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Multigene phylogeny of the family Cordycipitaceae (Hypocreales): new taxa and the new systematic position of the Chinese cordycipitoid fungus *Paecilomyces hepiali*

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Abstract
The phylogeny and systematics of cordycipitoid fungi have been extensively studied in the last two decades. However, systematic positions of some taxa in the family Cordycipitaceae have not yet been thoroughly resolved. In this study, a new phylogenetic framework of Cordycipitaceae is reconstructed using multigene (nr*SSU*, nr*LSU, tef-1α, rpb1* and *rpb2*) sequence data with large-scale taxon sampling. In addition, ITS sequence data of species belonging to the *Lecanicillium* lineage in the family Cordycipitaceae are used to further determine their phylogenetic placements. Based on molecular phylogenetic data together with morphological evidence, two new genera (*Flavocillium* and *Liangia*), 16 new species and four new combinations are introduced. In the new genus *Flavocillium*, one new species *F. bifurcatum* and three new combinations previously described as *Lecanicillium*, namely *F. acerosium, F. primulinium* and *F. subprimulinium*, are proposed. The genus *Liangia* is built by the new species *Lia. sinensis* with *Lecanicillium*-like asexual morph, isolated from an entomopathogenic fungus *Beauveria yunnanensis*. Due to the absence of *Paecilomyces hepiali*, an economically and medically significant fungus, in the earlier phylogenetic analyses, its systematic position has been puzzling in both business and academic communities for a long time. Here, *P. hepiali* is recharacterized using the holotype material along with seven additional samples. It is assigned to the genus *Samsoniella* (Cordycipitaceae, Hypocreales) possessing *Cordyceps*-like sexual morph and *Isaria*-like asexual morph, and thus a new combination, namely *S. hepiali* is proposed. An additional nine new species in *Samsoniella* are described: *S. alpina, S. antleroides, S. cardinalis, S. cristata, S. lanmaoa, S. kunmingensis, S. ramosa, S. tortricidae* and *S. yunnanensis*. Four new species in *Cordyceps* are described: *C. chaetoclavata, C. cocoonihabita, C. shuifuensis* and *C. subtenuipes*. *Simplicillium yunnanense*, isolated from synnemata of *Akanthomyces waltergamsii*, is described as a new species.

Keywords Cordycipitaceae · *Cordyceps* · *Flavocillium* · *Liangia* · *Paecilomyces hepiali* · Phylogeny · *Samsoniella*

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Introduction

In the taxonomic system of the twentieth century, *Cordyceps* Fr. sensu lato belonged to the family Clavicipitaceae s. l. characterized by possessing cylindrical asci, thickened ascus apices, and filiform ascospores that often disarticulate into secondary ascospores (Mains 1958; Kobayasi 1982; Rossman et al. 1999, 2002; Sung et al. 2007). This genus is the most diverse group of Clavicipitaceae s. l. due to the large number of species and wide host range. The host associations for *Cordyceps* s. l. are complex and diverse. Most of species are pathogens of more than 10 orders of invertebrates, while others are parasites of hypocrealean fungi, the truffle-like *Elaphomyces* Nees and myxomycetes (Kobayasi and Shimizu 1960; Kobayasi 1982; Sung et al. 2007; Kepler et al. 2013, 2017; Wang et al. 2015a,b). Phylogenetic analyses have indicated that neither *Cordyceps* s. l. nor Clavicipitaceae s. l. are monophyletic (Sung et al. 2007). Three cordycipitoid families are now recognized in the order Hypocreales: Clavicipitaceae, Cordycipitaceae and Ophiocordycipitaceae. At least 39 genera accommodating more than 1300 cordycipitoid species have been assigned to these three families (Sung et al. 2007; Chaverri et al. 2008; Johnson et al. 2009; Luangsa-ard et al. 2011, 2017; Kepler et al. 2013, 2014, 2017; Quandt et al. 2014; Spatafora et al. 2015; Tsang et al. 2016; Zare and Gams 2016; Mongkolsamrit et al. 2018).

The family Cordycipitaceae shares a common ancestor with Hypocreaceae and contains most of the species that have pallid or brightly pigmented, fleshy stromata (Sung et al. 2007; Maharachchikumbura et al. 2015). However, some species are characterized by possessing reduced stipes or subiculate stromata on the host. This family is the most complex group in Hypocreales with its varied morphological characteristics and wide-ranging hosts. Some genera with sexual or asexual morphs, such as *Akanthomyces* Lebert, *Beauveria* Vuill., *Cordyceps, Gibellula* Cavara*, Isaria* Pers., *Lecanicillium* W. Gams & Zare and *Torrubiella* Boud., present numerous taxonomical problems and exist competing names. Numerous species of *Cordyceps* are associated with genera described originally for asexual morphs, including *Akanthomyces, Beauveria, Evlachovaea* B.A. Borisov & Tarasov, *Isaria, Lecanicillium, Microhilum* H.Y. Yip & A.C. Rath and *Paecilomyces* Bainier. For example, in the genus *Akanthomyces* proposed by the type species *A. aculeatus* Lebert, *C. tuberculata* (Lebert) Maire is linked to an asexual morph *A. pistillariiformis* (Pat.) Samson & H.C. Evans (Samson and Evans 1974). The sexual morph *C. confragosa* (Mains) G.H. Sung et al. described by Mains (1949) in *Torrubiella*, is linked to the type species *Lecanicillium lecanii* (Zimm.) Zare & W. Gams of *Lecanicillium* and considered to be a synonym of *Akanthomyces* (Kepler et al. 2017). *Cordyceps militaris* (L.) Fr. also produces an asexual conidiogenous structure linked to *Lecanicillium* (Gams and Zare 2001). *Cordyceps bassiana* Z.Z. Li et al. was described as the sexual morph of *B. bassiana* (Bals.-Criv.) Vuill., the type species of *Beauveria*, which caused economically devastating epizootics of domestic larval silkworms in southern Europe during the eighteenth and nineteenth centuries (Li et al. 2001). *Evlachovaea kintrischica* B.A. Borisov & Tarasov, the type species of *Evlachovaea*, was demonstrated to be a synonym of *Isaria* and was later combined into *C. kintrischica* (B.A. Borisov & Tarasov) Kepler et al. (Humber et al. 2013; Kepler et al. 2017).

Kepler et al. (2017) provided the most complete taxonomic treatment of Cordycipitaceae and harmonized competing names based on principles of priority, recognition of monophyletic groups, and the practical usage of affected taxa, following Article 59 of the International Code of Nomenclature for algae, fungi and plants. They proposed to accommodate 11 genera within Cordycipitaceae, namely *Akanthomyces, Ascopolyporus* Möller, *Beauveria, Blackwellomyces* Spatafora & Luangsa-ard, *Cordyceps, Engyodontium* de Hoog, *Gibellula, Hyperdermium* J.F. White et al., *Hevansia* Luangsa-ard et al., *Parengyodontium* C.C. Tsang et al. and *Simplicillium* W. Gams & Zare. The other eight genera *Evlachovaea, Granulomanus* de Hoog & Samson, *Isaria, Lecanicillium, Microhilum, Phytocordyceps* C.H. Su & H.H. Wang, *Synsterigmatocystis* Costantin and *Torrubiella* were rejected. The genus *Leptobacillium* Zare & W. Gams, recently described with *L. leptobactrum* (W. Gams) Zare & W. Gams and two related new varieties, was added to the family Cordycipitaceae, presenting a sister generic relationship with *Simplicillium* (Zare and Gams 2016). The genus *Amphichorda* Fr. was established by Fries (1825) and comprised only one species, *Amp. felina* (DC.) Fr., which was later recombined into *B. felina* (DC.) J.W. Carmich. Recently, Zhang et al. (2017) described a species *Amp. guana* Z.F. Zhang, F. Liu & L. Cai on bat guano in this genus based on multigene phylogeny and morphology. Subsequently, Mongkolsamrit et al. (2018) erected the genus *Samsoniella* Mongkols et al. to accommodate three species with orange cylindrical to clavate stromata, superficial perithecia and orange conidiophores with *Isaria*-like phialides and white to cream conidia, and to segregate them from the *Akanthomyces* group. Although several taxonomic studies have been conducted, many species originally described in *Lecanicillium* remain incertae sedis members in the family Cordycipitaceae and are polyphyletic (Zare and Gams 2016; Kepler et al. 2017; Mongkolsamrit et al. 2018). To date, 32 *Lecanicillium* species have been formally described and recorded in the Index Fungorum (https://www.indexfungorum.org). Available data indicated that some species, such as *L. aranearum* (Petch) Zare & W. Gams, *L. antillanum* (R.F. Castañeda & G.R.W. Arnold) Zare & W. Gams, *L. primulinum* Kaifuchi et al. and *L. psalliotae* (Treschew) Zare & W. Gams represent basal to subbasal monophyletic clades in the family Cordycipitaceae (Kepler et al. 2017; Huang et al. 2018; Zhou et al. 2018). Therefore, new generic names for these species in the family Cordycipitaceae need to be introduced and supported by more detailed morphological and phylogenetic evidence combined with a larger taxon sampling.

The genus *Paecilomyces* erected by Bainier (1907), based on the type species *P. variotii* Bainier, was placed in the family Aspergillaceae (Eurotiales). Samson (1974) expanded *Paecilomyces* and recognized some mesophilic species previously placed in *Isaria* or *Spicaria* Harting as a distinguishing sect. *Isarioidea* with mostly insect hosts. However, a nr*SSU* phylogenetic analysis indicated that *Paecilomyces* is not monophyletic and the sect. *Isarioidea* is not a eurotialean lineage (Luangsa-ard et al. 2004). Based on the β-tubulin and ITS phylogentic data, Luangsa-ard et al. (2005) found that *Paecilomyces* sect. *Isarioidea* is polyphyletic in the order Hypocreales. The group designed as the *Isaria* clade is excluded from the genus *Paecilomyces*. It is monophyletic comprising of 10 *Paecilomyces* species, nine of which are subsequently transfered into *Cordyceps*.

Paecilomyces hepiali Q.T. Chen & R.Q. Dai ex R.Q. Dai et al. was first isolated from natural *Ophiocordyceps sinensis* (Berk.) G.H. Sung et al. (syn. *C. sinensis*) associated with the larvae of *Hepialus armoricanus* Oberthür in China (Dai et al. 1989). This is a very important fungus because of its therapeutic benefits. However, molecular phylogenetic position of *P. hepiali* has been unclear for a long time due to the absence of nucleotide sequences from the holotype material. Recent phylogenetic analyses based on mitochondrial genomic sequences from five families within the order Hypocreales indicated that the putative *P. hepiali* specimen belongs to the family Cordycipitaceae (Li et al. 2019). However, without any generic assignment, its well-established phylogenetic position within the family remains undetermined. For such a species that makes a significant contribution to human health, it is indispensable to elucidate its phylogeny and systematics using the holotype material.

During the last two decades, our efforts have been exerted in the investigation of cordycipitoid fungi especially in China and Southeast Asia. To date, over 18,000 specimens and 7500 strains of *Cordyceps* s. l., representing more than 450 species, have been deposited in Yunnan University, Kunming, Yunnan Province. In this study, 1568 specimens and 1075 strains of Cordycipitaceae from different regions in Yunnan Province of China and Vietnam were analyzed using molecular phylogeny and morphology. Among these materials, five-gene (nr*SSU*, nr*LSU, tef-1α, rpb1* and *rpb2*) data from 56 samples, and ITS data from two samples were selected and submitted to GenBank. We established phylogenetic and evolutionary trees by maximum likelihood (ML) and Bayesian inference (BI) analyses from the five-gene and ITS data. Two new genera, 16 new species and four new combinations are introduced.

Materials and methods

Fungal materials and isolation

The majority of Cordycipitaceae specimens were collected from Yunnan Province in China. Some specimens were collected from the Hoang Lien Mountains of Lao Cai Province in Vietnam. Specimens were noted and photographed in the fields. Collections were placed in sterilized plastic tubes and boxes, returned to the laboratory, and stored at 4 °C. The specimens were examined using an Olympus SZ61 stereomicroscope. To obtain axenic cultures, the stromata or synnemata were removed from insect bodies and divided into 5–10 segments, each 3 mm long. The segments were immersed in 30% H_2O_2 for 30 s and then rinsed five times in sterilized water. After drying on sterilized filter paper, segments were inoculated onto potato dextrose agar (PDA: potato 200 g/L, dextrose 20 g/L, agar 20 g/L) plates. The conidia of cordycipitoid fungi at the conidial masses were picked up with an inoculating loop and spread on PDA plates containing 0.1 g/l streptomycin and 0.05 g/l tetracycline. To isolate the strains from the sexual morph, the stroma containing mature perithecia was placed over a PDA plate and care was taken that the stroma was above the PDA plate and did not touch the agar surface in an effort to discharge ascospores. Discharged ascospores were removed with a sterile needle from the agar and transferred onto a new PDA plate containing 0.1 g/l streptomycin and 0.05 g/l tetracycline. Pure cultures were transferred onto PDA plates and incubated in a culture room at 25 °C. After isolation into pure cultures, they were transplanted to a PDA slant and stored at 4 °C. Specimens were deposited in Yunnan Herbal Herbarium (YHH) of Yunnan University. The cultures were deposited in Yunnan Fungal Culture Collection (YFCC) of Yunnan University.

Morphological observations

For descriptions of the sexual morph, fruiting bodies were photographed and measured using an Olympus SZ61 stereomicroscope. Hand sections of the fruiting structures were mounted in water or lactophenol cotton blue solution for microscopic studies and photomicrography. The micromorphological characteristics of fungi such as perithecia, asci and ascospores were examined using Olympus CX40 and BX53 microscopes. Cultures on slants were transferred to PDA plates and cultured in an incubator for 21 days at 25 °C. The circular agar blocks, circa 5 mm in diameter, from a colony were removed and placed on new PDA plates to observe colony morphology. Colonies were photographed and measured every fourth day. For asexual morphological descriptions, microscope slide cultures were prepared by placing a small amount of mycelia on 5-mm diameter PDA medium blocks overlaid by a cover slip. Micro-morphological observations and measurements were conducted using Olympus CX40 and BX53 microscopes, and a FEI QUANTA200 scanning electron microscope.

DNA extraction, PCR, and sequencing

Clean-washed specimens and axenic living cultures were prepared for DNA extraction. Total DNA was extracted using the CTAB method described by Liu et al. (2001). The following primer pairs were used for PCR amplification. The primer pair, nr*SSU*-CoF and nr*SSU*-CoR was used to amplify the nuclear ribosomal small subunit (nr*SSU*) (Wang et al. 2015a). The primer pair, LR5 and LR0R was used to amplify the nuclear ribosomal large subunit (nr*LSU*) (Vilgalys and Hester 1990; Rehner and Samuels 1994). The primer pair, EF1α-EF and EF1α-ER was used to amplify the translation elongation factor 1α (*tef-1α*) (Bischoff et al. 2006; Sung et al. 2007). The two primer pairs, RPB1-5′F and RPB1-5′R, RPB2-5′F and RPB2-5′R were used to amplify the largest and second largest subunits of RNA polymerase II (*rpb1*and *rpb2*), respectively (Bischoff et al. 2006; Sung et al. 2007). The primer pair, ITS4 and ITS5 was used to amplify the nuclear ribosomal internal transcribed spacer region (ITS) (White et al. 1990). Polymerase chain reaction (PCR) assays of five genes and ITS were performed as previously described (Bischoff et al. 2006; Wang et al. 2015b). The PCR assay was conducted as described by Wang et al. (2015b). PCR products were separated by electrophoresis in 1.0% agarose gels, purified using the Gel Band Purification Kit (Bio Teke Co., Ltd, Beijing, China) and then sequenced on an automatic sequence analyser (BGI Co., Ltd, Shenzhen, China). When PCR products could not be sequenced directly, coloning was performed by the TaKaRa PMD^{TM}18-T vector system (TaKaRa Biotechnology Co., Ltd, Dalian, China).

Phylogenetic analyses

Five-gene (nr*SSU*, nr*LSU, tef-1α, rpb1* and *rpb2*) sequences from 56 samples of 30 species belonging to six genera, and ITS sequences from two samples of the new species *Flavocillium bifurcatum*, were newly generated. Sequences of five genes and ITS were retrieved from GenBank, and then combined with the newly generated sequences. The taxon information and GenBank accession numbers of five genes were listed in Table 1. GenBank accession numbers of ITS sequences were placed in the front of the species name, appearing in the ITS phylogenetic tree (Fig. 3). Sequences of five genes and ITS were aligned using Clustal X2.0 and MEGA6 (Larkin 2007; Tamura et al. 2013). Ambiguously aligned sites were excluded from phylogenetic analyses, and gaps were treated as missing data. Adjustment to the computer-assisted alignment was necessary regarding the nr*SSU* sequences containing an intron. These sequences were manually adjusted and ambiguous regions created by insertions and deletions (indel) were eliminated. After sequence alignments, the aligned sequences of five genes were concatenated. Conflicts between the five genes were tested using PAUP* 4.0b10 (Swofford 2002). The results showed that the phylogenetic signals in the five genes were not in conflict. Eleven data partitions were defined for the combined five-gene dataset employing PartitionFinder V1.1.1 (Lanfear et al. 2012). These included one each for nr*SSU* and nr*LSU*, and three for each of the three codon positions of *tef-1α, rpb1* and *rpb2*. Phylogenetic analyses of the five-gene and ITS datasets were conducted using ML and BI methods. ML analyses were performed with RAxML v7.9.1 using the optimal model GTR + I with 1000 rapid bootstrap replicates on the five-gene and ITS datasets (Stamatakis 2006). The model was separately applied to each of the 11 partitions of five genes. BI analyses were performed with MrBayes v3.1.2 for five million generations using a GTR + G + I model determined by jModelTest version 2.1.4 and employed the model separately for each partition of five-gene analyses, whereas the default F81 model was used for the ITS analyses (Ronquist and Huelsenbeck 2003; Darriba et al. 2012). Trees were sampled every 100 generations. The first 25% trees were discarded as burn-in and the remaining trees were used to create a consensus tree using the sumt demand. Phylogenetic trees were visualised and modified using the Interactive Tree Of Life (iTOL) (https://itol.embl.de) online tool (Letunic and Bork 2019).

Results

In ML and BI phylogenetic analyses, five-gene sequences of 30 species collected in this study were employed to reconstruct phylogenetic framework of the family Cordycipitaceae. Taxa within the order Hypocreales consisted of four families, viz. Cordycipitaceae, Ophicordycipitaceae, Clavicipitaceae, Hypocreaceae, and two taxa of Nectriaceae (*Nectria cinnabarina* CBS 114055 and *Gliocephalotrichum bulbilium* ATCC 22228) designated as the outgroup. The concatenated sequence dataset of 241 taxa was composed of 4837 bp sequence data (1082 bp for nr*SSU*, 904 bp for nr*LSU*, 1064 bp for *tef-1*α, 802 bp for *rpb1* and 985 bp for *rpb2*). Phylogenetic trees obtained from ML and BI analyses were identical in overall topologies and were not significantly different (Fig. 1). Most well-resolved genera and lineages in Cordycipitaceae shared similar relationships with previous analyses (Sung et al. 2007; Sukarno et al. 2009; Kepler et al. 2017; Mongkolsamrit et al. 2018). Our ML and BI analyses showed that the placement of Cordycipitaceae in the order Hypocreales was well-supported by bootstrap proportions (BP = 70%) and posterior probabilities (PP = 95%), respectively.

Species in the typifed genus *Lecanicillium* were distributed throughout the family Cordycipitaceae and were polyphyletic (Fig. 1, 2). These species were clustered into the clades of *L. aranearum, L. antillanum, L. primulinum, L. fusisporum* and *L. psalliotae*, respectively. In the five-gene phylogenetic tree, the *L. primulinum* clade harbored *L. primulinum, L. acerosum* W. Gams et al., *Lecanicillium* sp. and another new species (YFCC 6101) described in this study. ML and BI phylogenetic

Table 1 Specimen information and GenBank accession numbers for sequences used in this study

Taxon	Voucher information	GenBank accession number				
		nr*SSU*	nr*LSU*	*tef-1α*	*rpb1*	*rpb2*
Akanthomyces aculeatus	HUA 186145	MF416572	MF416520	MF416465		
Akanthomyces aculeatus	HUA 772	KC519368	KC519370	KC519366		
Akanthomyces attenuatus	CBS 402.78	AF339614	AF339565	EF468782	EF468888	EF468935
Akanthomyces cf. *coccidioperitheciatus*	NHJ 5112	EU369109	EU369043	EU369026	EU369066	
Akanthomyces coccidioperitheciatus	NHJ 6709	EU369110	EU369042	EU369025	EU369067	EU369086
Akanthomyces dipterigenus	CBS 126.27	AF339605	AF339556	KM283820	KR064300	KR064303
Akanthomyces kanyawimiae	TBRC 7242		MF140718	MF140838	MF140784	MF140808
Akanthomyces kanyawimiae	TBRC 7244		MF140716	MF140836		
Akanthomyces lecanii	CBS 101247	AF339604	AF339555	DQ522359	DQ522407	DQ522466
Akanthomyces muscarius	CBS 143.62	KM283774	KM283798	KM283821	KM283841	KM283863
Akanthomyces pistillariaeformis	HUA 186131	MF416573	MF416521	MF416466		
Akanthomyces sabanensis	ANDES-F 1023	KC633253		KC633267	KC875222	
Akanthomyces sabanensis	ANDES-F 1024	KC633251	KC875225	KC633266		KC633249
Akanthomyces sulphureus	TBRC 7247		MF140720	MF140841	MF140785	MF140811
Akanthomyces sulphureus	TBRC 7248		MF140722	MF140843	MF140787	MF140812
Akanthomyces thailandicus	TBRC 7245			MF140839		MF140809
Akanthomyces thailandicus	TBRC 7246		MF140719	MF140840		MF140810
Akanthomyces tuberculatus	OSC 111002	DQ522553	DQ518767	DQ522338	DQ522384	DQ522435
Akanthomyces tuberculatus	BCC 16819	MF416600	MF416546	MF416490	MF416647	MF416444
Akanthomyces waltergamsii	TBRC 7251		MF140713	MF140833	MF140781	MF140805
Akanthomyces waltergamsii	TBRC 7252		MF140714	MF140834	MF140782	MF140806
Amphichorda guana	CGMCC 3.17908		KU746711	KX855211		
Ascopolyporus polychrous	P.C. 546		DQ118737	DQ118745	DQ127236	
Ascopolyporus villosus	ARSEF 6355		AY886544	DQ118750	DQ127241	
Beauveria acridophila	HUA 179220	JQ895527	JQ895536	JQ958614	JX003852	JX003842
Beauveria acridophila	HUA 179219		JQ895541	JQ958613	JX003857	JX003841
Beauveria amorpha	ARSEF 2641		AB100039	AY531917	HQ880880	HQ880952
Beauveria araneola	GZAC 150317			KT961699	KT961701	
Beauveria asiatica	ARSEF 4850			AY531937	HQ880859	HQ880931
Beauveria asiatica	YFCC 5600	MN576770	MN576826	MN576996	MN576886	MN576940
Beauveria australis	ARSEF 4598			HQ880995	HQ880861	HQ880933
Beauveria bassiana	ARSEF 1564	EU334676		HQ880974	HQ880833	HQ880905
Beauveria bassiana	YFCC 3369	MN576768	MN576824	MN576994	MN576884	MN576938
Beauveria blattidicola	MCA 1727	MF416593	MF416539	MF416483	MF416640	
Beauveria blattidicola	MCA 1814	MF416594	MF416540	MF416484	MF416641	
Beauveria brongniartii	**YFCC 3240**	**MN576769**	**MN576825**	**MN576995**	**MN576885**	**MN576939**
Beauveria brongniartii	ARSEF 617	AB027335	AB027381	HQ880991	HQ880854	HQ880926
Beauveria caledonica	ARSEF 2567	AF339570	AF339520	EF469057	HQ880889	HQ880961
Beauveria caledonica	**YFCC 7025**	**MN576771**	**MN576827**	**MN576997**	**MN576887**	**MN576941**
Beauveria diapheromeriphila	QCNE 186272	JQ895530	JQ895534	JQ958610	JX003848	
Beauveria diapheromeriphila	QCNE 186714	MF416601	MF416547	MF416491	MF416648	
Beauveria hoplocheli	MNHN-RF-06107			KC339702	KM453954	KM453963
Beauveria hoplocheli	Bt116			KC339703	KM453957	KM453966
Beauveria kipukae	ARSEF 7032			HQ881005	HQ880875	HQ880947
Beauveria locustiphila	HUA 179217	JQ958598	JQ958597		JX003847	
Beauveria locustiphila	HUA 179218	JQ895525	JQ895535	JQ958619	JX003846	JX003845
Beauveria malawiensis	ARSEF 7760			DQ376246	HQ880897	HQ880969
Beauveria pseudobassiana	**YFCC 7120**	**MN576772**	**MN576828**	**MN576998**	**MN576888**	**MN576942**

Table 1 (continued)

Taxon	Voucher information	GenBank accession number				
		nr*SSU*	nr*LSU*	*tef-1α*	*rpb1*	*rpb2*
Beauveria pseudobassiana	ARSEF 3405			AY531931	HQ880864	HQ880936
Beauveria scarabaeidicola	ARSEF 5689	AF339574	AF339524	DQ522335	DQ522380	DQ522431
Beauveria staphylinidicola	ARSEF 5718	EF468981	EF468836	EF468776	EF468881	
Beauveria varroae	ARSEF 8257			HQ881002	HQ880872	HQ880944
Beauveria vermiconia	ARSEF 2922			AY531920	HQ880894	HQ880966
Beauveria yunnanensis	**YFCC 3105**	**MN576773**	**MN576829**	**MN576999**	**MN576889**	**MN576943**
Blackwellomyces cardinalis	OSC 93609	AY184973	AY184962	DQ522325	DQ522370	DQ522422
Blackwellomyces cardinalis	OSC 93610	AY184974	AY184963	EF469059	EF469088	EF469106
Blackwellomyces pseudomilitaris	BCC 1919	MF416588	MF416534	MF416478		MF416440
Blackwellomyces pseudomilitaris	BCC 2091	MF416589	MF416535	MF416479		MF416441
Claviceps purpurea	S.A. cp11	EF469122	EF469075	EF469058	EF469087	EF469105
Cordyceps albocitrina	spat 07-174	MF416575		MF416467	MF416629	
Cordyceps amoenerosea	CBS 107.73	AY526464	MF416550	MF416494	MF416651	MF416445
Cordyceps amoenerosea	CBS 729.73	MF416604	MF416551	MF416495	MF416652	MF416446
Cordyceps bifusispora	spat 08-129	MF416576	MF416523	MF416468	MF416630	
Cordyceps bifusispora	spat 08-133.1	MF416577	MF416524	MF416469	MF416631	MF416434
Cordyceps bifusispora	EFCC 5690	EF468952	EF468806	EF468746	EF468854	EF468909
Cordyceps bifusispora	EFCC 8260	EF468953	EF468807	EF468747	EF468855	EF468910
Cordyceps blackwelliae	TBRC 7255		MF140703	MF140823	MF140772	MF140796
Cordyceps blackwelliae	TBRC 7256		MF140702	MF140822	MF140771	MF140795
Cordyceps caloceroides	MCA 2249	MF416578	MF416525	MF416470	MF416632	
Cordyceps cateniannulata	CBS 152.83	AY526465	MG665226	JQ425687		
Cordyceps cateniobliqua	**YFCC 3367**	**MN576765**	**MN576821**	**MN576991**	**MN576881**	**MN576935**
Cordyceps cateniobliqua	**YFCC 5935**	**MN576766**	**MN576822**	**MN576992**	**MN576882**	**MN576936**
Cordyceps cateniobliqua	CBS 153.83	AY526466		JQ425688		MG665236
Cordyceps cf. *ochraceostromata*	ARSEF 5691	EF468964	EF468819	EF468759	EF468867	EF468921
Cordyceps cf. *pruinosa*	NHJ 10627	EF468967	EF468822	EF468763	EF468870	
Cordyceps cf. *pruinosa*	NHJ 10684	EF468968	EF468823	EF468761	EF468871	
Cordyceps cf. *pruinosa*	EFCC 5693	EF468966	EF468821	EF468762	EF468869	
Cordyceps cf. *pruinosa*	EFCC 5197	EF468965	EF468820	EF468760	EF468868	
Cordyceps cf. *takaomontana*	BCC 12688	MF416599	MF416545	MF416489	MF416646	
Cordyceps cf. *takaomontana*	NHJ 12623	EF468984	EF468838	EF468778	EF468884	EF468932
Cordyceps chaetoclavata	**YHH 15101**	**MN576722**	**MN576778**	**MN576948**	**MN576838**	**MN576894**
Cordyceps cicadae	RCEF HP090724-31	MF416605	MF416552	MF416496	MF416653	MF416447
Cordyceps cocoonihabita	**YFCC 3415**	**MN576723**	**MN576779**	**MN576949**	**MN576839**	**MN576895**
Cordyceps cocoonihabita	**YFCC 3416**	**MN576724**	**MN576780**	**MN576950**	**MN576840**	**MN576896**
Cordyceps coleopterorum	CBS 110.73	JF415965	JF415988	JF416028	JN049903	JF416006
Cordyceps exasperata	MCA 2288	MF416592	MF416538	MF416482	MF416639	
Cordyceps farinosa	CBS 111113	AY526474	MF416554	MF416499	MF416656	MF416450
Cordyceps fumosorosea	**YFCC 4561**	**MN576761**	**MN576817**	**MN576987**	**MN576877**	**MN576931**
Cordyceps fumosorosea	CBS 244.31	MF416609	MF416557	MF416503	MF416660	MF416454
Cordyceps fumosorosea	CBS 375.70		AB083035	MF416501	MF416658	MF416452
Cordyceps fumosorosea	CBS 107.10		MG665227	HM161735		MG665237
Cordyceps grylli	MFLU 17-1023	MK863048	MK863055	MK860193		
Cordyceps grylli	MFLU 17-1024	MK863049	MK863056	MK860194		
Cordyceps javanica	**YFCC 3368**	**MN576767**	**MN576823**	**MN576993**	**MN576883**	**MN576937**
Cordyceps javanica	TBRC 7259		MF140711	MF140831	MF140780	MF140804
Cordyceps javanica	CBS 134.22	MF416610	MF416558	MF416504	MF416661	MF416455

