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New Species

寄生鳞翅目幼虫的线虫草属一新种：羽束梗孢状线虫草

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摘 要：线虫草属 *Ophiocordyceps* 是虫草类真菌中一个物种丰富、分布广泛、寄主多样的重要大属，目前已报道物种超过 400 种。中国西南的云南横断山区是生物多样性热点地区，也是该属多样性的重要集中分布区。本研究在云南兰坪县采集到一线虫草标本，结合形态特征、ITS 序列及联合 5 基因(*nr*SSU、*nr*LSU、*tef-1α*、*rpb1* 和 *rpb2*)系统发育分析，确定该物种为线虫草属一新种，命名为羽束梗孢状线虫草 *Ophiocordyceps paraisarioidea* sp. nov.。该种子座结构容易被误认为是 *Paraisaria* 属物种，但表现出更深的子座色泽、顶端具小突起的球形可孕部，以及不断裂的多隔梭形子囊孢子。5 基因系统发育结果显示，该种与虫根线虫草 *Ophiocordyceps entomorrhiza* 聚为一支，位于线虫草属的进化枝基部(basal clade)，但二者在形态和寄主选择上存在显著差异：*O. paraisarioidea* 子座深棕色，顶端灰白，寄主为鳞翅目蛾类幼虫；而 *O. entomorrhiza* 子座偏黑，寄主为鞘翅目步甲属幼虫及成虫。形态比较和 5 基因系统发育结果表明本文报道的 *O. paraisarioidea* 是线虫草属进化枝基部类群的一新物种，丰富了该分支物种多样性。此外，*O. paraisarioidea* 以鳞翅目昆虫为寄主的特征，拓宽了线虫草属基部类群物种寄主范畴，提示“线虫草属以鞘翅目为祖先寄主”这一观点或需进一步探讨，暗示该属在早期演化过程中可能经历了寄主转换。*O. paraisarioidea* 的发现对深入理解线虫草属的起源与早期辐射具有重要意义。

关键词：横断山区；多基因系统发育；线虫草属基部分支；球形可孕部；寄主转换；新种

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Ophiocordyceps paraisarioidea sp. nov. (Hypocreales, Ophiocordycipitaceae), a novel species of *Ophiocordyceps* parasitizing lepidopteran larvae

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Abstract: *Ophiocordyceps* is a diverse, widely distributed, and host-rich genus of entomogenous fungi, with over 400 species reported to date. The Hengduan Mountains in Yunnan of southwestern China, recognized as a global biodiversity hotspot, represent a major center of diversity for this genus. In this study, we describe a new species of *Ophiocordyceps* from Hengduan Mountains in Yunnan, designated *Ophiocordyceps paraisarioidea* sp. nov., based on morphological observations and phylogenetic analyses using both single ITS sequences and a combined dataset of five loci (*nr*SSU, *nr*LSU, *tef-1α*, *rpb1* and *rpb2*). Morphologically, this species is prone to misclassification as *Paraisaria* in virtue of stromatal structure, but it differs by having darker stromata, a spherical fertile part with apical protuberances, and multiseptate non-disarticulating ascospores. Five-gene phylogenetic analyses place *O. paraisarioidea* in the basal clade of *Ophiocordyceps*, clustering with *Ophiocordyceps entomorrhiza*. Nevertheless, the two species exhibit notable differences in morphology and host preference: *O. paraisarioidea* has dark brown stroma with grayish-white tips and parasitizes lepidopteran larvae, whereas *O. entomorrhiza* forms nearly black stromata and infects both larvae and adults of coleopteran insects (*Carabus* sp.). Notably, the lepidopteran host of *O. paraisarioidea* challenges the prevailing hypothesis that Coleopterans represent the ancestral hosts of *Ophiocordyceps*, implying the occurrence of multiple host shifts during the early evolutionary history. The discovery of *O. paraisarioidea* may provide valuable insight into the origin and early diversification of this genus.

Keywords: Hengduan Mountains; multigene phylogeny; the basal clade of *Ophiocordyceps*; spherical fertile part; host shift; new species

线虫草属 *Ophiocordyceps* Petch 是虫草类真菌(cordycepitoid fungi)中关注度非常高的大属。目前已报道 400 余种(含 *Hirsutella* Pat.、*Hymenostilbe* Petch 和 *Paraisaria* Samson & B.L. Brady) (http://www.indexfungorum.org)。线虫草属最初是 Petch (1931)根据 *Ophiocordyceps blattae* (Petch) Petch、*O. unilateralis* (Tul. & C. Tul.) Petch、*O. peltata* (Wakef.) Petch 和 *O. rhizoidea* (Höhn.) Petch 这 4 个物种而创建，定义其主要特征为不断裂的子囊孢子，以及顶端加厚的棒状子囊等。但 Kobayasi (1941, 1982)、Mains (1958)、臧穆等(1982)均将 *Ophiocordyceps* 作为亚属处理(*Cordyceps* subg. *Ophiocordyceps*)。Sung *et al*. (2007a)基于 *nr*SSU、*nr*LSU、*tef-1α* 等 7 基因分子系统学研究，在线虫草科 Ophiocordycipitaceae G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora 内重新确认线虫草属作为一个独立属的分类群特征，并强调该属区别于其他类群的显著特征是子座颜色较深或鲜艳，其质地柔韧或坚硬，细丝状或纤维状，并将其定为线虫草科的模式属。

