RESEARCH ARTICLE

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Morphological and Molecular Phylogenetic Data of the Chinese Medicinal Fungus Cordyceps liangshanensis Reveal Its New Systematic Position in the Family Ophiocordycipitaceae

Yao Wang^{a,b*}, Yong-Dong Dai^{a,b*}, Zhong-Lin Yang^{a,b}, Rui Guo^{a,b}, Yuan-Bing Wang^{a,b}, Zhu L. Yang^c, Lei Ding^d and Hong Yu^{a,b}

^aYunnan Herbal Laboratory, School of Ecology and Environmental Science, Yunnan University, Kunming, China; ^bThe International Joint Research Center for Sustainable Utilization of Cordyceps Bioresources in China and Southeast Asia, Yunnan University, Kunming, China; ^cYunnan Key Laboratory for Fungal Diversity and Green Development, Kunming, China; ^dSchool of Life Sciences, Yunnan University, Kunming, China

ABSTRACT

A cordycipitoid fungus infecting Hepialidae sp. in Nepal was supposed to be identical to Cordyceps liangshanensis, originally described from southwestern China, and thus, transferred to the genus Metacordyceps or Papiliomyces in previous studies. However, our multi-gene (nrSSU-nrLSU-tef-1α-rpb1-rpb2) phylogenetic and morphological studies based on the type specimen and additional collections of C. liangshanensis revealed that the fungus belongs to the genus Ophiocordyceps (Ophiocordycipitaceae). Therefore, a new combination O. liangshanensis was made, and a detailed description of this species was provided.

ARTICLE HISTORY

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KEYWORDS New combination; morphology; multiple genes; revision

1. Introduction

Cordyceps liangshanensis M. Zang, D.Q. Liu & R.Y. Hu is well-known in southwestern China and has been used as a Traditional Chinese Medicine (TCM) named "Mai-Gan-Chong-Cao" for a long time. Like Ophiocordyceps sinensis (Berk.) G.H. Sung et al., C. liangshanensis parasitizes soil-borne larvae of Hepialidae sp., and has a limited distribution in China [1]. The caterpillar-fungus resulting from fungal parasitism has been frequently used for the treatment of chronic cough, hemoptysis, asthma, lumbago, impotence and seminal emissions, and other diseases in Yi Nationality areas as it has special effects on cough expectorant, reinforcing kidney, nourishing lung, etc. [1,2]. The main ingredients of the natural C. liangshanensis are similar to the those of the natural O. sinensis, which contains amino acids, mannitol, adenosine, ergosterol, stearic acid, alkaloids, and organic acids [1,3]. The contents of polysaccharides, flavonoids, and nucleosides of C. liangshanensis were a little bit lower than those of O. sinensis, while the mannitol and saponins were higher than those of O. sinensis [3]. It has been long recognized as a prized medicinal fungus and a desirable alternative for natural O. sinensis by local people. This medicinal fungus was firstly recorded in "Sichuan Tongzhi," and it

was treated as a new species and named Cordyceps liangshanensis by Zang et al. [4]. The medicinal virtue of C. liangshanensis is also highly valued by herbalists. This fungus was included in the standardized herbal medicines of Sichuan (enlarged edition) in 1987.

With the rapid development of molecular phylogenetic techniques, considerable changes to the taxonomy of Cordyceps s. l. have occurred. Sung et al. [5] proposed the genus Metacordyceps to accommodate some species of Cordyceps s. l., which was characterized by solitary or grouped stromata which are simple or branched, with a fleshy or tough whitish stipe, a greenish yellow to greenish cylindrical to enlarged fertile part, and perithecia partially or completely immersed in stromata.

Specimens collected from Nepal were once regarded as Cordyceps liangshanensis and, subsequently this species was moved from Cordyceps to the genus Metacordyceps based on multi-gene phylogenetic evidence [5]. Based on the DNA sequences generated by Sung et al. [6], C. liangshanensis was transferred to Papiliomyces in the family Clavicipitaceae. However, the type or authentic materials of C. liangshanensis were not examined in the aforementioned studies. There is a need to

*These authors contributed equally to this work.

CONTACT Zhu L. Yang 🖾 fungi@mail.kib.ac.cn; Hong Yu 🖾 hongyu@ynu.edu.cn

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reinvestigate the type and additional collections of *C. liangshanensis.*

In this study, the type and other specimens from type locality of *C. liangshanensis* were collected and examined. The redescription was carried out on the basis of five-gene (nrSSU, nrLSU, *tef-1a*, *rpb1*, and *rpb2*) molecular phylogenetic analysis and morphological observations. Our data indicated that collections of *C. liangshanensis* differ from those from Nepal generated by Sung et al. [5], and the species transferred to *Metacordyceps* or *Papiliomyces* was not justified.

2. Materials and methods

2.1. Specimens

The type specimen of *Cordyceps liangshanensis* (KUN-HKAS 7723) was borrowed from Kunming Institute of Botany, Chinese Academy of Sciences. Additional collections were made in two locations in southwestern China, one location in Leibo County, Sichuan Province, and another in Shuifu County, Yunnan Province. Specimens were stored in plastic containers at low temperature and transported to the laboratory for identification and isolation. Afterward, they were deposited at Yunnan Herbal Herbarium (YHH), Yunnan University.

2.2. Fungal isolation and culture

Specimens were rinsed with tap water, and then washed with sterile distilled water. For the purpose of obtaining pure cultures, stromata were immersed in 30% H_2O_2 for 5 min, rinsed with sterile water, and then dried on sterilized filter paper. Stromata were then cut off and a small piece of tissue was inoculated onto potato dextrose agar (PDA: fresh diced potato 200 g, dextrose 20 g, agar 18 g, in 1000 ml distilled water) plates. The purified fungal strains were maintained in a culture room at 25 °C or transferred to PDA slants and stored at 4 °C, and were deposited to the Yunnan Fungal Culture Collection (YFCC) at the Institute of Herb Biotic Resources of Yunnan University.

2.3. Morphological observations

Specimens were examined in the laboratory using the Canon 750 D camera (Canon Inc., Tokyo, Japan) and Olympus SZ60 stereo dissecting microscope (Olympus Corporation, Tokyo, Japan). Cultures on PDA slants were transferred to PDA plates and incubated at 25 °C for 2 months. The colors of fresh specimens and cultures were characterized by the color standard [7]. Frozen sections and glass slides with lactic acid phenol cotton blue solution were prepared for morphological observation and measurement of sexual morph under a light microscope (BX53, Olympus Corporation, Tokyo, Japan). Morphological description of asexual morph was conducted as the method described by Wang et al. [8]. Micro-morphological observations and measurements were performed using the Olympus BX53 stereomicroscope and a scanning electron microscope (Quanta 200 FEG, FEI Company, Hillsboro, USA).

2.4. DNA extraction, PCR, and sequencing

Specimens and live axenic cultures were prepared for DNA extraction. Genomic DNA was extracted using a Genomic DNA Purification Kit (Qiagen GmbH, Hilden, Germany) according to the manufacturer's protocol. The primers used for PCR amplification of nrSSU, nrLSU, *tef-1a*, *rpb1*, and *rpb2* are listed in Table 1. All PCR reactions were performed in a final volume of 50 μ l containing 25 μ l 2 × Taq PCR Master Mix (Tiangen Biotech Co., Ltd, Beijing, China), 0.5 μ l of each primer (10 μ M), 1 μ l of genomic DNA, and 23 μ l of RNase-free water. Target gene amplification and sequencing were performed according to the methods described in our previous publication [9].

2.5. Phylogenetic analysis

Five gene sequences were retrieved from GenBank, and combined with those generated in our study (Table 2). The sequences were aligned using the programs Clustal X 2.0 and MEGA v6.06 [13,14]. After sequence alignment, the aligned sequences of five genes were concatenated. Partition homogeneity test was conducted using PAUP* 4.0b10 [15], and the result revealed that there was no significant conflict among different data partitions. Program PartitionFinder V1.1.1 identified eleven data partitions, one each for nrSSU and nrLSU, and nine for each of the three codon positions for the protein coding genes tef-1 α , rpb1, and rpb2 [16,17]. The results showed that the phylogenetic signals for the five genes were congruent (p = 0.02). Phylogenetic analysis of the five-gene dataset was conducted

Table 1. PCR primers used in this study.

		-	
Gene	Primer	5'-Sequence-3'	Reference
nrSSU	nrSSU-CoF	TCTCAAAGATTAAGCCATGC	[9]
	nrSSU-CoR	TCACCAACGGAGACCTTG	
nrLSU	LR5	ATCCTGAGGGAAACTTC	[10,11]
	LROR	GTACCCGCTGAACTTAAGC	
tef-1α	EF1α-EF	GCTCCYGGHCAYCGTGAYTTYAT	[5,12]
	EF1α-ER	ATGACACCRACRGCRACRGTYTG	
rpb1	RPB1-5'F	CAYCCWGGYTTYATCAAGAA	[5,12]
	RPB1-5'R	CCNGCDATNTCRTTRTCCATRTA	
rpb2	RPB2-5'F	CCCATRGCTTGTYYRCCCAT	[5,12]
	RPB2-5'R	GAYGAYMGWGATCAYTTYGG	

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Table 2.	