Table 1 (continued)

Taxon	Voucher information	GenBank accession number				
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Cordyceps kyusyuensis	EFCC 5886	EF468960	EF468813	EF468754	EF468863	EF468917
Cordyceps militaris	**YFCC 6587**	**MN576762**	**MN576818**	**MN576988**	**MN576878**	**MN576932**
Cordyceps militaris	**YFCC 5840**	**MN576763**	**MN576819**	**MN576989**	**MN576879**	**MN576933**
Cordyceps morakotii	BCC 55820		MF140730	KT261399		
Cordyceps morakotii	BCC 68398		MF140731	KT261398		
Cordyceps ninchukispora	EGS 38.165	EF468991	EF468846	EF468795	EF468900	
Cordyceps ninchukispora	EGS 38.166	EF468992	EF468847	EF468794	EF468901	
Cordyceps ningxiaensis	HMJAU 25074		KF309671			
Cordyceps ningxiaensis	HMJAU 25076		KF309673			
Cordyceps oncoperae	ARSEF 4358	AF339581	AF339532	EF468785	EF468891	EF468936
Cordyceps piperis	CBS 116719		AY466442	DQ118749	DQ127240	EU369083
Cordyceps polyarthra	MCA 996	MF416597	MF416543	MF416487	MF416644	
Cordyceps polyarthra	MCA 1009	MF416598	MF416544	MF416488	MF416645	
Cordyceps pruinosa	ARSEF 5413	AY184979	AY184968	DQ522351	DQ522397	DQ522451
Cordyceps rosea	spat 09-053	MF416590	MF416536	MF416480	MF416637	MF416442
Cordyceps roseostromata	ARSEF 4871	AF339573	AF339523			
Cordyceps shuifuensis	**YFCC 5230**	**MN576721**	**MN576777**	**MN576947**	**MN576837**	**MN576893**
Cordyceps sp.	CBS 101284	AF339613	AF339564	EF468803	EF468907	EF468948
Cordyceps sp.	EFCC 2535	EF468980	EF468835	EF468772		
***Cordyceps* sp.**	**YFCC 5833**	**MN576764**	**MN576820**	**MN576990**	**MN576880**	**MN576934**
Cordyceps spegazzinii	ARSF 7850		DQ196435			
Cordyceps subtenuipes	**YFCC 6051**	**MN576719**	**MN576775**	**MN576945**	**MN576835**	**MN576891**
Cordyceps subtenuipes	**YFCC 6084**	**MN576720**	**MN576776**	**MN576946**	**MN576836**	**MN576892**
Cordyceps succavus	MFLU 18-1890	MK086058	MK086062		MK084616	MK079353
Cordyceps tenuipes	ARSEF 5135	MF416612	JF415980	JF416020	JN049896	JF416000
Cordyceps tenuipes	**YFCC 4266**	**MN576774**	**MN576830**	**MN577000**	**MN576890**	**MN576944**
Drechmeria gunnii	OSC 76404	AF339572	AF339522	AY489616	AY489650	DQ522426
Engyodontium aranearum	CBS 309.85	AF339576	AF339526	DQ522341	DQ522387	DQ522439
Engyodontium parvisporum	IHEM 22910		LC092915			
Engyodontium rectidentatum	CBS 206.74		LC092912			
Engyodontium rectidentatum	CBS 641.74		LC092914			
Flavocillium bifurcatum	**YFCC 6101**	**MN576725**	**MN576781**	**MN576951**	**MN576841**	**MN576897**
Flavocillium primulinum	JCM 18525		AB712263			
Flavocillium primulinum	JCM 18526		AB712264			
Flavocillium primulinum	JCM 18527		AB712265			
Gibellula cf. *alba*	NHJ 11679			EU369016	EU369054	
Gibellula leiopus	BCC 16025	MF416602	MF416548	MF416492	MF416649	
Gibellula longispora	NHJ 12014	EU369098		EU369017	EU369055	EU369075
Gibellula pulchra	NHJ 10808	EU369099	EU369035	EU369018	EU369056	EU369076
Gibellula sp.	NHJ 10788	EU369101	EU369036	EU369019	EU369058	EU369078
Gibellula sp.	NHJ 5401	EU369102			EU369059	EU369079
Gibellula sp.	NHJ 13158	EU369100	EU369037	EU369020	EU369057	EU369077
Gliocephalotrichum bulbilium	ATCC 22228	AY489700	AY489732	AY489627	AY489664	EF469114
Harposporium harposporiferum	ARSEF 5472	AF339569	AF339519	DQ118747	DQ127238	
Hevansia arachnophilus	NHJ 10469	EU369090	EU369031	EU369008	EU369047	
Hevansia cinereus	NHJ 3510	EU369091		EU369009	EU369048	EU369070
Hevansia nelumboides	BCC 41864	JN201863	JN201873	JN201867		
Hevansia novoguineensis	NHJ 13161	EU369093		EU369011	EU369050	

Table 1 (continued)

Taxon	Voucher information	GenBank accession number				
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Hevansia novoguineensis	NHJ 13117	EU369092		EU369010	EU369049	EU369073
Hevansia novoguineensis	NHJ 4314	EU369094		EU369012	EU369051	EU369071
Hevansia novoguineensis	NHJ 11923	EU369095	EU369032	EU369013	EU369052	EU369072
Hevansia sp.	BCC 28584	GQ249965	GQ249989	GQ250040		
Hyperdermium caulium	Genebank AF242354		AF242354			
Hyperdermium pulvinatum	P.C. 602		DQ118738	DQ118746	DQ127237	
Hypocrella siamensis	BCC 8105	DQ522537	DQ518752	DQ522317	DQ522363	DQ522411
Isaria cf. *farinosa*	OSC 111004	EF468986	EF468840	EF468780	EF468886	
Isaria cicadae	**YFCC 7128**	**MN576759**	**MN576815**	**MN576985**	**MN576875**	**MN576929**
Isaria cicadae	**YFCC 7019**	**MN576760**	**MN576816**	**MN576986**	**MN576876**	**MN576930**
Isaria farinosa	OSC 111005	DQ522558	DQ518773	DQ522348	DQ522394	
Isaria farinosa	OSC 111006	EF469127	EF469080	EF469065	EF469094	
Isaria sp.	spat 09-050	MF416613	MF416559	MF416506	MF416663	MF416457
Isaria sp.	spat 09-051	MF416614	MF416560	MF416507	MF416664	MF416458
Isaria sp.	TNS 16333	MF416611		MF416505	MF416662	MF416456
Lecanicillium acerosum	CBS 418.81	KM283762	KM283786	KM283810	KM283832	KM283852
Lecanicillium antillanum	CBS 350.85	AF339585	AF339536	DQ522350	DQ522396	DQ522450
Lecanicillium aranearum	CBS 726.73a	AF339586	AF339537	EF468781	EF468887	EF468934
Lecanicillium fusisporum	CBS 164.70	KM283769	KM283793	KM283817	KM283836	KM283858
Lecanicillium psalliotae	CBS 363.86	AF339608	AF339559	EF468784	EF468890	
Lecanicillium psalliotae	CBS 101270	EF469128	EF469081	EF469066	EF469095	EF469113
Lecanicillium psalliotae	CBS 532.81	AF339609	AF339560	EF469067	EF469096	EF469112
Lecanicillium sp.	KYK00214		AB378528			
Lecanicillium sp.	KYK00305		AB378529			
Lecanicillium sp.	CBS 639.85	KM283777	KM283801	KM283824	KM283843	KM283865
Leptobacillium chinense	LC1345		JQ410322			
Leptobacillium coffeanum	CDA 734		MF066032			
Leptobacillium leptobactrum	CBS 771.69		KU382224			
Leptobacillium leptobactrum	IRAN 1230		KU382225			
Leptobacillium leptobactrum var. *calidius*	CBS 748.73		KU382227			
Leptobacillium leptobactrum var. *calidius*	CBS 703.86		KU382226			
Leptobacillium muralicola	CGMCC3.19014		MH379997			
Leptobacillium symbioticum	KYK00024		AB378539			
Leptobacillium symbioticum	Soy1-2		LC506046			
Leptobacillium symbioticum	OPTF00168		LC506047			
Liangia sinensis	**YFCC 3103**	**MN576726**	**MN576782**	**MN576952**	**MN576842**	**MN576898**
Liangia sinensis	**YFCC 3104**	**MN576727**	**MN576783**	**MN576953**	**MN576843**	**MN576899**
Metapochonia suchlasporia var. *suchlasporia*	CBS 251.83	AF339615	MH873311	KJ398790	KJ398601	KJ398697
Metarhizium guizhouense	CBS 258.90	MH143830	MH873894	EU248862	EU248914	EU248942
Nectria cinnabarina	CBS 114055	U32412	U00748	AF543785	AY489666	DQ522456
Ophiocordyceps sinensis	EFCC 7287	EF468971	EF468827	EF468767	EF468874	EF468924
Ophiocordyceps unilateralis	OSC 128574	DQ522554	DQ518768	DQ522339	DQ522385	DQ522436
Parengyodontium album	CBS 504.83		LC092899			
Parengyodontium album	IHEM 4198	JF797223	LC092906	DQ268655		
Parengyodontium album	CBS 368.72		LC092910			
Pochonia chlamydosporia var. *catenulata*	CBS 504.66	AF339593	AF339544	EF469069	EF469098	EF469120
Purpureocillium lilacinum	CBS 284.36	AY526475	FR775484	EF468792	EF468898	EF468941

Table 1 (continued)

Taxon	Voucher information	GenBank accession number				
		nr*SSU*	nr*LSU*	*tef-1α*	*rpb1*	*rpb2*
Samsoniella alboaurantium	CBS 240.32	JF415958	JF415979	JF416019	JN049895	JF415999
Samsoniella alboaurantium	CBS 262.58	MH869308	AB080087	MF416497	MF416654	MF416448
Samsoniella alpina	**YFCC 5818**	**MN576753**	**MN576809**	**MN576979**	**MN576869**	**MN576923**
Samsoniella alpina	**YFCC 5831**	**MN576754**	**MN576810**	**MN576980**	**MN576870**	**MN576924**
Samsoniella alpina	**YFCC 5836**	**MN576755**	**MN576811**	**MN576981**	**MN576871**	**MN576925**
Samsoniella antleroides	**YFCC 6016**	**MN576747**	**MN576803**	**MN576973**	**MN576863**	**MN576917**
Samsoniella antleroides	**YFCC 6113**	**MN576748**	**MN576804**	**MN576974**	**MN576864**	**MN576918**
Samsoniella aurantia	TBRC 7271		MF140728	MF140846	MF140791	MF140818
Samsoniella aurantia	TBRC 7272		MF140727	MF140845		MF140817
Samsoniella cardinalis	**YFCC 5830**	**MN576732**	**MN576788**	**MN576958**	**MN576848**	**MN576902**
Samsoniella cardinalis	**YFCC 6144**	**MN576730**	**MN576786**	**MN576956**	**MN576846**	**MN576900**
Samsoniella cardinalis	**YFCC 6320**	**MN576731**	**MN576787**	**MN576957**	**MN576847**	**MN576901**
Samsoniella cristata	**YFCC 6021**	**MN576735**	**MN576791**	**MN576961**	**MN576851**	**MN576905**
Samsoniella cristata	**YFCC 6023**	**MN576736**	**MN576792**	**MN576962**	**MN576852**	**MN576906**
Samsoniella cristata	**YFCC 7004**	**MN576737**	**MN576793**	**MN576963**	**MN576853**	**MN576907**
Samsoniella hepiali	**ICMM 82-2**	**MN576738**	**MN576794**	**MN576964**	**MN576854**	**MN576908**
Samsoniella hepiali	**Cor-4**	**MN576743**	**MN576799**	**MN576969**	**MN576859**	**MN576913**
Samsoniella hepiali	**YFCC 661**	**MN576739**	**MN576795**	**MN576965**	**MN576855**	**MN576909**
Samsoniella hepiali	**YFCC 2702**	**MN576740**	**MN576796**	**MN576966**	**MN576856**	**MN576910**
Samsoniella hepiali	**YFCC 5823**	**MN576745**	**MN576801**	**MN576971**	**MN576861**	**MN576915**
Samsoniella hepiali	**YFCC 5828**	**MN576744**	**MN576800**	**MN576970**	**MN576860**	**MN576914**
Samsoniella hepiali	**YFCC 7024**	**MN576741**	**MN576797**	**MN576967**	**MN576857**	**MN576911**
Samsoniella hepiali	**YFCC 7215**	**MN576742**	**MN576798**	**MN576968**	**MN576858**	**MN576912**
Samsoniella inthanonensis	TBRC 7915		MF140725	MF140849	MF140790	MF140815
Samsoniella kunmingensis	**YHH 16002**	**MN576746**	**MN576802**	**MN576972**	**MN576862**	**MN576916**
Samsoniella lanmaoa	**YFCC 6148**	**MN576733**	**MN576789**	**MN576959**	**MN576849**	**MN576903**
Samsoniella lanmaoa	**YFCC 6193**	**MN576734**	**MN576790**	**MN576960**	**MN576850**	**MN576904**
Samsoniella ramosa	**YFCC 6020**	**MN576749**	**MN576805**	**MN576975**	**MN576865**	**MN576919**
Samsoniella tortricidae	**YFCC 6013**	**MN576751**	**MN576807**	**MN576977**	**MN576867**	**MN576921**
Samsoniella tortricidae	**YFCC 6131**	**MN576750**	**MN576806**	**MN576976**	**MN576866**	**MN576920**
Samsoniella tortricidae	**YFCC 6142**	**MN576752**	**MN576808**	**MN576978**	**MN576868**	**MN576922**
Samsoniella yunnanensis	**YFCC 1527**	**MN576756**	**MN576812**	**MN576982**	**MN576872**	**MN576926**
Samsoniella yunnanensis	**YFCC 1824**	**MN576757**	**MN576813**	**MN576983**	**MN576873**	**MN576927**
Samsoniella yunnanensis	**YFCC 7282**	**MN576758**	**MN576814**	**MN576984**	**MN576874**	**MN576928**
Shimizuomyces paradoxus	EFCC 6279	EF469131	EF469084	EF469071	EF469100	EF469117
Simplicillium lamellicola	CBS 116.25	AF339601	AF339552	DQ522356	DQ522404	DQ522462
Simplicillium lanosoniveum	CBS 704.86	AF339602	AF339553	DQ522358	DQ522406	DQ522464
Simplicillium lanosoniveum	CBS 101267	AF339603	AF339554	DQ522357	DQ522405	DQ522463
Simplicillium obclavatum	CBS 311.74	AF339567	AF339517	EF468798		
Simplicillium yunnanense	**YFCC 7133**	**MN576728**	**MN576784**	**MN576954**	**MN576844**	
Simplicillium yunnanense	**YFCC 7134**	**MN576729**	**MN576785**	**MN576955**	**MN576845**	
Sphaerostilbella berkeleyana	CBS 102308	AF543770	U00756	AF543783	AY489671	DQ522465
Tolypocladium inflatum	OSC 71235	EF469124	EF469077	EF469061	EF469090	EF469108
Tolypocladium japonicum	OSC 110991	DQ522547	DQ518761	DQ522330	DQ522375	DQ522428
Torrubiella ratticaudata	ARSEF 1915	DQ522562	DQ518777	DQ522360	DQ522408	DQ522467
Torrubiella sp.	DJ 29	EU369108		EU369027	EU369065	
Torrubiella sp.	NHJ 7859	EU369107			EU369064	EU369085
Torrubiella wallacei	CBS 101237	AY184978	AY184967	EF469073	EF469102	EF469119
Trichoderma deliquescens	ATCC 208838	AF543768	AF543791	AF543781	AY489662	DQ522446
Trichoderma stercorarium	ATCC 62321	AF543769	AF543792	AF543782	AY489633	EF469103

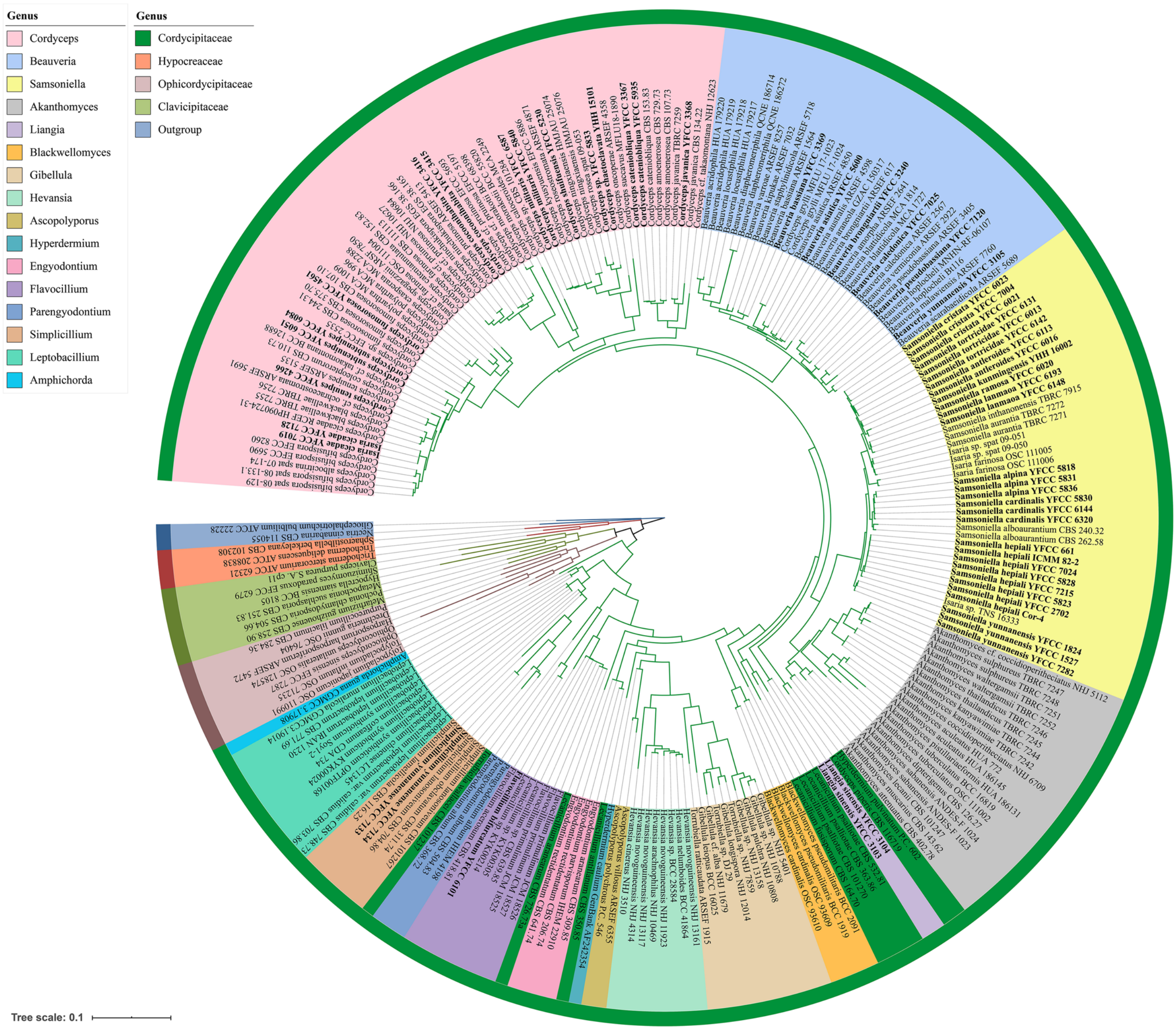


Fig. 1 Phylogenetic tree of Cordycipitaceae and related families inferred from a multigene dataset (nr*LSU*, nr*SSU*, *tef-1α*, *rpb1* and *rpb2*) based on maximum likelihood (ML) and Bayesian inference (BI) analyses. Families of Hypocreales and genera of Cordycipitaceae are differentiated with different colors. Phylogenetic relationships among families of Hypocreales are strongly supported by ML bootstrap proportions and BI posterior probabilities (BP ≥ 70%, PP ≥ 95%)

analyses based on ITS sequences containing 655 bp from 30 taxa arranged in *Lecanicillium* and *Simplicillium* clarified further phylogenetic relationships in *Lecanicillium*. The ITS phylogenetic tree showed that the *Lecanicillium* lineage was polyphyletic and composed of eight monophyletic clades. In addition to *L. primulinum, L. acerosum, Lecanicillium* sp. and one new species (YHH 15428, YFCC 6101), the *L. primulinum* clade contained one recently described species *L. subprimulinum* S.K. Huang & K.D. Hyde (Fig. 3). Five-gene phylogenetic analyses showed that a *Lecanicillium*-like species (YFCC 3103, YFCC 3104) isolated from *B. yunnanensis* Z.H. Chen & L. Xu was clustered in the central portion of phylogenetic tree within Cordycipitaceae and formed a monophyletic clade, being well supported by analyses (BP = 75%, PP = 100%) (Fig. 1, 2).

The systematic position of *P. hepiali* was determined by five-gene phylogeny with the holotype living culture ICMM 82–2 and seven other samples. These eight samples closely clustered together with a well-supported clade and were placed in the genus *Samsoniella*, all of which were phylogenetically distinct from *C. farinosa* (Holmsk.) Kepler et al. (type strain CBS 111113) belonging to the type genus *Cordyceps* of Cordycipitaceae (Fig. 1). Nine undescribed species collected from Yunnan in China also clustered in the

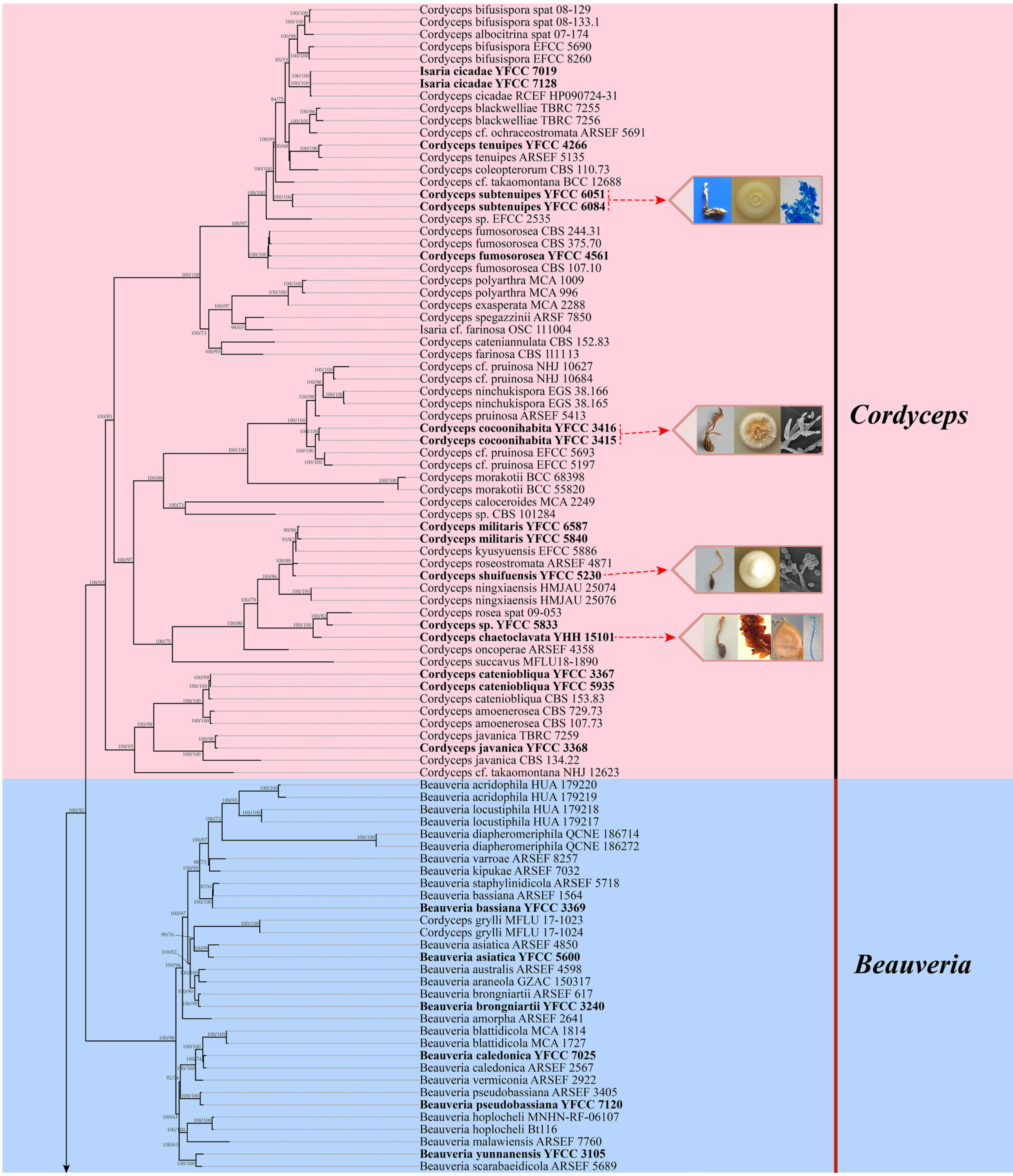


Fig. 2 Phylogenetic relationships among genera and related species in the family Cordycipitaceae inferred from a multigene dataset (nr*LSU*, nr*SSU, tef-1α, rpb1* and *rpb2*) based on ML and BI analyses. Values at the nodes before and after the backslash are BI posterior probabilities and ML bootstrap proportions, respectively. Support values greater than 50% are indicated at the nodes

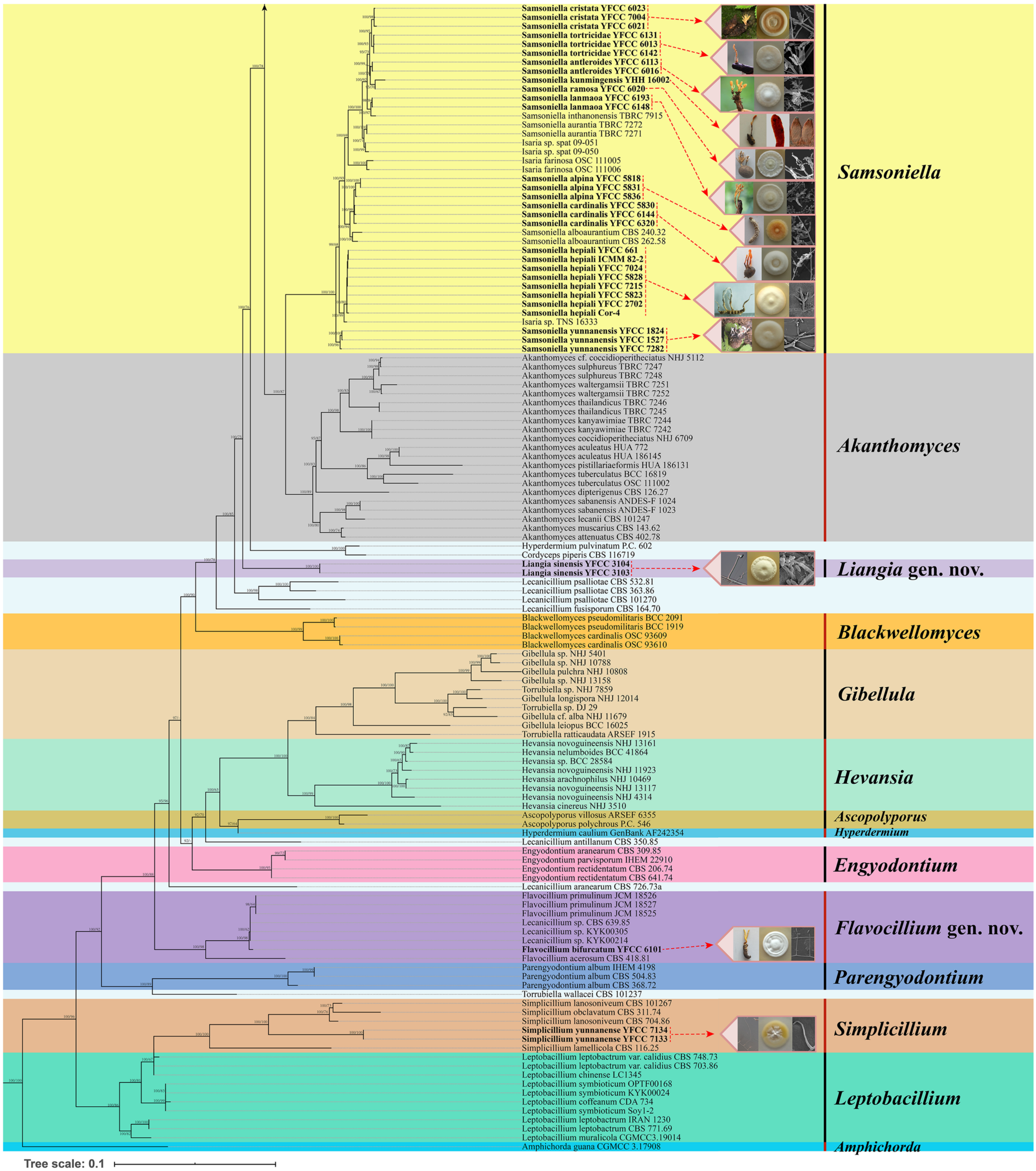


Fig. 2 (continued)

genus *Samsoniella* and were clearly distinct from *P. hepiali* and three described species, viz. *S. alboaurantia* (G. Sm.) Mongkolsamrit et al., *S. aurantia* Mongkolsamrit et al. and *S. inthanonensis* Mongkolsamrit et al. (Fig. 1, 2). Five-gene phylogenetic analyses showed that four new species in *Cordyceps* and one new species in *Simplicillium* represented distinctive taxa in the family Cordycipitaceae.