线虫草物种分布广泛，在亚洲、欧洲、大洋洲、北美洲和南美洲等地均有大量报道，是一个世界性的广布属。它们的寄主范围丰富，包括鳞翅目、膜翅目、鞘翅目、半翅目、双翅目、蜚蠊目、脉翅目和蜻蜓目等，从幼虫、蛹、若虫到成虫的不同生命周期阶段，呈现出极其丰富的物种多样性和寄主多样性(Kobayasi 1982；Sung *et al*. 2007a；Evans *et al*. 2011a；Sanjuan *et al*. 2015；Shrestha *et al*. 2016；Luangsa-Ard *et al*. 2018；Araújo & Hughes 2019；Zha *et al*. 2020；Tang *et al*. 2023；Dai *et al*. 2024；Fan *et al*. 2024；Xu *et al*. 2025)。

线虫草属物种具有丰富的应用价值。该属中冬虫夏草 *Ophiocordyceps sinensis* (Berk.) G.H. Sung *et al*.是中国著名的传统中药材，在营养、保健和疾病治疗中有重要应用价值(梁宗琦 2007；董彩虹等 2016)。此外，雪峰线虫草 *Ophiocordyceps xuefengensis* T.C. Wen *et al*.、凉山线虫草 *O. liangshanensis* (M. Zang, D.Q. Liu & R.Y. Hu) Hong Yu *et al*.、兰坪线虫草 *O. lanpingensis* Hong Yu & Zi H. Chen、细虫草 *O. gracilis* (Grev.) G.H. Sung *et al*.等，均具有良好的抗菌、抗肿瘤和抗病毒药理活性(喻东等 2010；叶星等 2015；郑兵等 2015；Wu *et al*. 2019；周树波 2021)。该属单侧生虫草复合群 *Ophiocordyceps unilateralis sensu lato* 感染蚂蚁后可操纵寄主，使蚂蚁失去自主行为如同“僵尸”一般，亦称为“僵尸蚂蚁真菌”(Evans *et al*. 2011b)。该类群是一类极具“操纵模型”代表的真菌资源，他们对蚂蚁特异性的操纵能力使其成为研究寄主特异性的良好模型(Will *et al*. 2020)。另外，线虫草属中 *Hirsutella minnesotensis* Sen Y. Chen, Xing Z. Liu & F.J. Chen、*H. rhossiliensis* Minter & Brady 和 *H. vermicola* M.C. Xiang & Xing Z. Liu 是大豆线虫主要生防真菌(刘淑芬 2004)，是农业害虫白蚁潜在的生防菌(Rath 2000)。

中国云南省拥有多样的生态环境和丰富的植被类型，是名副其实的“生物多样性王国”。该地区报道大量线虫草物种(代永东 2018；陈思琪 2021；邹维秋 2022；杨涛 2023；Dai *et al*. 2024；周云 2024)，有“虫草王国”的美誉(虞泓 2016)。而云南西北部横断山区，是潜在的虫草多样性中心，近年来还报道了若干与冬虫夏草有亲缘关系的线虫草新物种(Chen *et al*. 2011；Chen *et al*. 2013；Wang *et al*. 2021；Dai *et al*. 2024；Sun *et al*. 2022, 2024)，是研究冬虫夏草系统发育支系系统演化的重要区域。2023 年 7 月，我们在云南兰坪县中药材集市上发现一未知线虫草物种，寄主清晰可见为鳞翅目蛾类幼虫，其子座深色，可孕部呈球状位于子座顶端，子囊壳埋生等，有类似羽束梗孢 *Paraisaria* 相关特征，但与已知种均有差异。因此，对其开展详细的形态鉴定和系统发育分析，以期明确该物种分类及系统归属，以便更好地对线虫草属资源进行保护和利用。

1 材料与方法

1.1 标本来源

标本发现于云南省怒江傈僳族自治州兰坪县金顶镇集市(99°32′E, 26°41′N)，时间：2023 年 7 月。标本生长地理位置为兰坪县，属于云南横断山地区。

1.2 虫草标本形态及显微形态观察

观察标本子座、可孕部及菌核的形态及质地、寄主特征并拍照。使用体视显微镜(SZ61, Olympus)和倒置显微镜(Olympus CX40)对可孕部分切片，对标本的有性阶段进行观察。记录并描述子囊壳形状、大小和着生方式、子囊和子囊孢子等显微形态特征(代永东 2018)。

