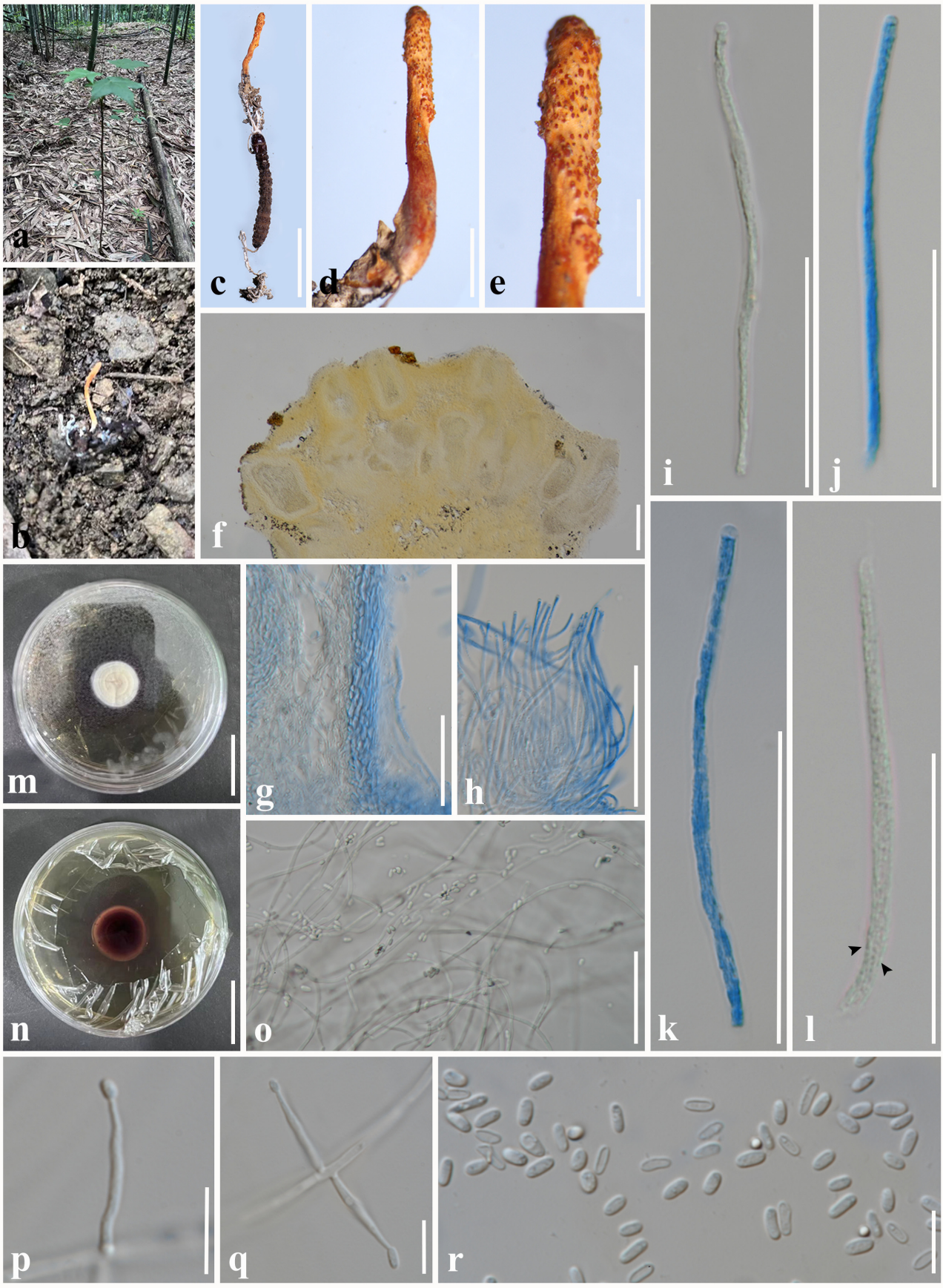

FIGURE 2. *Blackwellomyces larvatus* (HKAS 145947, holotype). a. Habitat of sampling site. b. Stromata produced on host buried in the soil. c. Appearance of fungus on lepidopteran larvae. d–e. Fertile part of stroma. f. Stroma in vertical section. g. Peridium. h–l. Asci. m–n. Colony on PDA (m obverse, n reverse). o–q. Phialides with conidia. r. Conidia. Notes: g–h, j–k stained in cotton blue reagent. Scale bars: c, m–n = 10 mm, d–e = 2 mm, f = 100 µm, g–l, o = 50 µm, p–r = 10 µm.

Holotype:—CHINA. Guizhou: Zunyi, Dabanshui Mountain (106.807671, 27.779294), on larvae of *Lepidoptera* in soil, 21 July 2024, Shi-Ke Huang (HKAS 145947, holotype); ex-type living culture (KUNCC 25-19105). Additional culture also isolated (KUNCC 25-19106).

Etymology:— referring to the fungus occurring on insect larvae.