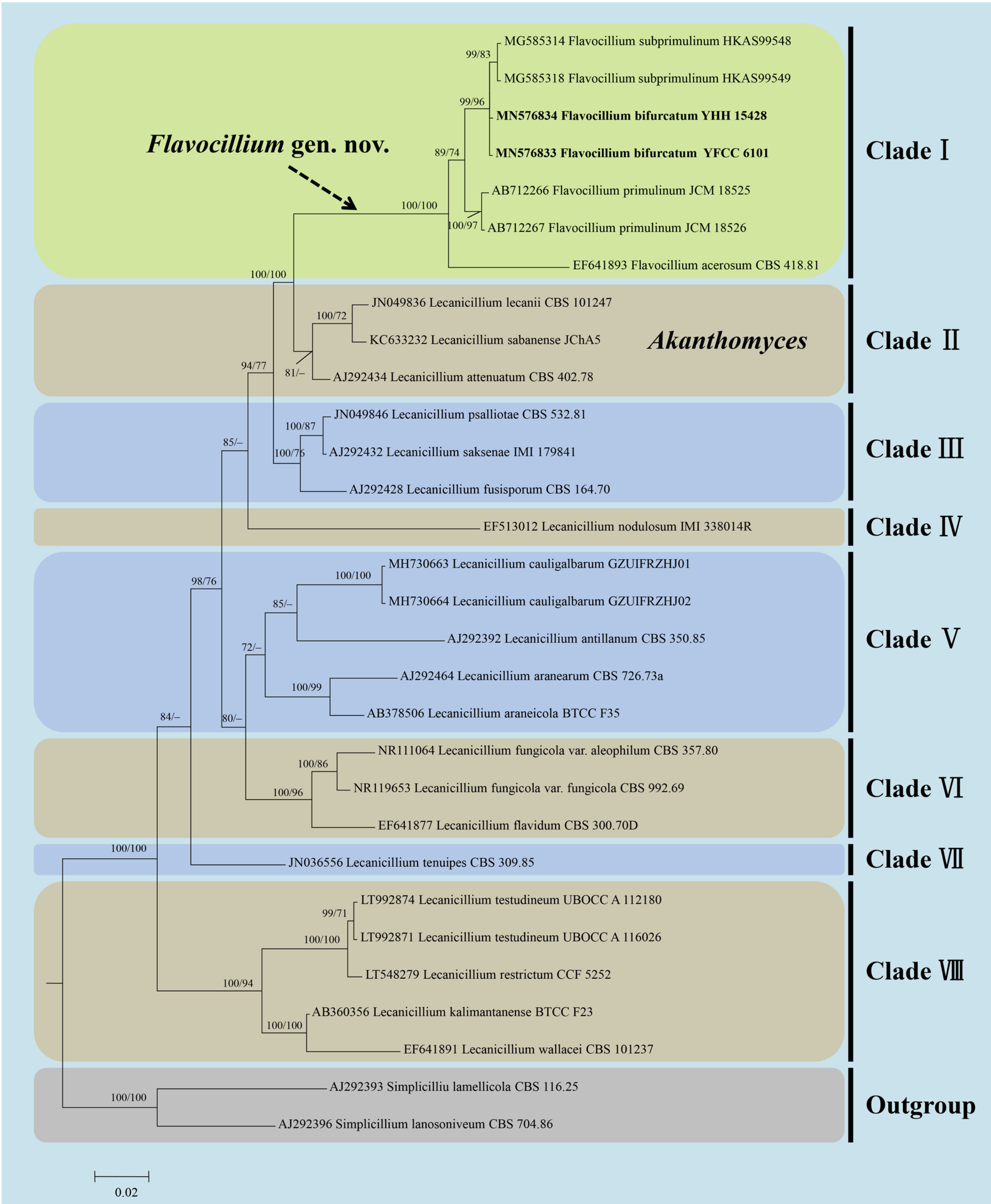


Fig. 3 Phylogenetic relationships of the genus *Flavocillium* and related *Lecanicillium* species in the family Cordycipitaceae inferred from ITS sequences based on ML and BI analyses. Statistical support values greater than 70% are shown at the nodes for BI posterior probabilities / ML boostrap proportions. *Simplicillium lanosoniveum* CBS 704.86 and *Sim. lamellicola* CBS 116.25 were designated as the outgroup taxa

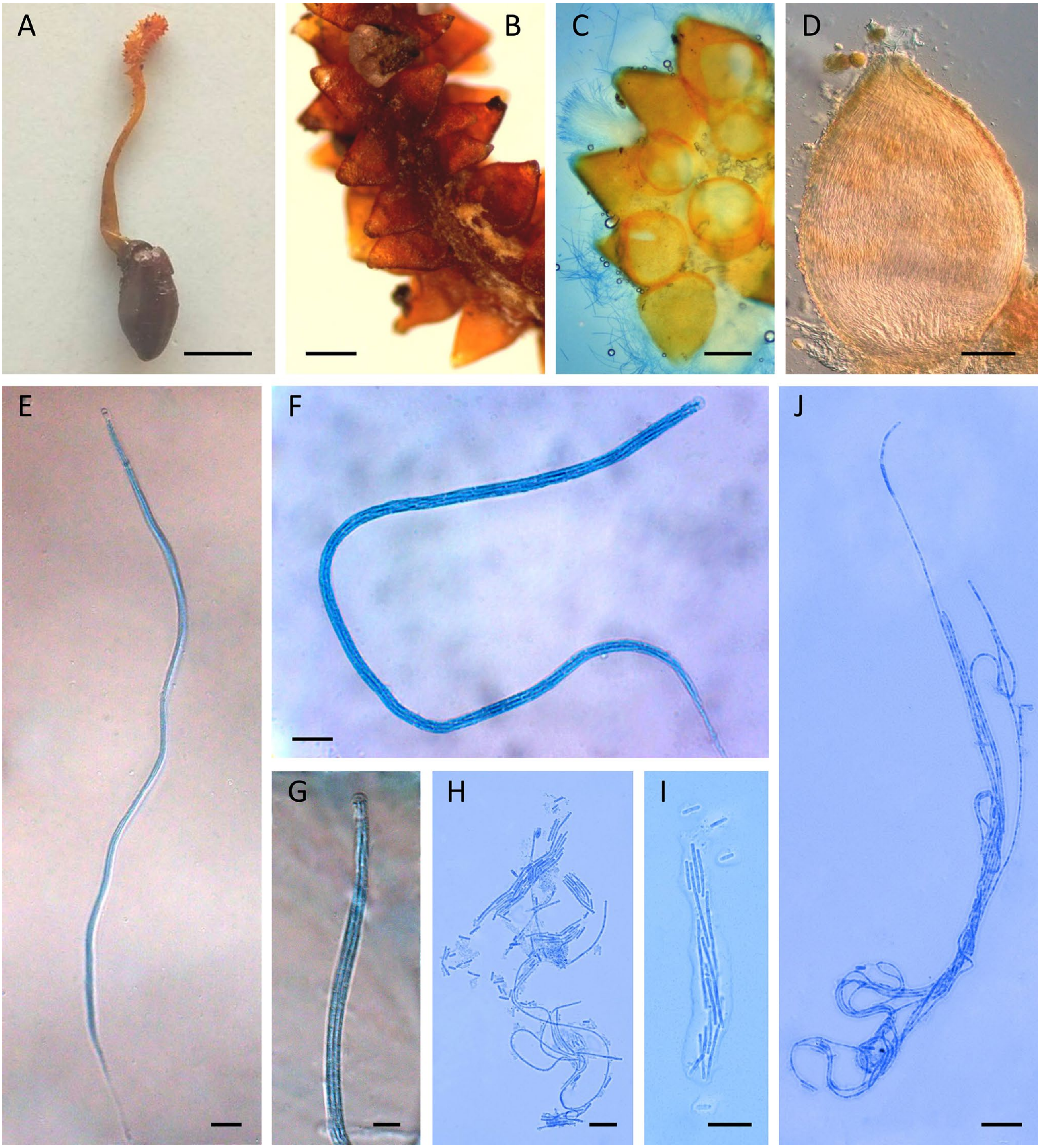


Fig. 4 *Cordyceps chaetoclavata*. **A** Fungus on the pupa of Lepidoptera. **B** Fertile part. **C**, **D** Perithecia. **E–G** Asci. **H** Ascospores and part-spores. **I** Part-spores. **J** Ascospores. Scale bars: **A** = 5 mm; **B, C** = 200 µm; **D** = 50 µm; **E, F** = 10 µm; **G** = 5 µm; **H–J** = 10 µm

Taxonomy

Cordyceps chaetoclavata H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833090; Fig. 4

Etymology: Referring to the clavate stromata with spinous fertile parts.

Holotype: YHH 15101.

Sexual morph: Stroma arising from the pupa of Lepidoptera buried in soil, solitary, cylindrical, reddish-orange to crimson, tapering gradually toward the apex, 2.3 cm long. Stipe cylindrical, orange to reddish-orange, 0.8 mm wide. Fertile part clavate, reddish-orange, covered by a spinous surface, up to 5.6 mm long, 0.7–1.1 mm wide, with sparsely distributed perithecia. Perithecia lageniform, crimson, superficial, 402–610 × 280–427 µm. Asci cylindrical, eight-spored, 274–385 × 3.7–4.8 µm, with a hemispheric apical cap of 3.1–4.3 × 2.1–2.7 µm. Ascospores 127–260 × 0.9–1.2 µm, filiform, multiseptate, breaking into cylindrical part-spores of 3–12 µm long. **Asexual morph:** Undetermined.

Host: Pupa of Lepidoptera.

Habitat: On the pupa of Lepidoptera buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Lepidoptera buried in soil, 12 August 2017, Qi Fan, (YHH 15101, holotype).

Notes: Five-gene phylogenetic analyses show that *C. chaetoclavata* is sister to *C. rosea* Kobayasi & Shimizu (spat 09–053) and an undescribed *Cordyceps* species (YFCC 5833). Based on the original description of *C. rosea*, it has rose stromata (1.1 cm long), immersed perithecia with ovoid shape, and the host of lepidopteran larvae (Kobayasi and Shimizu 1982). However, *C. chaetoclavata* differs from *C. rosea* by its longer stromata (2.3 cm long) with reddish-orange to crimson colors, spinous fertile parts, superficial lageniform perithecia, and the host of lepidopteran pupae. In addition, *C. chaetoclavata* is also morphologically similar to those of *C. militaris*, *C. ningxiaensis* T. Bau & J.Q. Yan, *C. kyusyuensis* Kawam, *C. roseostromata* Kobayasi & Shimizu, *C. shuifuensis* and *C. succavus* Y.P. Xiao et al. by sharing fleshy and cylindrical stipes, and orange to reddish-orange stromata (Kobayasi 1981; Kobayasi and Shimizu 1983; Liang 2007; Yang et al. 2012; Yan and Bau 2015; Hyde et al. 2019). The difference is that *C. chaetoclavata* has spinous fertile parts and superficial lageniform perithecia.

Cordyceps cocoonihabita H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833091; Fig. 5

Etymology: Referring to the host pupae of Lepidoptera inhabiting cocoons.

Holotype: YHH 8004.

Sexual morph: Stromata two or several, arising from the oval cocoon of the insect host, orange to pink, cylindrical, 15.2–57.8 mm long, unbranched or sometimes terminal branched. Stipes cylindrical, pink to reddish-orange, 0.1–1.3 mm wide. Fertile parts clavate, orange to pink or reddish-orange, 3.5–17.4 × 0.3–1.5 mm, often with aperithecial apices. Perithecia superficial, oblong-ovate, 346–435 × 125–199 µm. Asci cylindrical, 205–330 × 2.1–3.3 µm, eight-spored, with a hemispheric apical cap of 2.9–4.2 × 2.1–3.0 µm. Ascospores hyaline, cylindrical, septate, 140–269 × 1.4–2.1 µm, disarticulating into cylindrical part-spores of 2.9–8.0 µm long. **Asexual morph:** *Isaria*-like. Colonies on PDA moderately fast-growing, 38–45 mm diameter in 14 days at 25 °C, cottony, with high mycelial density; yellowish to pale orange at the centrum, white to yellowish at the edge, generating radially distributed stromata after 10 days, reverse brown. Hyphae smooth, septate, hyaline, 1.3–2.4 µm wide. Conidiophores smooth-walled, cylindrical, 5.8–8.3 × 1.4–2.0 µm. Phialides cylindrical to flask-shaped, solitary, alternate or whorled, 4.0–16.7 µm long, tapering gradually or abruptly from 1.5–2.7 µm at the base to 0.5–1.2 µm at the apex. Conidia in chains or solitary, hyaline, oval to fusiform, one-celled, 1.6–3.0 × 0.7–1.5 µm.

Host: Pupae of Limacodidae.

Habitat: On the pupae of Limacodidae in cocoons buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Shuanglong Village, on the pupa of Limacodidae in a cocoon buried in soil, 21 July 2011, Yuan-Bing Wang, (YHH 8004, holotype; YFCC 3415, ex-holotype living culture); *Ibid.*, (YHH 8005, paratype; YFCC 3416, ex-paratype living culture). Kunming City, Xishan Forest Park, on the pupa of Lepidoptera in a cocoon buried in soil, 13 August 2018, Yuan-Bing Wang, (YHH 16246; YFCC 6569, living culture).

Notes: Cordyceps cocoonihabita is characterized by unbranched or terminally branched stromata, clavate fertile parts often have aperithecial apices, orange to pink or reddish-orange, superficial perithecia with oblong-ovate shape, cylindrical ascospores, and the host of lepidopteran pupae in oval cocoons. The asexual morph from PDA culture produces conidiophores with cylindrical to flask-shaped phialides which are monothetic, alternate or whorled, as well as oval to fusiform conidia in chains.

It is phylogenetically closely related to a formally undescribed taxon *C.* cf. *pruinosa* (EFCC 5197, EFCC 5693) and is separated from *C. pruinosa* Petch and *C. ninchukispora* (C.H. Su & H.H. Wang) G.H. Sung et al. in this clade. *Cordyceps cocoonihabita, C. pruinosa* and *C. ninchukispora* have the similar macromorphological characteristics of stromata with orange to pink colors, pyriform-like perithecia, with the exception of the former fertile parts often have aperithecial apices (Petch 1924; Su and Wang 1986). The former two taxa have similar hosts of lepidopteran pupae in cocoons, they differ, however, from *C. ninchukispora* with hosts such as seeds of *Beilschmiedia* Nees. Ecologically, *C. cocoonihabita* and *C. obliquiordinata* Kobayasi & Shimizu have similar habitats that are in cocoons of Lepidoptera (Kobayasi and Shimizu 1982). However, *C. obliquiordinata* is morphologically different from *C. cocoonihabita* by having shorter stromata, brevis stipes, ovoid and irregular pars fertile parts, obliquely

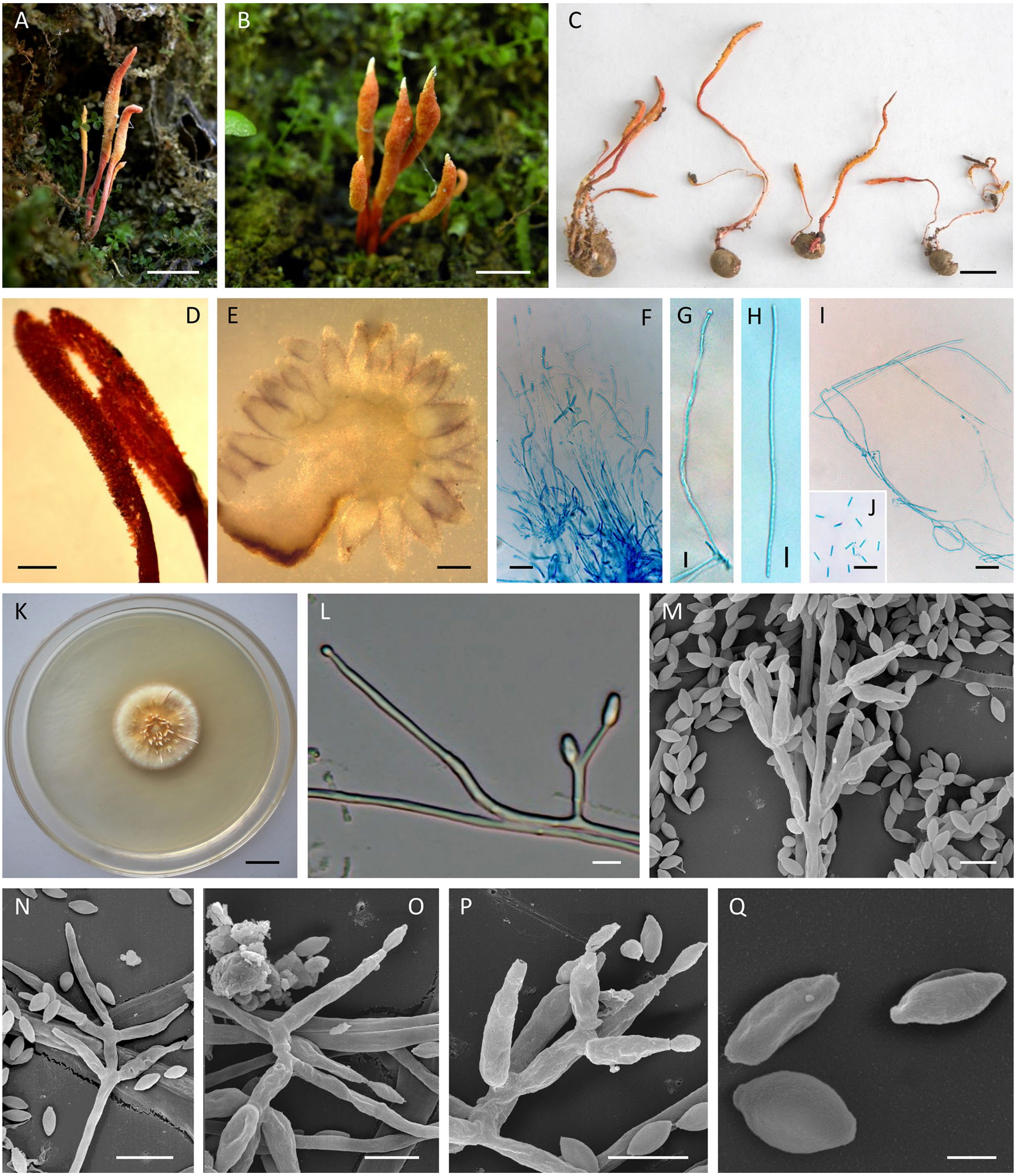


Fig. 5 *Cordyceps cocoonihabita*. **A, B** Stromata arising from hosts buried in soil. **C** Fungus on the pupae of Lepidoptera inhabiting cocoons. **D** Fertile part. **E** Perithecia. **F, G** Asci. **H, I** Ascospores. **J** Part-spores. **K** Colony on PDA. **L–P** Conidiophores and phialides. **Q** Conidia. Scale bars: **A–C** = 1 cm; **D** = 1 mm; **E** = 200 μm; **F** = 20 μm; **G** = 10 μm; **H** = 20 μm; **I, J** = 10 μm; **K** = 1 cm; **L** = 5 μm; **M** = 2 μm; **N–P** = 5 μm; **Q** = 1 μm

immersed perithecia, fairly short asci and ascospores. In terms of asexual morph, *C. cocoonihabita* has *Isaria*-like micromorphological characteristics and is significantly different from *C. pruinosa* and *C. ninchukispora* which respectively have morphs of *Mariannaea* G. Arnaud and *Acremonium* Link (Liang et al. 1983, 1991; Su and Wang 1986).

Cordyceps shuifuensis H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833092; Fig. 6

Etymology: Named after the location Shuifu City where this species was collected.

Holotype: YHH 14101.

Sexual morph: Stromata solitary, cylindrical to slightly clavate, 2.5 cm long. Stipes cylindrical, yellowish to orange, 21 × 1 mm. Fertile parts clavate, yellowish, reddish-orange, 4 × 1.5 mm. Perithecia ovoid, reddish-orange, losely-packed, pseudoimmersed, 450–620 × 300–430 µm. Asci cylindrical, 275–510 × 3.5–5.2 µm, with a hemispheric apical cap of 3.2–4.8 × 2.3–3.2 µm. Ascospores filiform, multiseptate, 180–410 × 1.2–1.7 µm, breaking into cylindrical part-spores of 2.8–6.5 µm long. **Asexual morph:** *Verticillium*-like. Colonies on PDA fast-growing, 45–50 mm diameter in 14 days at 25 °C, white, cottony, with protuberant mycelial density at the centrum, reverse yellowish. Hyphae smooth-walled, branched, septate, hyaline, 0.9–2.1 µm wide. Conidiophores smooth-walled, solitary, cylindrical, 5.5–9.2 × 1.6–2.7 µm. Phialides cylindrical or subulate, solitary or in whorls of two to three, 4.7–20.0 µm long, tapering gradually toward the apex, 1.1–2.0 µm wide at the base, 0.4–2.1 µm wide at the apex. Conidia have two types, hyaline, smooth-walled, one-celled, single or usually aggregate in subglobose to ellipsoidal heads at the apex of phialides. Macroconidia clavate to oblong-ovate, 5.1–11.8 × 1.3–2.4 µm. Microconidia globose to ellipsoidal, 1.8–3.0 × 1.6–2.5 µm.

Host: Pupa of Lepidoptera.

Habitat: On the pupa of Lepidoptera buried in soil.

Distribution: Shuifu City, China.

Material examined: CHINA. YUNNAN PROVINCE: Shuifu City, Tongluoba National Nature Reserve, on the pupa of Lepidoptera buried in soil, 07 September 2016, Yong-Dong Dai, (YHH 14101, holotype; YFCC 5230, ex-holotype living culture).

Notes: Cordyceps shuifuensis phylogenetically clusters with *C. militaris, C. kyusyuensis* Kawam and *C. roseostromata* Kobayasi & Shimizu, but is distinguished from these three by forming a separate clade in this group. This species is morphologically closest to *C. militaris* having cylindrical to slightly clavate stromata with yellowish to reddish-orange colors, superficial perithecia and *Verticillium*-like asexual morph, but differs from the latter in size. *Cordyceps shuifuensis* only has *Verticillium*-like asexual morph, whereas *C. militaris* has both *Verticillium*- and *Isaria*-like asexual morphs (Yang et al. 2012). *Cordyceps kyusyuensis* differs from *C. shuifuensis* by having mutiple rhizoid stromata, the host larvae of Sphingidae and being very large in size (Kobayasi 1981; Liang 2007). *Cordyceps roseostromata* differs from *C. shuifuensis* by its mutiple and rhizoid stromata, rose color, and the host larvae of Coleoptera (Kobayasi and Shimizu 1983).

Cordyceps subtenuipes H. Yu, Y.B. Wang, Y. Wang, D.E. Duan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833093; Fig. 7

Etymology: Referring to morphologically resembling *Cordyceps tenuipes* but phylogenetically distinct.

Holotype: YHH 15016.

Sexual morph: Undetermined. **Asexual morph:** *Isaria*-like. Synnemata arising from the pupae of Lepidoptera. Synnemata erect, solitary or two, flexuous, white, fleshy, up to 1.5 cm long, with terminal branches of 3–5 × 1.5–2.0 mm. Stipes cylindrical, 1 mm wide, producing a mass of conidia at the branches of synnemata, powdery and floccose. Conidiophores grouped together on th apex of synnemata, biverticillate with phialides in whorls of three to seven, 3.0–5.6 × 1.8–3.2 µm. Phialides with a globose basal portion, 3.7–6.2 × 2.3–3.9 µm, tapering abruptly into a narrow neck of 0.5–1.0 µm wide. Conidia usually single, one-celled, smooth-walled, hyaline, fusiform or oval, 2.2–3.2 × 1.5–2.7 µm. Colonies on PDA moderately fast-growing, 50–54 mm diameter in 14 days at 25 °C, white to yellowish, cottony, with low mycelial density, reverse deep yellow. Hyphae smooth-walled, branched, septate, hyaline, 1.3–2.7 µm wide. Conidiophores erect, arising from the aerial and prostrate hyphae, solitary or verticillate, with phialides in whorls of two to six, smooth-walled, cylindrical to ellipsoidal, 3.5–8.6 × 1.5–2.9 µm. Phialides solitary or verticillate, 5.3–42.5 µm long, with a cylindrical or flask-shaped basal portion, tapering gradually or abruptly toward the apex, 1.6–3.4 µm wide at the base, and 0.5–1.1 µm wide at the apex. Conidia hyaline, one-celled, ellipsoidal or fusiform, 1.9–3.4 × 1.7–2.5 µm, often in chains.

Host: Pupae of Lepidoptera.

Habitat: On the pupae of Lepidoptera buried in soil.

Distribution: Lanping County and Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Nujiang Lisu Autonomous Prefecture, Lanping County, Tongdian Town, on the pupa of Lepidoptera buried in soil, 05 August 2017, Yuan-Bing Wang, (YHH 15016, holotype; YFCC 6051, ex-holotype living culture). Kunming City, Xishan Forest Park, on the pupa of Lepidoptera buried in soil, 13 August 2018, Yuan-Bing Wang, (YHH 15002; YFCC 6084, living culture).