			Vouchar		Gen	Bank accession num	ber	
Manufactorization Instance Unstance Unstance <thunstance< th=""> Unstance Unstance</thunstance<>	Taxon	Host/substrate	information	nrSSU	nrLSU	tef1- α	rpb1	rpb2
Amenineries Environ	Akanthomyres cocridioneritherintus	Araneae	NH1 6709	FI 1360110	FI 1369047	FLI369075	FI 1369067	FII369086
Administration Inside of the constraint of t	Akanthomyces muscarius	Hemintera: Alevrodidae	CBS 143.67 ^T	KM283774	KM783798	KM783871	KM783841	KM783863
Butterington End (Waters) Constrained Merical Service	Akanthomyces tuberculatus	Lepidonteran adult	BCC 16819	MF416600	MF416546	MF416490	MF416647	MF416444
Botterrie Distribution End (Name) M53/35 M53/35 <	Balansia henninasiana	Plant (Panicum sp.)	AEG 96-27a	AY545723	AY545727	AY489610	AY489643	D0522413
Resumer fragment Exercise NMS/758 NMS/759 NMS/759 <thnms 759<="" th=""> NMS/759 NMS/759</thnms>	Balansia pilulaeformis	Plant (Poaceae sp.)	AEG 94-2	AF543764	AF543788	D0522319	D0522365	D0522414
Bounder formation Considered for the off AB2733 AB27333 AB27333 AB	Beauveria bassiana	Lepidoptera: Cossidae	YFCC 3369	MN576768	MN576824	MN576994	MN576884	MN576938
Methodise Constraint Constrai	Beauveria bronaniartii	Coleoptera: Scarabaeidae	ARSEF 617 ^T	AB027335	AB027381	HQ880991	HQ880854	HQ880926
Biochemistre Exploration Engloyeren M18403	Beauveria scarabaeidicola	Coleoptera: Scarabaeidae	ARSEF 5689	AF339574	AF339524	DQ522335	DQ522380	DQ522431
Conference Met Indian Met Ind	Blackwellomvces cardinalis	Lepidoptera: Tineidae	0SC 93609 ^T	AY184973	AY184962	D0522325	D0522370	D0522422
Curkeys project Data (proces sp.) MCC (392) U3/201 U4/255 D02/2311 D02/2313 Curkeys project Pennjener Cocroleko (scle Inecc) NU (12)(E46903 E46903 E46905	Blackwellomyces pseudomilitaris	Lepidopteran larva	BCC 2091	MF416589	MF416535	MF416479		MF416441
CurrentEnvironment <td>Claviceos paspali</td> <td>Plant (Poaceae sp.)</td> <td>ATCC 13892</td> <td>U32401</td> <td>U47826</td> <td>D0522321</td> <td>D0522367</td> <td>D0522416</td>	Claviceos paspali	Plant (Poaceae sp.)	ATCC 13892	U32401	U47826	D0522321	D0522367	D0522416
Condericing Interostrata Endensity Endensity<	Claviceos purpurea	Plant (Poaceae sp.)	S.A. cp11	EF469122	EF469075	EF469058	EF469087	EF469105
Condencemis Filterior UNI C23 EU36011 EU36012 EU36006 Condersent infance Endidateran papa FIC 588 MM57612 FIA6863 MM57613 MM5003 E156606 FE46805 M75023 M95033 E156605 FE46805 M75023 M76033 MM5003 E156605 E15561 M78033 M780333 M780333 M780333 M780333 <td>Conoideocrella luteorostrata</td> <td>Hemiptera: Coccoidea (scale insect)</td> <td>NHJ 12516</td> <td>EF468994</td> <td>EF468849</td> <td>EF468800</td> <td>EF468905</td> <td>EF468946</td>	Conoideocrella luteorostrata	Hemiptera: Coccoidea (scale insect)	NHJ 12516	EF468994	EF468849	EF468800	EF468905	EF468946
Codycarp synupsion EndC 588 End 578 End 574 End 586 Codycarp printion Lepidoptent luma coldae REC 588 End 574 End 574 End 586 Codycarp printion Lepidoptent luma coldae RESE 513 MIS7675 MIS7688 MIS7689	Conoideocrella tenuis	Hemiptera: Coccoidea (scale insect)	NHJ 6293	EU369112	EU369044	EU369029	EU369068	EU369087
Cordycars milarisLepidopteran puisNTC 6557NTS7752NTS7753NTS9753 </td <td>Cordvceps kvusvuensis</td> <td>Lepidopteran pupa</td> <td>EFCC 5886</td> <td>EF468960</td> <td>EF468813</td> <td>EF468754</td> <td>EF468863</td> <td>EF468917</td>	Cordvceps kvusvuensis	Lepidopteran pupa	EFCC 5886	EF468960	EF468813	EF468754	EF468863	EF468917
Codycast prinodCodycast prinodMSEF 513M148493M149493D023321D023321Codycast prinodEiglobateran JunaMSEF 5135M33953F51520D023323Derhmerio balandesLepidoperen Jima-coldaeMSEF 5135M33953F51520D023324Derhmerio balandesLepidoperen Jima-coldaeMSEF 5135M33953E1399505D023324Derhmerio balandesLepidoperen ILD071325M33953E139503E139503D023324Derhmerio balandAraneaMSEF 1915D033737D033295D033973D033920Derhmerio balandAraneaMSEF 1915D033950E139603E139603E139603HarnoodAraneaMREF 1915D033950E139603E139603E139603HarnoodAraneaMREF 1915D033950E139603E139603E139603HarnoodAraneaMREF 1915M45303UK2000E139603E139603HarnoodAraneaMREF 1915M45303UK2000E139603E139603HarnoodCaleopresi Candidae (EnformiMSEF 134MK52005WK52006WK5203HarnoodCaleopresi Candidae (EnformiMSEF 134MK52005WK52006WK5203HarnoodCaleopresi Candidae (EnformiMK5716WK5206WK5206WK5203HarnoodCaleopresi Candidae (EnformiMK5716WK5206WK5206WK5206HarnoodHarnoodMK57103WK5206WK5206WK5206HarnoodHarno	Cordyceps militaris	Lepidopteran pupa	YFCC 6587	MN576762	MN576818	MN576988	MN576878	MN576932
CordnersEndoptent pupaASEF 515'MrI 166.1Jr 160.00Jr 160.00Jr 160.00Derdneris bulnotesEnglopten (Heplaldae Iava)CGS 764.2173395.23A73395.23D0522340D0522340Derdneria parniLepidopten (Heplaldae Iava)CGS 764.2173395.53A73395.23A73395.23A73955.24A78966.6Derdneria parniLepidopten (Heplaldae Iava)CGS 764.01A7335.72A73395.23A73950.23.400D0522400Derdneria parniAnneeAnneeAnneeArresA71C 222.24A73395.73A73395.73A73956.73A74956.43Geblalta particulariaAnneeAnneeArresArresA71C 222.24A73395.73A73957.73A74956.73Herosoparium horpospritumAnneeArresArresA71C 222.25A73357.73A74956.73A74956.73Herosoparium horpospritumArresArresA71C 222.24A73357.73A74956.73A74956.73Herosoparium horpospritumArresArresA71C 222.54A73357.73A74956.73A74956.73Herosoparium horpospritumArresArresA715.73A73357.73A74956.73A74956.73Herosoparium horpospritumArresArresArresA745.72.73A7497.73A7486.73HerosopariaArresArresArresA745.72.73A745.77A745.77A745.77HerosopariaArresArresArresArresArresA745.77A745.77HerosopariaArresArres <td< td=""><td>Cordyceps pruinosa</td><td>Lepidoptera: Limacodidae</td><td>ARSEF 5413</td><td>AY184979</td><td>AY184968</td><td>DQ522351</td><td>DQ522397</td><td>DQ522451</td></td<>	Cordyceps pruinosa	Lepidoptera: Limacodidae	ARSEF 5413	AY184979	AY184968	DQ522351	DQ522397	DQ522451
Derfineria gania families manace de la construction	Cordyceps tenuipes	Lepidopteran pupa	ARSEF 5135 ^T	MF416612	JF415980	JF416020	JN049896	JF416000
DefendenciaEpidoptera (hepalidae lava)NGZ 7644A733572A733572A7439516N439516N439556Geldula carticuadaraGeldula carticuadaraGeldula carticuadaraGeldula carticuadaraMaster 317N439516N439557N439557N439557N439557N439557N439556D05723468D0772348HarondorinemisAnneaeNHU 11923E1380095E1380093E1380013E1380013E1380013E1380052E1380013E1380052E1386072E1386072E1386072E1386072E1	Drechmeria balanoides	Nematode	CBS 250.82 ^T	AF339588	AF339539	DQ522342	DQ522388	DQ522442
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Attraction<	Gliocephalotrichum bulbilium	Soil	ATCC 22228 ^T	AY489700	AY489732	AY489627	AY489664	EF469114
Hargosporium helicoidesInteractedRRSEF 53:4AT333577AT333577AT333577AT333577AT333577AT333577AT333577AT333577AT335073EU369093EU369043EU369	Harposporium harposporiferum	Arthropod	ARSEF 5472 ^T	AF339569	AF339519	DQ118747	DQ127238	
Heransia arachrophilisAraneeNHJ 10459EU36903EU369031EU36903EU36903EU36903HeransiaAraneeNHJ 11923EU36903EU369032EU369032EU36903EU36903Hisratelia (informisHemptera: CircliniaKM652067KM652106KM651993KM65203Hirstella garateHimperonen:ARSEF 547KM652067KM651993KM65203Hirstella garateHimperonen:ARSEF 539KM652069KM651993KM65203Hirstella garateHemptera: Cidaelidae (Enosona langerum)ARSEF 539KM652069KM651995KM65203Hirstella lustrisHemptera: Cidaelidae (Enosona langerum)ARSEF 539KM652069KM651996KM65203Hirstella lustrisHarnelHarnel (Kannel)ARSEF 539KM652073KM651996KM65203Hirstella lustrisHarnel locensisHirstella (Kannel)ARSEF 539KM652073KM651995KM55203Hirstella lustrisHirstella lustrisKM652073KM652073KM651995KM55203Hirstella lustrisLepidoptera: Cocidae (Jarne comin com)ARSEF 553KM652073KM651995KM55203Hirstella numescensisVietariaARSEF 543KM652073KM65193KM55203Hirstella numescensisLepidoptera: Cicclenelidae (Revocrionen com)ARSEF 543KM652073KM65193KM55203Hirstella numescensisVietariaNietariaNietariaNietariaNietariaNietariaHirstella numescensisVietariaARSEF 543 <td>Harposporium helicoides</td> <td>Nematode</td> <td>ARSEF 5354</td> <td>AF339577</td> <td>AF339527</td> <td></td> <td></td> <td></td>	Harposporium helicoides	Nematode	ARSEF 5354	AF339577	AF339527			
HeurarisAnaneaeNHI 11923EU36005EU366012EU369013EU369032EU369013EU369032HeurarisHemptera: CividaeRSEF 1446KM652055KM651990KM651939KM652033Histarella giganteaHemptera: CividaeRSEF 1446KM652057KM651993KM652033Histarella giganteaHemptera: CircalulaeRSEF 30XM652058KM651993KM652033Histarella giganteaHemptera: CircalulaeRSEF 30XM652050KM651994KM652035Histarella giganteaHemptera: CircalulaeRSEF 53KM652050KM651994KM652035Histarella giustrisHemptera: Costada (Partnenolecrnium com)RSEF 551KM652071KM651994KM652035Histarella kernisciaHemptera: Costada (Partnenolecrnium com)RSEF 553KM652073KM65193KM652035Histarella kernisciaHemptera: Costada (Partnenolecrnium com)RSEF 553KM652073KM65193KM652035Histarella kernisciaLepidoptera: Pyralidae (Eroosona karneno)RSEF 553KM652073KM65193KM652035Histarella kernisciaLepidoptera: Pyralidae (Roosorta zimmeran)RSEF 553KM652073KM65193KM652035Histarella kernisciaLepidoptera: Pyralidae (Roosorta zimmeran)RSEF 554KM652073KM652035KM652035Histarella kernisciaTyle nchicaLepidoptera: Pyralidae (Roosorta zimmeran)RSEF 554KM652073KM652032KM652035Histarella kernisciaTyle nchicaLepidoptera: Pyralidae (Roosorta zimmeran) </td <td>Hevansia arachnophilus</td> <td>Araneae</td> <td>NHJ 10469</td> <td>EU369090</td> <td>EU369031</td> <td>EU369008</td> <td>EU369047</td> <td></td>	Hevansia arachnophilus	Araneae	NHJ 10469	EU369090	EU369031	EU369008	EU369047	