1.3 标本 DNA 提取、序列 PCR 扩增及测序

对标本开展DNA提取和基因片段PCR扩增及测序。分别使用真菌基因组 DNA 提取试剂盒(离心柱型，TransGen Biotech)提取标本菌核和子座部分的 DNA。DNA 提取完成后，利用 PCR 扩增其 ITS (internal transcribed spacer)、*nr*SSU (small subunit ribosomal RNA)、*nr*LSU (large subunit ribosomal RNA)、*tef-1α* (transcription elongationfactor-1 alpha)、*rpb1* (largest subunits of RNA polymerase Ⅱ) 和 *rpb2* (second largest subunits of RNA polymeraseⅡ)序列，所用引物见

表 1。所有 PCR 反应的总体积为 25 μL，其中含有 12.5 μL 2× *Taq* PCR Master Mix (TransGen Biotech)，每种引物 1.25 μL (10 μmol/L)，基因组 DNA 1 μL，RNase-Free water 9 μL。扩增程序参考试剂盒说明。使用 1.5%琼脂糖胶检测 PCR 产物，使用 EasyPureTM Quick Gel Extraction Kit (TransGen Biotech)进行纯化，在生工生物工程(上海)股份有限公司利用 ABI 3700 自动测序仪进行测序。

1.4 多基因分子系统发育分析

测序结果首先使用 MEGA 5 (Tamura *et al*. 2011)检查测序序列的 AB1 峰图，查看测序文件是否为单峰，若存在双峰、套峰等情况，重新优化程序进行 PCR 扩增及测序。基于广泛的文献收集及整理，本研究汇总了线虫草属已发表的多基因测序数据，建立了涵盖该属已报道物种的 5 基因序列数据库(附表 1，国家微生物科学数据中心编号 NMDCX0002185)，并进一步突出与本研究物种相关的近缘类群分类与序列信息(表 2)。在不同基因序列的比对中，*nr*SSU 和 *nr*LSU 比对参数默认，*tef-1α*、*rpb1* 和 *rpb2* 去掉内含子区，且比对后利用 codon 模式查看序列是否能正常翻译成蛋白质，并避免出现终止子等情况，必要时进行人工纠错。构建该数据库后，我们直接将本研究标本扩增的 5 基因序列加入已构建的线虫草属序列库中，形成 5 基因(*nr*SSU、*nr*LSU、*tef-1α*、*rpb1* 和 *rpb2*)数据集合。设置线虫草属近缘属 *Drechmeria* 物种为外类群。比对拼接完成的 5 基因序列总长度为 4 536 bp，其中 *nr*SSU 1 104 bp、*nr*LSU 1 011 bp、*tef-1α* 933 bp、*rpb1* 552 bp，以及 *rpb2* 936 bp。将 5 基因序列分为 11 个区，分别是 Partition 1：*nr*SSU；Partition 2：*nr*LSU；Partition 3–5：*tef-1α* 密码子 1–3 位；Partition 6–8：*rpb1* 密码子 1–3 位；Partition 9–11：*rpb2* 密码子 1–3 位。考虑各基因各位点选择压力，以及不同基因最佳模型差异，使用 PartitionFinder 2 (Lanfear *et al*. 2017)进行分区优化，并获得优化分区及适用模型。运算结果为：Partition 1—*nr*SSU；Partition 2—*nr*LSU；Partition 3—*tef-1α* codon1；Partition 4—*tef-1α* codon2；Partition 5—*tef-1α* codon3；Partition 6—*rpb1* codon1、*rpb2* codon1；Partition 7—*rpb1* codon2；Partition 8—*rpb1* codon3、*rpb2* codon3；Partition 9—*rpb2* codon2。

使用最大似然法(maximum likelihood, ML)和贝叶斯推论运算(Bayesian inference, BI)进行系统发育运算。ML 运算使用 RAxML-HPC BlackBox (8.2.12) (Stamatakis 2006)软件，设置 Use a mixed/partitioned model 为 9，bootstrap= 1 000 开展运算，各区替代模型从 PartitionFinder 2 中自动输出。BI 运算使用软件 Mrbayes 3.2 (Ronquist *et al*. 2012)，各分区模型和相关先验参数由 PartitionFinder 2 运算获得、自动调取并生成 nex 文件。设置 mcmc ngen=3×10^{8}，以确保系统发育结构的可靠性。