Notes: Phylogenetically, the new species *C. subtenuipes* forms a separate clade from the other species of *Cordyceps* with high credible support (100%). *Cordyceps subtenuipes* is similar to *C. tenuipes* (Peck) Kepler et al. by its

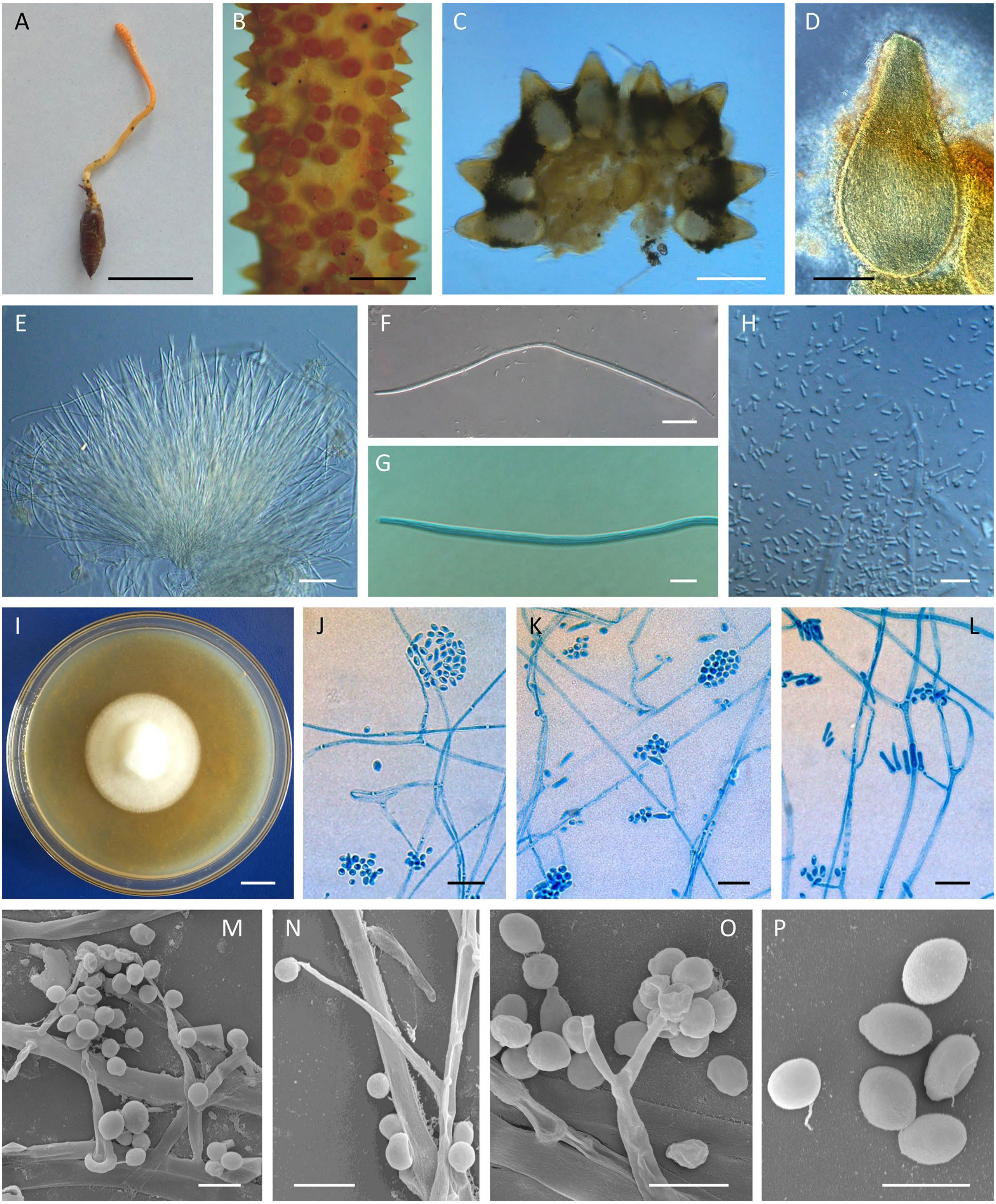


Fig. 6 *Cordyceps shuifuensis*. **A** Fungus on the pupa of Lepidoptera. **B** Fertile part. **C, D** Perithecia. **E–G** Asci. **H** Part-spores. **I** Colony on PDA. **J–O** Conidiophores and phialides. **P** Conidia. Scale bars: **A** = 1 mm; **B, C** = 500 μm; **D** = 200 μm; **E** = 50 μm; **F, G** = 10 μm; **H** = 5 μm; **I** = 1 cm; **J–L** = 10 μm; **M–O** = 5 μm; **P** = 2 μm

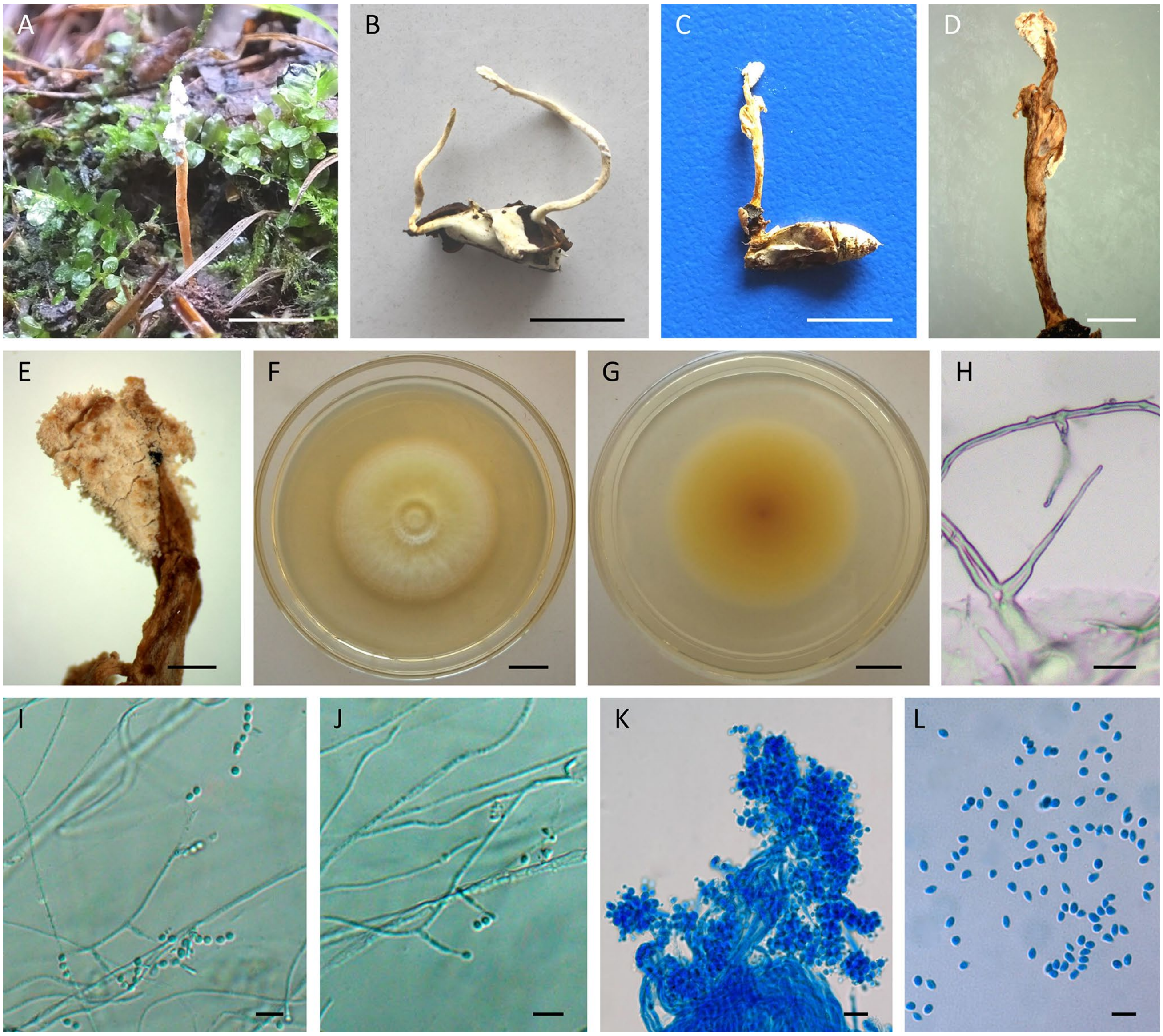


Fig. 7 *Cordyceps subtenuipes*. **A** Synnemata arising from the pupa of Lepidoptera buried in soil. **B, C** Fungus on the pupae of Lepidoptera. **D, E** Stipe producing a mass of conidia at the apex. **F** Colony on PDA. **G** Reverse of colony. **H–K** Conidiophores and phialides. **L** Conidia. Scale bars: **A–C** = 5 mm; **D** = 1 mm; **E** = 500 μm; **F, G** = 1 cm; **H** = 10 μm; **I, J** = 5 μm; **K** = 10 μm; **L** = 5 μm

conspicuous synnemata and *Isaria*-like asexual conidiogenous structure producing phialides with a swollen basal portion. It differs from *C. tenuipes* by its single or two synnemata, white color, phialides with a globose basal portion and smaller fusiform or oval conidia measuring 1.9–3.4 × 1.5–2.7 μm. *Cordyceps tenuipes* has mutiple synnemata, larger cylindrical to botuliform conidia with the size of 2.0–7.5 × 1.0–2.5 μm (Samson 1974). The sexual morph of *C. tenuipes* as proposed by the name *C. takaomontana* Yakush & Kumaz has yellowish stromata and often co-occurs with its asexual morph (Liang 2007). However, the sexual morph of *C. subtenuipes* was not found in this study.

Flavocillium H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **gen. nov.**

Mycobank: MB 833094.

Etymology: Referring to the yellowish stromata and colonies.

Type species: Flavocillium bifurcatum H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang.

Sexual morph: Stromata arising from the insect buried in soil, clavate to flake-like, solitary, flexuous, yellowish, fleshy, up to 5 cm long, with a furcate terminal branch; stipe clavate, flexuous; fertile part contorted, clavate; perithecia densely packed, yellowish. **Asexual morph:** *Lecanicillium*-like. Colonies yellowish, slow-growing. Conidiophores mononematous, cylindrical, with two to five phialides at the terminal nodes. Phialides lanceolate, solitary or in whorls of two to five, tapering gradually toward the apex. Two types of conidia hyaline, one-celled and smooth-walled, single or usually aggregate in subglobose to ellipsoidal heads at the apex of the phialides. Macroconidia fusiform, cymbiform or ellipsoidal to cylindrical. Microconidia oval to ellipsoidal or fusiform.

Notes: Five-gene phylogenetic analyses show that *L. acerosum, L. primulinum, Lecanicillium* sp. and our samples (YHH 15428, YFCC 6101) group together, in a monophyletic clade in the family Cordycipitaceae (Fig. 1, 2). This *L. primulinum* clade is clustered in the subbasal portion of phylogenetic tree within Cordycipitaceae and has a close phylogenetic relationship with *Engyodontium* and *Parengyodontium*, but forms a distinct lineage. ML and BI phylogenetic analyses based on ITS sequences from 30 taxa in *Lecanicillium* and *Simplicillium* show that the *Lecanicillium* group is polyphyletic and consists of eight monophyletic clades (Fig. 3). The *L. primulinum* clade includes *L. acerosum, L. primulinum, Lecanicillium* sp., *L. subprimulinum* and one new species with yellowish stromata (Fig. 3). This result is also supported by the previous phylogenetic analyses of *Lecanicillium* species from a combined nr*SSU*, nr*LSU, tef-1* and ITS sequence dataset (Huang et al. 2018). In this clade, *L. acerosum* was first described by its distinguishing morphological characteristics producing the large straight macroconidia (Zare and Gams 2001). Recently, two species (*L. primulinum* and *L. subprimulinum*) producing pastel yellow pigment were added, which were respectively isolated from soil and an ophioceras-like taxon on the dead submerged wood (Kaifuchi et al. 2013; Huang et al. 2018).

Morphologically, the *L. primulinum* clade is similar to other *Lecanicillium* species in terms of conidiophores, phialides and two types of conidia (Zare and Gams 2001; Zhou et al. 2018). However, these species of *Flavocillium* possess yellowish stromata with a furcate terminal branch, contorted fertile parts with yellowish perithecia and colonies that usually produce pastel yellow pigment, are obviously different from other members of the *Lecanicillium* lineage. In addition, the *L. primulinum* clade also can be distinguished from these phylogenetically related genera *Engyodontium* and *Parengyodontium* based on the morphological characteristics of the latters, both of which usually produce white colonies, conidiiferous rachids with denticles on phialides and terminal fertile regions that are zigzag-shaped (Gams et al. 1984; Tsang et al. 2016). Therefore, the new genus *Flavocillium* is introduced by the type species *F. bifurcatum* in order to accomodate the three following new combinations previously treated as members of *Lecanicillium.*

Flavocillium acerosum (W. Gams et al.) H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **comb. nov.**

Mycobank: MB 833101.

Basionym: *Lecanicillium acerosum* W. Gams et al., Nova Hedwigia 73(1–2): 37 (2001).

Descriptions and illustrations: Zare and Gams (2001).

Distribution: Known from Brazil, Amazon (Zare and Gams 2001).

Notes: Flavocillium acerosum was first isolated from *Crinipellis perniciosa* (Stahel) Singer on *Theobroma cacao* Linn. (Zare and Gams 2001). This species is characterized by producing phialides solitary or up to two to five at the node, which gradually taper toward the apex (30–32 × 1.8–2.2 μm), fusiform macr- and microconidia with acute ends, presenting octahedral crystals (Zare and Gams 2001). It morphologically resembles *L. antillanum*, but its straight conidia are distinct from the sigmoidally curved conidia of the latter. Five-gene and ITS phylogenetic analyses indicate that *F. acerosum* and *L. antillanum* are located in different clades which represent a genus level difference in the family Cordycipitaceae.

Flavocillium bifurcatum H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833096; Fig. 8

Etymology: Referring to the stromata with a bifurcate terminal branch.

Holotype: YHH 15428.

Sexual morph: Stromata arising from the insect buried in soil, clavate to flake-like, solitary, flexuous, yellowish, fleshy, up to 2.0 cm long, with a furcate terminal branch of 13–16 × 1.5–2.0 mm. Stipe clavate, flexuous, 2.2 mm wide. Fertile parts contorted, clavate, 11–14 × 1.4–2.0 mm. Perithecia densely packed, yellowish, immature. Asci not observed. **Asexual morph:** Colonies on PDA slow-growing, up to 3 cm diameter in 14 days at 25 °C, white to yellowish, cottony with raised mycelial density at the centrum, generating several concentric rings at the edge, reverse pale yellow to brown. Hyphae hyaline, septate, branched, smooth-walled, 1.0–2.3 μm wide. Conidiophores mononematous, cylindrical, 50.0–64.2 × 0.9–1.8 μm. Phialides on conidiophores or arising from prostrate hyphae, lanceolate, solitary or in whorls of two to five, tapering gradually toward the apex, 18.1–44.5 μm long, 1.1–2.4 μm wide at the base, and 0.7–1.5 μm wide at the apex. Two types of conidia hyaline, one-celled and smooth-walled, single or usually aggregate in subglobose to ellipsoidal heads at the apex of the phialides. Macroconidia cymbiform, 5.5–9.2 × 1.3–2.7 μm. Microconidia ellipsoidal to reniform, 2.1–4.2 × 0.9–1.5 μm.

Host: Larva of Noctuidae.

Habitat: On the larva of Noctuidae buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the larva of Noctuidae buried in soil, 12 August 2017, Hong Yu, (YHH 15428, holotype; YFCC 6101, ex-holotype living culture).

Fig. 8 *Flavocillium bifurcatum*. **A** Fungus on the host. **B** The host larva of Noctuidae. **C** Stroma with a bifurcate terminal branch. **D** Colony on PDA. **E–I** Conidiophores with phialides. **J, K** Phialides with conidia. **L** Conidia. Scale bars: **A** = 5 mm; **B, C** = 2 mm; **D** = 1 cm; **E–J** = 10 μm; **K** = 5 μm; **L** = 2 μm

Notes: Flavocillium bifurcatum is characterized by the fleshy stromata with a bifurcate terminal branch, solitary, yellowish, contorted fertile parts, long conidiophores, lanceolate phialides, two types of cymbiform macroconidia and ellipsoidal to reniform microconidia.

Five-gene phylogenetic analyses suggest that *F. bifurcatum* is close to *Lecanicillium* sp. and *F. primulinum.* In addition, ITS phylogenetic analyses from more complete sequence data in this clade show that *F. bifurcatum* is sister to *F. subprimulinum*. Morphologically, *F. bifurcatum* is similar to *F. subprimulinum* and *F. primulinum* by the yellowish colonies, solitary or whorled phialides, macro- and microconidia aggregate in subglobose to ellipsoidal heads at the apex of phialides (Kaifuchi et al. 2013; Huang et al. 2018). However, the sexual morphs of *F. subprimulinum* and *F. primulinum* have not been observed. *Flavocillium bifurcatum* differs from *F. subprimulinum* and *F. primulinum* by its cymbiform macroconidia and longer conidiophores up to 64 μm. Ecologically, *F. bifurcatum* is parasitic on the larva of Noctuidae buried in soil and is quite different from other congeneric species.

Flavocillium primulinum (Kaifuchi et al.) H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **comb. nov.**

Mycobank: MB 833103.

Basionym: *Lecanicillium primulinum* Kaifuchi et al., Mycoscience. 54: 294–293 (2013).

Descriptions and illustrations: Kaifuchi et al. (2013).

Distribution: Known from Okinawa Prefecture, Japan (Kaifuchi et al. 2013).

Notes: The type strain of *F. primulinum* was isolated from soil under an unidentified plant. It is characterized by phialides produced on prostrate aerial hyphae, solitary or in whorls of two to five which taper toward the apex, ellipsoidal to cylindrical macroconidia and oval to ellipsoidal microconidia aggregate in subglobose to ellipsoidal heads at the apex of the phialides, presenting octahedral crystals (Kaifuchi et al. 2013). Phylogenetically, this species is close to *F. bifurcatum* and *F. subprimulinum*, but it differs morphologically from *F. bifurcatum* by the latter's cymbiform macroconidia and smaller microconidia of 2.1–4.2 × 0.9–1.5 µm in size.

Flavocillium subprimulinum (S.K. Huang & K.D. Hyde) H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **comb. nov.**

Mycobank: MB 833106.

Basionym: *Lecanicillium subprimulinum* S.K. Huang & K.D. Hyde, Phytotaxa 348 (2): 102 (2018).

Descriptions and illustrations: Huang et al. (2018).

Distribution: Known from Baoshan City, China (Huang et al. 2018).

Notes: Flavocillium subprimulinum is characterized by solitary or two to three phialides on conidiophores arising from hyaline hyphae, with gregarious, ovoid to ellipsoidal conidia (Huang et al. 2018). Ecologically, this species is associated with a sexual morph of an ophioceras-like taxon on submerged wood and is different from those of *F. bifurcatum* on the larva of Noctuidae and *F. subprimulinum* isolated from soil. Phylogenetically, *F. subprimulinum* is sister to *F. bifurcatum* based on ITS phylogenetic analyses of *Lecanicillium* lineage, but it differs morphologically from *F. bifurcatum* because the latter has bifurcate stromata, cymbiform macroconidia and longer conidiophores.

Liangia H. Yu, Y.B. Wang, Y. Wang, Z.H. Chen & Zhu L. Yang, **gen. nov.**

Mycobank: MB 833107.

Etymology: In honor of Prof. Zong-Qi Liang, acknowledging his contributions to our knowledge of cordycipitoid fungi.

Type species: Liangia sinensis H. Yu, Y.B. Wang, Y. Wang, Z.H. Chen & Zhu L. Yang.

Colonies on PDA slow-growing, effuse or stellate, white, usually raising dome-shaped mycelial density with a sunken zone at the centrum, verrucose around the margin. Conidiophores not observed. Phialides lanceolate, occurring directly from the prostrate hyphae, solitary, gradually attenuated toward the apex. Two types of macro- and microconidia, aseptate, smooth-walled, one-celled, both of them existing singly or in pairs at the the apex of phialides. Macroconidia positioned at a right angle to the apex of phialides, straight, oblong-oval to fusiform. Microconidia oval to ellipsoidal.

Notes: Liangia sinensis, isolated from an entomopathogenic fungus *B. yunnanensis*, represents a well-supported monophyletic lineage in the family Cordycipitaceae (Fig. 1). The new genus *Liangia* with *Lecanicillium*-like asexual morph is proposed for the type species *Lia. sinensis* based on its phylogenetic placement. In this study, it appears more closely related to *C. piperis* (J.F. Bisch. & J.F. White) D. Johnson et al. and *L. psalliotae* clades by the five-gene phylogenetic analyses. The genus *Liangia* is morphologically similar to these two clades which possess asexual morph of *Lecanicillium* (Zare and Gams 2001; Bischoff and White 2004). However, it differs from the latter two groups by the shape and size of its colonies, phialides and conidia.

Liangia sinensis H. Yu, Y.B. Wang, Y. Wang, Z.H. Chen & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833109; Fig. 9

Etymology: Named after China where the species is distributed.

Holotype: YHH 7455.

Sexual morph: Undetermined. **Asexual morph:** *Lecanicillium*-like. Strains isolated from the stromata of *Beauveria yunnanensis* associated with the pupa of Lepidoptera. Colonies on PDA slow-growing, 28–34 mm in diameter after 14 days at 25 °C, effuse or stellate, white, usually raising dome-shaped mycelial density with a sunken zone at the centrum, verrucose around the margin. Reverse pale brown, causing a brown concentric ring outside of the inoculum. Hyphae hyaline, septate, branched, smooth-walled, and 0.7–2.4 µm wide. Phialides lanceolate, occurring directly from the prostrate hyphae, solitary, gradually attenuated toward the apex, 16.7–59.0 µm long, 0.7–1.6 µm wide at the base and 0.3–0.7 µm wide at the apex. Conidia existing in two types, macro- and microconidia, aseptate, hyaline, smooth-walled, one-celled, straight, both existing singly or in pairs at the apex of phialides. Macroconidia positioned at a right angle to the apex of phialides, oblong-oval to fusiform, 4.5–9.3 × 1.2–1.9 µm. Microconidia oval to ellipsoidal, 1.8–3.3 × 1.1–1.8 µm.

Substratum: Beauveria yunnanensis.

Habitat: On the stromata of *B. yunnanensis* associated with the pupa of Lepidoptera buried in soil.

Distribution: Baoshan City, China.

Material examined: CHINA. YUNNAN PROVINCE: Baoshan City, Mangkuan Village, isolated from *B. yunnanensis* associated with the pupa of Lepidoptera buried in soil, 22 July 2016, Zi-Hong Chen, (YHH 7455, holotype; YFCC 3103, ex-holotype living culture); *Ibid.*, (YHH 7456; YFCC 3104, living culture).

Notes: Liangia sinensis possesses *Lecanicillium*-like asexual morph and is characterized by white colonies forming a sunken zone at the centrum of dome-shaped mycelial density and verrucose around the margin, solitary and lanceolate phialides occurring directly from the prostrate

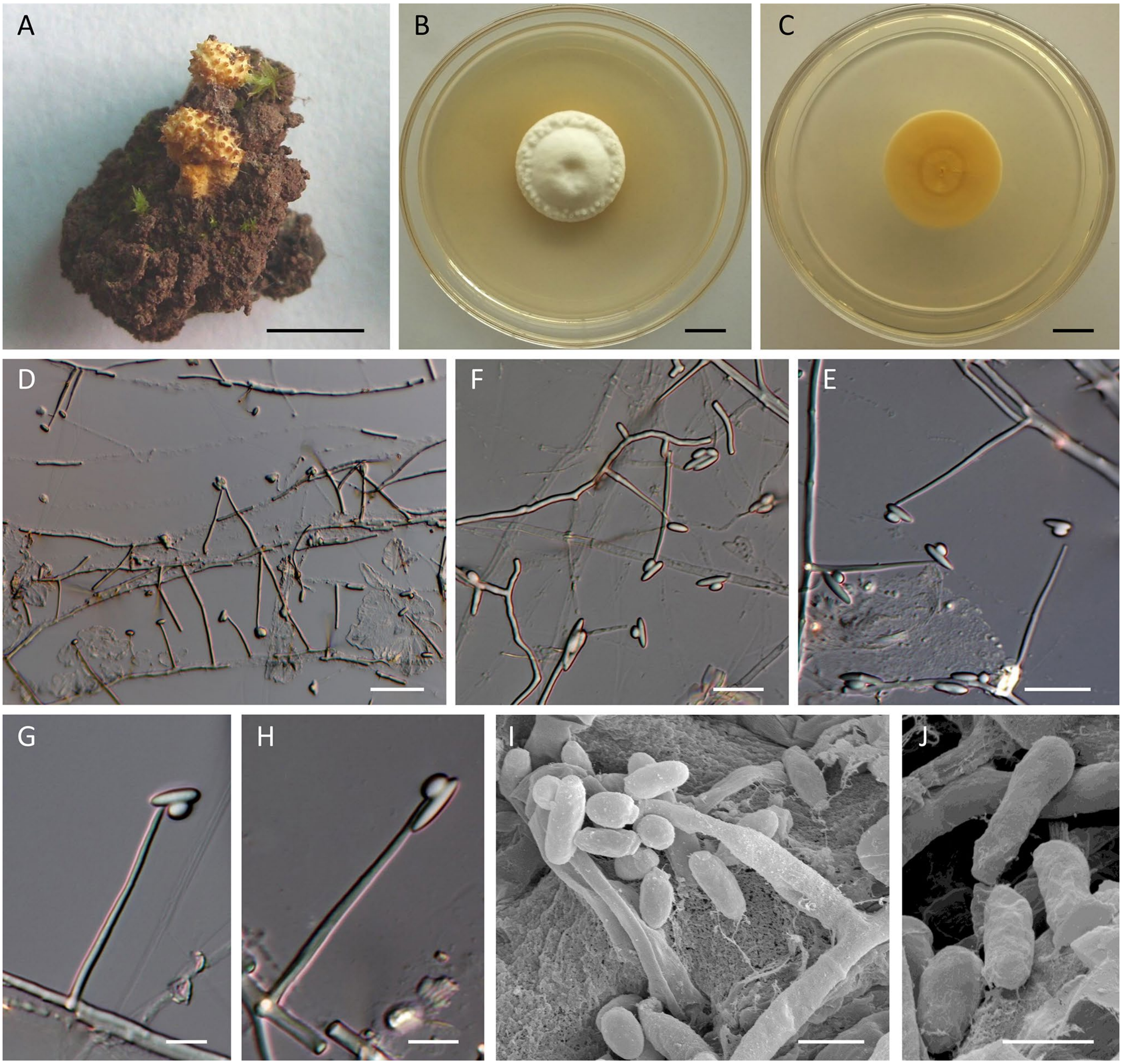


Fig. 9 *Liangia sinensis*. **A** Stromata of *Beauveria yunnanensis* arising from the pupa of Lepidoptera buried in soil, from which *Lia. sinensis* was isolated. **B** Colony on PDA. **C** Reverse of colony. **D, E** Phialides. **F–H** Macro- and microconidia existing in pairs at the apex of phialides. **I** Phialides and conidia. **J** Conidia. Scale bars: **A** = 5 mm; **B, C** = 1 cm; **D** = 20 µm; **E, F** = 10 µm; **G–I** = 5 µm; **J** = 2 µm

hyphae, oblong-oval to fusiform macroconidia, and oval to ellipsoidal microconidia existing singly or in pairs at the apex of phialides.

It is similar to the two phylogenetically more closely related *C. piperis* and *L. psalliotae* clades with asexual morph of *Lecanicillium* (Zare and Gams 2001; Bischoff and White 2004). However, *Lia. sinensis* differs from *C. piperis* and *L. psalliotae* by its distinguished colonies, solitary and lanceolate phialides without conidiophores and oblong-oval to fusiform macroconidia. *Cordyceps piperis*, originally named *T. piperis* J.F. Bischoff & J.F. White, was reported to have the sexual morph of *Torrubiella* with sessile perithecial stromata which covered the corpses of scale insects attached to Piperaceae (Bischoff and White 2004). *Lecanicillium psalliotae* was originally described as *Verticillium psalliotae* Treschew which caused diseases of cultivated mushrooms (Treschew 1941), and later were widely discovered from insects, nematodes, soil, mushrooms, *Rhopalomyces* Corda and other fungi (Dayal and Barron 1970; Zare and Gams 2001; Yang et al. 2005). *Liangia sinensis* is distinctive for its isolates from the newly described cordycipitoid fungus *B. yunnanensis* parasitic on the lepidopteran pupa (Chen et al. 2019).