Histerla cirtíomisHubitera: CixidaeMRSF 1446KM652055KM652106KM651990KM652031Histerla dirafomisCleoptera: Curculonidae (Brachyderes incanus)ARSF 547KM652057KM651993KM652033Histerla gigarteaHimuoptera: Curculonidae (Brachyderes incanus)ARSF 539KM652068KM651994KM652033Histerla gigarteaHemiptera: Curculonidae (Entosona Ingreum)ARSF 539KM652059KM652037KM652035Histerla gigarteaHemiptera: Cicadelidae (Entosona Ingreum)ARSF 539KM652017KM651996KM652037Histerla kindiRainHemiptera: Cocide (Parthenolecanium com)ARSF 539KM652017KM651996KM652037Histerla kindiHemiptera: Cocide (Parthenolecanium com)ARSF 539KM652017KM651996KM652037Histerla kindiHemiptera: Cocide (Parthenolecanium com)ARSF 530KM652017KM652037KM652037Histerla kindiaUponologiaHomiptera: Cocide (Parthenolecanium com)ARSF 5403KM652017KM652037Histerla kindiaUponologiaHimiptera: Cocide (Parthenolecanium com)ARSF 5403KM652017KM652037Histerla kindiaNinaARSF 5403KM652017KM652037KM652037Histerla noduosaLepidoptera: Vircice/Idae (Neocritorem xeroplux)ARSF 5417KM652037KM652037Histerla noduosaLepidoptera: Vircice/Idae (Neocritorem xeroplux)ARSF 5417KM652037KM652037Histerla noduosaLepidoptera: Vircice/Idae (Neocritorem xeroplux)ARSF 1347<	Hevansia novoguineensis	Araneae	NHJ 11923	EU369095	EU369032	EU369013	EU369052	EU369072
Histarella fasiformisKimosofiesKimos	Hirsutella citriformis	Hemiptera: Cixiidae	ARSEF 1446	KM652065	KM652106	KM651990	KM652031	
Histuella giganteaHymenoptera: PamphilidaeARSE F30X566977X566980KM652034Histuella giganteaHimpitera: Cicaellidae (Frposca kraemer)ARSE F38KM652068KM652111KM651994KM652035Histuella giugraHempitera: Cicaellidae (Frposca kraemer)ARSE F539KM652070KM651995KM651035Histuella liustrella giugraHempitera: Coscidae (Parthenolecanium com)ARSE F539KM652017KM651995KM652035Histuella liunesisisLepidoptera: Coscidae (Parthenolecanium com)ARSE F539KM652017KM652113KM651995KM652036Histuella linnesisisLepidoptera: Coscidae (Parthenolecanium com)ARSE F539KM652017KM652193KM652036Histuella neosisisTyle nchida (Heerodera gi/srin)ARSE F549KM652017KM652019KM652036Histuella neodiosaLadia (Heerodera gi/srin)ARSE F549KM652017KM652019KM652030Histuella neodiosaLadia nodiosaLadia (Heerodera gi/srin)ARSE F549KM652014KM652019KM652030Histuella neodiosaLadia nodiosaLadia nodiosaKM652014KM652019KM652019KM652020Histuella neodiosaLadia nodiosaLadia nodiosaKM652013KM652019KM652013KM652013Histuella neodiosaLadia nodiosaKM652014KM652013KM652013KM652013KM6520203Histuella neodiosaLadia nodiosaKM652014KM652013KM652013KM652013KM6520203Histuella nonsonisisLadia nodiosa	Hirsutella fusiformis	Coleoptera: Curculionidae (Brachyderes incanus)	ARSEF 5474	KM652067	KM652110	KM651993	KM652033	
Hisutella guyana Hemiptera: Cicadellidae (Ernosarca kraemeri) ARSEF 8738 KM652068 KM652111 KM651994 KM652035 Hisutella kirchneri Hemiptera: Aphidiae (Ernosarca kraemeri) ARSEF 5539 KM652071 KM652112 KM651996 KM652037 Hisutella kirchneri Hemiptera: Aphidiae (Ernosarca kraemeri) ARSEF 5539 KM652071 KM652113 KM651996 KM652038 Hisutella kecnificio Hemiptera: Costidae (Parthenolecanium comi) ARSEF 8888 KM652071 KM652114 KM651997 KM652038 Hisutella minnesotensis Tuje nchida (Heterodera glycin) ARSEF 9603 [†] KM652072 KM652013 KM652013 KM652039 KM652039 Hisutella minnesotensis Tuje nchida (Heterodera glycin) ARSEF 9603 [†] KM652073 KM652014 KM652040 Hisutella minnesotensis Tuje nchida (Heterodera glycin) ARSEF 9543 KM652073 KM652014 KM652040 Hisutella modulosa Diptera Uphidae (Zonyctria zimmerann) ARSEF 9543 KM652073 KM652014 KM652040 Hisutella andulosa Diptera Uphidae (Aceria zimmerann) ARSEF 9543 KM652073 KM652014 KM652040 Hisutella andulosa Diptera Uphidae (Aceria zimmerann) ARSEF 9543 KM652073 KM652013 KM652040 Hisutella andulosa Diptera Uphidae (Aceria zimmerann) ARSEF 9543 KM652073 KM652013 KM652040 Hisutella tonosiliensis Hisutella tonosonii var. symematosa Aceri Hisutella tonosonii var. symematosa Aceri Eriophyidae (Areira sheldon) ARSEF 2543 KM652015 KM652013 KM652013 KM652050 Hisutella thompsonii var. th	Hirsutella gigantea	Hymenoptera: Pamphiliidae	ARSEF 30		JX566977	JX566980	KM652034	
Hisurella illustris Hisurella lilustris Hisurella kirchneri Hisurella necatrix Hisurella thompsonii var. Nonesoni Hisurella thompsonii var. Intomosoni Hisurella thompsonii var. Intomosoni Hisurella thompsonii var. Intomosoni Hisurella thompsonii var. Intomosoni Hisurella thompsonii var. Intomosoni var. Intomo	Hirsutella guyana	Hemiptera: Cicadellidae (<i>Empoasca kraemeri</i>)	ARSEF 878	KM652068	KM652111	KM651994	KM652035	
Histatella kirchneriAcari: Eriophyidae (Abacarus hystrix)ARSEF 5551KM652070KM655113KM655197Histatella kirchneriHemiptera: Cocidae (Parthenolecanium com)ARSEF 9603KM652071KM6551015KM655198KM652038Histatella lecanificidaHemiptera: Cocidae (Parthenolecanium com)ARSEF 9603KM652072KM652073KM655198KM652038Histatella mimesotensisTyle nchida (Heterodera glycin)3608JPUM01000376JPUM01000376JPUM01000376JPUM01000376Histatella mimesotensisTyle nchida (Heterodera glycin)ARSEF 543KM652074KM652039KM652040Histatella mecatrixDipteraLepidoptera: Pyralidae (Dioryctria zimmerann)ARSEF 543KM652074KM652030KM652040Histatella necatrixDipteraDipteraTylenchidae (Mesocriconema zenoplax)ARSEF 374KM652076KM652002KM652040Histatella nadiataTylenchidae (Nephotetix virescens)ARSEF 347KM652080KM652012KM652020KM652020Histatella subulataLepidoptera: MicrolepidopteaMicrolepidopteaARSEF 2227KM652080KM652013KM652013KM652020Histatella thompsonii var. ynnematosaLepidoptera: MicrolepidopteaARSEF 2227KM652080KM652013KM652013KM652013KM652021Histatella thompsonii var. ynnematosaArariLepidoptera: MicrolepidopteaARSEF 2227KM652080KM652013KM652013KM652013Histatella thompsonii var. ynneeaArariArariArariArari <t< td=""><td>Hirsutella illustris</td><td>Hemiptera: Aphididae (<i>Eriosoma lanigerum</i>)</td><td>ARSEF 5539</td><td>KM652069</td><td>KM652112</td><td>KM651996</td><td>KM652037</td><td></td></t<>	Hirsutella illustris	Hemiptera: Aphididae (<i>Eriosoma lanigerum</i>)	ARSEF 5539	KM652069	KM652112	KM651996	KM652037	
Hisutella lecaniicola Hemiptera: Cocidae (Parthenolecanium corni) ARSEF 8888 KM652071 KM652114 KM651998 KM652038 Hisutella liboensis Lepidoptera: Cosidae (Jarva) ARSEF 9603 ^T KM652072 KM652115 KY415588 KY945567 Hisutella liboensis Tyle nchida (Heterodera glycin) 3608 JPUM01000376 JPUM01000211 JPUM0100013 Hisutella minesotensis Tyle nchida (Heterodera glycin) ARSEF 5549 KM652073 KM652116 KM652199 KM652040 Hisutella nodulosa Diptera Pyralidae (<i>Dioyctria zimmermani</i>) ARSEF 5549 KM652074 KM652119 KM652000 KM652040 Hisutella radiar Diptera Diptera Diptera Diptera ARSEF 5137 KM652074 KM652119 KM652002 KM652040 Hisutella radiar and tara Diptera Diptera Diptera Diptera ARSEF 2197 KM652080 KM652123 KM652012 KM652050 Hisutella tanopsonii var. synematosa Arai Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2197 KM652099 KM652013 KM652013 KM652050 Hisutella thompsonii var. synematosa Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652013 KM652013 KM652050 Hisutella thompsonii var. synematosa Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652013 KM652013 KM652050 Hisutella thompsonii var. synematosa Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652099 KM652013 KM652050 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652099 KM652013 KM6520207 KM652050 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652099 KM652014 KM6520207 HK652050 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2459 KM652099 KM652099 KM652014 KM6520207 HK652060 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2450 KM652099 KM652099 KM652014 KM6520207 HK652060 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2450 KM652099 KM652099 KM652014 KM6520207 HK652060 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) ARSEF 2450 KM652099 KM652099 KM652014 KM6520207 HK652060 Hisutella thompsonii var. vinacea Arai: Eriophyidae (<i>Aeria sheldoni</i>) BCC 1	Hirsutella kirchneri	Acari: Eriophyidae (<i>Abacarus hystrix</i>)	ARSEF 5551	KM652070	KM652113	KM651997		
Hisutella liboensisLepidoptera: Cossidae (lava)ARSEF 9603KM652072KM652115KY415588KY945367Hisutella minesotensisTyle nchida (Heterodera glycin)3608JPUM01000376JPUM01000211JPUM01000211JPUM01000211Hisutella minesotensisTyle nchida (Heterodera glycin)36083608M652073KM652073KM652109KM652003Hisutella neatrixLepidoptera: Pyralidae (Dioryctria zimmermani)ARSEF 549KM652074KM652117KM652002KM652024Hisutella nodulosaLipetedDipteraArster 1369KM652075KM652013KM652020KM652025Hisutella nodulosaDipteraTisutella evolutaArsEF 1369KM652076KM652020KM6520205Hisutella nossiliensisTylenchida: Criconematidae (Mesocriconema zenoplax)ARSEF 1377KM652036KM6520205KM6520205Hisutella strigosaHemiptera: Cicadellidae (Nephotettix virescens)ARSEF 2197KM652036KM652123KM652013KM6520205Hisutella thompsoniiastrigosaAraiiLepidoptera: MiccolepidopteaMTCC 3556ARSEF 2197KM652120KM6520207KM6520205Hisutella thompsonii var. synnematosaAcarii Eriophyidae (Aceria sheldoni)ARSEF 2459KM652039KM652134KM6520207KM6520207Hisutella thompsonii var. vinaceaAcarii thompsonii var. vinaceaAraii Eriophyidae (Aceria sheldoni)ARSEF 2459KM652039KM6521347KM652027KM6520207Hisutella thompsonii var. vinaceaAcarii triophoraARSEF 2459	Hirsutella lecaniicola	Hemiptera: Coccidae (Parthenolecanium corní)	ARSEF 8888	KM652071	KM652114	KM651998	KM652038	
Hisutella minesotensisTyle nchida (Heterodera glycin)3608JPUM01000376JPUM01000376JPUM01000211JPUM01000013Hisutella minesotensisTyle ncdariAcariARSEF 5549KM652073KM652073KM652030KM652030Hisutella ncdulosaLepidoptera: Pyralidae (Dioyctria zimmermani)ARSEF 5349KM652074KM652016KM652002KM652030Hisutella ncdulosaLepidoptera: Pyralidae (Dioyctria zimmermani)ARSEF 5347KM652076KM652019KM652002KM652030Hirsutella nodulosaLepidoptera: Cicadellidae (Mesocriconema xenoplax)ARSEF 1369KM652080KM652123KM652012KM652060Hirsutella triososiliensisTylenchida: Criconentidae (Mesocriconema xenoplax)ARSEF 2197KM652080KM652012KM652060Hirsutella triososiLepidoptera: MicrolepidopteaMTCC 3556APK601000383AFK601000383AFK601000383AFK601000211Hirsutella trompsoniNar. Eriophyidae (Aceria sheldoni)ARSEF 2217KM652099KM652093KM652012KM652061Hirsutella trompsoniNar. symematosaArari: Eriophyidae (Phyllocoptruta oleivora)ARSEF 137KM652099KM652013KM652012KM652062Hirsutella trompsoniNar. symematosaArari: Eriophyidae (Acalitus vaccini)ARSEF 254KM652099KM652013KM652014KM652014Hirsutella trompsoniNar. symematosaArari: Eriophyidae (Acalitus vaccini)ARSEF 254KM652099KM652014KM652014KM652014Hirsutella trompsoniNar. vinacea <td< td=""><td>Hirsutella liboensis</td><td>Lepidoptera: Cossidae (larva)</td><td>ARSEF 9603^T</td><td>KM652072</td><td>KM652115</td><td>KY415588</td><td>KY945367</td><td></td></td<>	Hirsutella liboensis	Lepidoptera: Cossidae (larva)	ARSEF 9603 ^T	KM652072	KM652115	KY415588	KY945367	