Description:—Sexual morph: *Stromata* multiple, fleshly, unbranched, about 10 mm long and 1 mm wide, reddish to orange-red, cylindrical. *Rhizoids* flexuous, emerging from the head and base of lepidoptera larva in soil. *Stipe* flesh, reddish to orange-red, cylindrical to enlarging apically. *Fertile area* bright reddish to reddish orange, clavate, irregularly distributed at the apex, with the longer side measuring about 4 mm and the shorter side about 1.5 mm in length, 0.6–1 mm in width. *Perithecia* 210–340 × 90–160 μm ($\bar{x}$ = 265 × 125 μm, n = 30), semi-immersed, narrowly ovoid to ampulliform, thick-walled, with ostiole on the top. *Peridium* 20–38 μm ($\bar{x}$ = 25 μm, n = 50), comprising two layers, inner layer composed of hyaline to pale orange cells of *textura porrecta*, outer layer composed of yellow to orange cells of *textura angularis*. *Asci* 8-spored, cylindrical, 95–125 × 3.6–6 μm ($\bar{x}$ = 110 × 4.5 μm, n = 50), with a thick hemispheric apex. *Ascospores* filiform, hyaline, irregularly multiseptate, 75–95 × 0.7–1.2 μm ($\bar{x}$ = 80 × 1.0 μm, n = 50), not separating into part-spores when they reach maturity. Asexual morph: Colonies white to purplish red on PDA, cottony with dense mycelium, 20 mm diameter after 10 days at 25 ℃, purplish pigment spreading in PDA. *Phialides* arising from aerial hyphae, solitary or in whorls of 2–3 on each branch, cylindrical, sometimes swollen at the base, about 10 μm long and 2 μm wide, tapering from the base to thin neck. *Conidia* hyaline, ovoid to cylindrical, smooth-walled, one-celled, 3.5–5.5 × 1.5–2.5 μm ($\bar{x}$ = 4.5–2 μm, n = 50).

Morphological distinguishing features of all *Blackwellomyces* species are listed in Table 2 and are highlighted in the Discussion.

TABLE 2. Morphological comparison between *Blackwellomyces* species.

Species	Host/Locality	Stromata	Rhizoids	Fertile part (mm)	Ascospores (μm)	Colony on PDA	Reference
Blackwellomyces aurantiacus	Lepidoptera (larva) Thailand	Solitary or multiple	Flexuous, arising from the head	Reddish orange, cylindrical to clavate, 2.0–6.0 × 1.5–2.5	Multiseptate,235–295 × 1.0–1.5	White to strong purplish red, reddish pigment diffusing in medium	Mongkolsamrit *et al.* (2020)
B. calendulinus	Coleoptera (larva) Thailand	Solitary or multiple	Flexuous, arising from the head	Orange, cylindrical to clavate, 2.0–5.0 × 1.0–2.0	Multiseptate,150–180 × 1.0–1.5	White	Mongkolsamrit *et al.* (2020)
B. cardinalis	Lepidoptera (larva) USA, Japan, Republic of Korea, China	Solitary or multiple		Reddish orange to reddish, elliptical to fusiform, 2.0–9.0 × 1.0–4.0	Multiseptate, not fragmenting into part-spores, 160–320 × 1.0	White, red pigment diffusing in medium	Sung & Spatafora (2004)
B. changningensis	Lepidoptera (larva) China	Multiple		Reddish orange, cylindrical to clavate, 2.0–5.0 × 1.0–1.5	Multiseptate, disarticulating into cylindrical part-spores	White to yellow, red pigment diffusing in medium	Ma *et al.* (2024)
B. kaihuaensis	Lepidoptera (larva) China	Solitary or multiple	Flexuous, arising from the head	Reddish orange, clavate or palmated, 1.5–4.0 × 1.0–1.6	Multiseptate, not fragmenting into part-spores, 160–220 × 1.0–1.5	White to purplish red, purplish pigment diffusing in medium	Li *et al.* (2023)
B. lateris	Lepidoptera (larva) Thailand	Solitary or multiple		Yellow to yellowish, cylindrical, 5–25 × 1.5–2.0	Multiseptate, not fragmenting into part-spores, 160–217 × 1.0–1.5		Hyde *et al.* (2019)

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TABLE 2. (Continued)

Species	Host/Locality	Stromata	Rhizoids	Fertile part (mm)	Ascospores (µm)	Colony on PDA	Reference
B. larvatus	Lepidoptera (larva), China	Multiple	Flexuous, arising from the head and base	Bright reddish to reddish orange, clavate, 1.5–4.0 × 0.6–1.0	Multiseptate, not fragmenting into part-spores, 75–95 × 0.7–1.2	White to purplish red, purplish pigment diffusing in medium	This study
B. minutus	Coleoptera (larva), Thailand	Multiple	Flexuous, arising from the head and abdomen	Orange yellow, subglobose, 1.5–2.0 × 1.5	Multiseptate, 180–300 × 1.0	White	Mongkolsamrit *et al.* (2020)
B. pseudomilitaris	Lepidoptera (larva), Thailand	Solitary or multiple		Orange, variably clavate to flattened clavate or obclavate, 2.0–8.0 × 1.2–4.0	Multiseptate, not fragmenting into part-spores, 280–390 × 1.0	White	Hywel-Jones (1994)
B. roseostromatus	Lepidoptera (larva), China, Thailand	Solitary or multiple	Flexuous, arising from the head	Orange to yellowish pink, cylindrical to clavate, 4.0–7.0 × 2.0–3.0	Multiseptate, 200–285 × 1–1.5	White to yellowish pink, reddish pigment diffusing in medium	Mongkolsamrit *et al.* (2020), Ma *et al.* (2024)
B. taiwanensis	Coleoptera (larva), China	Solitary or multiple		Orange, clavate	Multiseptate, disarticulating into cylindrical part-spores, 123–160 × 1–1.5	Light yellow	Chuang *et al.* (2024)