表 1 用于基因片段扩增和测序的引物

Table 1 Primer pairs for gene amplification and sequencing used in this study

基因 Gene	引物名称 Primer	引物序列 Primer sequence (5′→3′)	来源 Reference
ITS	ITS5	GGAAGTAAAAGTCGTAACAAGG	White *et al*. 1990
	ITS4	TCCTCCGCTTATTGATATGC	
*nr*SSU	CSSU3F	TCTCAAAGATTAAGCCATGC	Chen *et al*. 2013
	CSSU18R	TCACCAACGGAGACCTTG	
*nr*LSU	LR5	ATCCTGAGGGAAACTTC	Vilgalys & Hester 1990
	LR0R	GTACCCGCTGAACTTAAGC	
tef-1α	EF1α-EF	GCTCCYGGHCAYCGTGAYTTYAT	Bischoff *et al*. 2006; Sung *et al*. 2007b
	EF1α-ER	ATGACACCRACRGCRACRGTYTG	
rpb1	rpb1-5'F	CAYCCWGGYTTYATCAAGAA	
	rpb1-5'R	CCNGCDATNTCRTTRTCCATRTA	
rpb2	rpb2-5'F	CCCATRGCTTGTYYRCCCAT	
	rpb2-5'R	GAYGAYMGWGATCAYTTYGG	

表 2 线虫草属中 **basal clade** 和 ***Ophiocordyceps ravenelii*** **clade** 物种 5 基因(***nr*SSU, *nr*LSU, *tef-1α*, *rpb1*, and *rpb2***)序列信息
Table 2 Specimens and GenBank accession numbers of the basal clade and *Ophiocordyceps ravenelii* clade for *nr*SSU, *nr*LSU, *tef*-1α, *rpb1*, and *rpb2* sequences

物种 Species	菌株 Voucher	寄主 Host	GenBank 登录号 GenBank accession number					文献引证 References
			*nr*SSU	*nr*LSU	*tef-1α*	*rpb1*	*rpb2*	
O. borealis	GACPR_16002	Coleoptera	MK863045	MK863052	MK860190	–	–	Zha *et al*. 2021
O. borealis	MFLU_18_0163	Coleoptera	MK863044	MK863051	MK860189	–	–	Zha *et al*. 2021
O. clavata	BCC_95653	Coleoptera	–	–	OR855796	OR855816	OR855838	Mongkolsamrit *et al*. 2024
O. clavata	BUO_545	Coleoptera	–	MH879601	MH879672	MH885450	–	
O. clavata	CEM_1762	Coleoptera	KJ878916	KJ878882	KJ878963	KJ878996	–	Quandt *et al*. 2014
O. clavata	NBRC_106961	Coleoptera	–	JN941414	AB968586	JN992461	AB968547	Ban *et al*. 2015
O. clavata	NBRC_106962	Coleoptera	JN941726	JN941415	AB968587	JN992460	AB968548	Ban *et al*. 2015
O. entomorrhiza	KEW_53484	Coleoptera	EF468954	EF468809	EF468749	EF468857	EF468911	Sung *et al*. 2007a
O. formosana	MFLU:15-3888	Coleoptera: Tenebrionoidea	KU854951	–	KU854949	KU854947	–	Li *et al*. 2016
O. formosana	NTU_00035	Coleoptera: Tenebrionoidea	–	–	KT275192	KT275190	KT275191	Wang YW *et al*. 2015
O. formosana	TNMF_13893	Coleoptera	KJ878908	–	KJ878956	KJ878988	KJ878943	Wang YW *et al*. 2015
O. highlandensis	HKAS83207	Coleoptera: Scarabaeoidea	KM581284	–	–	KM581274	KM581278	Yang *et al*. 2015
O. hignlandensis	YHH_OH1301	Coleoptera: Melolonthidae	KR479869	–	KR479870	KR479872	KR479874	Wang YB *et al*. 2015
O. konnoana	EFCC_7295	Coleoptera	EF468958	–	–	EF468862	EF468915	Sung *et al*. 2007a
O. konnoana	EFCC_7315	Coleoptera	EF468959	–	EF468753	EF468861	EF468916	Sung *et al*. 2007a
O. krachonicola	BCC_79666	Coleoptera	–	MK632080	MK632054	MK632161	MK632132	Thanakitpipattana *et al*. 2020
O. krachonicola	BCC_79667	Coleoptera	–	MK632081	MK632055	MK632162	MK632133	Thanakitpipattana *et al*. 2020
O. kuchinaraiensis	BCC_95830	Coleoptera	–	OQ627397	OQ625474	–	OQ625475	Crous *et al*. 2023
O. melolonthae	OSC_110993	Coleoptera	DQ522548	DQ518762	DQ522331	DQ522376	–	Sung *et al*. 2007a
O. melolonthae	Ophgrc_679	Coleoptera	–	KC610768	KC610744	KF658666	–	Sanjuan *et al*. 2015
O. neovolkiana	OSC_151903	Coleoptera	KJ878930	KJ878896	KJ878976	KJ879010	–	Sung *et al*. 2007a
O. nigrella	EFCC_9247	Coleoptera	EF468963	EF468818	EF468758	EF468866	EF468920	Sung *et al*. 2007a
O. paraisariaoidea	GZY_OPNJ2023-1	Lepidoptara	PV890077	PV890078	PV897478	PV897480	–	本研究 This study
O. paraisariaoidea	GZY_OPNJ2023-2	Lepidoptara	PX105295	PV890079	PV897479	PV897481	–	本研究 This study
O. pseudovariabilis	BCC_88311	Coleoptera	–	–	OR855800	OR855824	OR855844	Mongkolsamrit *et al*. 2024
O. purpureostromata	TNS_F18430	Coleoptera	KJ878931	KJ878897	KJ878977	KJ879011	–	Quandt *et al*. 2014