In the five-gene phylogenetic tree, *B. yunnanensis* (ex-holotype living culture CCTCC AF 2018010 = YFCC 3105) is closely clustered with *B. scarabaeidicola* (Kobayasi) S.A. Rehner & Kepler, and remotely related to *Lia. sinensis* (Fig. 1, 2). In this study, there is no strong hyperparasitic evidence that *Lia. sinensis* grows on the stromata of *B. yunnanensis*. However, two strains of *Lia. sinensis* were truly isolated from the stromata of *B. yunnanensis*. The possibility that *Lia. sinensis* is a hyperparasitic fungus of *B. yunnanensis* requires confirmation.

Samsoniella alpina H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833110; Fig. 10

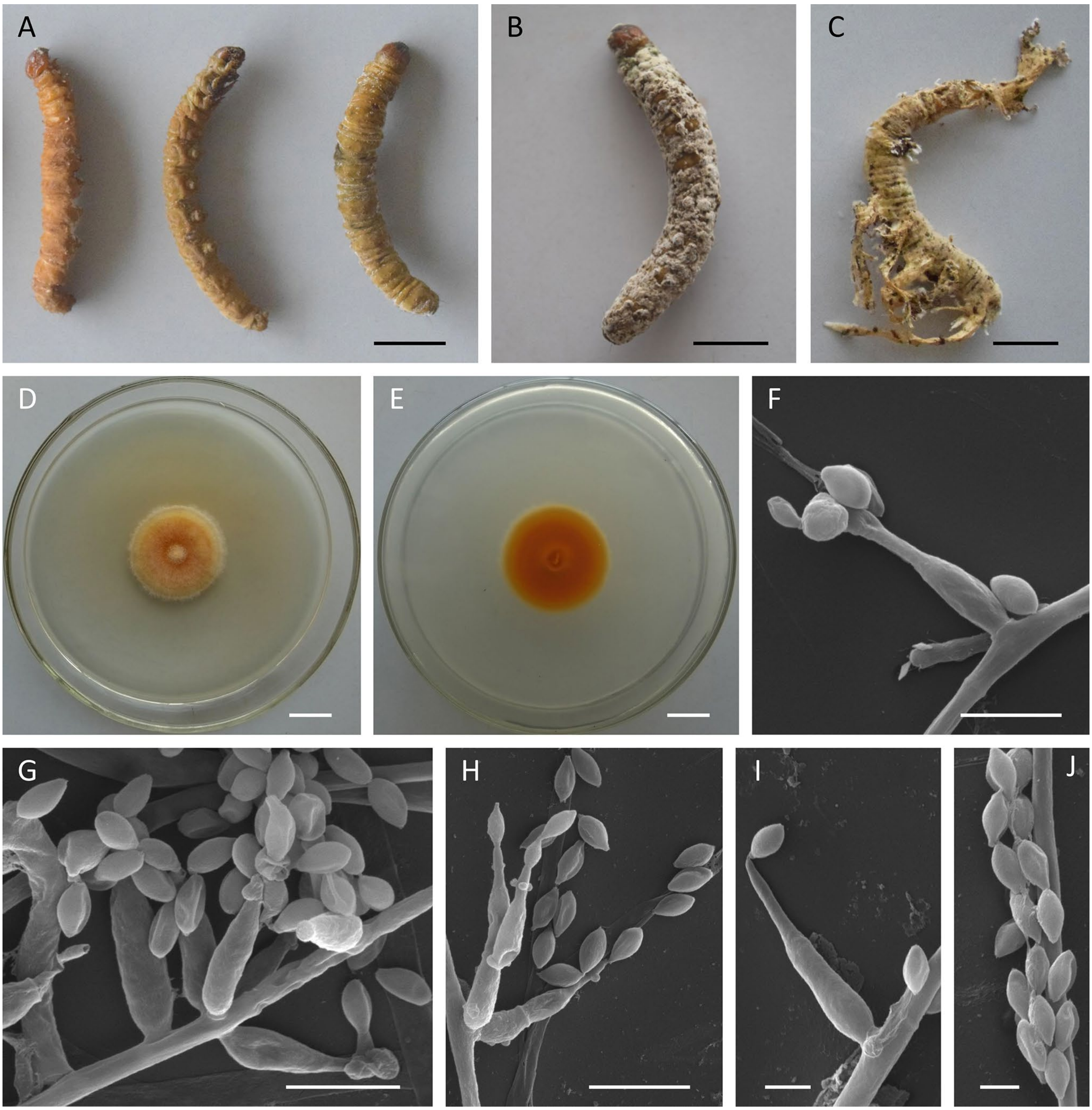


Fig. 10 *Samsoniella alpina*. **A, B** Larvae of *Hepialus baimaensis* infected by *S. alpina.* **C** Synnemata arising from the whole body of *H. baimaensis*. **D** Colony on PDA. **E** Reverse of colony. **F** Solitary phialides on hyphae. **G, H** Verticillate phialides. **I** Solitary phialides on hyphae. **J** Conidia in chains. Scale bars: **A–E** = 1 cm; **F–H** = 5 μm; **I, J** = 2 μm

Etymology: Named after the alpine locations where this species is distributed.

Holotype: YHH 15316

Sexual morph: Undetermined. **Asexual morph:** *Isaria*-like. Synnemata arising from the whole body of larvae of *Hepialus*. Synnemata irregularly branched, 0.3–2.0 cm long, 0.1–0.3 mm wide; cylindrical or clavate stipes with white powdery heads, white to orange yellow. Conidiophores on the apex of synnemata, biverticillate with phialides in whorls of two to seven, cylindrical, 4.5–7.2 × 1.5–3.0 µm. Phialides with a basal portion cylindrical to narrowly lageniform, 4.3–10.3 × 1.6–2.9 µm, tapering abruptly into a narrow neck of 0.5–1.0 µm wide. Conidia in chains, one-celled, smooth-walled, hyaline, fusiform or oval, 2.2–2.9 × 1.3–2.0 µm. Colonies on PDA growing fairly well at 25 °C, up to 40 mm diameter in 14 days, hairy, floccose, light orange to orange-red. Reverse cream, turning yellowish. Hyphae smooth-walled, branched, septate, hyaline, 0.9–2.7 µm wide. Conidiophores cylindrical, usually biverticillate with phialides in whorls of two to seven, 3.1–6.5 × 1.6–2.8 µm. Phialides verticillate on conidiophores, solitary or verticillate on hyphae, occasionally verruculose, basal portion cylindrical to narrowly lageniform, tapering abruptly toward the apex, 4.7–9.5 µm long, 1.9–3.1 µm wide at the base, 0.5–1.1 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–3.1 × 1.3–2.1 µm, often in chains.

Host: Larvae of *Hepialus baimaensis* Liang.

Habitat: On the larvae of *Hepialus baimaensis* (Hepialidae) buried in soil.

Distribution: Diqing Tibetan Autonomous Prefecture, China.

Material examined: CHINA. YUNNAN PROVINCE: Diqing Tibetan Autonomous Prefecture, Shangrila City, Xiaozhongdian Town, on the larva of *Hepialus baimaensis* (Hepialidae) buried in soil, 6 May 2017, Can-Ming Zhang, (YHH 15316, holotype; YFCC 5818, ex-holotype living culture); *Ibid.*, (YHH 15317, paratype; YFCC 5831, ex-paratype living culture); *Ibid.*, (YHH 15319, paratype; YFCC 5836, ex-paratype living culture).

Notes: Samsoniella alpina has *Isaria*-like asexual morph and is characterized by irregularly branched synnemata, cylindrical or clavate stipes with white powdery heads, white to orange yellow, hairy and floccose colonies with light orange to orange-red colors, solitary or verticillate phialides with cylindrical to narrowly lageniform basal portion, fusiform or oval conidia.

Samsoniella alpina is phylogenetically sister to *S. cardinalis* with high statistical supports by BP = 99% and PP = 100%. It is similar to *S. cardinalis* in producing phialides with cylindrical to narrowly lageniform basal portion, fusiform or oval conidia. However, it differs from *S. cardinalis* by irregularly branched synnemata with white powdery heads, white to orange yellow, colonies produing light orange to orange-red colors and parasitizing larvae of *H. baimaensis*.

Samsoniella antleroides H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833111; Fig. 11

Etymology: Referring to the antler-like stromata.

Holotype: YHH 15758

Sexual morph: Stromata fasciculate, antler-like, arising from the larvae of Noctuidae, 22.3–57.8 mm long, cylindrical to clavate, with oblate terminal branches of 4.6–26.2 mm long. Stipes flexuous, 16.4–43.5 × 0.7–2.2 mm. Fertile parts clavate to flake-like, lateral sides usually have a longitudinal ditch without producing perithecia, orange to orange-red, 6.3–9.5 × 0.6–2.3 mm. Perithecia superficial, fusiform, 294–442 × 131–216 µm. Asci eight-spored, hyaline, cylindrical, 160–248 × 2.1–2.7 µm. Ascus caps hemispherical, 1.9–3.2 × 1.8–2.5 µm. Ascospores hyaline, bola-shaped, septate, 110–184 × 0.8–1.3 µm, central part filiform, terminal part narrowly fusiform, don't disarticulate into part-spores. **Asexual morph:** *Isaria*-like. Colonies fast-growing on PDA, 35–40 mm diameter in 14 days at 25 °C, white to light orange, cottony, producing high mycelial density at the centrum. Reverse light orange, turning deep yellow brown, appearing a brown concentric ring and radiate stria out of the inoculum. Hyphae smooth, septate, hyaline, 1.1–1.9 µm wide. Conidiophores cylindrical, solitary or verticillate, 3.5–9.7 × 1.3–3.2 µm. Phialides verticillate, in whorls of two to nine, sometimes solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering abruptly toward the apex; 3.5–16.3 µm long, 1.7–2.9 µm wide at the base, and 0.5–1.0 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.3–3.5 × 1.6–2.5 µm, often in chains.

Host: Larvae of Noctuidae.

Habitat: On the larvae of Noctuidae buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the larva of Noctuidae buried in soil, 12 August 2017, Hong Yu, (YHH 15758, holotype; YFCC 6016, ex-holotype living culture); *Ibid.*, (YHH 16034, paratype; YFCC 6113, ex-paratype living culture).

Notes: Samsoniella antleroides is characterized by fasciculate and antler-like stromata with oblate terminal branches, clavate to flake-like fertile parts, orange to orange-red, superficial and fusiform perithecia, cylindrical asci with bola-shaped ascospores, light orange to orange-red colonies, having *Isaria*-like asexual conidiogenous structure, and on the larvae of Noctuidae buried in soil.

Phylogenetic analyses reveal that *S. antleroides* forms a sister lineage with *S. tortricidae* and *S. cristata*. *Samsoniella antleroides* resembles the latter two species in having stromata with terminal branches, superficial and fusiform

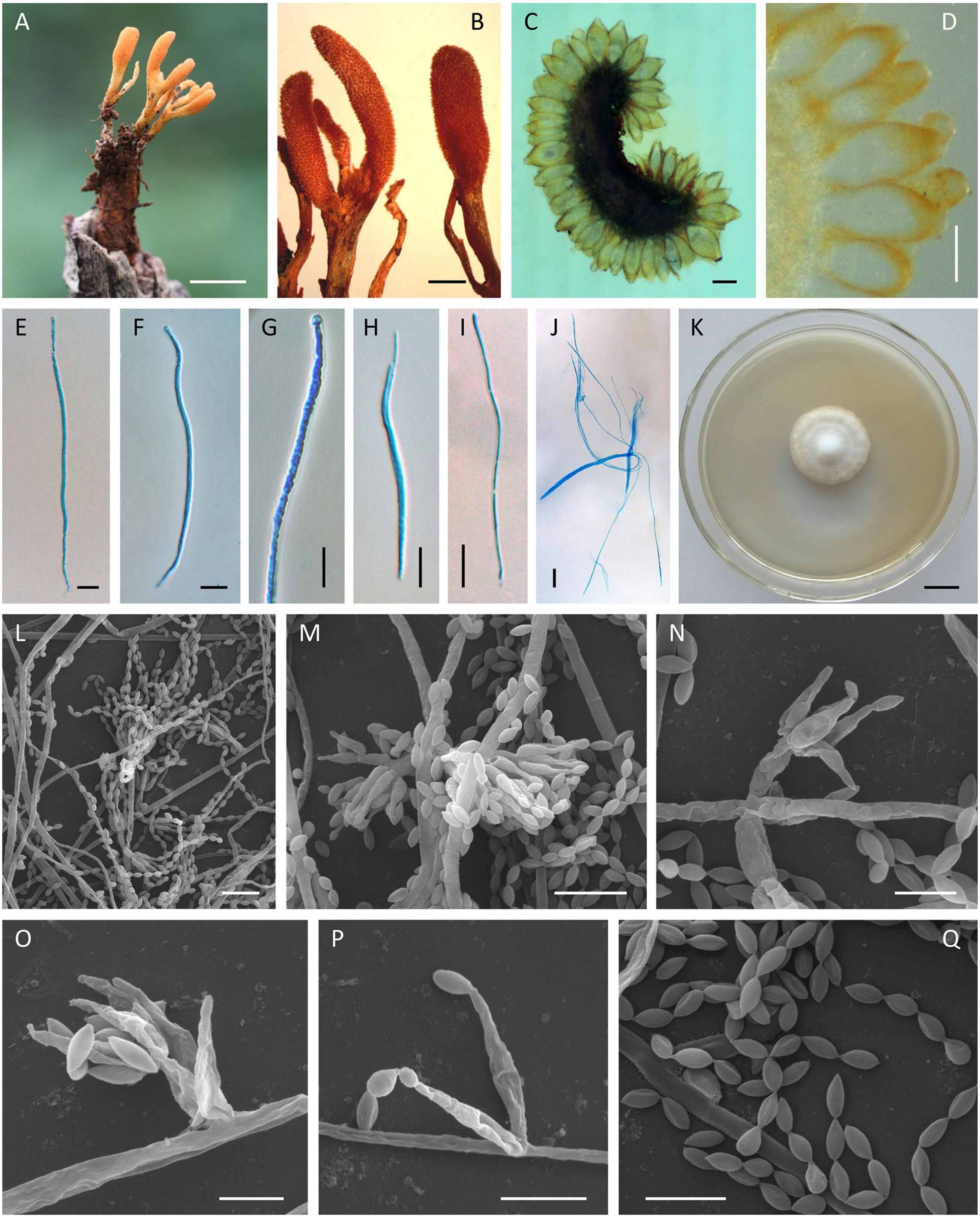


Fig. 11 *Samsoniella antleroides*. **A** Antler-like stromata arising from the larva of Noctuidae. **B** Fertile parts. **C, D** Perithecia. **E–G** Asci. **H, I** Immature ascospores. **J** Mature ascospores. **K** Colony on PDA. **L–O** Verticillate phialides on conidiophores. **P** Phialides in whorls of two on hypha. **Q** Conidia in chains. Scale bars: **A** = 1 cm; **B** = 1 mm; **C, D** = 200 µm; **E, F** = 20 µm; **G–J** = 10 µm; **K** = 1 cm; **L, M** = 10 µm; **N–Q** = 5 µm

perithecia, cylindrical asci with bola-shaped ascospores and *Isaria*-like asexual morph. However, it differs from *S. cristata* and *S. tortricidae* in the production of fasciculate and antler-like stromata with oblate terminal branches, clavate to flake-like fertile parts, conidiophores forming verticillate branches with shorter phialides in whorls of up to nine. Ecologically, *S. antleroides* is parasitic on the larvae of Noctuidae buried in soil and is different from *S. cristata* and *S. tortricidae*, both of which parasitize the pupae of Saturniidae in cocoons buried in soil and the pupae of Tortricidae in cocoons rolled in fallen leaves, respectively.

Samsoniella cardinalis H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833112; Fig. 12

Etymology: Referring to the scarlet stromata arising from the host in cocoons.

Holotype: YHH 15732

Sexual morph: Several stromata arising from oval cocoons of insect host, scarlet, cylindrical, 11.5–18.6 mm long. Stipes reddish-orange, 0.4–1.8 mm wide. Fertile parts clavate, ateral sides usually have a longitudinal ditch without producing perithecia, scarlet, 2.5–6.8 × 0.5–2.6 mm. Perithecia superficial, oblong-ovate to fusiform, 370–485 × 140–238 um. Asci eight-spored, hyaline, cylindrical 163–320 × 3.2–4.3 µm. Ascus caps hemispherical, 1.9–3.0 × 1.4–2.6 µm. Ascospores hyaline, bola-shaped, septate, 165–230 × 0.5–0.9 µm, central part filiform, terminal part narrowly fusiform, do not disarticulate into part-spores. **Asexual morph:** *Isaria*-like. Colonies on PDA growing fairly well at 25 °C, 35–38 mm in 14 days, floccose, crater-shaped, white to pale pink, sporulating abundantly at the centrum. Reverse pale yellow to reddish-brown. Hyphae smooth-walled, branched, septate, hyaline, 1.3–2.2 µm wide. Conidiophores cylindrical, solitary or verticillate, 3.1–9.5 × 1.3–2.0 µm. Phialides verticillate, in whorls of two to five, sometimes solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 4.1–43.5 µm long, 1.3–2.4 µm wide at the base, and 0.6–1.2 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.4–3.2 × 1.4–2.2 µm, often in chains.

Host: Pupae of Limacodidae.

Habitat: On the pupae of Limacodidae in cocoons buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Limacodidae in a cocoon buried in soil, 12 August 2017, Hong Yu, (YHH 15732, holotype; YFCC 6144, ex-holotype living culture). Kunming City, Xishan Forest Park, on the pupa of Limacodidae in a cocoon buried in soil, 13 August 2018, Qi Fan, (YHH 15764; YFCC 6320, living culture). VIETNAM. LAOCAI PROVINCE: Sapa County, Hoang Lien Mountains, on the pupa of Limacodidae in a cocoon buried in soil, 26 October 2016, Yuan-Bing Wang, (YHH 14891; YFCC 5830, living culture).

Notes: Samsoniella cardinalis is characterized by scarlet stromata with clavate fertile parts, superficial perithecia, oblong-ovate to fusiform, cylindrical asci, bola-shaped ascospores, crater-shaped colonies with white to pale pink, having *Isaria*-like asexual conidiogenous structure, and on the pupae of Limacodidae in cocoons buried in soil.

It is similar to *S. alpina* in sharing *Isaria*-like asexual conidiogenous structure which produces phialides with cylindrical to narrowly lageniform basal portion, fusiform or oval conidia. However, it differs from *S. alpina* by its scarlet stromata with clavate fertile parts and superficial perithecia, crater-shaped colonies with white to pale pink colors, and longer phialides up to 43.5 µm. Ecologically, it is parasitic on the pupae of Limacodidae in cocoons and is significantly different from *S. alpina* which parasitizes the larvae of *H. baimaensis* (Hepialidae).

Samsoniella cristata H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833113; Fig. 13

Etymology: Referring to the crista-like stromata.

Holotype: YHH 16982

Sexual morph: Stromata arising from the insect cocoons, solitary or two, much branched, 25–40 mm long, orange, crista-like. Stipes fleshly, white at the rhizine, becoming orange towards the upper part, 1.0–1.5 mm wide. Fertile parts reddish orange, crista-like or subulate, 3.1–18.5 × 0.9–8.0 mm. Perithecia crowded, superficial, narrowly ovoid, 370–485 × 150–245 µm. Asci eight-spored, hyaline, cylindrical 180–356 × 3.0–4.8 µm. Ascus caps hemispherical, 2.7–3.8 × 1.5–2.4 µm. Ascospores hyaline, bola-shaped, septate, 155–290 × 1.0–1.3 µm, central part filiform, terminal part narrowly fusiform, do not disarticulate into part-spores. **Asexual morph:** *Isaria*-like. Colonies on PDA fast-growing, 43–50 mm diameter in 14 days at 25 °C, floccose, crater-shaped, white to light orange, forming yellow-brown concentric rings around the inoculum, sporulating abundantly, cottony, with high mycelial density around the edge, reverse pale brown. Hyphae smooth-walled, branched, septate, hyaline, 1.3–2.5 µm wide. Conidiophores smooth-walled, cylindrical, solitary or verticillate, 3.6–11.5 × 1.7–2.5 µm. Phialides verticillate, in whorls of two to five, usually solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 4.5–23.2 µm long, 1.6–2.7 µm wide at the base, and 0.5–1.1 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.4–3.2 × 1.6–2.3 µm, often in chains.

Host: Pupae of Saturniidae.

Habitat: On the pupae of Saturniidae in cocoons buried in soil.

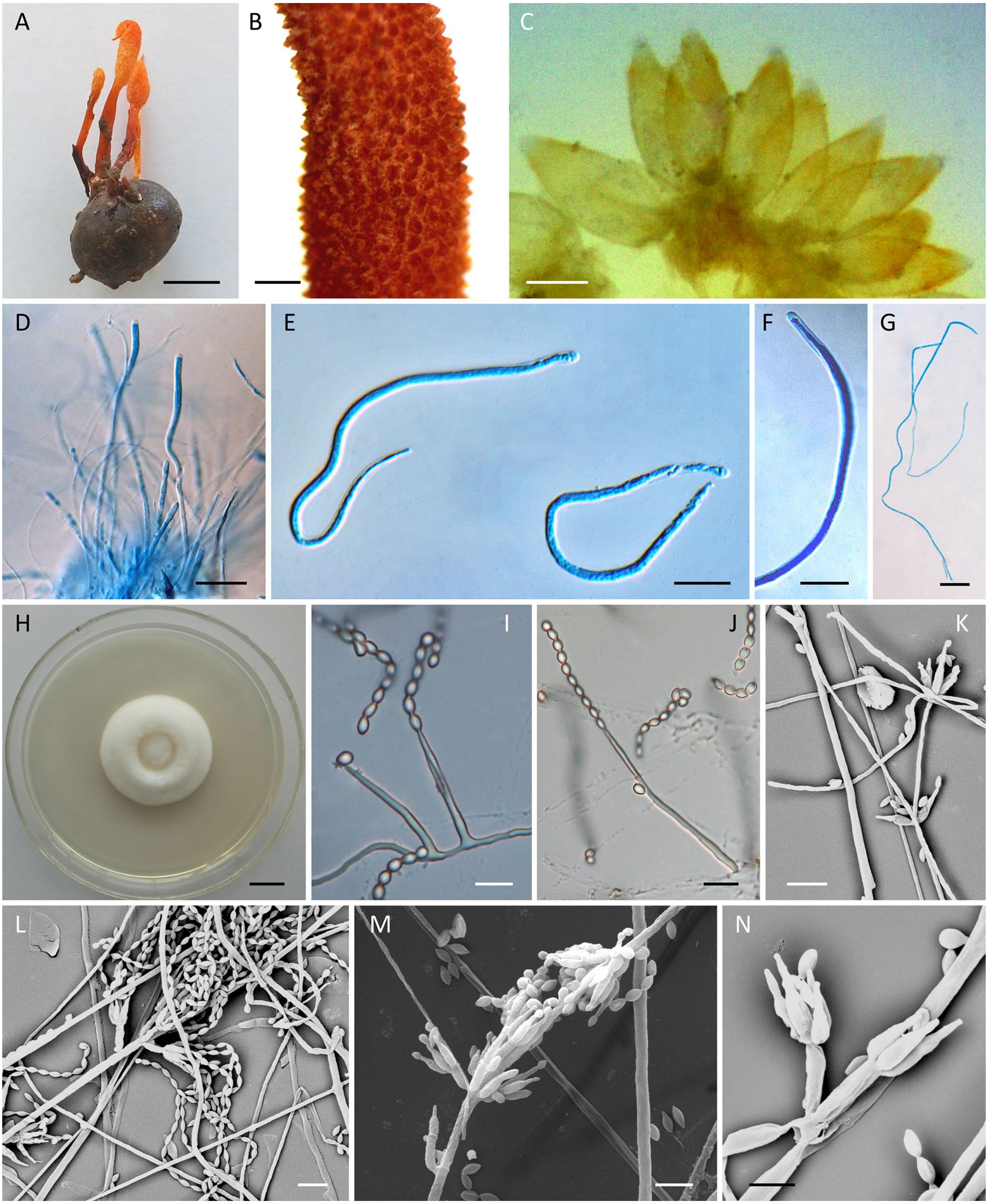
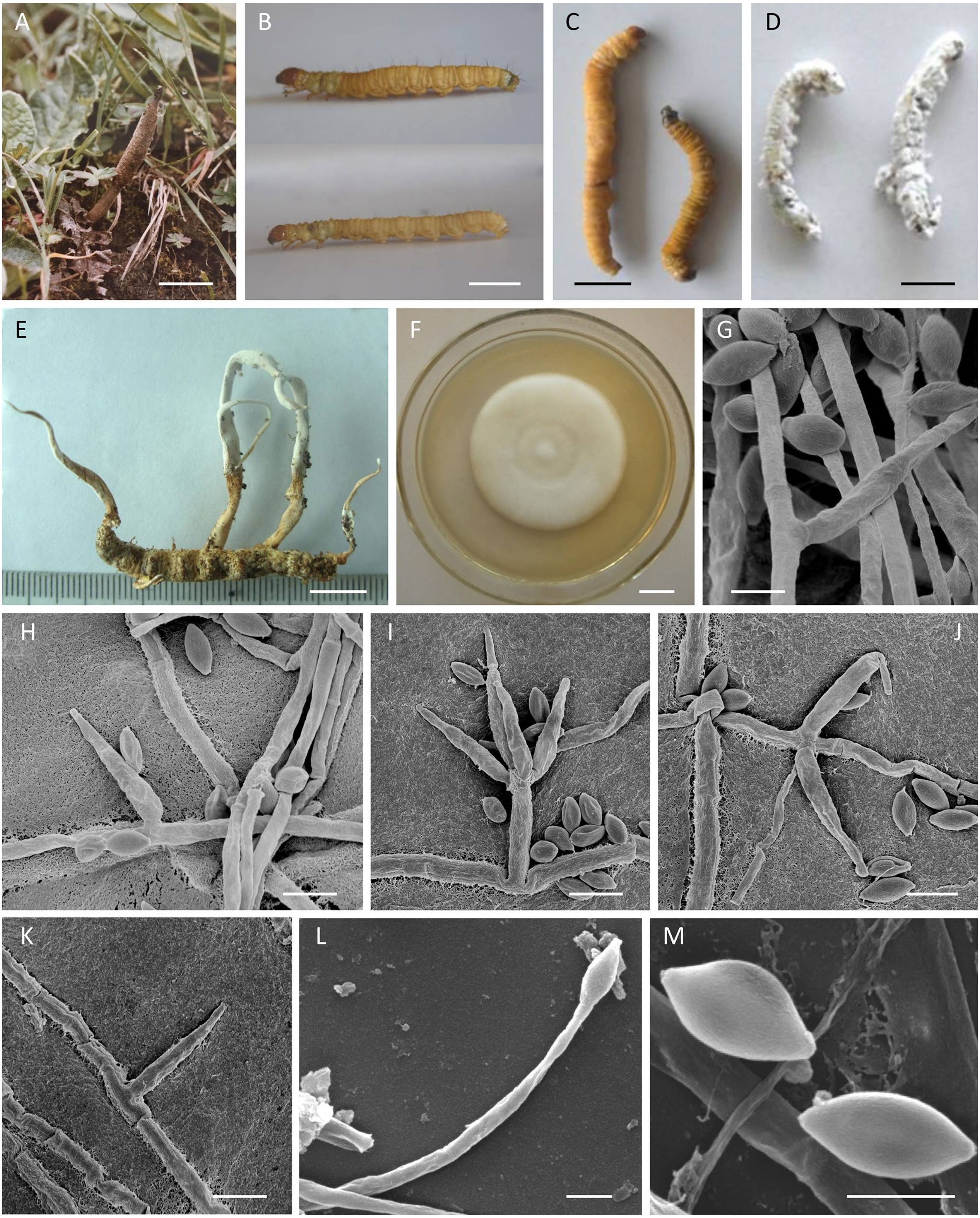


Fig. 12 *Samsoniella cardinalis*. **A** Fungus on the pupa of Limacodidae in a cocoon. **B** Fertile part. **C** Perithecia. **D–F** Asci. **G** Ascospores. **H** Colony on PDA. **I, J** Solitary phialides on hyphae. **K–N** Verticillate phialides on conidiophores. Scale bars: **A** = 5 mm; **B, C** = 200 μm; **D, E** = 20 μm; **F, G** = 10 μm; **H** = 1 cm; **I–N** = 5 μm

Fig. 13 *Samsoniella cristata*. **A** Crista-like stromata arising from the host. **B** Fungus on the pupa of Saturniidae in a cocoon. **C, D** Fertile parts. **E** Perithecia. **F** Asus. **G** Ascospore. **H** Colony on PDA. **I** Solitary phialides on hyphae. **J** Verticillate phialides on conidiophores. **K** Solitary phialides on hyphae. **L–N** Verticillate phialides on conidiophores. **O** Conidia. Scale bars: **A, B** = 1 cm; **C, D** = 500 μm; **E** = 200 μm; **F** = 5 μm; **G** = 10 μm; **H** = 1 cm; **I–N** = 5 μm; **O** = 2 μm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◂**Fig. 14** *Samsoniella hepiali*. **A** Stroma of *Ophiocordyceps sinensis* arising from the larva of *Hepialus* buried in soil in the Baima Snow Mountain, Yunnan Province (This picture taken in June 1982 was provided by Ru-Qin Dai); the holotype material of *S. hepiali* was isolated from this specimen. **B** The host larvae of *Hepialus baimaensis*. **C, D** Larvae of *H. baimaensis* infected by *S. hepiali*. **E** Synnemata arising from the whole body of *H. yunnanensis*. **F** Colony on PDA. **G–J** Verticillate phialides on conidiophores. **K, L** Solitary phialides on hyphae. **M** Conidia. Scale bars: **A–F** = 1 cm; **G–K** = 5 μm; **L, M** = 2 μm

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Saturniidae in a cocoon buried in soil, 14 August 2018, Hong Yu, (YHH 16982, holotype; YFCC 7004, ex-holotype living culture); *Ibid.* (YHH 15760, paratype; YFCC 6021, ex-paratype living culture); *Ibid.* (YHH 15761, paratype; YFCC 6023, ex-paratype living culture).