Discussion

This study introduces a new species, *Blackwellomyces larvatus*. Morphologically, *Blackwellomyces* species typically have rhizoids that arise from the head or abdomen of the host, extending to form a reddish-orange or yellowish thallus (Mongkolsamrit *et al.* 2020, Li *et al.* 2023, Ma *et al.* 2024). However, *B. larvatus* not only has rhizoids on the head of its host forming an orange stroma, but also has many rhizoids at the base, without forming stromata. Phylogenetic analysis based on ML and BI suggests a very close evolutionary relationship between *B. aurantiacus*, *B. kaihuaensis*, *B. lateris* and *B. larvatus*, with 100%, BS/1.00, PP support. *Blackwellomyces lateris* produces yellow fruiting bodies, unlike *B. aurantiacus*, *B. kaihuaensis*, and *B. larvatus*, which have orange fruiting bodies (Hyde *et al.* 2019, Mongkolsamrit *et al.* 2020, Li *et al.* 2023). The latter three species are morphologically similar, all growing on Lepidoptera larvae, and in pure culture produce a purple-red pigment that diffuses into the culture medium (Mongkolsamrit *et al.* 2020, Li *et al.* 2023). However, *B. kaihuaensis* and *B. larvatus* were collected from China, while *B. aurantiacus* was collected from Thailand, with a significantly larger fertile part in *B. aurantiacus* (2–6 × 1.5–2.5 mm) compared to *B. kaihuaensis* (1.5–4 × 1.0–1.6 mm) and *B. larvatus* (1.5–4 × 0.6–1 mm) (Mongkolsamrit *et al.* 2020, Li *et al.* 2023). Furthermore, *B. larvatus* produces smaller spores (75–95 × 0.7–1.2 µm) compared to *B. kaihuaensis* (160–220 × 1–1.5 µm) (Li *et al.* 2023). Our phylogenetic tree also shows that *B. larvatus* and *B. kaihuaensis* form a strongly supported monophyletic clade (100%, BS/1.00, PP). To further examine the differences between *B. kaihuaensis* and *B. larvatus*, we compared 795 nucleotides in the *tef1-α* region and found 7 bp (1%) difference, and examined the 948 bp *rpb2* region with 2 bp (1%) difference. Thus, *B. larvatus* is established following the guidelines of Jeewon & Hyde (2016).

The fertile parts of *Blackwellomyces* species are typically small, predominantly less than 10 mm and reddish (Hywel-Jones 1994, Sung & Spatafora 2004, Hyde *et al.* 2019, Mongkolsamrit *et al.* 2020, Li *et al.* 2023, Chuang *et al.* 2024, Ma *et al.* 2024). The ascospores produced are usually multi-septate but do not divide into part-spores, which is one of the distinguishing factors that separates *Blackwellomyces* from *Cordyceps* (Kepler *et al.* 2017). However, the ascospores of *B. changningensis* and *B. taiwanensis* divide into part-spores upon maturation, and these two species occupy different positions in the *Blackwellomyces* phylogenetic tree, both with stable support values. Thus, this characteristic may not be a reliable feature for identifying *Blackwellomyces* species. In our phylogenetic tree,

species exhibiting the characteristic of pigment diffusion into the medium, including *B. aurantiacus*, *B. cardinalis*, *B. changningensis*, *B. kaihuaensis*, *B. larvatus* and *B. roseostromatus*, cluster into the same well-supported phylogenetic branch (100%, BS/1.00, PP) (the *B. lateris* is not discussed here due to lack of data on its cultures). Phutthacharoen *et al.* (2024) reported that certain compounds isolated from *B. roseostromatus* BCC56290 exhibited significant antimicrobial, cytotoxic and nematicidal activities, highlighting the potential for further development as biological control agents (BCA) within the genus. The Hypocreales entomopathogenic fungi, including several genera such as *Beauveria* (family *Cordycipitaceae*) and *Metarhizium* (family *Clavicipitaceae*), are currently the most commercially used BCAs. The increasing diversity of *Blackwellomyces* species may serve as a valuable resource for driving development and utilization of the genus.