(待续)

(续表 2)

物种 Species	菌株 Voucher	寄主 Host	GenBank 登录号 GenBank accession number					文献引证 References
			*nr*SSU	*nr*LSU	*tef-1α*	*rpb1*	*rpb2*	
O. ravenelii	OSC_110995	Coleoptera: Beetle larva	DQ522550	DQ518764	DQ522334	DQ522379	DQ522430	Sung *et al*. 2007a
O. ravenelii	OSC_151914	Coleoptera	KJ878932	–	KJ878978	KJ879012	KJ878950	Sung *et al*. 2007a
O. spicatus	MFLU18-0164	Coleoptera: Tenebrionoidea	MK863047	MK863054	MK860192	–	–	Zha *et al*. 2021
O. variabilis	ARSEF_5365	Diptera: Xylophagidae	DQ522555	DQ518769	DQ522340	DQ522386	DQ522437	Spatafora *et al*. 2007
O. variabilis	OSC_111003	Diptera: Xylophagidae	EF468985	EF468839	EF468779	EF468885	EF468933	Mongkolsamrit *et al*. 2019
Parisaria alba	HKAS_102484	Orthoptera	MN943843	MN943839	MN929085	MN929078	MN929082	Wei *et al*. 2021
Par. amazonica	HUA_186094	Orthoptera	KJ917565	–	KM411986	KP212906	–	Sanjuan *et al*. 2015
Par. amazonica	HUA_186100	Orthoptera	KJ917564	–	KM411987	KP212907	–	Sanjuan *et al*. 2015
Par. amazonica	HUA_186101	Orthoptera	–	–	KM411988	KP212908	KM411981	Sanjuan *et al*. 2015
Par. amazonica	HUA_186113	Orthoptera	KJ917566	KJ917572	–	KP212903	KM411980	Sanjuan *et al*. 2015
Par. amazonica	HUA_186136	Orthoptera	KJ917560	–	KM411991	KP212905	–	Sanjuan *et al*. 2015
Par. amazonica	Ophama2026	Orthoptera	KJ917562	KJ917571	KM411989	KP212902	KM411982	Sanjuan *et al*. 2015
Par. arcta	HKAS 102552	Lepidoptera	MN943844	MN943840	MN929086	MN929079	MN929083	Wei *et al*. 2021
Par. arcta	HKAS_102553	Lepidoptera	MN943845	MN943841	MN929087	MN929080	–	Wei *et al*. 2021
Par. blattarioides	HUA_186108	Blattodea, Dyctioptera	KJ917558	KJ917569	–	KP212912	KM411984	Sanjuan *et al*. 2015
Par. blattarioides	HUA_186093	Blattodea, cockroach	KJ917559	KJ917570	KM411992	KP212910	–	Sanjuan *et al*. 2015
Par. cascadensis	OSC-M-052010	Orthoptera	OQ800918	OQ708931	OR199814	OR199828	OR199838	Tehan *et al*. 2023
Par. cascadensis	OSC-M-052012	Orthoptera	OQ800920	OQ708933	OR199816	OR199830	–	Tehan *et al*. 2023
Par. cascadensis	OSC-M-052017	Orthoptera	OQ800921	OQ708934	OR199817	OR199831	–	Tehan *et al*. 2023
Par. coenomyiae	NBRC_108993	Diptera: Coenomyia	AB968384	AB968412	AB968570	–	AB968532	Ban *et al*. 2015
Par. coenomyiae	NBRC_106964	Diptera: Coenomyiidae	AB968385	AB968413	AB968571	–	AB968533	Ban *et al*. 2015
Par. gracilioides	Ophgrc934	Coleoptera (Elateridae larva)	KJ917556	–	KM411994	KP212914	–	Sanjuan *et al*. 2015
Par. gracilioides	HUA 186092	Coleoptera	KJ917555	KJ130992	–	KP212915	–	Sanjuan *et al*. 2015
Par. cf. gracilis	EFCC_3101	Lepidoptera	EF468955	EF468810	EF468750	EF468858	EF468913	Sung *et al*. 2007a
Par. gracilis	EFCC_8572	Lepidoptera	EF468956	EF468811	EF468751	EF468859	EF468912	Sung *et al*. 2007a
Par. heteropoda	EFCC 10125	Hemiptera: Cicada	EF468957	EF468812	EF468752	EF468860	EF468914	Quandt *et al*. 2014
Par. heteropoda	NBRC 100642	Hemiptera	JN941720	JN941421	AB968594	JN992454	AB968555	Ban *et al*. 2015