Hirsutella necatrixAcariAcariARSEF 5349KM652073KM652116KM65199KM652030Hirsutella necatrixLepidoptera: Pyralidae (Dioyctria zimmermani)ARSEF 5473KM652074KM652017KM652000KM652040Hirsutella nodulosaLepidoptera: Pyralidae (Dioyctria zimmermani)ARSEF 5473KM652074KM652017KM652002KM652040Hirsutella nodulosaDipteraDipteraPylenchida: Criconematidae (Mesocriconema xenoplax)ARSEF 1369KM652018KM652012KM6520205Hirsutella triososiliensisTylenchida: Criconematidae (Mesocriconema xenoplax)ARSEF 2197KM652108KM652123KM652012KM652050Hirsutella subulataLepidoptera: MicrolepidopteaMTCC 3556APK601000383APK601000383APK601000051APK00100061APK00100001Hirsutella tompsoniNar. SymematosaAcari. Eriophylidae (Phyllocoptruta oleivora)ARSEF 137KM652099KM652013KM652012KM652051Hirsutella tompsoni var. symematosaAcari. Eriophylidae (Phyllocoptruta oleivora)ARSEF 137KM652099KM652014KM652062Hirsutella tompsoni var. symematosaAcari. Eriophylidae (Acaritus varcini)ARSEF 137KM652099KM652014KM652014Hirsutella tompsoni var. symematosaAcari. Eriophylidae (Acaritus varcini)ARSEF 137KM652099KM652014KM652014Hirsutella tompsoni var. symematosaAcari. Eriophylidae (Acaritus varcini)ARSEF 137KM652099KM652014KM652014Hirsutella tompsoni var. symematosaAcari. Er	Hirsutella minnesotensis	Tyle nchida (<i>Heterodera glycin</i>)	3608	JPUM01000376	JPUM01000376	JPUM01000211	JPUM01000139	JPUM01000138
<i>Hisutella nodulosa</i> Lepidoptera: Pyralidae (<i>Dioryctria zimmermani</i>) ARSEF 5473 KM652074 KM652117 KM652000 KM652042 <i>Hisutella radiata</i> Diptera Diptera <i>Hisutella radiata</i> Diptera <i>Tylenchida: Ciconematidae (Mesocriconema xenoplax)</i> ARSEF 1369 KM652086 KM652129 KM652012 KM652045 <i>Hisutella subulata tw652012</i> KM652012 KM652050 <i>Hisutella subulata cicolellidae (Nephatettix virescens</i>) ARSEF 2197 KM652086 KM652129 KM652012 KM652050 <i>Hisutella subulata cicolellidae (Nephatettix virescens</i>) ARSEF 2197 KM652086 KM652129 KM652012 KM652050 <i>Hisutella subulata cicolellidae (Nephatettix virescens</i>) ARSEF 227 KM652086 KM652130 KM652013 KM652050 <i>Hisutella thompsonii</i> Acari. Eriophyidae (<i>Aceria sheldon</i>) ARSEF 227 KM652099 KM652130 AFKB01000051 AFKB01000051 <i>Hisutella thompsonii</i> var. <i>symematosa</i> Acari. Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 137 KM652087 KM6520131 KM652051 <i>Hisutella thompsonii</i> var. <i>vinacea</i> Acari. Eriophyidae (<i>Acalitus vaccinii</i>) BCC 14123 D0522557 D0518771 D0522346 D0522392 <i>Hypocrella schizostachyi</i> Hemiptera: Coccoidea (scale insect) BCC 14123 D0522557 D0518771 D0522346 D0522392	Hirsutella necatrix	Acari	ARSEF 5549	KM652073	KM652116	KM651999	KM652039	
<i>Hisutella radiata</i> Diptera Diptera Diptera Mescriconematidae (<i>Mesocriconema xenoplax</i>) ARSEF 1369 KM652076 KM652119 KM652002 KM652045 <i>Hisutella radiata</i> Tylenchida: Criconematidae (<i>Mesocriconema xenoplax</i>) ARSEF 3747 KM652080 KM652123 KM652066 KM652045 <i>Hisutella strigosa</i> Hemiptera: Cicadellidae (<i>Nesocriconema xenoplax</i>) ARSEF 2197 KM652080 KM652129 KM652012 KM652050 Hisutella strigosa taria a distributed a thompsonii var. Symematosa Acari Eriophyidae (<i>Neria sheldoni</i>) ARSEF 2227 KM652086 KM652130 KM652013 KM652051 Hisutella thompsonii var. Symematosa Acari Eriophyidae (<i>Phyllocoptrua oleivora</i>) ARSEF 2459 KM652099 KM6520147 KM652026 Hisutella thompsonii var. Symematosa Acari. Eriophyidae (<i>Phyllocoptrua oleivora</i>) ARSEF 254 KM652091 KM6520147 KM652024 Hisutella thompsonii var. vinacea Acari. Eriophyidae (<i>Phyllocoptrua oleivora</i>) ARSEF 254 KM652011 KM6520149 KM652024 Hisotschi Arstiella thompsonii var. vinacea Acari. Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 254 KM652087 KM652131 KM652024 KM652052 Hisotella thompsonii var. vinacea Acari. Eriophyidae (scale insect) BCC 14123 D0522557 D0518771 D0522346 D0522392	Hirsutella nodulosa	Lepidoptera: Pyralidae (<i>Dioryctria zimmermani</i>)	ARSEF 5473	KM652074	KM652117	KM652000	KM652040	
<i>Hisutella rhossiliensis</i> Tylenchida: Criconematidae (<i>Mesocriconema xenoplax</i>) ARSEF 3747 KM652080 KM652123 KM652066 KM652050 <i>Hisutella strigosa</i> Hemiptera: Cicadellidae (<i>Nephotettix virescens</i>) ARSEF 2197 KM652086 KM652012 KM652050 <i>Hisutella subulata KM652013</i> KM652013 KM652013 KM652050 <i>Hisutella thompsonii var. Symematosa</i> Acari Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2257 KM652089 KM652013 KM652051 APKB0100013 <i>Hisutella thompsonii var. Symematosa</i> Aerai: Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2459 KM652089 KM652131 KM652027 KM652061 <i>Hisutella thompsonii var. thompsonii var. thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 137 KM652087 KM652131 KM652024 KM652052 <i>Hisutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) BCC 14123 DQ522557 DQ518771 DQ522346 DQ522392	Hirsutella radiata	Diptera	ARSEF 1369	KM652076	KM652119	KM652002	KM652042	
<i>Hirsutella strigosa</i> Hemiptera: Cicadellidae (<i>Nephotettix virescens</i>) ARSEF 2197 KM652085 KM652129 KM652012 KM652050 <i>Hirsutella subulata</i> Lepidoptera: Microlepidoptea ARSEF 2227 KM652086 KM652130 KM652013 KM652051 <i>Hirsutella thompsonii</i> Acari Lepidoptea (<i>Aceria sheldoni</i>) ARSEF 2256 APKB01000383 APKB0100061 APKB0100012. <i>Hirsutella thompsonii</i> var. <i>synnematosa</i> Acari: Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2459 KM652099 KM652147 KM652027 KM652061 <i>Hirsutella thompsonii</i> var. <i>synnematosa</i> Acari: Eriophyidae (<i>Acelitus vaccini</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 <i>Hirsutella thompsonii</i> var. <i>vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 <i>Hirsutella thompsonii</i> var. <i>vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccini</i>) BCC 14123 DQ522557 DQ518771 DQ522346 DQ52232	Hirsutella rhossiliensis	Tylenchida: Criconematidae (Mesocriconema xenoplax)	ARSEF 3747	KM652080	KM652123	KM652006	KM652045	
<i>Hirsutella subulata</i> Lepidoptera: Microlepidoptea ARSEF 227 KM652086 KM652130 KM652013 KM652051 Hirsutella subulata thompsonii Acari Lepidoptea: Microlepidopta MTCC 3556 APKB01000383 APKB0100061 APKB0100012 Hirsutella thompsonii var. synnematosa Acari: Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2459 KM652099 KM652147 KM652027 KM652061 Hirsutella thompsonii var. thompsonii Acari: Eriophyidae (<i>Phyllocoptruta oleivora</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652027 KM652052 Hirsutella thompsonii var. vinacea Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 Hirsutella thompsonii var. vinacea Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 137 KM652087 KM652149 KM652014 KM652062 Hirsutella thompsonii var. vinacea Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 254 KM652101 KM6520149 KM652028 KM652062 Hirsutella thompsonii var. vinacea Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 254 KM652101 KM652028 KM652062 Hirsutella thompsonii var. vinacea Acari: Eriophyidae (<i>Acalitus vaccini</i>) BCC 14123 DQ522557 DQ518771 DQ522346 DQ522392	Hirsutella strigosa	Hemiptera: Cicadellidae (Nephotettix virescens)	ARSEF 2197	KM652085	KM652129	KM652012	KM652050	
<i>Hirsutella thompsonii</i> Acari APKB0100061 APKB01000383 APKB01000383 APKB0100061 APKB0100012 <i>Hirsutella thompsonii var. synnematosa</i> Acari: Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2459 KM652099 KM652147 KM652027 KM652061 <i>Hirsutella thompsonii var. thompsonii</i> Acari: Eriophyidae (<i>Phyllocoptruta oleivora</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 <i>Hirsutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 137 KM652087 KM652149 KM652028 KM652062 <i>Hirsutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 254 KM652101 KM652149 KM652028 KM652062 <i>Hypocrella schizostachyi</i> Berci Prompsonii var. Coccoidea (scale insect) BCC 14123 DQ522557 DQ518771 DQ522346 DQ52392	Hirsutella subulata	Lepidoptera: Microlepidoptea	ARSEF 2227	KM652086	KM652130	KM652013	KM652051	
<i>Hirsutella thompsonii var. synnematosa</i> Acari: Eriophyidae (<i>Aceria sheldoni</i>) ARSEF 2459 KM652099 KM652147 KM652027 KM652061 <i>Hirsutella thompsonii var. thompsonii</i> Acari: Eriophyidae (<i>Phyllocoptruta oleivora</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 <i>Hirsutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 254 KM652101 KM652149 KM652028 KM652062 <i>Hypocrella schizostachyi</i> DQ518771 DQ522346 DQ522322	Hirsutella thompsonii	Acari	MTCC 3556	APKB01000383	APKB01000383	APKB01000061	APKB01000125	APKB01000164
<i>Hirsutella thompsonii var. thompsonii</i> Acari: Eriophyidae (<i>Phyllocoptruta oleivora</i>) ARSEF 137 KM652087 KM652131 KM652014 KM652052 <i>Hirsutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccinii</i>) ARSEF 254 KM652101 KM652149 KM652028 KM652062 <i>Hypocrella schizostachyi</i> DQ518771 DQ522346 DQ522392	Hirsutella thompsonii var. synnematosa	Acari: Eriophyidae (<i>Aceria sheldoni</i>)	ARSEF 2459	KM652099	KM652147	KM652027	KM652061	
<i>Hirsutella thompsonii var. vinacea</i> Acari: Eriophyidae (<i>Acalitus vaccini</i>) ARSEF 254 KM652101 KM652149 KM652028 KM652062 <i>Hypocrella schizostachyi</i> DQ518771 DQ522346 DQ522392	Hirsutella thompsonii var. thompsonii	Acari: Eriophyidae (Phyllocoptruta oleivora)	ARSEF 137	KM652087	KM652131	KM652014	KM652052	
	Hirsutella thompsonii var. vinacea	Acarr: Errophyldae (Acalitus vaccinii) Lomintom: Cocceidos (scolo incod)	AKSEF 254	KM652101	KM652149	KM652028	KM652062	
	пуростена эслигознасную	nemiptera: Loccoldea (scale insect)	DLL 14123	10077cDU	1//01000	04522CDU	76577cDU	14422cDU