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References

Bischoff, J.F., Chaverri, P. & White Jr, J.F. (2005) Clarification of the host substrate of *Ascopolyporus* and description of *Ascopolyporus philodendrus* sp. nov. *Mycologia* 97 (3): 710–717.
https://doi.org/10.1080/15572536.2006.11832800

Chaverri, P., Bischoff, J.F., Evans, H.C. & Hodge, K.T. (2005) *Regiocrella*, a new entomopathogenic genus with a pycnidial anamorph and its phylogenetic placement in the Clavicipitaceae. *Mycologia* 97 (6): 1225–1237.
https://doi.org/10.1080/15572536.2006.11832732

Chuang, W., Lin, Y., Shrestha, B., Luangsa-ard, J., Stadler, M., Tzean, S., Wu, S., Ko, C., Hsieh, S., Wu, M., Shen, T.L. & Ariyawansa, H.A. (2024) Phylogenetic diversity and morphological characterization of cordycipitaceous species in Taiwan. *Studies in Mycology* 109: 1–56.
https://doi.org/10.3114/sim.2024.109.01

Huang, S.K., Hyde, K.D., Maharachchikumbura, S.S.N, McKenzie, E.H.C. & Wen, T.C. (2021) Taxonomic studies of Coronophorales and Niessliaceae (Hypocreomycetidae). *Mycosphere* 12 (1): 875–992.
https://doi.org/10.5943/mycosphere/12/1/9

Hyde, K.D., Tennakoon, D.S., Jeewon, R., Bhat, D.J., Maharachchikumbura, S.S.N., Rossi, W., Leonardi, M., Lee, H.B., Mun, H.Y., Houbraken, J., Nguyen, T.T.T., Jeon, S.J., Frisvad, J.C., Wanasinghe, D.N., Lücking, R., Aptroot, A., Cáceres, M.E.S., Karunarathna, S.C., Hongsanan, S., Phookamsak, R., de Silva, N.I., Thambugala, K.M., Jayawardena, R.S., Senanayake, I.C., Boonmee, S., Chen, J., Luo, Z.-L., Phukhamsakda, C., Pereira, O.L., Abreu, V.P., Rosado, A.W.C., Bart, B., Randrianjohany, E., Hofstetter, V., Gibertoni, T.B., Soares, A.M.S., Plautz Jr., H.L., Sotão, H.M.P., Xavier, W.K.S., Bezerra, J.D.P., de Oliveira, T.G.L., de Souza-Motta, C.M., Magalhães, O.M.C., Bundhun, D., Harishchandra, D., Manawasinghe, I.S., Dong, W., Zhang, S.-N., Bao, D.-F., Samarakoon, M.C., Pem, D., Karunarathna, A., Lin, C.-G., Yang, J., Perera, R.H., Kumar, V., Huang, S.-K., Dayarathne, M.C., Ekanayaka, A.H., Jayasiri, S.C., Xiao, Y., Konta, S., Niskanen, T., Liimatainen, K., Dai, Y.-C., Ji, X.-H., Tian, X.-M., Mešić, A., Singh, S.K., Phutthacharoen, K., Cai, L., Sorvongxay, T., Thiyagaraja, V., Norphanphoun, C., Chaiwan, N., Lu, Y.-Z., Jiang, H.-B., Zhang, J.-F., Abeywickrama, P.D., Aluthmuhandiram, J.V.S., Brahmanage, R.S., Zeng, M., Chethana, T., Wei, D., Réblová, M., Fournier, J., Nekvindová, J., Barbosa, R.N., dos Santos, J.E.F., de Oliveira, N.T., Li, G.-J., Ertz, D., Shang, Q.-J., Phillips, A.J.L., Kuo, C.-H., Camporesi, E., Bulgakov, T.S., Lumyong, S., Jones, E.B.G., Chomnunti, P., Gentekaki, E., Bungartz, F., Zeng, X.-Y., Fryar, S., Tkalčec, Z., Liang, J., Li, G., Wen, T.-C., Singh, P.N., Gafforov, Y., Promputtha, I., Yasanthika, E., Goonasekara, I.D., Zhao, R.-L., Zhao, Q., Kirk, P.M., Liu, J.-K., Yan, J., Mortimer, P.E., Xu, J. & Doilom, M. (2019) Fungal diversity notes 1036–1150: taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity* 96: 1–242.
https://doi.org/10.1007/s13225-019-00429-2

Hyde, K.D., Noorabadi, M.T., Thiyagaraja, V., He, M.Q., Johnston, P.R., Wijesinghe, S.N., Armand, A., Biketova, A.Y., Chethana, K.W.T., Erdoğdu, M., Ge, Z.W., Groenewald, J.Z., Hongsanan, S., Kušan, I., Leontyev, D.V., Li, D.W., Lin, C.G., Liu, N.G.,