(待续)

(续表 2)

物种 Species	菌株 Voucher	寄主 Host	GenBank 登录号 GenBank accession number *nr*SSU	*nr*LSU	*tef-1α*	*rpb1*	*rpb2*	文献引证 References
Par. heteropoda	NBRC 100643	Hemiptera	JN941719	JN941422	AB968595	JN992453	AB968556	Ban *et al*. 2015
Par. heteropoda	NBRC_100644	Hemiptera	JN941718	JN941423	AB968596	JN992452	AB968557	Ban *et al*. 2015
Par. heteropoda	NBRC 33060	Hemiptera	AB113352	–	MK214083	MK214087	–	Mongkolsamrit *et al*. 2019
Par. heteropoda	OSC_106404	Hemiptera	AY489690	AY489722	AY489617	AY489651	–	Sung *et al*. 2007a
Par. insignis	OSC.164134	Coleoptera	OQ800911	OQ708924	OR199807	OR199822	–	Tehan *et al*. 2023
Par. insignis	OSC.164135	Coleoptera	OQ800912	OQ708925	OR199808	OR199823	–	Tehan *et al*. 2023
Par. insignis	OSC.164137	Coleoptera	OQ800913	OQ708926	OR199809	OR199824	–	Tehan *et al*. 2023
Par. insignis	OSC-M-052004	Coleoptera	OQ800914	OQ708927	OR199810	–	–	Tehan *et al*. 2023
Par. insignis	OSC-M-052008	Coleoptera	OQ800917	OQ708930	OR199813	OR199827	–	Tehan *et al*. 2023
Par. insignis	OSC-M-052013	Coleoptera	OQ800924	OQ708938	OR199820	OR199834	–	Tehan *et al*. 2023
Par. orthopterorum	BBC88305	Orthoptera	–	MK332583	MK214080	MK214084	–	Mongkolsamrit *et al*. 2019
Par. orthopterorum	TBRC 9710	Orthoptera	–	MK332582	MK214081	MK214085	–	Mongkolsamrit *et al*. 2019
Par. phuwiangensis	BBH 43492	Coleoptera	–	MH201169	MH211355	MH211352	–	Mongkolsamrit *et al*. 2019
Par. phuwiangensis	TBRC9709	Coleoptera: Elateridae	–	MK192057	MK214082	MK214086	–	Mongkolsamrit *et al*. 2019
Par. pseudoheteropoda	OSC-M-052005	Hemiptera	OQ800915	OQ708928	OR199811	OR199825	OR199836	Tehan *et al*. 2023
Par. pseudoheteropoda	OSC-M-052007	Hemiptera	OQ800916	OQ708929	OR199812	OR199826	OR199837	Tehan *et al*. 2023
Par. pseudoheteropoda	OSC-M-052009	Hemiptera	OQ800922	OQ708935	OR199818	OR199832	OR199840	Tehan *et al*. 2023
Par. pseudoheteropoda	OSC-M-052020	Hemiptera	OQ800923	OQ708937	OR199819	OR199833	–	Tehan *et al*. 2023
Par. pseudoheteropoda	OSC-M-052022	Hemiptera	OQ800925	OQ708939	OR199821	OR199835	OR199841	Tehan *et al*. 2023
Par. rosea	HKAS_102546	Coleoptera	MN943846	MN943842	MN929088	MN929081	MN929084	Wei *et al*. 2021
Par. tettigonia	GZUHCS14062709	Orthoptera: Tettigoniidae	KT345955	–	KT375440	KT375441	–	Wen *et al*. 2016
Par. yodhathaii	BBH43163	Coleoptera: Elateridae	–	MK332584	MH211353	MH211349	–	Mongkolsamrit *et al*. 2019
Par. yodhathaii	TBRC 8502	Coleoptera	–	MH201168	MH211354	MH211350	–	Mongkolsamrit *et al*. 2019
Tilachlidiopsis nigra	TNS_16252	Coleoptera	KJ878941	KJ878906	KJ878986	–	–	Quandt *et al*. 2014
Tilachlidiopsis nigra	TNS_16250	Coleoptera	KJ878942	–	KJ878987	KJ879021	–	Quandt *et al*. 2014

注：–表示序列缺失

Note: – Denotes missing sequence data.