Notes: Samsoniella cristata is characterized by solitary or two stromata, crista-like, reddish orange fertile parts, superficial and narrowly ovoid perithecia, cylindrical asci, bola-shaped ascospores, crater-shaped colonies with white to light orange colors, *Isaria*-like asexual conidiogenous structure, and on the pupae of Saturniidae in cocoons.

Phylogenetically, *S. cristata* is sister to *S. tortricidae*, a novel species described in this study. *Samsoniella cristata* resembles *S. tortricidae* in sharing stromata with terminal branches, subulate fertile parts, and *Isaria*-like asexual conidiogenous structure. However, it differs in having fewer and shorter stromata, crista-like, crater-shaped colonies, shorter phialides, and it is parasitic on the pupae of Saturniidae in cocoons buried in soil.

Samsoniella hepiali (Q.T. Chen & R.Q. Dai ex R.Q. Dai et al.) H. Yu, R.Q. Dai, Y.B. Wang, Y. Wang & Zhu L. Yang, **comb. nov.**

Mycobank: MB 833114; Fig. 14

Basionym: *Paecilomyces hepiali* Q.T. Chen & R.Q. Dai ex R.Q. Dai et al., Mycosystema 27 (5): 642 (2008); *Paecilomyces hepiali* Q.T. Chen & R.Q. Dai, Acta Agric. Univ. Pekin. 6(2): 223 (1989), invalid.

Holotype: IMM 82–2 [as "CHICMM 82–2"]

Sexual morph: Undetermined. **Asexual morph:** *Isaria*-like. Synnemata arising from the whole body of lepidopteran insects, branched or unbranched, 0.5–4.1 cm long. Stipes cylindrical or clavate, 0.6–3.2 mm wide, with powdery conidia at the apex, white to yellowish. Conidiophores along the apex of synnemata, solitary, with phialides in whorls of two to five, cylindrical, 4.1–7.3 × 1.4–2.0 μm. Phialides with a basal portion cylindrical to narrowly lageniform, 4.5–12.6 × 1.5–2.6 μm, tapering gradually or abruptly into a narrow neck of 0.5–1.0 μm wide. Conidia in chains, one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–3.1 × 1.4–1.9 μm. Colonies on PDA moderately fast-growing, 50–55 mm diameter in 14 days at 25 °C, cottony, with high mycelial density, white to yellowish, forming concentric rings around the inoculum. Reverse white to yellowish, turning orange when old. Hyphae smooth-walled, branched, septate, hyaline, 1.3–2.2 μm wide. Conidiophores smooth-walled, cylindrical, solitary, 4.0–7.6 × 1.4–2.2 μm. Phialides on conidiophores verticillate, in whorls of two to five, solitary or opposite on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 3.5–13.6 μm long, 1.3–2.1 μm wide at the base, 0.5–1.0 μm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 1.8–3.3 × 1.4–2.2 μm, often in chains.

Host: Larvae and pupae of Lepidoptera.

Habitat: On the larvae and pupae of Lepidoptera, the larvae of *Hepialus* parasitized by *O. sinensis* buried in soil or clinging to fallen leaves.

Distribution: Deqin County, Shangrila City, Huanglong County, China; Sapa County, Vietnam.

Material examined: CHINA. YUNNAN PROVINCE: Diqing Tibetan Autonomous Prefecture, Deqin County, Baima Snow Mountain, isolated from the larva of *H. armoricanus* parasitized by *O. sinensis*, June 1982, Ru-Qin Dai, (IMM 82–2 = CHICMM 82–2, holotype; ICMM 82–2, ex-holotype living culture); same location, isolated from the larva of *H. baimaensis* associated with *O. sinensis*, May 2002, Zhuo Zhang, (YHH 1056; YFCC 661, living culture); same location, on the larva of *H. baimaensis* associated with *O. sinensis*, 26 May 2010, Hong Yu, (YHH 4258; YFCC 2702, living culture); same location, associated with *O. sinensis* on the larva of *H. baimaensis*, 18 May 2018, Hong Yu, (YHH 16883; YFCC 7024, living culture); Diqing Tibetan Autonomous Prefecture, Shangrila City, Xiaozhongdian Town, on the larva of *H. yunnanensis*, 24 December 2017, Hong Yu, (YHH 16827; YFCC 7215, living culture). QINHAI PROVINCE: Haidong City, Huanglong County, (Cor-4, dried culture). VIETNAM. LAOCAI PROVINCE: Sapa County, Hoang Lien Mountains, on the pupa of Lepidoptera buried in soil, 26 October 2016, Yuan-Bing Wang, (YHH 14896; YFCC 5823, living culture); same location, on the larva of Lepidoptera clinging to fallen leaves, 26 October 2016, Yao Wang, (YHH 14898; YFCC 5828, living culture).

Notes: This fungus, named as *Paecilomyces hepiali* by Dai et al. (1989), was originally collected from the Baima Snow Mountain in Yunnan Province, China based on isolates from the larvae of *H. armoricanus* parasitized by *O. sinensis*. However, the name was effectively, but not formally published due to the failure of the authors to comply with the requirements of the Code for type indication, and the only cited material was a living culture (Dai et al. 2008; Turland et al. 2018). *Paecilomyces hepiali* was later validly published and the holotype IMM 82–2 was designated using a dried culture from the living culture 82–2 (ICMM 82–2) (Dai et al. 2008, 2018a).

Based on the original description, *P. hepiali* was morphologically similar to *P. xylariiformis* (Lloyd) Samson, originally named as *I. xylariiformis* Lloyd, but it differs in the globose or subglobose conidia with smaller size and the host of hepialid larvae (Dai et al. 1989). In addition, *P. hepiali* differed from *I. farinosa* (Holmsk.) Fr., currently recombined into *C. farinosa*, by the shape and arrangement of phialides, the shape of conidia, its host belonging to the genus *Hepialus*, and its habitat of an extremely cold area at an altitude of 4000−4500 m (Dai et al. 1989).

Paecilomyces xylariiformis, probably belonging to *Isaria*, is only known from dried type herbarium material no. 42613, and its phylogenetic analyses have not been conducted (Samson 1974; Luangsa-ard et al. 2005). Its generic status, and even so, higher taxonomic rank remain unresolved. Recent phylogenetic analyses together with our five-gene phylogeny of the family Cordycipitaceae show that *C. farinosa* belongs to the type genus *Cordyceps* of this family (Kepler et al. 2017; Mongkolsamrit et al. 2018). In our phylogenetic analyses, the holotype material ICMM 82–2 and seven other samples of *P. hepiali* were used to determined its systematic position. Our results show that the eight samples of *P. hepiali* group together with strong statistical support (BP = 80% and PP = 100%), are clustered within the recently established genus *Samsoniella* of Cordycipitaceae, and form a single clade related to an undescribed taxon *Isaria* sp. TNS 16333 (Fig. 1, 2). Consequently, *P. hepiali* is phylogenetically distinguished from *C. farinosa* which also produces *Isaria*-like asexual morph. Based on the strong phylogenetic and morphological evidence, a new combination, namely *S. hepiali* is proposed for *P. hepiali*.

Here, a redescription of *S. hepiali* is made on the basis of morphological observations of the ex-holotype living culture ICMM 82–2 and related samples collected in this study. *Samsoniella hepiali* has *Isaria*-like asexual morph and is characterized by branched or unbranched synnemata arising from the whole body of lepidopteran insects, cylindrical or clavate stipes with a powdery conidia at the apex, white to yellowish, moderately fast-growing colonies with white to yellowish colors, cottony, solitary conidiophores with cylindrical shape, solitary or verticillate phialides with cylindrical to narrowly lageniform basal portion, fusiform or oval conidia often in chains.

Samsoniella hepiali is morphologically similar to *S. alpina* and *S. yunnanensis* in the *Isaria*-like asexual conidiogenous structure, producing synnemata with powdery conidia at the apex. However, *S. hepiali* differs from *S. alpina* by its white to yellowish colonies, solitary conidiophores with phialides in whorls of two to five and longer phialides. It differs from *S. yunnanensis* because the latter has synnemata with orange to pink stipes, white colonies, solitary or verticillate conidiophores up to 23.5 µm long with phialides in whorls of two to seven. Ecologically, *S. hepiali* and *S. alpina* share similar host larvae of *Hepialus*, whereas *S. hepiali* has a wider lepidopteran species host range.

Samsoniella kunmingensis H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833116; Fig. 15

Etymology: Named after the location Kunming City where the species was collected.

Holotype: YHH 6002

Sexual morph: Stromata arising from the lepidopteran pupa buried in soil, solitary, up to 23 mm long, cylindrical to clavate, bifurcated. Stipes fleshly, white to orange, 0.5–0.9 mm wide, with a terminal bifurcated branch of 5.2–11.4 mm long. Fertile parts reddish orange, clavate, ateral sides usually have a longitudinal ditch without producing perithecia, 3.3–4.2 × 0.8–1.2 mm. Perithecia crowded, superficial, narrowly ovoid to fusiform, 330–395 × 110–185 µm. Asci eight-spored, hyaline, cylindrical, 150–297 × 3.0–4.6 µm. Ascus caps hemispherical, 2.3–3.6 × 1.5–2.5 µm. Ascospores hyaline, bola-shaped, septate, 127–190 × 0.8–1.5 µm, central part filiform, terminal part narrowly fusiform, do not disarticulate into part-spores. **Asexual morph:** Undetermined.

Host: Pupa of Lepidoptera.

Habitat: On the pupa of Lepidoptera buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Lepidoptera buried in soil, 12 August 2017, Qi Fan, (YHH 16002, holotype).

Notes: Samsoniella kunmingensis is characterized by solitary stromata, bifurcated, clavate fertile parts with reddish orange color, ateral sides usually have a longitudinal ditch without producing perithecia, superficial perithecia, narrowly ovoid to fusiform, and cylindrical asci with bola-shaped ascospores.

Phylogenetically, it is closely related to the new species *S. ramosa* described in this study. However, *S. kunmingensis* is morphologically similar to *S. antleroides*, *S. lanmaoa* and *S. inthanonensis* by producing superficial perithecia, narrowly ovoid to fusiform, cylindrical asci with bola-shaped ascospores. *Samsoniella kunmingensis* differs from *S. antleroides*, *S. lanmaoa*, *S. inthanonensis* and *S. ramosa* by its solitary and bifurcated stromata, and clavate fertile parts with reddish orange color. The latter three species have *Isaria*-like asexual morphs, whereas asexual morph of *S. kunmingensis* was not determined in this study.

Samsoniella lanmaoa H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833115; Fig. 16

Etymology: Lanmaoa is named for Mr. Lan Mao (1397–1476, Ming Dynasty), an ancient Chinese botanist, who recorded medicinal fungi in the famous Chinese literature "Dian Nan Ben Cao".

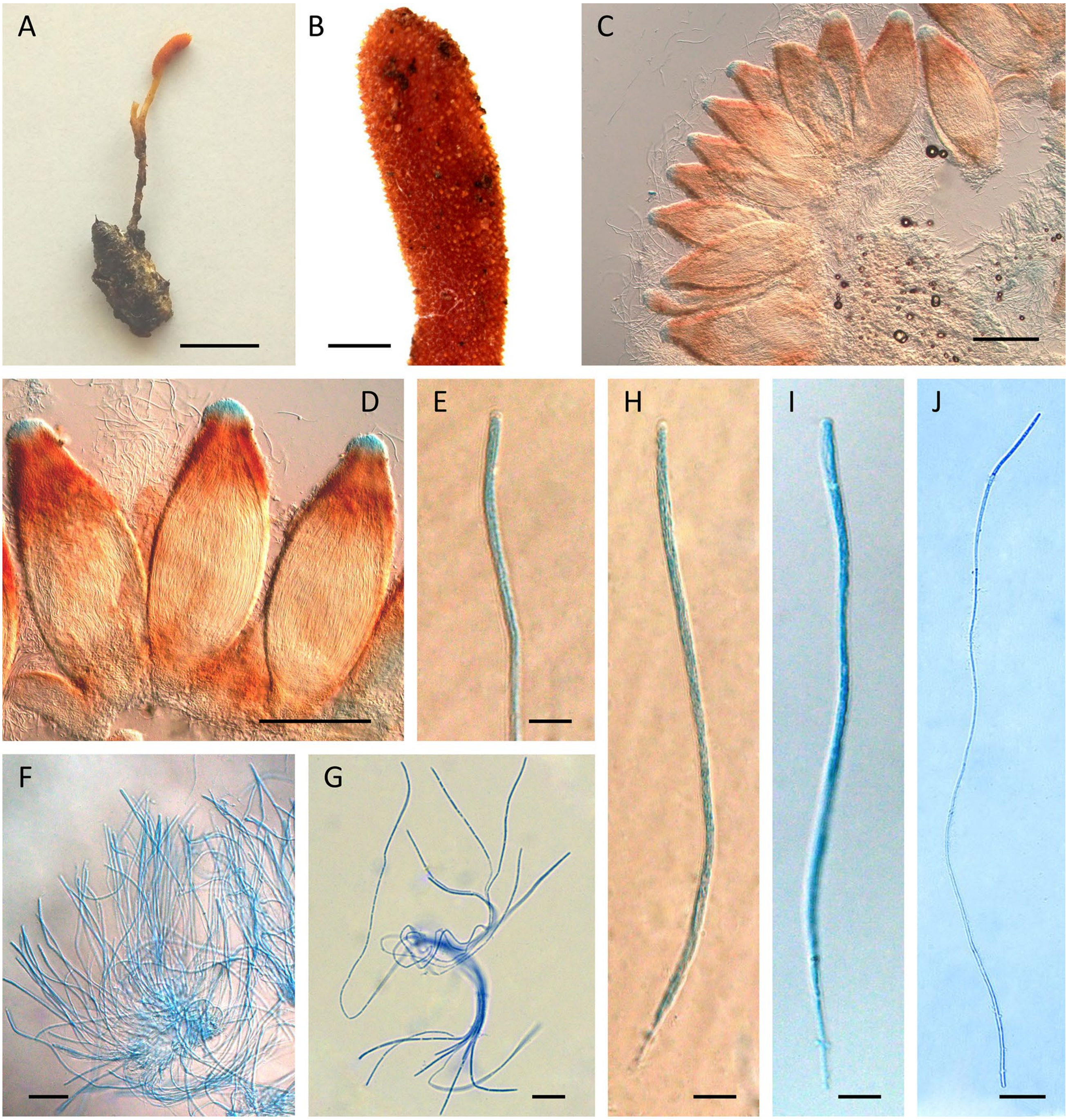
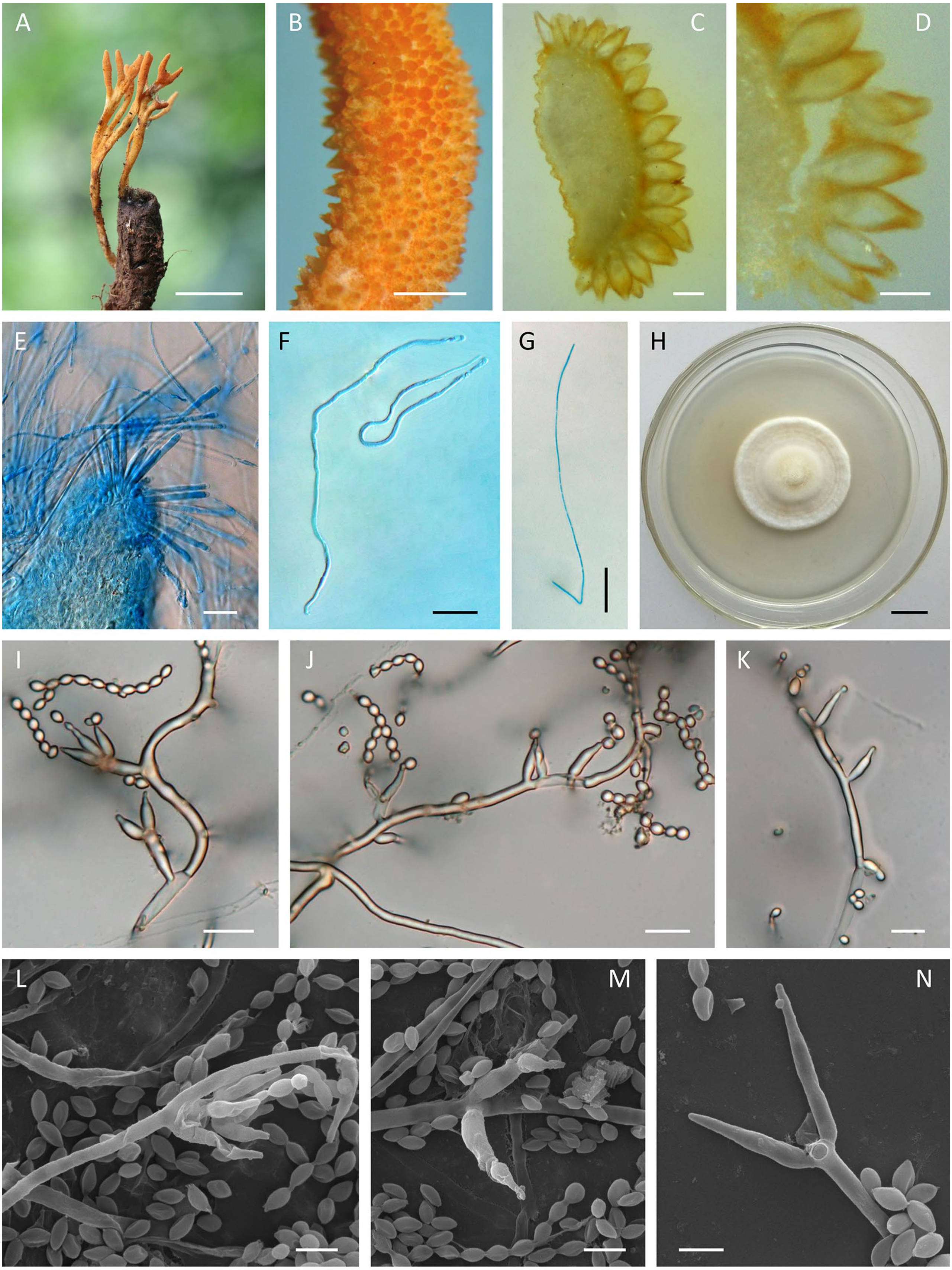


Fig. 15 *Samsoniella kunmingensis.* **A** Fungus on the pupa of Lepidoptera. **B** Fertile parts. **C, D** Perithecia. **E, F** Asci. **G** Ascospores. **H, I** Asci. **J** Ascospore. Scale bars: **A** = 1 cm; **B** = 500 μm; **C, D** = 200 μm; **E** = 5 μm; **F** = 20 μm; **G–I** = 5 μm; **J** = 10 μm

Holotype: YHH 15740

Sexual morph: Stromata arising from insect cocoons, two to five, 38–69 mm long, palmately branched, orange. Stipes fleshly, clavate, palmated at the branching portion, 1.2–3.9 mm wide. Fertile parts reddish orange, clavate, ateral sides usually have a longitudinal ditch without producing perithecia, 8.5–11.2 × 0.6–2.3 mm. Perithecia crowded, superficial, narrowly ovoid to fusiform, 360–467 × 124–210 μm. Asci eight-spored, hyaline, cylindrical, 160–325 × 3.3–4.8 μm. Ascus caps hemispherical, 2.5–3.8 × 1.6–2.3 μm. Ascospores hyaline, bola-shaped, septate, 135–260 × 0.9–1.4 μm, central part filiform, terminal part narrowly fusiform, do not disarticulate into part-spores. **Asexual morph:** *Isaria*-like. Colonies on PDA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◂**Fig. 16** *Samsoniella lanmaoa*. **A** Stromata arising from the pupa of Lepidoptera. **B** Fertile parts. **C, D** Perithecia. **E–F** Asci. **G** Ascospore. **H** Colony on PDA. **I, J** Verticillate phialides on conidiophores. **K** Solitary phialides on hypha. **L, N** Verticillate phialides on conidiophores. Scale bars: **A** = 1 cm; **B** = 500 µm; **C–E** = 200 µm; **E–G** = 20 µm; **H** = 1 cm; **I–N** = 5 µm

fast-growing, 38–40 mm diameter in 14 days at 25 °C, white to cream-colored, cottony, with high mycelial density at the centrum, forming concentric rings around the inoculum, reverse pale yellow to yellowish-brown. Hyphae smooth-walled, branched, septate, hyaline, 1.2–1.9 µm wide. Conidiophores smooth-walled, cylindrical, solitary or verticillate, 3.8–13.3 × 1.5–2.1 µm. Phialides verticillate, in whorls of two to six, usually solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 3.5–20.7 µm long, 1.7–2.6 µm wide at the base, and 0.5–1.1 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 1.9–2.7 × 1.4–2.0 µm, often in chains.

Host: Pupae of Lepidoptera.

Habitat: On the pupae of Lepidoptera in cocoons buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Lepidoptera in a cocoon buried in soil, 12 August 2017, Hong Yu, (YHH 15740, holotype; YFCC 6148, ex-holotype living culture); *Ibid.*, (YHH 15753, paratype; YFCC 6193, ex-paratype living culture).

Notes: Samsoniella lanmaoa is characterized by palmately branched stromata, clavate fertile parts with reddish orange color, superficial perithecia with narrowly ovoid to fusiform shapes, bola-shaped ascospores, white to cream-colored colonies, and *Isaria*-like asexual conidiogenous structure.

Phylogenetic analyses show that *S. lanmaoa* is sister to the recently described species *S. inthanonensis*, by which the genus *Samsoniella* was established. Morphologically, *S. lanmaoa* is similar to *S. inthanonensis* in producing branched stromata with reddish to orange colors, bola-shaped ascospores and *Isaria*-like asexual conidiogenous structure (Mongkolsamrit et al. 2018). However, it differs from *S. inthanonensis* by its longer stromata (38–69 mm), narrowly ovoid to fusiform perithecia, white to cream-colored colonies and larger phialides (3.5–20.7 µm long). Ecologically, *S. lanmaoa* is parasitic on the lepidopteran pupae in cocoons buried in soil, whereas *S. inthanonensis* was reported as a parasite of the lepidopteran larvae in leaf litter (Mongkolsamrit et al. 2018).

Samsoniella ramosa H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833117; Fig. 17

Etymology: Referring to the ramose stromata.

Holotype: YHH 15988

Sexual morph: Stromata arising directly from an insect cocoon, fascicular, multi-branched, often confluent at the base 15–32 × 0.8–1.5 mm. Stipes oblate or flaky, white at first, then turning into fulvous, rusty-brown when old. Fertile parts having no obvious boundary with stipes, white to pale brown, with a tapering sterile part, 1.6–7.8 mm long, white to khaki. Perithecia crowded, superficial, narrowly ovoid to fusiform, 340–435 × 130–197 µm. Asci and ascospores not observed. **Asexual morph:** *Isaria*-like. A mass of conidia producing toward the apex of stromatic branches, white, powdery and floccose. Conidiophores on the apex of stromata with phialides in whorls of two to five, cylindrical, 5.1–12.3 × 1.4–2.5 µm. Phialides with a basal portion cylindrical to narrowly lageniform, 4.5–12.6 × 1.5–2.6 µm, tapering abruptly into a narrow neck of 0.5–1.1 µm wide. Conidia in chains, one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–3.3 × 1.4–2.0 µm. Colonies on PDA moderately fast-growing, 45–50 mm diameter in 14 days at 25 °C, floccose, crater-shaped, white to cream-coloured, sporulating abundantly, reverse off-white. Hyphae smooth-walled, branched, septate, hyaline, 1.5–2.8 µm wide. Conidiophores smooth-walled, cylindrical, solitary or verticillate, 4.3–10.5 × 1.3–2.4 µm. Phialides verticillate, in whorls of two to six, usually solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 5.3–14.6 µm long, 1.3–2.8 µm wide at the base, and 0.6–1.2 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–3.6 × 1.5–2.2 µm, often in chains.

Host: Pupa of Limacodidae.

Habitat: On the pupa of Limacodidae in a cocoon buried in soil.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Limacodidae in a cocoon buried in soil, 12 August 2017, Hong Yu, (YHH 15988, holotype; YFCC 6020, ex-holotype living culture).

Notes: Samsoniella ramosa is characterized by fascicular stromata, multi-branched, oblate or flaky stipes, fertile parts with no obvious boundary with stipes, superficial perithecia, narrowly ovoid to fusiform, floccose and crater-shaped colonies, having *Isaria*-like asexual conidiogenous structure, and on the pupa of Limacodidae in a cocoon buried in soil.

It is similar to its phylogenetically closely related species *S. kunmingensis* in producing superficial perithecia, narrowly ovoid to fusiform. However, *S. ramosa* is easily distinguished by its fascicular stromata, multi-branched, oblate or flaky stipes and fertile parts having no obvious boundary with stipes.