Table 2. Continued.							
		Voucher			ibank accession num	Der 	C -1
laxon	Host/substrate	information	nrssu	nrLSU	ter1-α	rpb 1	rpb2
Hypocrella siamensis	Hemiptera: Coccoidea (scale insect)	BCC 8105	DQ522537	DQ518752	DQ522317	DQ522363	DQ522411
"Metacordyceps liangshanensis"	Lepidoptera (pupa)	EFCC 1452	EF468962	EF468815	EF468756		
"Metacordyceps liangshanensis"	Lepidoptera (pupa)	EFCC 1523	EF468961	EF468814	EF468755		EF468918
Metacordyceps shibinensis	Lepidoptera (pupa)	GZUHSB13050311	KR153588		KR153589	KR153590	
Metacordyceps neogunnii	Lepidoptera (pupa)	GZUHSB13050302	KU729722		KU729727	KU729732	
Metacordyceps neogunnii	Lepidoptera (pupa)	GZUHHS14061253	KU729725		KU729730	KU729735	
Metapochonia goniodes	Fungi	CBS 891.72	AF339599	AF339550	DQ522354	DQ522401	DQ522458
Metapochonia microbactrospora	Rotifera: Bdelloidea (bdelloid rotifer)	CBS 101433	AF339587	AF339538	KJ398794	KJ398605	KJ398701
Metapochonia rubescens	Nematode eggs	CBS 464.88 ^T	AF339615	AF339566	EF468797	EF468903	EF468944
Metarhizium album	Hemiptera	ARSEF 2082	DQ522560	DQ518775	DQ522352	KJ398617	KJ398715
Metarhizium anisopliae	Soil	BUM 1900	MH143837	MH143820	MH143854	MH143869	MH143884
Metarhizium carneum	Dune sand	CBS 239.32 ^T	EF468988	EF 468843	EF468789	EF468894	EF468938
Metarhizium flavoviride	Coleoptera: Curculionidae (<i>Ceutorrhynchus macula-alba</i>)	CBS 218.56 ^T		MH869139	KJ398787	KJ398598	KJ398694
Metarhizium indigoticum	Lepidoptera (Hepialidae larva)	TNS-F 18553	JF415952	JF415968	JF416010	JN049886	JF415992
Metarhizium khaoyaiense	Lepidoptera (larva)	BCC 14290	KX983469	KX 983463	KJ398797	JN049888	KJ398704
Metarhizium kusanagiense	Lepidoptera	NBRC 109322	JF415954	JF415972	JF416014	JN049890	
Metarhizium majus	Coleoptera	ARSEF 3145	AF339579	AF339530	AF543774	DQ522399	DQ522453
Metarhizium marquandii	Soil	CBS 182.27	EF468990	EF468845	EF468793	EF468899	EF468942
Metarhizium minus	Hemiptera	ARSEF 2037 ^T	AF339580	AF339531	DQ522353	DQ522400	DQ522454
Metarhizium owariense	Hemiptera	NBRC 33258	HQ165669	HQ165730	JF416017	KJ398596	JF415996
Metarhizium samlanense	Hemiptera: Cicadellidae (leafhopper)	BCC 17093	HQ165666	HQ165728	HQ165687	HQ165746	HQ165647
Metarhizium takense	Hemiptera: Cicadidae (cicada nymph)	BCC 30934	HQ165658	HQ165720	HQ165679	HQ165740	HQ165639
Metarhizium yongmunense	Lepidoptera (pupa)	EFCC 2131	EF468977	EF 468833	EF468770	EF468876	
Nectria cinnabarina	Plant (<i>Betula</i> sp.)	CBS 114055	U32412	U00748	AF543785	AY489666	DQ522456
Ophiocordyceps acicularis	Coleoptera (larva)	OSC 110987	EF468950	EF468805	EF 468744	EF468852	
Ophiocordyceps acicularis	Coleoptera (larva)	OSC 110988	EF468951	EF468804	EF468745	EF468853	
Ophiocordyceps agriotidis	Coleoptera (larva)	ARSEF 5692	DQ522540	DQ518754	DQ522322	DQ522368	DQ522418
Ophiocordyceps amazonica	Orthoptera (Acrididae adult)	HUA 186143	KJ917562	KJ917571	KM411989	KP212902	KM411982
Ophiocordyceps aphodii	Coleoptera (Scarabaeidae larva)	ARSEF 5498	DQ522541	DQ518755	DQ522323		DQ522419
Ophiocordyceps appendiculata	Coleoptera (larva)	NBRC 106960	JN941728	JN941413	AB968577	JN992462	AB968539
Uphiocordyceps arborescens	Lepidoptera (<i>Pueraria Jobata</i> Jarva)	NBKC 105891	AB968386	AB968414	AB9685/2		AB968534
Ophiocordyceps bispora	Isoptera (adult termite)	EKS11230//	FKNF01000183	FKNF01000183	FKNF0100002	FKNF01000038	FKNF01000031
Ophiocorayceps brunneanigra	Hemiptera: Licadellidae			MF014054	MF014038	MF014008	MF014081
Ophiocolayceps branningpentitiectata	Coloontoria (laiva) Coloontoria (Elatoridae Java)	101 0 100					
Ophinocol dyceps of drifter particular Ophinocol dyceps citring	Coreoptera (Liateriuae Talva) Hamintara	TNS F18537	74077000	UC 101 CD/J	K1878083	60C77CD/1	K 187805A
Ophiccolar copy contraction of the contraction of t	Lenidontera (Cochlididae muna)	HMAS 199612	K 1878917	K1878884	KI878965	K IR 7 8 9 9 8	
Ophiocordyceps coenomyja	Dintera: Coenomvildae (<i>Coenomvia</i> sp. Jarva)	NBRC 106964	AB968385	AB968413	AB968571		AB968533
Ophiocordyceps crinalis	Lepidoptera (larva)	GDGM 17327	KF226253	KF226254	KF226256	KF226255	
Ophiocordyceps evansii	Hymenoptera (Pachycondyla harpax adult ant)	HUA 186159 ^T	KC610796	KC610770	KC610736	KP212916	
Ophiocordyceps formicarum	Hymenoptera: Formicidae	TNS F18565	KJ878921	KJ878888	KJ878968	KJ879002	KJ878946
Ophiocordyceps forquignonii	Diptera (adult fly)	OSC 151902	KJ878912	KJ878876		KJ878991	KJ878945
Ophiocordyceps fulgoromorphila	Hemiptera (Fulgoridae adult)	HUA 186139 ^T	KC610794	KC610760	KC610729	KF658676	KC610719
Ophiocordyceps geometridicola	Lepidoptera (Geometridae larva)	TBRC 8095 ^T		MF614648	MF614632	MF614663	MF614679
Ophiocordyceps gracilis	Lepidoptera (larva)	EFCC 8572	EF468956	EF468811	EF468751	EF468859	EF468912
Ophiocordyceps heteropoda	Hemiptera (cicada nymph)	NBRC 100644	JN941718	JN941423	AB968596	JN992452	AB968557
Uphiocordyceps karstii	Lepidoptera (<i>Hepialus Jianchuanensis</i>)	MFLU:15-3884	KU854952		KU854945	KU854943	
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Table 2. Continued.