以上两种运算均在系统发育分析平台 CIPRES Science Gateway (https://www.phylo.org/portal2/)完成。Raxml 运行结束后获得的一致树(bipartitions tree)和 mrbayes 运算完成获得的 tre 文件使用 Figtree 1.6 (http://tree.bio.ed.ac.uk/software/figtree/)查看并编辑。在分析平台(https://www.chiplot.online)进一步优化系统树。将 ML 的 bootstrap 支持率(bootstrap support, BS)和 BI 的后验概率(posterior probability, PP)同时标注在系统发育树分支上。由于 ITS 在线虫草属不同物种中差异较大，考虑到替代饱和及长枝吸引问题，不适宜将 ITS 与 5 基因数据集进行联合分析，但 ITS 对于物种亲缘关系判别特别是近缘物种有较高的分辨率(Dai *et al*. 2024)，因此我们单独利用 IT 序列开展系统发育分析。基于 BLAST 在线比对，下载相关物种的序列，尤其是在 5 基因数据集中与本研究物种有较近亲缘关系的物种。使用软件 Mrbayes 3.2 (Ronquist *et al*. 2012)进行运算。我们在运行程序中加入 mcmc stoprule=yes stopval=0.005 (通常设置为 0.01)，以确保系统发育结果更加稳定可靠。

2 结果与分析

2.1 5 基因(*nr*SSU、*nr*LSU、*tef-1α*、*rpb1* 和 *rpb2*)系统发育分析

我们构建了线虫草属 439 个标本的包含 210 个已知物种的 5 基因系统发育树。结果显示本研究构建的线虫草属系统发育框架与之前的研究结果基本保持一致(Sanjuan *et al*. 2015；Dai *et al*. 2024；Xu *et al*. 2025)，但系统发育整体结构框架更加明显，主要形成 5 个支系：*Ophiocordyceps ravenelii* clade、*O. sinensis* clade、*O. unilateralis* clade、*O. sphecocephala* clade 和 *O. soblifera* clade (图 1A)。

本研究报道的羽束梗孢状线虫草 *Ophiocordyceps paraisarioidea* 系统位置位于线虫草属基部，基于其特殊的系统发育位置，我们定义该分支为基部分支(basal clade)，包含 *O. paraisarioidea*、虫根线虫草 *O. entomorrhiza* (Dicks.) G.H. Sung *et al*.和黑拟多头束霉 *Tilachlidiopsis nigra* Yakush. & Kumaz.。在该分支内，羽束梗孢状线虫草与另 2 个物种系统位置差异显著，支持其作为独立的物种(BS=100, PP=1.0)。

基于 BLAST 相似性搜索，利用 ITS 序列构建了 *O. paraisarioidea* 及其近缘物种的系统树(图 2)，结果显示 *O. paraisarioidea* 与其近缘种的关系与 5 基因系统树有一定差异，这可能与二者进化速率不一致有关。*O. paraisarioidea* 与 *O. entomorrhiza* 仍处于线虫草属末端，但 *O. paraisarioidea* 与 *O. entomorrhiza* 并不在同一个分支。*O. paraisarioidea* 与 *O. ravenelii* clade 有较近的亲缘关系，而 *O. entomorrhiza* 则与弯颈霉属 *Tolypocladium* 更近。这种分子层面的接近关系也提示 *O. paraisarioidea* 与 *O. entomorrhiza* 可能代表线虫草属中一个较为原始的类群，且可能是线虫草属和弯颈霉属之间的过渡物种。

此外，我们将线虫草物种寄主种类映射至线虫草属系统发育关系中，结果显示，线虫草属不同系统发育分支与寄主类群(节肢动物)形成较为一致的对应关系(图 1B)，提示线虫草属物种与寄主之间可能存在显著的协同进化模式。

O. paraisarioidea 所在基部分支(basal clade)及近缘分支 *O. ravenelii* clade 寄主为鞘翅目昆虫(仅 *O. variabilis* 例外，寄主为 Diptera)，本研究描述的 *O. paraisarioidea* 寄主为鳞翅目蛾类幼虫，为线虫草属，尤其是基部类群物种的寄主多样性提供了实例。

2.2 物种分类

羽束梗孢状线虫草　图 3 新种

Ophiocordyceps paraisarioidea Y.D. Dai & Ch. X. Chang **sp. nov.**　Fig. 3

MycoBank: MB 859746

Etymology: *Paraisaria*+*oidea*, refers to several characters of this species similar to the *Paraisaria* species.

Holotype: GZY_OPNJ2023-1, China. Yunnan Province: Lanping county, Jinding town (99°32′E, 26°41′N), on the larva of species of Lepidoptera. July 2023, collected by Yongdong Dai and Dehua Hou (Fig. 3A, 3B). Preserved in the Miao Medicine Museum of Guizhou University of Traditional Chinese Medicine.

Host: the larvae of Lepidoptera, 2.6–4.0 cm × 0.3–0.4 cm.