Maharachchikumbura, S.S.N., Matočec, N., May, T.W., McKenzie, E.H.C., Mešić, A., Perera, R.H., Phukhamsakda, C., Piątek, M., Samarakoon, M.C., Selcuk, F., Senanayake, I.C., Tanney, J.B., Tian, Q., Vizzini, A., Wanasinghe, D.N., Wannasawang, N., Wijayawardene, N.N., Zhao, R.L., Abdel-Wahab, M.A., Abdollahzadeh, J., Abeywickrama, P.D., Abhinav, Absalan, S., Acharya, K., Afshari, N., Afshan, N.S., Afzalinia, S., Ahmadpour, S.A., Akulov, O., Alizadeh, A., Alizadeh, M., Al-Sadi, A.M., Alves, A., Alves, V.C.S., Alves-Silva, G., Antonín, V., Aouali, S., Aptroot, A., Apurillo, C.C.S., Arias, R.M., Asgari, B., Asghari, R., Assis, D.M.A., Assyov, B., Atienza, V., Aumentado, H.D.R., Avasthi, S., Azevedo, E., Bakhshi, M., Bao, D.F., Baral, H.O., Barata, M., Barbosa, K.D., Barbosa, R.N., Barbosa, F.R., Baroncelli, R., Barreto, G.G., Baschien, C., Bennett, R.M., Bera, I., Bezerra, J.D.P., Bhunjun, C.S., Bianchinotti, M.V., Błaszkowski, J., Boekhout, T., Bonito, G.M., Boonmee, S., Boonyuen, N., Bortnikov, F.M., Bregant, C., Bundhun, D., Burgaud, G., Buyck, B., Caeiro, M.F., Cabarroi-Hernández, M., Cai, M.F., Cai, L., Calabon, M.S., Calaça, F.J.S., Callalli, M., Câmara, M.P.S., Cano-Lira, J., Cao, B., Carlavilla, J.R., Carvalho, A., Carvalho, T.G., Castañeda-Ruiz, R.F., Catania, M.D.V., Cazabonne, J., Cedeño-Sanchez, M., Chaiwan, N., Chakraborty, N., Cheewankoon, R., Chen, C., Chen, J., Chen, Q., Chen, Y.P., Chinaglia, S., Coelho-Nascimento, C.C., Coleine, C., Costa-Rezende, D.H., Cortés-Pérez, A., Crouch, J.A., Crous, P.W., Cruz, R.H.S.F., Czachura, P., Damm, U., Darmostuk, V., Daroodi, Z., Das, K., Das, K., Davoodian, N., Davydov, E.A., da Silva, G.A., da Silva, I.R., da Silva, R.M.F., da Silva Santos, A.C., Dai, D.Q., Dai, Y.C., de Groot, M.D., De Kesel, A., De Lange, R., de Medeiros, E.V., de Souza, C.F.A., de Souza, F.A., dela Cruz, T.E.E., Decock, C., Delgado, G., Denchev, C.M., Denchev, T.T., Deng, Y.L., Dentinger, B.T.M., Devadatha, B., Dianese, J.C., Dima, B., Doilom, M., Dissanayake, A.J., Dissanayake, D.M.L.S., Dissanayake, L.S., Diniz, A.G., Dolatabadi, S., Dong, J.H., Dong, W., Dong, Z.Y., Drechsler-Santos, E.R., Druzhinina, I.S., Du, T.Y., Dubey, M.K., Dutta, A.K., Elliott, T.F., Elshahed, M.S., Egidi, E., Eisvand, P., Fan, L., Fan, X., Fan, X.L., Fedosova, A.G., Ferro, L.O., Fiuza, P.O., Flakus, A., W. Fonseca, E.O., Fryar, S.C., Gabaldón, T., Gajanayake, A.J., Gannibal, P.B., Gao, F., García-Sánchez, D., García-Sandoval, R., Garrido-Benavent, I., Garzoli, L., Gasca-Pineda, J., Gautam, A.K., Gené, J., Ghobad-Nejhad, M., Ghosh, A., Giachini, A.J., Gibertoni, T.B., Gentekaki, E., Gmoshinskiy, V., Góes-Neto, A., Gomdola, D., Gorjón, S.P., Goto, B.T., Granados-Montero, M.M., Griffith, G.W., Groenewald, M., Grossart, H.-P., Gu, Z.R., Gueidan, C., Gunarathne, A., Gunaseelan, S., Guo, S.L., Gusmão, L.F.P., Gutierrez, A.C., Guzmán-Dávalos, L., Haelewaters, D., Haituk, H., Halling, R.E., He, S.C., Heredia, G., Hernández-Restrepo, M., Hosoya, T., Hoog, S.D., Horak, E., Hou, C.L., Houbraken, J., Htet, Z.H., Huang, S.K., Huang, W.J., Hurdeal, V.G., Hustad, V.P., Inácio, C.A., Janik, P., Jayalal, R.G.U., Jayasiri, S.C., Jayawardena, R.S., Jeewon, R., Jerônimo, G.H., Jin, J., Jones, E.B.G., Joshi, Y., Jurjević, Ž., Justo, A., Kakishima, M., Kaliyaperumal, M., Kang, G.P., Kang, J.C., Karimi, O., Karunarathna, S.C., Karpov, S.A., Kezo, K., Khalid, A.N., Khan, M.K., Khuna, S., Khyaju, S., Kirchmair, M., Klawonn, I., Kraisitudomsook, N., Kukwa, M., Kularathnage, N.D., Kumar, S., Lachance, M.A., Lado, C., Latha, K.P.D., Lee, H.B., Leonardi, M., Lestari, A.S., Li, C., Li, H., Li, J., Li, Q., Li, Y., Li, Y.C., Li, Y.X., Liao, C.F., Lima, J.L.R., Lima, J.M.S., Lima, N.B., Lin, L., Linaldeddu, B.T., Linn, M.M., Liu, F., Liu, J.K., Liu, J.W., Liu, S., Liu, S.L., Liu, X.F., Liu, X.Y., Longcore, J.E., Luangharn, T., Luangsa-ard, J.J., Lu, L., Lu, Y.Z., Lumbsch, H.T., Luo, L., Luo, M., Luo, Z.L., Ma, J., Madagammana, A.D., Madhushan, A., Madrid, H., Magurno, F., Magyar, D., Mahadevakumar, S., Malosso, E., Malysh, J.M., Mamarabadi, M., Manawasinghe, I.S., Manfrino, R.G., Manimohan, P., Mao, N., Mapook, A., Marchese, P., Marasinghe, D.S., Mardones, M., Marin-Felix, Y., Masigol, H., Mehrabi, M., Mehrabi-Koushki, M., Meiras-Ottoni, A. de, Melo, R.F.R., Mendes-Alvarenga, R.L., Mendieta, S., Meng, Q.F., Menkis, A., Menolli Jr, N., Mikšík, M., Miller, S.L., Moncada, B., Moncalvo, J.M., Monteiro, J.S., Monteiro, M., Mora-Montes, H.M., Moroz, E.L., Moura, J.C., Muhammad, U., Mukhopadhyay, S., Nagy, G.L., Najam ul Sehar, A., Najafiniya, M., Nanayakkara, C.M., Naseer, A., Nascimento, E.C.R., Nascimento, S.S., Neuhauser, S., Neves, M.A., Niazi, A.R., Nie, Y., Nilsson, R.H., Nogueira, P.T.S., Novozhilov, Y.K., Noordeloos, M., Norphanphoun, C., Nuñez, Otaño, N., O'Donnell, R.P., Oehl, F., Oliveira, J.A., Oliveira Junior, I., Oliveira, N.V.L., Oliveira, P.H.F., Orihara, T., Oset, M., Pang, K.L., Papp, V., Pathirana, L.S., Peintner, U., Pem, D., Pereira, O.L., Pérez-Moreno, J., Pérez-Ortega, S., Péter, G., Pires-Zottarelli, C.L.A., Phonemany, M., Phongeun, S., Pošta, A., Prazeres, J.F.S.A., Quan, Y., Quandt, C.A., Queiroz, M.B., Radek, R., Rahnama, K., Raj, K.N.A., Rajeshkumar, K.C., Rajwar, S., Ralaiveloarisoa, A.B., Rämä, T., Ramírez-Cruz, V., Rambold, G., Rathnayaka, A.R., Raza, M., Ren, G.C., Rinaldi, A.C., Rivas-Ferreiro, M., Robledo, G.L., Ronikier, A., Rossi, W., Rusevska, K., Ryberg, M., Safi, A., Salimi, F., Salvador-Montoya, C.A., Samant, B., Samaradiwakara, N.P., Sánchez-Castro, I., Sandoval-Denis, M., Santiago, A.L.C.M.A., Santos, A.C.D.S., Santos, L.A. dos, Sarma, V.V., Sarwar, S., Savchenko, A., Savchenko, K., Saxena, R.K., Schoutteten, N., Selbmann, L., Ševčíková, H., Sharma, A., Shen, H.W., Shen, Y.M., Shu, Y.X., Silva, H.F., Silva-Filho, A.G.S., Silva, V.S.H., Simmons, D.R., Singh, R., Sir, E.B., Sohrabi, M., Souza, F.A., Souza-Motta, C.M., Sri-indrasutdhi, V., Sruthi, O.P., Stadler, M., Stemler, J., Stephenson, S.L., Stoyneva-Gaertner, M.P., Strassert, J.F.H., Stryjak-Bogacka, M., Su, H., Sun, Y.R., Svantesson, S., Takamatsu, S., Tan, T.H., Tanaka, K., Tang, C., Tang, X., Taylor, J.E., Taylor, P.W.J., Tennakoon, D.S., Thakshila, S.A.D., Thambugala, K.M., Thamodini, G.K., Thilanga, D., Thines, M., Tiago, P.V., Tian, X.G., Tian, W.H., Tibpromma, S., Tkalčec, Z., Tokarev, Y.S., Tomšovský, M., Torruella, G., Tsurykau, A., Udayanga, D., Ulukapı, M., Untereiner, W.A., Uzunov, B.A., Vadthanarat, S., Valenzuela, R., Van den Wyngaert, S., Van Vooren, N., Velez, P., Verma, R.K., Vieira, L.C., Vieira, W.A.S., Vinzelj, J.M., Tang, A.M.C., Walker, A., Walker, A.K., Wang, Q.M., Wang, Y., Wang, X.Y., Wang, Z.Y., Wannathes, N., Wartchow, F., Weerakoon, G., Wei, D.P., Wei, X., White, J.F., Wijesundara, D.S.A., Wisitrassameewong, K., Worobiec, G., Wu, H.X., Wu, N., Xiong, Y.R., Xu, B., Xu, J.P., Xu, R., Xu, R.F., Xu, R.J., Yadav, S., Yakovchenko, L.S., Yang, H.D., Yang, X., Yang, Y.H., Yang, Y., Yang, Y.Y., Yoshioka, R., Youssef, N.H., Yu, F.M., Yu, Z.F., Yuan, L.L., Yuan, Q., Zabin, D.A., Zamora, J.C., Zapata, C.V., Zare, R., Zeng, M., Zeng, X.Y., Zhang, J.F., Zhang, J.Y., Zhang, S., Zhang, X.C., Zhao, C.L., Zhao, H., Zhao, Q., Zhao, H., Zhao, H.J., Zhou,