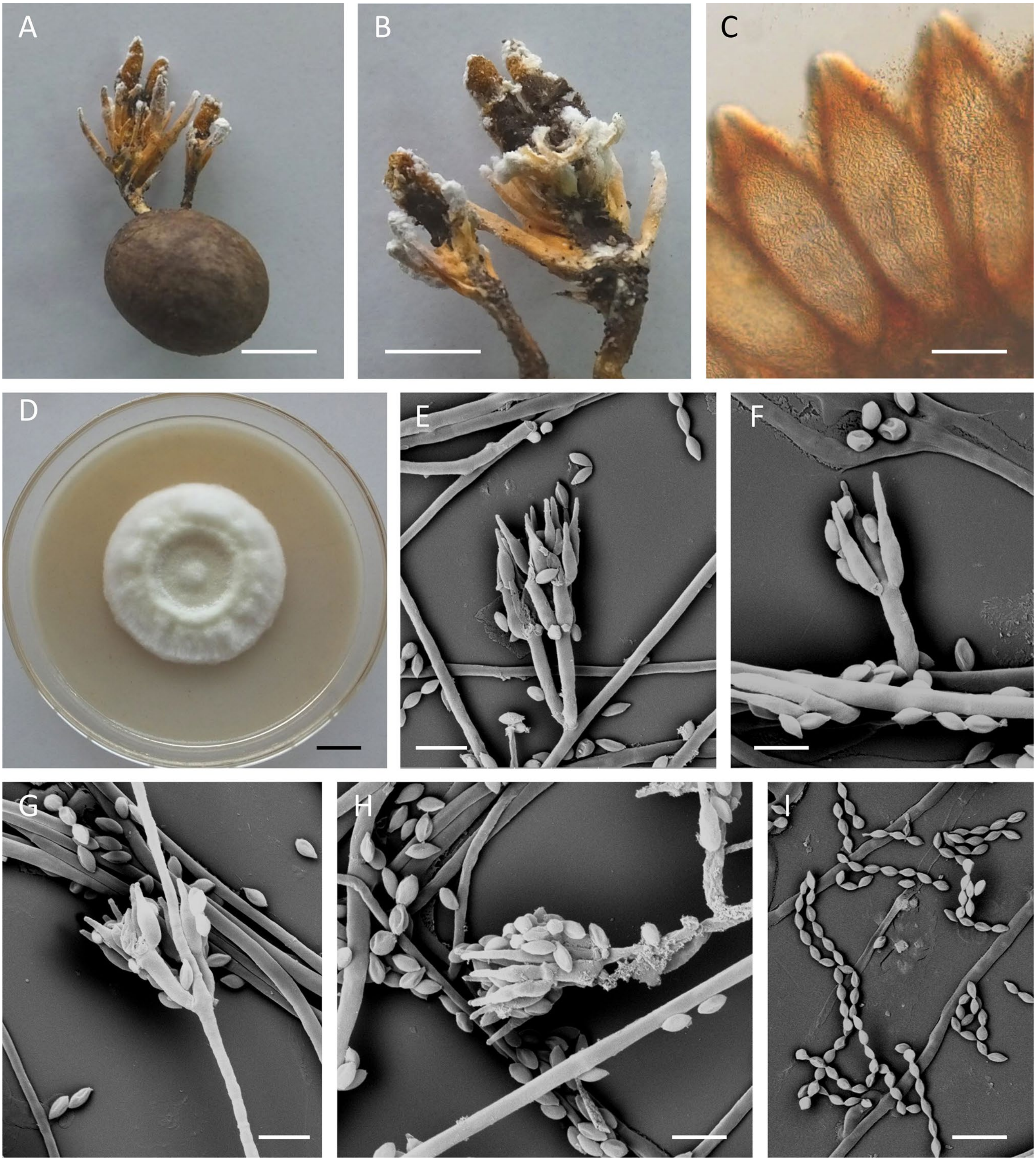

Fig. 17 *Samsoniella ramosa*. **A** Fungus on the pupa of Limacodidae in a cocoon. **B** Ramose stromata. **C** Perithecia. **D** Colony on PDA. **E–H** Verticillate phialides on conidiophores. **I** Conidia in chains. Scale bars: **A, B** = 5 mm; **C** = 200 μm; **D** = 1 cm; **E–I** = 5 μm

Samsoniella tortricidae H. Yu, Y.B. Wang, Y. Wang, Q. Fan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833118; Fig. 18

Etymology: Named after the host belonging to the family Tortricidae (Lepidoptera).

Holotype: YHH 16050

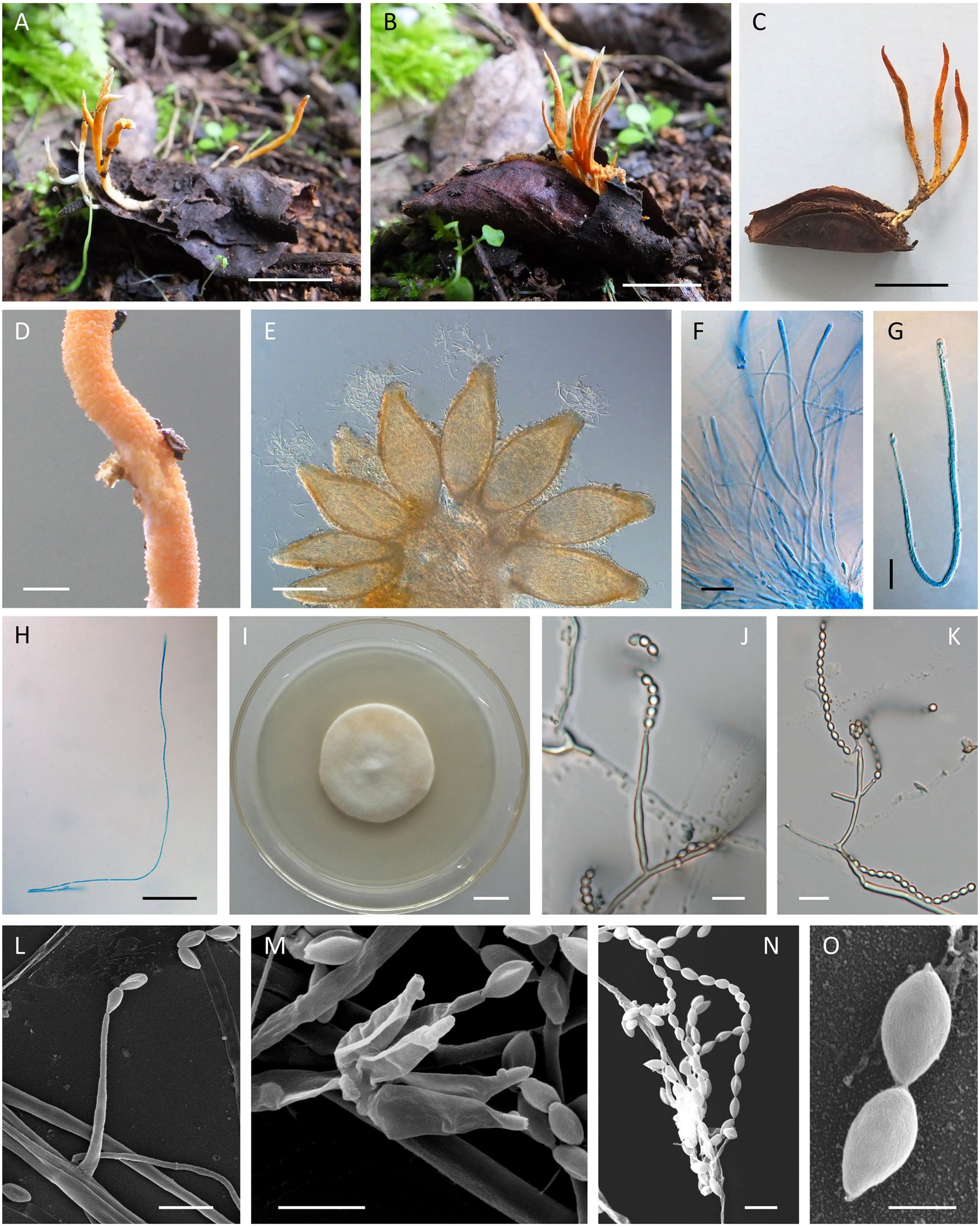

Fig. 18 *Samsoniella tortricidae*. **A–C** Stromata arising from the pupae of Tortricidae in cocoons rolled in fallen leaves. **D** Fertile parts. **E** Perithecia. **F**, **G** Asci. **H** Ascospore. **I** Colony on PDA. **J–M** Conidiophores and phialides. **N, O** Conidia in chains. Scale bars: **A–C** = 1 cm; **D** = 1 mm; **E** = 200 µm; **F–H** = 20 µm; **I** = 1 cm; **J–N** = 5 µm; **O** = 2 µm

Sexual morph: Stromata gregarious, arising from insect cocoons rolled in fallen leaves, up to 25–60 mm long, unbranched or dichotomous. Stipes flexuous, yellowish to orange, cylindrical to clavate, 12–46 × 1.1–3.0 mm. Fertile parts reddish orange, clavate to subulate, ateral side usually has a longitudinal section without producing perithecia, 5–15 × 1.2–2.3 mm. Perithecia crowded, superficial, narrowly ovoid to fusiform, 350–468 × 140–225 µm. Asci eight-spored, hyaline, cylindrical, up to 170–285 × 2.8–4.0 µm. Ascus caps hemispherical, 2.2–3.3 × 1.4–2.2 µm. Ascospores hyaline, bola-shaped, septate, 120–235 × 0.8–1.3 µm, central part filiform, terminal part narrowly fusiform, do not disarticulate into part-spores. **Asexual morph:** *Isaria*-like. Colonies on PDA grow well, 30–36 mm diameter in 14 days at 25 °C, white to pale pink, cottony, sporulating abundantly, reverse orange to reddish-brown. Hyphae smooth-walled, branched, septate, hyaline, 1.1–2.4 µm wide. Conidiophores smooth-walled, cylindrical, solitary, 4.2–12.5 × 1.4–2.4 µm. Phialides verticillate, in whorls of two to five, usually solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 3.6–42.4 µm long, 1.1–2.6 µm wide at the base, and 0.4–0.9 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.1–3.0 × 1.3–1.7 µm, often in chains.

Host: Pupae of Tortricidae (Lepidoptera)

Habitat: On the pupae of Tortricidae (Lepidoptera) in cocoons rolled in fallen leaves.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, on the pupa of Tortricidae (Lepidoptera) in a cocoon rolled in fallen leaves, 12 August 2017, Hong Yu, (YHH 16050, holotype; YFCC 6131, ex-holotype living culture); *Ibid.*, (YHH 15989, paratype; YFCC 6013, ex-paratype living culture); *Ibid.*, (YHH 16064, paratype; YFCC 6142, ex-paratype living culture).

Notes: Samsoniella tortricidae is characterized by gregarious stromata, unbranched or dichotomous, cylindrical to clavate stipes, clavate to subulate fertile parts with reddish orange color, superficial perithecia, narrowly ovoid to fusiform, cylindrical asci with bola-shaped ascospores, and having *Isaria*-like asexual conidiogenous structure.

Samsoniella tortricidae resembles the phylogenetic sister species *S. cristata* in producing stromata with terminal branches, subulate fertile parts, and *Isaria*-like asexual conidiogenous structure. However, it differs from *S. cristata* by its gregarious stromata up to 25–60 mm long, unbranched or dichotomous, white to pale pink cottony colonies, sporulating abundantly, longer phialides (3.6–42.4 µm). Ecologically, *S. tortricidae* is parasitic on the pupae of Tortricidae (Lepidoptera) in cocoons rolled in fallen leaves and is very different from *S. cristata*, which is parasitic on the pupae of Saturniidae in cocoons buried in soil.

Samsoniella yunnanensis H. Yu, Y.B. Wang, Y. Wang, D.E. Duan & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833119; Fig. 19

Etymology: Named after the location Yunnan Province where the species was collected.

Holotype: YHH 3126

Sexual morph: Undetermined. **Asexual morph:** *Isaria*-like. Synnemata arising from the insect cocoons, gregarious, flexuous, fleshy, 0.4–1.8 cm long, with terminal branches of 3–7 × 1.0–2.0 mm. Stipes clavate to spatulate, orange to pink, about 1 mm wide, producing a mass of conidia toward the apex of synnemata, powdery and floccose. Conidiophores biverticillate with phialides in whorls of two to seven, cylindrical, 4.0–22.7 × 1.5–2.5 µm. Phialides with a basal portion cylindrical to narrowly lageniform, 4.2–12.1 × 1.3–2.5 µm, tapering gradually or abruptly into a narrow neck of 0.5–1.0 µm wide. Conidia in chains, one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–2.8 × 1.2–2.0 µm. Colonies on PDA fast-growing, 48–50 mm diameter in 14 days at 25 °C, white, consisting of high mycelial density, loose and hairy, sporulating abundantly, reverse reddish-brown. Hyphae smooth-walled, branched, septate, hyaline, 1.2–2.3 µm wide. Conidiophores smooth-walled, cylindrical, solitary or verticillate, 4.2–23.5 × 1.4–2.3 µm. Phialides verticillate, in whorls of two to seven, usually solitary on hyphae, basal portion cylindrical to narrowly lageniform, tapering gradually or abruptly toward the apex; 4.5–11.6 µm long, 1.2–2.4 µm wide at the base, and 0.6–1.0 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, fusiform or oval, 2.0–3.3 × 1.1–2.2 µm, often in chains.

Host/Substratum: Pupae of Limacodidae, *Cordyceps* sp. and *Cordyceps cicadae* Shing.

Habitat: On the pupae of Limacodidae in cocoons, *Cordyceps* sp. associated with the pupae of Lepidoptera and *C. cicadae* associated with the nymphs of Cicadidae buried in soil.

Distribution: Kunming City and Shangrila City, China.

Material examined: CHINA. YUNNAN PROVINCE: Diqing Tibetan Autonomous Prefecture, Shangrila City, Hutiaoxia Town, isolated from *C. cicadae* associated with the nymph of Cicadidae buried in soil, 26 July 2007, Yi-Jian Chen, (YHH 3126, holotype); YFCC 1527, ex-holoype living culture); same location, isolated from *C. cicadae* associated with the nymph of Cicadidae buried in soil, 10 July 2008, Zi-Hong Chen, (YHH 3715; YFCC 1824, living culture); same location, on the pupa of Limacodidae in a cocoon buried in soil, 08 October 2010, Yuan-Bing Wang, (YHH 4520; YFCC 2830, living culture). Kunming City, Wild Duck Lake Forest Park, on *Cordyceps* sp. associated with the pupa of Lepidoptera buried in soil, 14 August 2018, Yao Wang, (YHH 17053; YFCC 7282, living culture).

Notes: Samsoniella yunnanensis is characterized by gregarious synnemata with terminal branches, clavate to

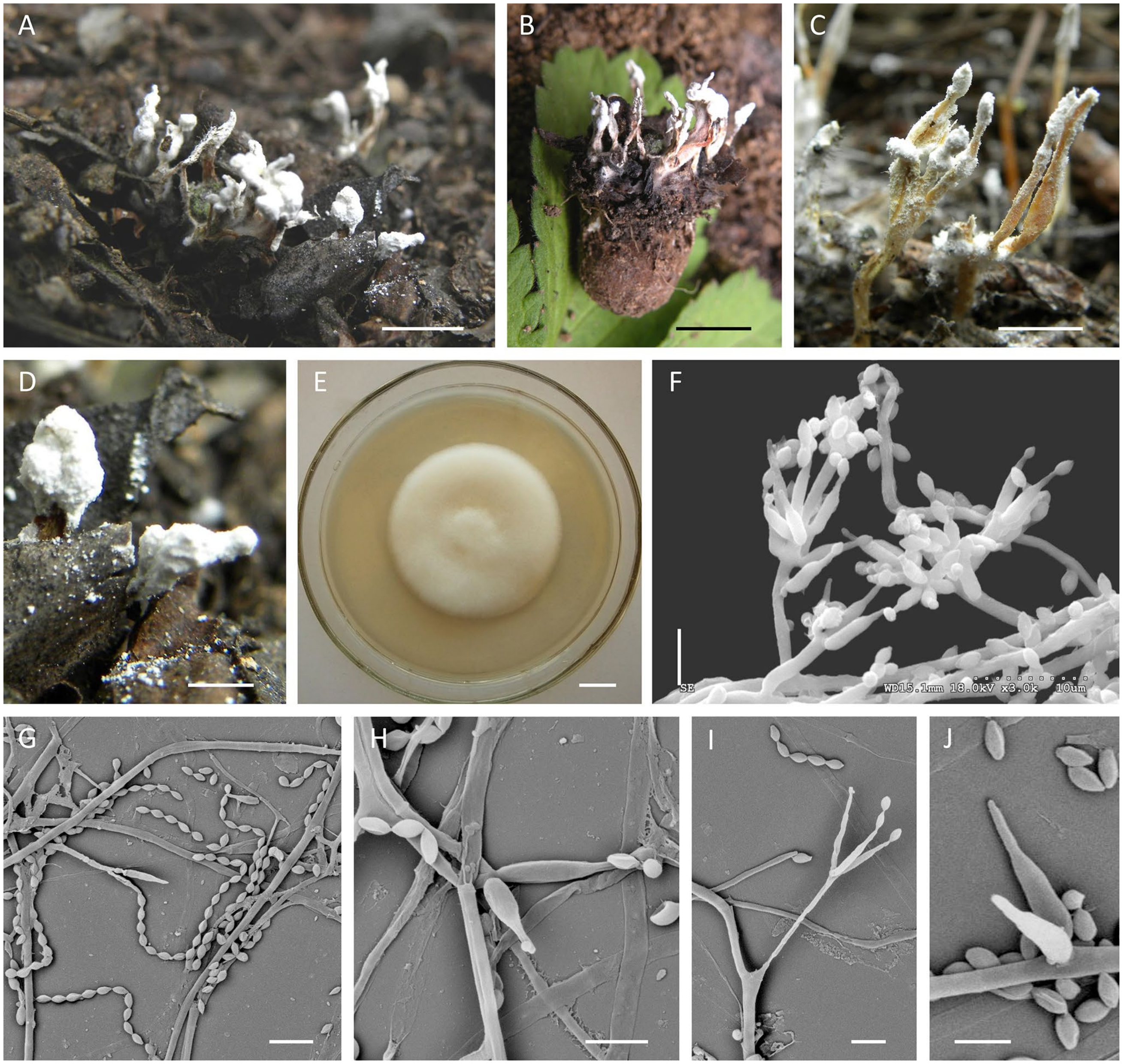

Fig. 19 *Samsoniella yunnanensis.* **A, B** Synnemata arising from the pupa of Limacodidae in a cocoon. **C**, **D** Stipes producing a white mass of conidia toward the apex. **E** Colony on PDA. **F–I** Verticillate phialides on conidiophores. **J** Verticillate phialides on hypha. Scale bars: **A–D** = 5 mm; **E** = 1 cm; **F–J** = 5 µm

spatulate stipes with orange to pink colors, producing a mass of conidia toward the apex of synnemata, powdery and floccose, loose and hairy colonies, sporulating abundantly, having *Isaria*-like asexual conidiogenous structure, and it is associated with pupae of Limacodidae and *Cordyceps* spp.

Phylogenetically, three samples of *S. yunnanensis* group together with strong statistical support, and form a separate clade at the basal portion of *Samsoniella* lineage. It is similar to *S. alpina* and *S. hepiali* in producing a mass of conidia toward the apex synnemata with terminal branches and *Isaria*-like asexual conidiogenous structure. Additionally, none of these three fungal sexual morphs have been determined yet. However, it differs from the latter two by its orange to pink stipes, and associations with the pupae of Limacodidae in cocoons, *Cordyceps* sp. associated with the pupa of Lepidoptera, and *C. cicadae* associated with the nymphs of Cicadidae buried in soil.

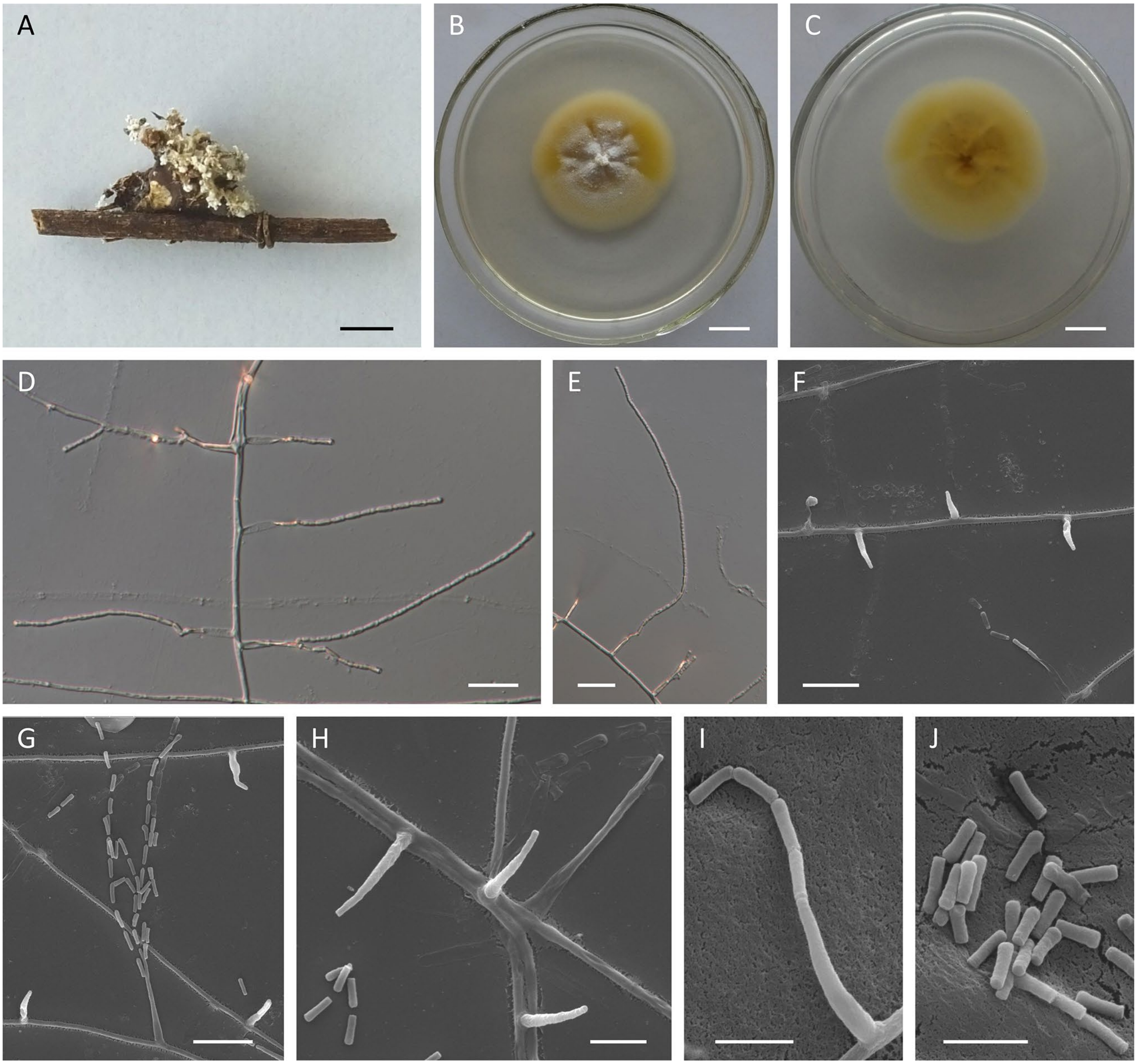

Fig. 20 *Simplicillium yunnanense*. **A** *Akanthomyces waltergamsii* associated with the spider on a dead stem, from which *Sim. yunnanense* was isolated. **B** Colony on PDA. **C** Reverse of colony. **D–I** Solitary phialides with conidia in chains produced on prostrate aerial hyphae. **J** Cylindrical conidia. Scale bars: **A** = 2 mm; **B, C** = 1 cm; **D–G** = 10 µm; **H–J** = 5 µm

Simplicillium yunnanense H. Yu, Y.B. Wang, Y. Wang & Zhu L. Yang, **sp. nov.**

Mycobank: MB 833120; Fig. 20

Etymology: Named after the location Yunnan Province where this species was collected.

Holotype: YHH 16988

Sexual morph: Undetermined. **Asexual morph:** Colonies on PDA fast-growing, 39–42 mm diameter in 14 days at 25 °C, convex, white to light yellow, with very low mycelial density, producing hyaline droplets on the felty aerial mycelium, generating radially distributed grooves. Reverse grayish orange to brown. Hyphae smooth-walled, branched, septate, hyaline, 0.8–1.7 µm wide. Phialides produced on prostrate aerial hyphae, solitary, discrete, subulate, tapering gradually toward the apex, 5.8–16.9 µm long, 1.1–1.5 µm wide at the base, and 0.6–1.1 µm wide at the apex. Conidia one-celled, smooth-walled, hyaline, cylindrical, 2.5–3.4 × 0.7–1.1 µm, usually in chains at the phialidic apex.

Substratum: Akanthomyces waltergamsii Mongkols et al.

Habitat: On *A. waltergamsii* associated with the spider on a dead stem.

Distribution: Kunming City, China.

Material examined: CHINA. YUNNAN PROVINCE: Kunming City, Wild Duck Lake Forest Park, isolated from synnemata of *A. waltergamsii* associated with the spider on a dead stem, 14 August 2018, Yao Wang, (YHH 16988, holotype; YFCC 7133, ex-holotype living culture); *Ibid.*, (YHH 16989; YFCC 7134, living culture).

Notes: *Simplicillium yunnanense* is characterized by white to light yellow colonies with very low mycelial density, convex, generating radially distributed grooves, solitary phialides, discrete, subulate, produing cylindrical conidia usually in chains at the apex of phialides, and on *A. waltergamsii* associated with the spider on the dead stem.

In our five-gene phylogenetic analyses (Fig. 1, 2), *Sim. yunnanense* forms a separate clade in *Simplicillium* and is likely to be related to *Sim. lanosoniveum* (J.F.H. Beyma) Zare & W. Gams and *Sim. obclavatum* (W. Gams) Zare & W. Gams. However, it differs from the latter two by its shorter phialides with subulate shape and producing cylindrical conidia usually in chains at the apex of phialides. *Simplicillium lanosoniveum* and *Sim. obclavatum* have much narrower and longer phialides, producing respectively oval or ellipsoidal to subcylindrical, obclavate to ellipsoidal conidia, and form respectively globose heads and short imbricate chains at the apex of phialides (Zare and Gams 2001). Ecologically, *Sim. yunnanense* can be differentiated due to its association with synnemata of *A. waltergamsii* parasitizing the spider.

Discussion

Many high-level phylogenetic classifications for entomopathogenic fungi have been undertaken, thus more and more available molecular data can be efficiently used to facilitate systematics and evolutionary biology of cordycipitoid fungi (Sung et al. 2007; Chaverri et al. 2008; Kepler et al. 2013, 2014, 2017; Quandt et al. 2014; Maharachchikumbura et al. 2015; Hongsanan et al. 2017; Luangsa-ard et al. 2017; Mongkolsamrit et al. 2018). In this study, we focused on the phylogenetic investigation of the family Cordycipitaceae, with special emphasis on species collected from Yunnan Province, China. Our phylogenetic study supports recognition of the genera *Cordyceps, Samsoniella, Lecanicillium* and *Simplicillium*, as previously reported (Kepler et al. 2017; Mongkolsamrit et al. 2018). We proposed two new genera *Flavocillium* and *Liangia*, 16 new species and four new combinations in the family Cordycipitaceae.

The genus *Flavocillium* was erected to accommodate *F. bifurcatum, F. acerosium, F. primulinium*, and *F. subprimulinium.* Even though *Flavocillium* is morphologically similar to other *Lecanicillium* species in conidiophores, phialides and two types of conidia, the genus is sufficiently distinct by possessing yellowish stromata with a furcate terminal branch, contorted fertile parts, and colonies that usually produce pastel yellow pigment (Zare and Gams 2001; Kaifuchi et al. 2013; Huang et al. 2018; Su et al. 2019). In addition, *Flavocillium* is distinguished from phylogenetically close relatives *Engyodontium* and *Parengyodontium* because the latter two genera usually produce white colonies, conidiiferous rachids with denticles on phialides, and terminal fertile regions that are zigzag-shaped (Gams et al. 1984; Tsang et al. 2016). *Liangia* is established for the new species *Lia. sinensis* isolated from the cordycipitoid fungus *B. yunnanensis*. *Liangia* is more closely related to *C. piperis* and *L. psalliotae* clades in the five-gene phylogenetic analyses. However, this genus differs morphologically from *C. piperis* that produces the *Verticillium*-like anamorph with verticillate conidiophores and phialides, subcylindrical conidia aggregating into heads and conjoined polyhedral crystals (Bischoff and White 2004). *Liangia* is similar to *L. psalliotae* in sharing the *Lecanicillium*-like asexual morph, but it differs from the latter that produces erect conidiophores, relatively short verticillate phialides, short-ellipsoidal conidia formed in heads and octahedral crystals (Zare and Gams 2001). The new genera *Flavocillium* and *Liangia* can be distinguished from each other by having distinct morphological characteristics and phylogenetic positions.