		Voucher		9	enBank accession nu	umber	
Taxon	Host/substrate	information	nrSSU	nrLSU	tef1- α	rpb1	rpb2
Ophiocordyceps kimfleminaiae	Hymenoptera (Camponotus castaneus/americanus)	SC09B	KX713631	KX713620	KX713698	KX713724	
Ophiocordyceps kniphofioides	Hymenoptera (<i>Cephalotes atratus</i> adult ant)	HUA 186148	KC610790	KF658679	KC610739	KF658667	KC610717
Onhiocordvcens konnoana	Coleontera (larva)	EECC 7315	FF468959		FF468753	FF468861	EF468916
Onhiocorducens lanningensis	lenidontera (Henialidae larva)	VHOSOZOS	KC417458	KC 417460	KC417462	KC417464	KC456333
Ophiocordyceps lianashanensis	Lepidoptera (Henialidae Jarva)	KUN-HKAS7723				MW168192	
Onhiorordyrens lianashanensis	lenidontera (Henialidae larva)	YECC 8577	MT774218	MT774225	MT774246	MT74232	MT774239
Ophiocordycens lianashanensis	Lepidontera (Henialidae Jarva)	YECC 8578	MT774219	MT774226	MT774247	MT774233	MT774240
Ophiocordyceps nangonancius Ophiocordycens lianashanensis	Lepidoptera (Henialidae Jarva) Lepidoptera (Henialidae Jarva)	VHH 17007	MT74220	TCCATTM	MT774248	MT7A23A	MT77A241
	Lepiuopiera (rreplanuae rarva) Homistono (fizedidoo (zizedo sumuch)						
			AD900392	AD900420	4000044		AD900340
Uphiocordyceps macroacicularis	Lepidoptera (Lossidae larva)	NBKC 100685	AB968388	AB968416	AB9685/4		AB968536
Ophiocordyceps multiperitheciata	Lepidoptera (larva)	BCC 69008 ¹		MF614657	MF614641		MF614682
Ophiocordyceps myrmicarum	Hymenoptera: Formicidae	HIRS 45	KJ680150	JX566965	JX566973	KJ680151	
Ophiocordyceps nigrella	Lepidoptera (larva)	EFCC 9247	EF468963	EF468818	EF468758	EF468866	EF468920
Ophiocordyceps pseudoacicularis	Lepidoptera (larva)	TBRC 8102 ¹		MF614646	MF614630	MF614661	MF614677
Ophiocordyceps pruinosa	Hemiptera	NHJ 12994	EU369106	EU369041	EU369024	EU369063	EU369084
Ophiocordyceps pulvinata	Hymenoptera (Camponotus adult ant)	TNS-F 30044	GU904208	AB721305	GU904209	GU904210	
Ophiocordyceps ramosissimum	Lepidoptera (<i>Phassus nodus</i> larva)	GZUHHN8	KJ028012		KJ028014	KJ028017	
Ophiocordyceps ravenelii	Coleoptera (beetle larva)	OSC 110995	DQ522550	DQ518764	DQ522334	DQ522379	DQ522430
Ophiocordyceps robertsii	Lepidoptera (Hepialidae larva)	KEW 27083		EF468826	EF468766		
Onhiocordyceps rubiaino sineritheciata	Coleontera (larva)	NBRC 106966	IN941704	IN941437	AB968582	JN992438	AB968544
Ophiccol a) ceps racignosiperintectada Ophiccordicens entroi	Hymenontera (Polyrhochis lamellidens)	110	KX713650	KX713601	2000021 XX713684	KX713710	
Ophilocol dy ceps such On history dy ceps such	Instruction (University and Instruction)						r costraa
Ophilocol dyceps sinerisis On history dycons rimansis	Lepiuopiera (riepianuae raiva) Lonidonton (Unoninidon lonio)					LF 4000/4	
Optilocordyceps sinerisis	Lepidoptera (nepiditade larva)						
Upniocorayceps sobolitera	Hemiptera: Licadidae (cicada nymph)	KEW /8842	EF408972	EF408828		C/988/3	C2408925
Ophiocordyceps sobolitera	Hemiptera: Cicadidae (cicada nymph)	INS F18521	KJ878933	KJ8/8898	KU878979	KU879013	
Ophiocordyceps spataforae	Hemiptera (adult)	NHJ 12525	EF469125	EF469078	EF469063	EF469092	EF469111
Ophiocordyceps sphecocephala	Hymenoptera (adult wasp)	NBRC 101753	JN941695	JN941446	AB968592	JN992429	AB968553
Ophiocordyceps stylophora	Coleoptera (Elateridae Iarva)	OSC 110999	EF468982	EF468837	EF468777	EF468882	EF468931
Ophiocordyceps tiputinii	Megaloptera (larva)	QCNE 186287 ¹	KC610792	KC610773	KC610745	KF658671	
Ophiocordyceps thanathonensis	Hymenotera (adult ant)	MFLU 16-2910	MF882926	MF850377	MF872614	MF872616	
Ophiocordyceps tricentri	Hemiptera (Cercopoidea adult)	NBRC 106968	AB968393	AB968423	AB968593		AB968554
Ophiocordyceps unilateralis	Hymenoptera (<i>Camponotus</i> adult ant)	OSC 128574	DQ522554	DQ518768	DQ522339	DQ522385	DQ522436
Ophiocordyceps unituberculata	Lepidoptera (larva)	YFCC HU1301	KY923214	KY923212	KY923216	KY923218	KY923220
Ophiocordyceps xuefengensis	Lepidoptera (<i>Phassus nodus</i> larva)	GZUH2012HN14 ¹	KC631789		KC631793	KC631798	
Ophiocordyceps yakusimensis	Hemiptera: Cicadidae (cicada nymph)	HMAS 199604	KJ878938	KJ878902		KJ879018	KJ878953
Orbiocrella petchii	Hemiptera: Coccoidea (scale insect)	NHJ 6209	EU369104	EU369039	EU369023	EU369061	EU369081
Orbiocrella petchii	Hemiptera: Coccoidea (scale insect)	NHJ 6240	EU369103	EU369038	EU369022	EU369060	EU369082
Pochonia chlamydosporia	Mollusca	CBS 101244	DQ522544	DQ518758	DQ522327	DQ522372	DQ522424
Pochonia chlamydosporia var. catenulata	Soil	CBS 504.66 ^T	AF339593	AF339544	EF469069	EF469098	EF469120
Pochonia chlamydosporia var. chlamydosporia	Soil under Brassica napus	CBS 103.65 ^T			KJ398786	KU398597	KJ398693
Pochonia boninensis	Soil	JCM 18597	AB758255	AB709831	AB758463	AB758666	AB758693
Purpureocillium atypicolum	Araneae	CBS 744.73	EF468987	EF468841	EF468786	EF468892	
Purpureocillium lilacinum	Soil	CBS 284.36 ^T	AY526475	FR775484	EF468792	EF468898	EF468941
Rotiferophthora angustispora	Rotifera: Bdelloidea (bdelloid rotifer)	CBS 101437	AF339584	AF339535	AF543776	DQ522402	DQ522460
Samsoniella alboaurantium	Soil	CBS 262.58 ^T	AB023943	AB080087	MF416497	MF416654	MF416448
Samsoniella inthanonensis	Lepidopteran pupa	TBRC 7915 ¹		MF140725	MF140849	MF140790	MF140815
Shimizuomyces paradoxus	Plant (Smilax sieboldii)	EFCC 6279	EF469131	EF469084	EF 469071	EF 469100	EF469117
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Taxon	Host/substrate	voucner information	nrSSU	nrLSU	tef1-α	rpb 1	rpb2
Shimizuomyces paradoxus	Plant (Smilax sieboldii)	EFCC 6564	EF469130	EF469083	EF469072	EF469101	EF469118
Simplicillium lamellicola	Fungi (<i>Agaricus bisporus</i>)	CBS 116.25 ^T	AF339601	AF339552	DQ522356	DQ522404	DQ522462
Simplicillium lanosoniveum	Fungi (Hemileia vastatrix)	CBS 704.86	AF339602	AF339553	DQ522358	DQ522406	DQ522464
Sphaerostilbella berkeleyana	Fungi (Polyporaceae sp.)	CBS 102308	AF543770	U00756	AF543783	AY489671	DQ522465
Tolypocladium capitatum	Fungi (Elaphomyces sp.)	NBRC 100997	JN941740	JN941401	AB968597	JN992474	AB968558
Tolypocladium inflatum	Soil	OSC 71235	EF469124	EF469077	EF469061	EF469090	EF469108
Tolypocladium paradoxum	Hemiptera: Cicadidae (larva)	NBRC 100945	JN941731	JN941410	AB968599	JN992465	AB968560
Trichoderma deliquescens	On decorticated conifer wood	ATCC 208838	AF543768	AF543791	AF543781	AY489662	DQ522446
Trichoderma stercorarium	Cow dung	ATCC 62321	AF543769	AF543792	AF543782	AY489633	EF469103
Notes: ^T ex-type culture.							