H.M., Zhu, X.Y., Zmitrovich, I.V., Zucconi, L. & Zvyagina, E. (2024) The 2024 Outline of Fungi and fungus-like taxa. *Mycosphere* 15 (1): 5146–6239.
https://doi.org/10.5943/mycosphere/15/1/25

Hywel-Jones, N.L. (1994) *Cordyceps khaoyaiensis* and *C. pseudomilitaris*, two new pathogens of lepidopteran larvae from Thailand. *Mycological Research* 98: 939–942.

Index Fungorum. (2025) Available from: https://www.indexfungorum.org/Names/Names.asp (accessed 5 March 2025)

Jayasiri, S.C., Hyde, K.D., Ariyawansa, H.A., Bhat, J., Buyck, B., Cai, L., Dai, Y.-C., Abd-Elsalam, K.A., Ertz, D. & Hidayat, I. (2015) The Faces of Fungi database: fungal names linked with morphology, phylogeny and human impacts. *Fungal Diversity* 74: 3–18.
https://doi.org/10.1007/s13225-015-0351-8

Jayawardena, R.S., Bhunjun, C.S., Hyde, K.D., Gentekaki, E. & Itthayakorn, P. (2021) *Colletotrichum*: lifestyles, biology, morpho-species, species complexes and accepted species. *Mycosphere* 12 (1): 519–669.
https://doi.org/10.5943/mycosphere/12/1/7

Jeewon, R. & Hyde, K.D. (2016) Establishing species boundaries and new taxa among fungi: recommendations to resolve taxonomic ambiguities. *Mycosphere* 7 (11): 1669–1677.
https://doi.org/10.5943/mycosphere/7/11/4

Kepler, R., Sung, G.-H., Ban, S., Nakagiri, A., Chen, M.-J., Huang, B., Li, Z.Z. & Spatafora, J. (2012) New teleomorph combinations in the entomopathogenic genus *Metacordyceps*. *Mycologia* 104 (1): 182–197.
https://doi.org/10.3852/11-070

Kepler, R.M., Luangsa-ard, J.J., Hywel-Jones, N.L., Quandt, C.A., Sung, G.-H., Rehner, S.A., Aime, M.C., Henkel, T.W., Sanjuan, T., Zare, R., Chen, M.J., Li, Z.Z., Rossman, A.Y., Spatafora, J.W. & Shrestha, B. (2017) A phylogenetically-based nomenclature for Cordycipitaceae (Hypocreales). *IMA Fungus* 8: 335–353.
https://doi.org/10.5598/imafungus.2017.08.02.08

Li, Y., Zhao, X.-C., Wu, L.-X., Wang, Y., Xu, A. & Lin, W.-F. (2023) *Blackwellomyces kaihuaensis* and *Metarhizium putuoense* (Hypocreales), two new entomogenous fungi from subtropical forests in Zhejiang Province, Eastern China. *Forests* 14 (12): 2333.
https://doi.org/10.3390/f14122333

Liu, Y.J., Whelen, S. & Hall, B.D. (1999) Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. *Molecular Biology and Evolution* 16 (12): 1799–1808.
https://doi.org/10.1093/oxfordjournals.molbev.a026092

Luangsa-ard, J., Houbraken, J., van Doorn, T., Hong, S.-B., Borman, A.M., Hywel-Jones, N.L. & Samson, R.A. (2011) *Purpureocillium*, a new genus for the medically important *Paecilomyces lilacinus*. *FEMS Microbiology Letters* 321 (2): 141–149.
https://doi.org/10.1111/j.1574-6968.2011.02322.x

Ma, J., Wang, Z., Yang, Z., Sun, T., Yang, S. & Yu, H. (2024) Morphology, phylogeny, and mitogenomics reveal a new entomopathogenic fungus, *Blackwellomyces changningensis* (Hypocreales, Clavicipitaceae), from southwestern China. *Mycologia* 117 (1): 166–182.
https://doi.org/10.1080/00275514.2024.2399996

Matheny, P.B. (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (Inocybe; Agaricales). *Molecular Phylogenetics and Evolution* 35 (1): 1–20.
https://doi.org/10.1016/j.ympev.2004.11.014

Mongkolsamrit, S., Noisripoom, W., Thanakitpipattana, D., Wutikhun, T., Spatafora, J.W. & Luangsa-ard, J. (2018) Disentangling cryptic species with isaria-like morphs in Cordycipitaceae. *Mycologia* 110 (1): 230–257.
https://doi.org/10.1080/00275514.2018.1446651

Mongkolsamrit, S., Noisripoom, W., Tasanathai, K., Khonsanit, A., Thanakitpipattana, D., Himaman, W., Kobmoo, N. & Luangsa-ard, J.J. (2020) Molecular phylogeny and morphology reveal cryptic species in *Blackwellomyces* and *Cordyceps* (Cordycipitaceae) from Thailand. *Mycological Progress* 19: 957–983.
https://doi.org/10.1007/s11557-020-01615-2

Nguyen, L.-T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32 (1): 268–274.
https://doi.org/10.1093/molbev/msu300

Nylander, J. (2004) *MrModeltest* 2.2. Program distributed by the author. Uppsala University, Uppsala: Department of Systematic Zoology.