The economically and medically significant fungus *P. hepiali* was reexamined and assigned to the genus *Samsoniella* based on study of the holotype IMM 82–2 and its ex-holotype living culture, as well as seven other samples of *P. hepiali*. The systematic position of *P. hepiali* is most appropriate in the genus *Samsoniella.* Therefore, the new taxonomic combination *S. hepiali* is proposed for *P. hepiali*. Collections of unknown identity are found to represent nine new species of *Samsoniella*, which are named *S. alpina, S. antleroides, S. cardinalis, S. cristata, S. kunmingensis, S. lanmaoa, S. ramosa, S. tortricidae* and *S. yunnanensis*. Four new species of *Cordyceps* are described and named *C. subtenuipes, C. shuifuensis, C. chaetoclavata* and *C. cocoonihabita.* Two isolations from *A. waltergamsii* associated with the spider on the dead stem represent a new species in the genus *Simplicillium*, viz. *Sim. yunnanense.* All of the above species are recognized as new members of the family Cordycipitaceae by well-supported morphological and molecular phylogenetic evidence.

The asexual genus *Lecanicillium* is typified by *L. lecanii* with the sexual morph *T. confragosa* and previously contained 32 species (Zare and Gams 2001, 2008; Sukarno et al. 2009; Crous et al. 2018; Huang et al. 2018; Su et al. 2019; Zhou et al. 2018). However, the recent taxonomic revision rejected *L. lecanii*, the type species of *Lecanicillium*, and considered that it was a synonym of *Akanthomyces* (Kepler et al. 2017). This treatment seeks to harmonize competing names by principles of priority, recognition of monophyletic groups, and the practical usage of the affected taxa. Based on this, *Akanthomyces* was proposed to be maintained and *Lecanicillium* was rejected, although the generic name *Lecanicillium* was still being used thereafter (Crous et al. 2018; Huang et al. 2018; Su et al. 2019; Zhou et al. 2018). Species of different lineages may have similar micromorphological characteristics like those of *Lecanicillium* in the family Cordycipitaceae. Unfortunately, many species in the *Lecanicillium* lineage are published with singular gene data, such as ITS sequences. Few multigene sequences are available in online databases. Reconstructing the credible phylogenetic framework of *Lecanicillium* clades in the family Cordycipitaceae is difficult due to a lack of large-scale multigene sequence sampling. Thus, in this study, the phylogenetic tree of *Lecanicillium* inferred from ITS sequences includes eight clades, which does not match those of the tree generated from five-gene data because of differentiated available data sampling. To be prudent, we did not make major revisions to the *Lecanicillium* lineage but only added two genera, *Flavocillium* and *Liangia*, based on their monophyly and distinct morphological characteristics in the family Cordycipitaceae. A credible phylogenetic framework of *Lecanicillium* species, which have not been assigned appropriate generic names, will require more future extensive multigene taxon sampling.

Phylogenetic classifcations of entomopathogenic fungi showed that most diagnostic characteristics used in current classifcations of cordycepitoid fungi (e.g., arrangement of perithecia, ascospores fragmentation, conidiogenous structures, conidial shape and size) are not phylogenetically informative (Sung et al. 2007; Kepler et al. 2013, 2017; Ban et al. 2015; Mongkolsamrit et al. 2018). However, the characteristics that are most consistent with the phylogeny are texture, pigmentation and morphology of the stromata and synnemata. Even so, these macro- and micro-morphological characteristics could aid the identification of *Cordyceps*, *Isaria*-like and *Lecanicillium*-like fungi. Sexual morphs of *Cordyceps* are characterized by fleshy stromata, red to orange colors, superficial perithecia, asci cylindrical with thickened ascus apex, ascospores usually cylindrical and multiseptate. These are very similar to those of *Samsoniella*, which mainly have lepidopteran hosts. Previous studies of cordycipitoid fungi as well as our study show that both *Samsoniella* and *Cordyceps* species produce similar asexual conidiogenous structures (Samson 1974; Mongkolsamrit et al. 2018). *Samsoniella* and *Cordyceps* share similar *Isaria*-like asexual morphs that produce branched and white to orange synnemata, a dry mass of white to cream conidia on the synnemata, flask-shaped phialides that are produced in whorls, conidia with divergent chains. Therefore, the *C. farinosa* morphology is not diagnostic and represents a polyphyletic species complex as exemplified by the isolates delimited as *S. alboaurantium* (G. Sm.) Mongkolsamrit et al. (Kepler et al. 2017; Mongkolsamrit et al. 2018).

A review of the taxonomic history of *Cordyceps* concluded that *Cordyceps* is the oldest accepted generic name in the family Cordycipitaceae (Shrestha et al. 2014). Based on the cylindrical shape of stroma, pre-Linnaean literature of the 17th and early eighteenth centuries had recorded *C. militaris*. It is noteworthy that *Cordyceps* has a much longer history and culture in China. The famous Chinese medicine monograph "Shennong's Materia Medica" (Qin and Han Dynasties, second century BC) recorded the white muscardin silkworms infected by *B. bassiana* as a medicine. The archaeology of Haihun marquis (Western Han Dynasty, first century AD) discovered *Cordyceps* sp. in He Liu's funerary objects, proving that *Cordyceps* sp. had been used for health care in China as early as 2075 years ago. The "Mister Lei's Treatise on Processing Drugs" (Southern and Northern Dynasties, 5th Century AD) recorded *I. cicadae* Miq. as a traditional medicine. Tibetan Materia Medica "Medical King's Drugs for Medicine" (Tibetan Empire, 8th Century AD) recorded *O. sinensis* as a medicine.

In the phylogenetic classification of cordycipitoid fungi, the desire to preserve the term "cordyceps" within the family Ophiocordycipitaceae to reflect the cultural and economic importance of *O. sinensis* was expressed (Sung et al. 2007). This taxonomic revision ultimately benefits humanity, especially in Asia. *Samsoniella hepiali* (syn. *P. hepiali*) is also termed "cordyceps", and it is internationally known. Based on the above, we suggest that the Chinese name "鳞翅虫草属" (Lín Chì Chóng Cǎo Shǔ), be given to *Samsoniella*, taking into account the similarity of its morphological and ecological characteristics with *Cordyceps* and practical usage.

Samsoniella hepiali is a very important fungus to humans, due to its therapeutic effects in cardiovascular, respiratory disorders, immunomodulatory, hyposexuality, hyperglycemia, renal disorder and antitumor conditions (Lou et al. 1986; Huang et al. 1988; Wang and Huang 1988; Dai et al. 1989; Zou and Huang 1993; Xiang et al. 2006; Jiang et al. 2010). The Ministry of Health of the P. R. China issued a new drug certificate (WYZZ2-67 05) in July, 1987 and listed the *S. hepiali* strain Cs-4 as a protected and confidential strain. The product of strain Cs-4, Jinshuibao capsule, was introduced into the market in 1987. The Ministry of Health of the P. R. China issued File No. 84 on 23 March 2001 and approved *S. hepiali* mycelia to be used as a stand-alone or a component of health foods (equivalent to dietary supplements in other countries) (Dai et al. 2018b). Thus, *S. hepiali* is widely used as a medicinal and edible cordycipitoid fungus, creating an annual economic value of approximately 10 billion RMB in China. In addition to the Jinshuibao capsule, over 260 healthcare products have been developed with *S. hepiali* as a raw material. Its therapeutic effects have been demonstrated and are now widely recognized by doctors and patients. Many companies have put these products into Chinese markets and globally exported them to nearly 80 countries or regions as medicine and dietary supplements, including northeastern and southeastern Asia, the United States of America, Canada, Australia, New Zealand and other countries (Dai et al. 2018b). *Samsoniella hepiali* is economically, medicinally and culturally important, and share the morphologically and ecologically similar characteristics with *Cordyceps*. Based on its significant contribution as "cordyceps", here we strongly suggest that the Chinese name "蝙蝠蛾虫草" (Biān Fú É Chóng Cǎo), be given to this cordycipitoid fungus, which will allow for the convenient and unambiguous communication among the biomedical and health industries of China.

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References

Ban S, Sakane T, Nakagiri A (2015) Three new species of *Ophiocordyceps* and overview of anamorph types in the genus and the family Ophiocordyceptaceae. Mycol Prog 14:1017

Bainer G (1907) Mycotheque del' Ecole de Pharmacie XI. *Paecilomyces*, Genre Noveau de Mucedinees. Bull Soc Mycol France 23:26–27

Bischoff JF, White JF (2004) *Torrubiella piperis* sp. nov. (Clavicipitaceae, Hypocreales), a new teleomorph of the *Lecanicillium* complex. Stud Mycol 50:89–94

Bischoff JF, Rehner SA, Humber RA (2006) *Metarhizium frigidum* sp. nov.: a cryptic species of *M. anisopliae* and a member of the *M. flavoviride* Complex. Mycologia 98(5):737–745

Chaverri P, Liu M, Hodge KT (2008) A monograph of the entomopathogenic genera *Hypocrella, Moelleriella*, and *Samuelsia* gen. nov. (Ascomycota, Hypocreales, Clavicipitaceae), and their aschersonia-like anamorphs in the Neotropics. Stud Mycol 60:1–66

Chen ZH, Chen K, Dai YD, Zheng Y, Wang YB, Yang XN, Yu H, Yang YM, Xu L (2019) *Beauveria* species diversity in the Gaoligong Mountains of China. Mycol Prog 18(7):933–943

Crous PW, Wingfield MJ, Burgess TI, Hardy GEStJ, Gené J, Guarro J, Baseia IG, García D, Gusmão LFP, Souza-Motta CM, Thangave R, Adamčík S, Barili A, Barnes CW, Bezerra JDP, Bordallo JJ, Cano-Lira JF, de Oliveira RJV, Ercole E, Hubka V, Iturrieta-González I, Kubátová A, Martín MP, Moreau PA, Morte A, Ordoñez ME, Rodríguez A, Stchige AM, Vizzini A, Abdollahzadeh J, Abreu VP, Adamčíková K, Albuquerque GMR, Alexandrova AV,Álvarez Duarte E, Armstrong-Cho C, Banniza S, Barbosa RN, Bellanger JM, Bezerra JL, Cabral TS, Caboň M, Caicedo E, Cantillo T, Carnegie AJ, Carmo LT, Castañeda-Ruiz RF, Clement CR, Čmoková A, Conceição LB, Cruz RHSF, Damm U, da Silva BDB, da Silva GA, da Silva RMF, de A. Santiago ALCM, de Oliveira LF, de Souza CAF, Déniel F, Dima B, Dong G, Edwards J, Félix CR, Fournier J, Gibertoni TB, Hosaka K, Iturriaga T, Jadan M, Jany JL, Jurjević Ž, Kolařík M, Kušan I, Landell MF, Leite Cordeiro TR, Lima DX, Loizides M, Luo S, Machado AR, Madrid H, Magalhães OMC, Marinho P, Matočec N, Mešić A, Miller AN, Morozova OV, Neves RP, Nonaka K, Nováková A, Oberlies NH, Oliveira-Filho JRC, Oliveira TGL, Papp V, Pereira OL, Perrone G, Peterson SW, Pham THG, Raja HA, Raudabaugh DB, Řehulka J, Rodríguez-Andrade E, Saba M, Schauflerová A, Shivas RG, Simonini G, Siqueira JPZ, Sousa JO, Stajsic V, Svetasheva T, Tan YP, Tkalčec Z, Ullah S, Valente P, Valenzuela-Lopez N, Abrinbana M, Viana Marques DA, Wong PTW, Xavier de Lima V, Groenewald JZ (2018) Fungal Planet description sheets: 716–784. Persoonia 40:240–393

Dai RQ, Lan JL, Chen WH, Li XM, Chen QT, Shen CY (1989) Research on *Paecilomyces hepiali* Chen et Dai, sp. nov. Acta Agric Univ Pekin 15(2):221–224

Dai RQ, Li XM, Shao AJ, Lin SF, Lan JL, Chen WH, Shen CY (2008) Nomenclatural validation of *Paecilomyces hepiali*. Mycosystema 27(5):641–644

Dai RQ, Shen CY, Li XM, Lan JL, Lin SF, Shao AJ (2018a) Discussion on related problems of model species of fungus: *Paecilomyces hepialid*. China J Chin Mater Med 42(19):3843–3846

Dai RQ, Shen CY, Li XM, Lan JL, Lin SF, Shao AJ (2018b) Response to neotypification of *Paecilomyces hepiali* (Hypocreales) (Wang & al., 2015). Taxon 67 (4):784–786

Dayal R, Barron GL (1970) *Verticillium psalliotae* as a parasite of *Rhopalomyces*. Mycologia 62(4):826–830

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772

Gams W, de Hoog GS, Samson RA, Evans HC (1984) The hyphomycete genus *Engyodontium*: a link between *Verticillium* and *Aphanocladium*. Persoonia 12:135–147

Hongsanan S, Maharachchikumbura SSN, Hyde KD, Samarakoon MC, JeewonR ZQ, Al-Sadi AM, Bahkali AH (2017) An updated phylogeny of Sordariomycetes based on phylogenetic and molecular clock evidence. Fungal Divers 84(1):25–41

Huang MM, Zhang JF, Pang L, Jiang Z, Wang DW (1988) Studies on immunopharmacology of *Cordyceps* (Fr.) Link IV. Observations on the immunosuppressive activity of artificial substance of *Paecilomyces hapiali* Chen. Acta Univ Med Tongji 5:329–331

Huang SK, Maharachchikumbura SSN, Jeewon R, Bhat DJ, Phookamsak R, Hyde KD, Al-Sadi AM, Kang JC (2018) *Lecanicillium subprimulinum* (Cordycipitaceae, Hypocreales), a novel species from Baoshan, Yunnan. Phytotaxa 348(2):099–108

Humber RA, Rocha LFN, Inglis PW, Kipnis A, Luz C (2013) Morphology and molecular taxonomy of *Evlachovaea*-like fungi, and the status of this unusual conidial genus. Fungal Biol 117:1–12

Hyde KD, Tennakoon DS, Jeewon R, Bhat DJ, Maharachchikumbura SSN, Rossi W, Leonardi M, Lee HB, Mun HY, Houbraken J, Nguyen TTT, Jeon SJ, Frisvad JC, Wanasinghe DN, Lücking R, Aptroot A, Caceres MES, Karunarathna SC, Hongsanan S, Phookamsak R, de Silva NI, Thambugala KM, Jayawardena RS, Senanayake IC, Boonmee S, Chen J, Luo ZL, Phukhamsakda C, Pereira OL, Abreu VP, Rosado AWC, Buyck B, Randrianjohany E, Hofstetter V, Gibertoni TB, da Silva Soares AM, Plautz HL Jr, Pontes Sotão HM, Xavier WKS, Bezerra JDP, de Oliveira TGL, de Souza-Motta CM, Magalhães OMC, Bundhun D, Harishchandra D, Manawasinghe IS, Dong W, Zhang SN, Bao DF, Samarakoon MC, Pem D, Karunarathna A, Lin CG, Yang J, Perera RH, Kumar V, Huang SK, Dayarathne MC, Ekanayaka AH, Jayasiri SC, Xiao YP, Konta S, Niskanen T, Liimatainen K, Dai YC, Ji XH, Tian XM, Mešić A, Singh SK, Phutthacharoen K, Cai L, Sorvongxay T, Thiyagaraja V, Norphanphoun C, Chaiwan N, Lu YZ, Jiang HB, Zhang JF, Abeywickrama PD, Aluthmuhandiram JVS, Brahmanage RS, Zeng M, Chethana T, Wei DP, Réblová M, Fournier J, Nekvindová J, Barbosa RN, Felinto dos Santos JE, Oliveira NT, Li GJ, Ertz D, Shang QJ, Phillips AJL, Kuo CH, Camporesi E, Bulgakov TS, Lumyong S, Jones EBG, Chomnunti P, Gentekaki E, Bungartz F, Zeng XY, Fryar S, Tkalčec Z, Liang JM, Li GS, Wen TC, Singh PN, Gafforov Y, Promputtha I, Yasanthika E, Goonasekara ID, Zhao RL, Zhao Q, Kirk PM, Liu JK, Yan JY, Mortimer PE, Xu JC, Doilom MW (2019) Fungal diversity notes 1036–1150: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Divers 96:1–242

Hywel-Jones NL (2002) Multiples of eight in *Cordyceps* ascospores. Mycol Res 106:2–3

Jiang L, Bao HY, Yang M (2010) Antitumor activity of a petroleum ether extract from *Paecilomyces hepiali* mycelium. Acta Edulis Fungi 17:58–60

Johnson D, Sung GH, Hywel-Jones NL, Luangsa-Ard JJ, Bischoff JF, Kepler RM, Spatafora JW (2009) Systematics and evolution of the genus *Torrubiella* (Hypocreales, Ascomycota). Mycol Res 113:279–289

Kaifuchi S, Nonaka K, Mori M, Shiomi K, Ômura S, Masuma R (2013) *Lecanicillium primulinum*, a new hyphomycete (Cordycipitaceae) from soils in the Okinawa's main island and the Bonin Islands, Japan. Mycoscience 54:291–296

Kepler RM, Ban S, Nakagiri A, Bischoff JF, Hywel-Jones NL, Owensby CA, Spatafora JW (2013) The phylogenetic placement of hypocrealean insect pathogens in the genus *Polycephalomyces*: an application of one fungus one name. Fungal Biol 117(9):611–622

Kepler RM, Humber RA, Bischoff JF, Rehner SA (2014) Clarifcation of generic and species boundaries for *Metarhizium* and related fungi through multigene phylogenetics. Mycologia 106(4):811–829

Kepler RM, Luangsa-ard JJ, Hywel-Jones NL, Quandt CA, Sung GH, Rehner SA, Aime MC, Henkel TW, Sanjuan T, Zare R, Chen M, Li Z, Rossman AY, Spatafora JW, Shrestha B (2017) A phylogenetically-based nomenclature for Cordycipitaceae (Hypocreales). IMA Fungus 8(2):335–353

Kobayasi Y, Shimizu D (1960) Monographic studies of *Cordyceps* 1. Group parasitic on *Elaphomyces*. Bull Natl Sci Mus Tokyo 5:69–85

Kobayasi Y (1981) Revision of the genus *Cordyceps* and its allies 1. Bull Natl Sci Mus Tokyo Ser B 7(1):1–13

Kobayasi Y (1982) Keys to the taxa of the genera *Cordyceps* and *Torrubiella*. Trans Mycol Soc Japan 23:329–364

Kobayasi Y, Shimizu D (1982) *Cordyceps* species from Japan 5. Bull Natl Sci Mus Tokyo Ser B 8(4):111–123

Kobayasi Y, Shimizu D (1983) *Cordyceps* species from Japan 6. Bull Natl Sci Mus Tokyo Ser B 9(1):2–21

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Biol Evol 29(2):1695–1701

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23(21):2947–2948

Letunic I, Bork P (2019) Interactive Tree Of Life (iTOL) v4: recent updates and new developments. Nucleic Acids Res 47(W1):W256–W259

Liu ZY, Liang ZQ, Whalley AJS, Yao YJ, Liu AY (2001) *Cordyceps brittlebankisoides*, a new pathogen of grubs and its anamorph, *Metarhizium anisopliae* var. *majus*. J Invertebr Pathol 78:178–182

Luangsa-ard JJ, Hywel-Jones NL, Samson RA (2004) The order level polyphyletic nature of *Paecilomyces* sensu lato as revealed through 18S-generated rRNA phylogeny. Mycologia 96(4):773–780

Luangsa-ard JJ, Hywel-Jones NL, Manoch L, Samson RA (2005) On the relationships of *Paecilomyces* sect. *Isarioidea* species. Mycol Res 109(5):581–589

Luangsa-ard JJ, Houbraken J, van Doorn T, Hong SB, Borman AM, Hywel-Jones NL, Samson RA (2011) *Purpureocillium*, a new genus for the medically important *Paecilomyces lilacinus*. FEMS Microbiol Lett 321(2):141–149

Luangsa-Ard JJ, Mongkolsamrit S, Thanakitpipattana D, Khonsanit A, Tasanathai K, Noisripoom W, Humber RA (2017) Clavicipitaceous entomopathogens: new species in *Metarhizium* and a new genus *Nigelia*. Mycol Prog 16(4):369–391

Lou YQ, Liao XM, Lu YC (1986) Cardiovascular pharmacological studies of ethanol extracts of *Cordyceps* mycelia and *Cordyceps* fermentation solution. Chin Tradit Herbal Drugs 17:17–21

Li DD, Zhang GD, Huang LD, Wang YB, Yu H (2019) Complete mitochondrial genome of the important entomopathogenic fungus *Cordyceps tenuipes* (Hypocreales, Cordycipitaceae). Mitochondrial DNA B 4(1):1329–1331

Li ZZ, Li CR, Huang B, Fan MZ (2001) Discovery and demonstration of the telemorph of *Beauveria bassiana*, an important entomogenous fungus. Chin Sci Bull 46(6):470–473

Liang ZQ (1983) A record and description on *Cordyceps pruinosa* Petch and its conidial state. J Guizhou Agric Coll 2:72–80

Liang ZQ (1991) Verification and identification of the anomorph of *Cordyceps pruinosa* Petch. Acta Mycol Sin 10(2):104–107

Liang ZQ (2007) Flora fungorum sinicorum vol 32 Cordyceps, vol 32. Science Press, Beijing

Maharachchikumbura SSN, Hyde KD, Jones EBG, McKenzie EHC, Huang SK, Abdel-Wahab MA, Daranagama DA, Dayarathne M, D'souza MJ, Goonasekara ID, Hongsanan S, Jayawardena RS, Kirk PM, Konta S, Liu JK, Liu ZY, Norphanphoun C, Pang KL, Perera RH, Senanayake IC, Shang QJ, Shenoy BD, Xiao YP, Bahkali AH, Kang JC, Somrothipol S, Suetrong S, Wen TC, Xu

JC (2015) Towards a natural classification and backbone tree for Sordariomycetes. Fungal Divers 72:199–301

Mains EB (1949) New species of *Torrubiella*, *Hirsutella* and *Gibellula*. Mycologia 41:303–310

Mains EB (1958) North American entomogenous species of *Cordyceps*. Mycologia 50:169–222

Mongkolsamrit S, Noisripoom W, Thanakitpipattana D, Wutikhun T, Spatafora JW, Luangsa-ard JJ (2018) Disentangling cryptic species with isaria-like morphs in Cordycipitaceae. Mycologia 110(1):230–257

Petch T (1924) Studies in entomogenous fungus. IV. Some Ceylon *Cordyceps*. Trans Br Mycol Soc 10:28–45

Quandt CA, Kepler RM, Gams W, Araújo JPM, Ban S, Evans HC, Hughes D, Humber R, Hywel-Jones NL, Li ZZ, Luangsa-ard JJ, Rehner SA, Sanjuan T, Sato H, Shrestha B, Sung GH, Yao YJ, Zare R, Spatafora JW (2014) Phylogenetic-based nomenclatural proposals for Ophiocordycipitaceae (Hypocreales) with new combinations in *Tolypocladium*. IMA Fungus 5(1):121–134

Rehner SA, Samuels GJ (1994) Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. Mycol Res 98(6):625–634

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12):1572–1574

Rossman AY, Samuels GJ, Rogers JS, Lowen R (1999) Genera of Bionectriaceae, Nectriaceae and Hypocreaceae (Hypocreales, Ascomycetes). Stud Mycol 42:1–248

Samson RA, Evans HC (1974) Notes on entomogenous fungi from Ghana. II. The genus *Akanthomyces*. Acta Bot Neerl 23:28–35

Samson RA (1974) *Paecilomyces* and some allied hyphomycetes. Stud Mycol 6:1–119

Shrestha B, Tanaka E, Han JG, Oh J, Han SK, Lee KH, Sung GH (2014) A brief chronicle of the genus *Cordyceps* Fr., the oldest valid genus in Cordycipitaceae (Hypocreales, Ascomycota). Mycobiology 42(2):93–99

Spatafora JW, Quandt CA, Kepler RM, Sung GH, Shrestha B, Hywel-Jones NL, Luangsa-ard JJ (2015) New 1F1N species combinations in Ophiocordycipitaceae (Hypocreales). IMA Fungus 6(2):357–362

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21):2688–2690

Su CH, Wang HH (1986) *Phytocordyceps*, a new genus of the Clavicipitaceae. Mycotaxon 26:337–344

Su L, Zhu H, Guo YX, Du XP, Guo JG, Zhang L, Qin C (2019) *Lecanicillium coprophilum* (Cordycipitaceae, Hypocreales), a new species of fungus from the feces of *Marmota monax* in China. Phytotaxa 387:55–62

Sukarno N, Kurihara Y, Ilyas M, Mangunwardoyo W, Yuniarti E, Sjamsuridzal W, Park JY, Saraswati R, Inaba S, Widyastuti Y, Ando K, Harayama S (2009) *Lecanicillium* and *Verticillium* species from Indonesia and Japan including three new species. Mycoscience 50(5):369–379

Sung GH, Hywel-Jones NL, Sung JM, Luangsa-Ard JJ, Shrestha B, Spatafora JW (2007) Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. Stud Mycol 57:5–59

Swofford DL (2002) PAUP*: Phylogenetic analysis using parsimony (*and other methods), Version 4. Sinauer Associates, Sunderland

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30(12):2725–2729

Treschew D (1941) The *Verticillium* diseases of cultivated mushrooms. Dansk bot Ark 11(1):1–31

Tsang CC, Chan JFW, Pong WM, Chen JHK, Ngan AHY, Cheung M, Lai CKC, Tsang DNC, Lau SKP, Woo PCY (2016) Cutaneous hyalohyphomycosis due to *Parengyodontium album* gen. et comb. Nov. Med Mycol 54:699–713

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (eds.) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. [Regnum Vegetabile no. 159.] Glashütten: Koeltz Botanical Books.

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172(8):4238–4246

Wang DW, Huang MM (1988) Studies on immunopharmacology of *Cordyceps* (Fr.) Link V. Influence of artificial fermentative substance of *Paecilomyces hapiali* Chen on the function of T cell and its subgroup in mice. Acta Univ Med Tongji 5:332–334

Wang YB, Yu H, Dai YD, Wu CK, Zeng WB, Yuan F, Liang ZQ (2015a) Polycephalomyces agaricus, a new hyperparasite of *Ophiocordyceps* sp. infecting melolonthid larvae in southwestern China. Mycol Prog 14:70

Wang YB, Yu H, Dai YD, Chen ZH, Zeng WB, Yuan F, Liang ZQ (2015b) *Polycephalomyces yunnanensis* (Hypocreales), a new species of *Polycephalomyces* parasitizing *Ophiocordyceps nutans* and stink bugs (hemipteran adults). Phytotaxa 208:034–044

White TJ, Bruns TD, Lee SB, Taylor JW (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, New York, pp 315–322

Yan JQ, Bau T (2015) *Cordyceps ningxiaensis* sp. nov., a new species from dipteran pupae in Ningxia Hui Autonomous Region of China. Nova Hedwigia 100:251–258

Yang JK, Huang XW, Tian BY, Sun H, Duan JX, Wu WP, Zhang KQ (2005) Characterization of an Extracellular Serine Protease Gene from the Nematophagous Fungus *Lecanicillium psalliotae*. Biotechnol Lett 27(17):1329–1334

Xiang M, Tang J, Chu T, Zhang CL, Zou XL (2006) Hypoglycemic effect and mechanism study on streptozocin induced diabetes in mice by *Paecilomyces hepiali* Chen mycelium. Chin J Hosp Pharm 26:556–559

Yang ZL, Yu H, Chen ZH, Wang YB (2012) Study on the Biological and Ecological Habits of Populations of *Cordyceps militaris* in Middle of Yunnan Edible Fungi of China. Edible Fungi China 30(5):43–47

Zhang ZF, Liu F, Zhou X, Liu X, Liu SJ, Cai L (2017) Culturable mycobiota from Karst caves in China, with descriptions of 20 new species. Persoonia 39(1):1–31

Zare R, Gams W (2001) A revision of *Verticillium* section *Prostrata*. IV. The genera *Lecanicillium* and *Simplicillium* gen. nov. Nova Hedwigia 73(1):1–50

Zare R, Gams W (2008) A revision of the *Verticillium fungicola* species complex and its affinity with the genus *Lecanicillium*. Mycol Res 112(7):811–824

Zare R, Gams W (2016) More white verticillium-like anamorphs with erect conidiophores. Mycol Prog 15:993–1030

Zhou YM, Zhi JR, Ye M, Zhang ZY, Yue WB, Zou X (2018) *Lecanicillium cauligalbarum* sp. nov. (Cordycipitaceae, Hypocreales), a novel fungus isolated from a stemborer in the Yao Ren National Forest Mountain Park. MycoKeys 43:59–74

Zou WP, Huang MM (1993) Primary studies on the mechanism of *Paecilomyces hepiali* Chen against the rejection reaction. Acta Univ Med Tongji 22:282–284

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