wees. ex-type culture. Boldface: *Ophiocordyceps lianshanensis* and *"Metacordyceps liangshensis"* were treated as two different species here using maximum-likelihood (ML) methods. The ML analysis was run on RaxML v7.9.1 using the optimal model GTR + I with 1000 rapid bootstrap replicates [18]. The reliability of nodes was assessed 1000 replicates of non-parametric bootstrap proportions on the combined 5-gene dataset.

3. Results

3.1. Phylogenetic analysis

The 149 taxa were used for phylogenetic analysis four from families (Ophicordycipitaceae, Clavicipitaceae, Cordycipitaceae, and Hypocreaceae), with Gliocephalotrichum bulbilium and Nectria cinnabarina included as outgroups. The concatenated sequence dataset of five genes was composed of 5567 bp sequence data (1690 bp for nrSSU, 972 bp for nrLSU, 1035 bp for tef-1a, 781 bp for rpb1, and 1089 bp for rpb2). Phylogenetic tree inferred from ML analysis recognized four statistically well-supported clades in Ophiocordyceps, designated as Hirsutella Pat., O. sobolifera (Hill ex Watson) G.H. Sung et al., O. sphecocephala (Klotzsch ex Berk.) G.H. Sung et al. and O. ravenelii (Berk. & M.A. Curtis) G.H. Sung et al. clades (Figure 1). The Hirsutella clade included six distinct subclades, namely, H. citriformis Speare, H. thompsonii F.E. Fisher, H. nodulosa Petch, H. Guyana Minter & B.L. Brady, H. sinensis X.J. Liu et al., and the Hirsutella ant pathogen subclades. Phylogenetic analysis of combined dataset placed four samples of C. liangshanensis in the H. sinensis subclade. Cordyceps liangshanensis was closely clustered with O. karstii T.C. Wen, Y.P. Xiao & K.D. Hyde and well-supported by ML bootstrap proportions (ML-BP = 100%). However, three samples of C. liangshanensis clustered together and formed a separate clade from O. karstii with 100% statistical support.

3.2. Morphological features

The morphological characteristics of various specimens of *C. liangshanensis* are shown, and the photomicrographs of morphological structures are shown in Figure 2. The detailed fungal morphological descriptions are in the Taxonomy section. Distinct morphological features between *C. liangshanensis* and its related species are summarized in Table 3.

3.3. Taxonomy

Ophiocordyceps liangshanensis (M. Zang, D.Q. Liu & R.Y. Hu) H. Yu, Y. Wang, Y.D. Dai, Zhu L. Yang & Y.B. Wang, comb. nov. (Figure 2). MycoBank MB837859



Figure 1. Phylogenetic tree of *Ophiocordyceps liangshanensis* with related species based on maximum likelihood analysis from a five-locus (nrLSU, nrSSU, *tef-1a*, *rpb1*, and *rpb2*) dataset. Statistical support values (50%) are shown at the nodes for ML bootstrap support.

 \equiv Cordyceps liangshanensis M. Zang, D.Q. Liu & R.Y. Hu, Acta Botonic Yunnanica 4(2): 174 (1982).

= Metacordyceps liangshanensis (M. Zang, D. Liu & R.Y. Hu) G.H. Sung, J.M. Sung, Hywel-Jones &

Spatafora, Studies in Mycology 57: 35 (2007, misinterpretation).

= Papiliomyces liangshanensis (M. Zang, D. Liu & R.Y. Hu) Luangsa-ard, Samson &



Figure 2. Morphology of *Ophiocordyceps liangshanensis*. (A) Slender stromata arising from Hepialidae larvae; (B) Mature stroma arising from the larva of Hepialidae. (C) The type specimen of *O. liangshanensis* (KUN-HKAS7723). (D) The reddish dark brown host of *O. liangshanensis*. (E) Fertile part; (F–G) Perithecia. (H–J) Asci. (K–M) Ascospores; (N) Colony on PDA; (O–S) Conidiogenous cells; (T–X) Conidia embedded in mucous sheaths. Scale bars: A-C = 3 cm; D, E, N = 1 cm; F = 500 µm; G = 200 µm; H-M = 50 µm; O-S = 10 µm; T-X = 5 µm.