Phutthacharoen, K., Llanos-Lopez, N.A., Toshe, R., Noisripoom, W., Khonsanit, A., Luangsa-ard, J.J., Hyde, K.D., Ebada, S.S. & Stadler, M. (2024) Bioactive bioxanthracene and cyclodepsipeptides from the entomopathogenic fungus *Blackwellomyces roseostromatus* BCC56290. *Antibiotics (Basel)* 13 (7): 585.
https://doi.org/10.3390/antibiotics13070585

Rehner, S.A., Minnis, A.M., Sung, G.-H., Luangsa-ard, J.J., Devotto, L. & Humber, R.A. (2011) Phylogeny and systematics of the anamorphic, entomopathogenic genus *Beauveria*. *Mycologia* 103 (5): 1055–1073.
https://doi.org/10.3852/10-302

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Sanjuan, T., Tabima, J., Restrepo, S., Læssøe, T., Spatafora, J.W. & Franco-Molano, A.E. (2014) Entomopathogens of Amazonian stick insects and locusts are members of the *Beauveria* species complex (*Cordyceps sensu stricto*). *Mycologia* 106 (2): 260–275.
https://doi.org/10.3852/13-020

Schoch, C., Seifert, K., Huhndorf, S., Robert, V., Spouge, J., Levesque, C. & Chen, W. (2012) The internal transcribed spacer as a universal DNA barcode marker for Fungi. Fungal Barcoding Consortium. *Proceedings of the National Academy of Sciences of the United States of America* 109: 6241–6246.
https://doi.org/10.1073/pnas.1117018109

Spatafora, J., Sung, G.H., Sung, J.M., Hywel-Jones, N. & White Jr, J. (2007) Phylogenetic evidence for an animal pathogen origin of ergot and the grass endophytes. *Molecular Ecology* 16 (8): 1701–1711.
https://doi.org/10.1111/j.1365-294X.2007.03225.x

Sung, G.-H. & Spatafora, J.W. (2004) *Cordyceps cardinalis* sp. nov., a new species of *Cordyceps* with an east Asian-eastern North American distribution. *Mycologia* 96 (3): 658–666.
https://doi.org/10.1080/15572536.2005.11832962

Sung, G.-H., Spatafora, J.W., Zare, R., Hodge, K.T. & Gams, W. (2001) A revision of *Verticillium* sect. Prostrata. II. Phylogenetic analyses of SSU and LSU nuclear rDNA sequences from anamorphs and teleomorphs of the Clavicipitaceae. *Nova Hedwigia* 72 (3–4): 311–328.
https://doi.org/10.1127/nova.hedwigia/72/2001/311

Sung, G.-H., Hywel-Jones, N.L., Sung, J.-M., Luangsa-ard, J.J., Shrestha, B. & Spatafora, J.W. (2007a) Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. *Studies in Mycology* 57: 5–59.
https://doi.org/10.3114/sim.2007.57.01

Sung, G.-H., Sung, J.-M., Hywel-Jones, N.L. & Spatafora, J.W. (2007b) A multi-gene phylogeny of Clavicipitaceae (Ascomycota, Fungi): identification of localized incongruence using a combinational bootstrap approach. *Molecular Phylogenetics and Evolution* 44 (3): 1204–1223.
https://doi.org/10.1016/j.ympev.2007.03.011

Thanakitpipattana, D., Tasanathai, K., Mongkolsamrit, S., Khonsanit, A., Lamlertthon, S. & Luangsa-ard, J. (2020) Fungal pathogens occurring on *Orthopterida* in Thailand. *Persoonia* 44 (1): 140–160.
https://doi.org/10.3767/persoonia.2020.44.06

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172 (8): 4238–4246.
https://doi.org/10.1128/jb.172.8.4238-4246.1990

Vu, D., Groenewald, M., De Vries, M., Gehrmann, T., Stielow, B., Eberhardt, U., Al-Hatmi, A., Groenewald, J.Z., Cardinali, G., Houbraken, J., Boekhout, T., Crous, P.W., Robert, V. & Verkley, G.J.M. (2019) Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* 92: 135–154.
https://doi.org/10.1016/j.simyco.2018.05.001

Wang, Y.-B., Wang, Y., Fan, Q., Duan, D.-E., Zhang, G.-D., Dai, R.-Q., Dai, Y.-D., Zeng, W.-B., Chen, Z.-H., Li, D.-D., Tang, D.-X., Xu, Z.-H., Sun, T., Nguyen, T.-T., Tran, N.-L., Dao, V.-M., Zhang, C.-M., Huang, L.-D., Liu, Y.-J., Zhang, X.-M., Yang, D.-R., Sanjuan, T., Liu, X.-Z., Yang, Z.L. & Yu, H. (2020) Multigene phylogeny of the family Cordycipitaceae (Hypocreales): new taxa and the new systematic position of the Chinese cordycipitoid fungus *Paecilomyces hepiali*. *Fungal Diversity* 103: 1–46.
https://doi.org/10.1007/s13225-020-00457-3

Wei, D., Gentekaki, E., Wanasinghe, D., Tang, S. & Hyde, K. (2022) Diversity, molecular dating and ancestral characters state reconstruction of entomopathogenic fungi in Hypocreales. *Mycoshpere* 13 (2): 281–351.
https://doi.org/10.5943/mycosphere/si/1f/8

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR protocols: a guide to methods and applications* 18: 315–322.
https://doi.org/10.1016/B978-0-12-372180-8.50042-1