Thanakitpipattana, Studies in Mycology 95: 240 (2020, misinterpretation).

Holotype: CHINA. Sichuan Province: Liangshan Yi Autonomous Prefecture, Leibo County, alt. 1500 m, on the larva of Hepialidae sp. living in *Qiongzhuea tumidinoda* forest, 25 July 1980, Jiyuan Li (KUN-HKAS7723, holotype).

Sexual morph: Stromata cylindrical, solid, yellowbrown to brown, 1–2 arising mainly from the head of host, 200–300 mm long, 1.5–2.5 mm wide. Stipes

Table 3. Morphological c	omparisons of <i>Ophio</i>	ocordyceps liangshanensis with it	s related species.			
Species	Host	Stromata	Perithecia	Asci	Ascospores	Reference
Ophiocordyceps liangshanensis	Hepialidae larva	Single or occasionally branched, cylindrical, 200–300 × 1.5–2.5 mm	Superficial, long ovoid, 450–740 × 300–450 μm	Cylindrical, 260–480 $ imes$ 8–12 μ m	170–240 × 2.5–4.1 μm. Septa, 5.5–19.8 × 2.5–4.1 μm	This study
Ophiocordyceps robertsii	Hepialidae larva	Single, cylindrical, 100–380 × 3–4 mm	Superficial, elongate-obvate or elliptical, 600–880 × 300–400 µm	Narrowly cylindrical, $280-400 \times 9-10 \mu m$	280 × 3 μm. Secondly ascospores, 5.0–6.0 × 3.0 μm	[19]
Ophiocordyceps xuefenensis	Hepialidae larva	Single or occasionally branched, cylindrical, 140–460 × 2–7 mm	Superficial, long ovoid, 416–625 × 161–318 μm	Cylindrical, $191-392 \times 4.5-8.9 \mu m$	130–380 × 1.4–5.2 µm. Septa not measured	[20]
Ophiocordyceps ramosissimum	Hepialidae larva	One or two, 70-150 × 2-4 mm	Superficial, ovoid, 340–350 × 225–255 µm	Cylindrical, 172–265 $ imes$ 6.9–17.3 μm	$130-245 \times 2.0-3.5 \mu$ m. Septa not measured.	[21]
Ophiocordyceps karstii	Hepialidae larva	Mostly single, 140–145 $ imes$ 2–4 mm	Superficial, flask-shaped, thick-walled, 600–765 × 247–323 µm	Narrowly cylindrical, with a thickened apex. 186–228 × 8–12 µm	173–202 × 3.0–5.0 μm. Septa not measured	[22]
Ophiocordyceps Ianpinaensis	Hepialidae larva	Single to several, or fascioled, 50–160 × 0.2–1.3 mm	Superficial, ovoid, 310–370 × 200–240 um	Cylindrical, 240–300 $ imes$ 5.1–6.5 μm	$240-300 imes 1.4 \ \mu m. \ Septa, 3.3-4.9 imes 1.1-1.4 \ \mu m$	[23]
Ophiocordyceps emeiensis	Hepialidae larva	Single, occasionally 2, $100-160 \times 1.5-3.0 \text{mm}$	Superficial, ellipsoidal to ovoid, 320–460 × 220–320 µm	Cylindrical, $170-215 \times 7.5-8 \mu m$	Whole ascospore was not measured. Septa, 9.8–16.0 \times 1.0–1.5 μm	[24]
Ophiocordyceps larvarum	Lepidoptera larva	$100-380 imes 2.0-2.5\mathrm{mm}$	Superficial, ovoid, 600–700 × 330–370 μm	Narrowly cylindrical, 180–200 $ imes$ 8.5 μm	Whole ascospore was not measured. Septa, 4.0–9.0 \times 2.0–2.5 μm	[2,25]
Ophiocordyceps sinensis	Hepialidae larva	Single, occasionally 2–3, $40-110 \times 1.5-4.0 \text{mm}$	Nearly superficial, ellipsoidal to ovoid, 380– 550 × 140–240 μm	Slender, long, 240–485 $ imes$ 12–16 μ m	160–470 × 5.0–6.0 μm. Septa, 5.0–6.3 × 4.6–6.0 μm	[2]

subcylindrical, slender, and long. Fertile parts cylindrical or clavate, yellow-brown to dark brown, covering apex to middle part of stromata, 30–60 mm long, 2–2.5 mm diam., often with a 3–5 mm long sterile apex (n=5). Perithecia dense, superficial, long ovoid, with a basal stipe connected to the stromata, becoming yellowish brown to black brown when mature, 450–740 × 300–450 µm (n=10). Asci hyaline, cylindrical, 8-spored, 260–480 × 8–12 µm (n=10). Apical caps conspicuous and thick, hemiglobose to taper, 7.2–10.0 µm wide, 4.4–6.4 µm high (n=10). Ascospores hyaline, fasciculate, thread-like, slender and long, 170–240 × 2.5–4.1 µm (n=10), with many septa, not breaking into secondary ascospores. Septa, 5.5–19.8 × 2.5–4.1 µm (n=10).

Asexual morph: Hirsutella. Colonies on PDA growing very slowly, reaching 12-15 mm diam after 2 months at 25 °C, hard, round, irregular swell, brown, and radial growth of white. Cell secretoried dark brown pigment material. Hyphae hyaline, septate, branched, smooth-walled, $3.2-5.4 \,\mu\text{m}$ wide (n = 10). Conidiogenous cells monophialidic, sometimes polyphialidic with swollen base and slender neck, generating on hyphae laterally or terminally, hyaline, 46.9–75.6 μ m long (n = 20), smooth and subcylindrical in the basal region, reaching $3.8-4.7 \,\mu\text{m}$ wide (n = 20), tapering gradually or abruptly to a straight neck, minutely warty, 2.0–3.0 μ m wide at the tip (n = 20). Conidia hyaline, aseptate, smooth-walled, arising in groups at the apex of the neck, ellipsoid, citriform or shape of an orange segment, $8.0-12.6 \times 3.6-5.0 \,\mu m$ (n = 25), single or 2-4 aggregated, embedded in a pigmented mucous sheath.

Host: Larvae of Hepialidae sp., reddish dark brown, $31-55 \text{ mm} \log 6-10 \text{ mm} \text{ wide } (n = 10)$.

Other materials examined: CHINA. Sichuan Province: Liangshan Yi Autonomous Prefecture, Leibo County, Xining Town (N 28.26°, E 103.57°), alt. 1540 m, on larvae of Hepialidae sp. living in *Qiongzhuea tumidinoda* forests, 12 July 2011, Hong Yu (YHH 16800, epitype, designated here; YFCC 8577, ex-epitype living culture); Ibid., 5 August 2016, Lei Ding (YHH 17007–YHH 17050). CHINA. Yunnan Province: Zhaotong City, Shuifu County, Taiping Town, Tongluoba National Forest Park (N 28.41°, E 104.15°), alt. 1750 m, on larvae of Hepialidae sp. living in *Q. tumidinoda* forests, 20 June 2015, Yong-Dong Dai (YHH 16861–YHH 16900; YFCC 8578, living culture).

Known distribution: this species is distributed in Sichuan, Yunnan, and Guizhou, southwestern China.

4. Discussion

Ophiocordyceps liangshanensis and O. robertsii share similar morphological characteristics by producing

long stromata with a sterile apex, wide, and brown perithecia, long and cylindrical asci, except that O. robertsii produces secondary ascospores [19]. There are more than 270 known species of Ophiocordyceps but only a few species (i.e., O. liangshanensis, O. xuefenensis T.C. Wen, R.C. Zhu, J.C. Kang & K.D. Hyde, O. ramosissimum T.C. Wen, J.C. Kang & K.D. Hyde, O. karstii, O. lanpingensis H. Yu & Z. H. Chen, O. emeiensis (A.Y. Liu & Z.Q. Liang) G.H. Sung et al., O. larvarum (Westwood) G.H. Sung et al., and O. sinensis) have long stromata, superficial perithecia and ascospores not breaking into secondary ascospores. Ophiocordyceps liangshanensis differs from the other species mentioned above in having relatively wide perithecia (300-450 µm) (Table 3). Its asexual state has long conidiogenous cells, and is similar to that of H. illustris Minter & B.L. Brady and H. strigosa Petch. However, O. liangshanensis differs from H. illustris by its smaller size in conidia $(8.0-12.6 \times 3.6-5.0 \,\mu\text{m})$. The conidiogenous cells of O. liangshanensis generate on hyaline hyphae laterally or terminally, whereas those of H. strigosa arise at right angle from brown hyphae. To fix the species concept, a recently collected specimen (YHH 16800), is designated here as the epitype of O. liangshanensis.

No serious comparison was made for the materials of *C. liangshanensis* from China and those from Nepal previously [4,5]. Based on multi-gene phylogeny, "*C. liangshanensis*" from Nepal reported by Sung et al. [5] was identified as a member in Clavicipitaceae, whereas "*C. liangshanensis*" from Sichuan (type locality) and Yunnan, China, belongs to Ophiocordycipitaceae in the present study. Thus, its new combination is proposed as *Ophiocordyceps liangshanensis* instead of the previous names, "*Metacordyceps liangshanensis*" and "*Papiliomyces liangshanensis*."

The genus *Papiliomyces*, consisting of two species, was proposed for the type species "*P. liangshanensis*" by Mongkolsamrit et al. [6] based on its phylogenetic placement. However, it is clear that the Nepalese collections differ from the Chinese collections, and should be restudied and described in detail, as well as other nomenclatural and taxonomic confusions should be verified in the future.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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