Stromata: arising from the head of host, 5.0–10.0 cm long, clavate, solid, lignified, usually single, a few with branches (2 to 5) from the middle part, dark brown, with the apex being off-white.

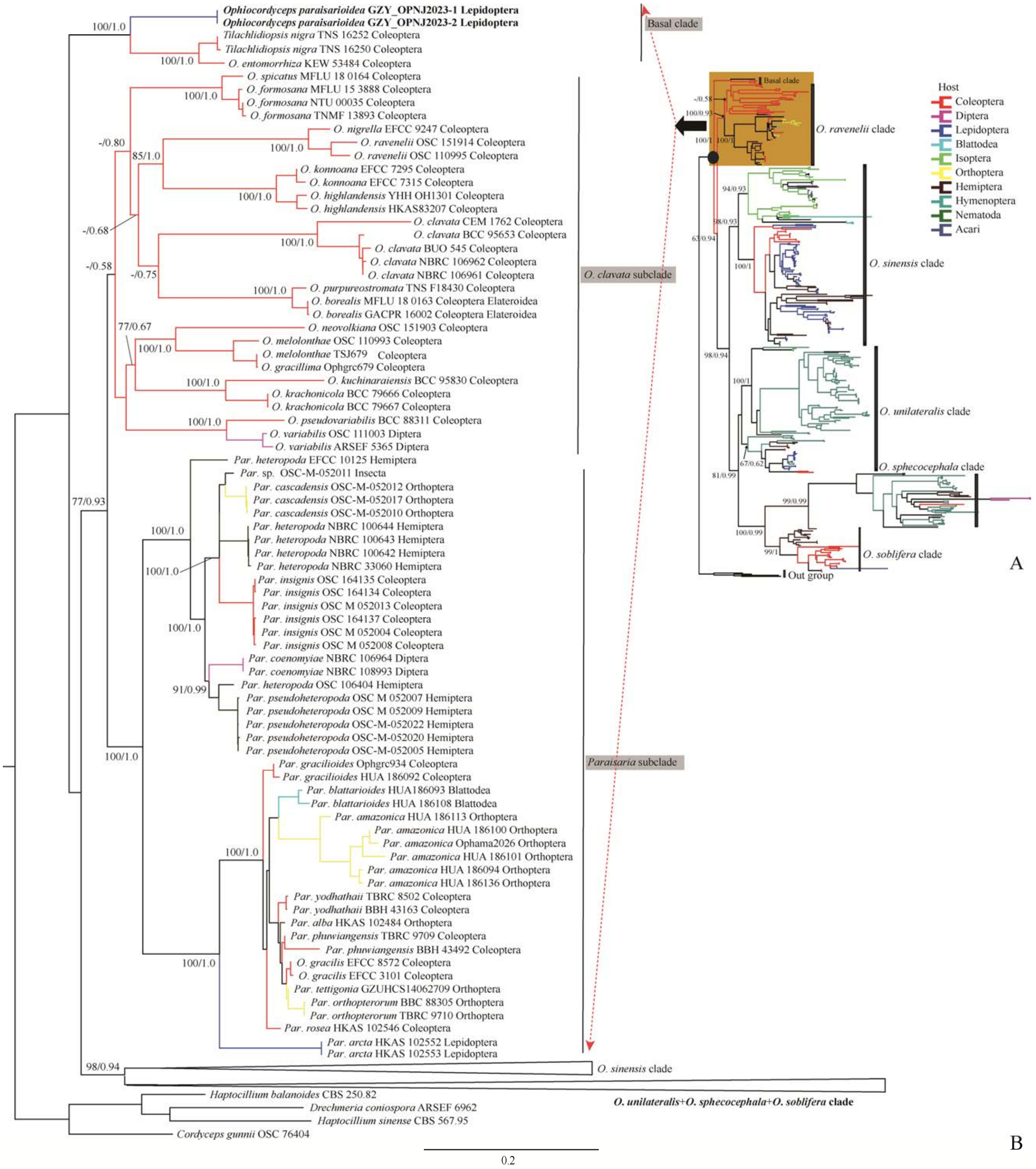

图 1 基于 5 基因(*nr*SSU、*nr*LSU、*tef-1α*、*rpb1* 和 *rpb2*)的羽束梗孢状线虫草系统位置及线虫草属 *Ophiocordyceps* 系统发育树 A：*Ophiocordyceps* 属系统发育树；B：*Ophiocordyceps paraisarioidea* 及其近缘 *O. ravenelii* clade 物种系统发育树

Fig. 1 The phylogeny of *Ophiocordyceps* with emphasis on *Ophiocordyceps paraisarioidea* and its related species based on 5-locus (*nr*SSU, *nr*LSU, *tef-1α*, *rpb1*, and *rpb2*) datasets. A: Phylogeny of *Ophiocordyceps*; B: Phylogeny of *Ophiocordyceps paraisarioidea* and its related species.

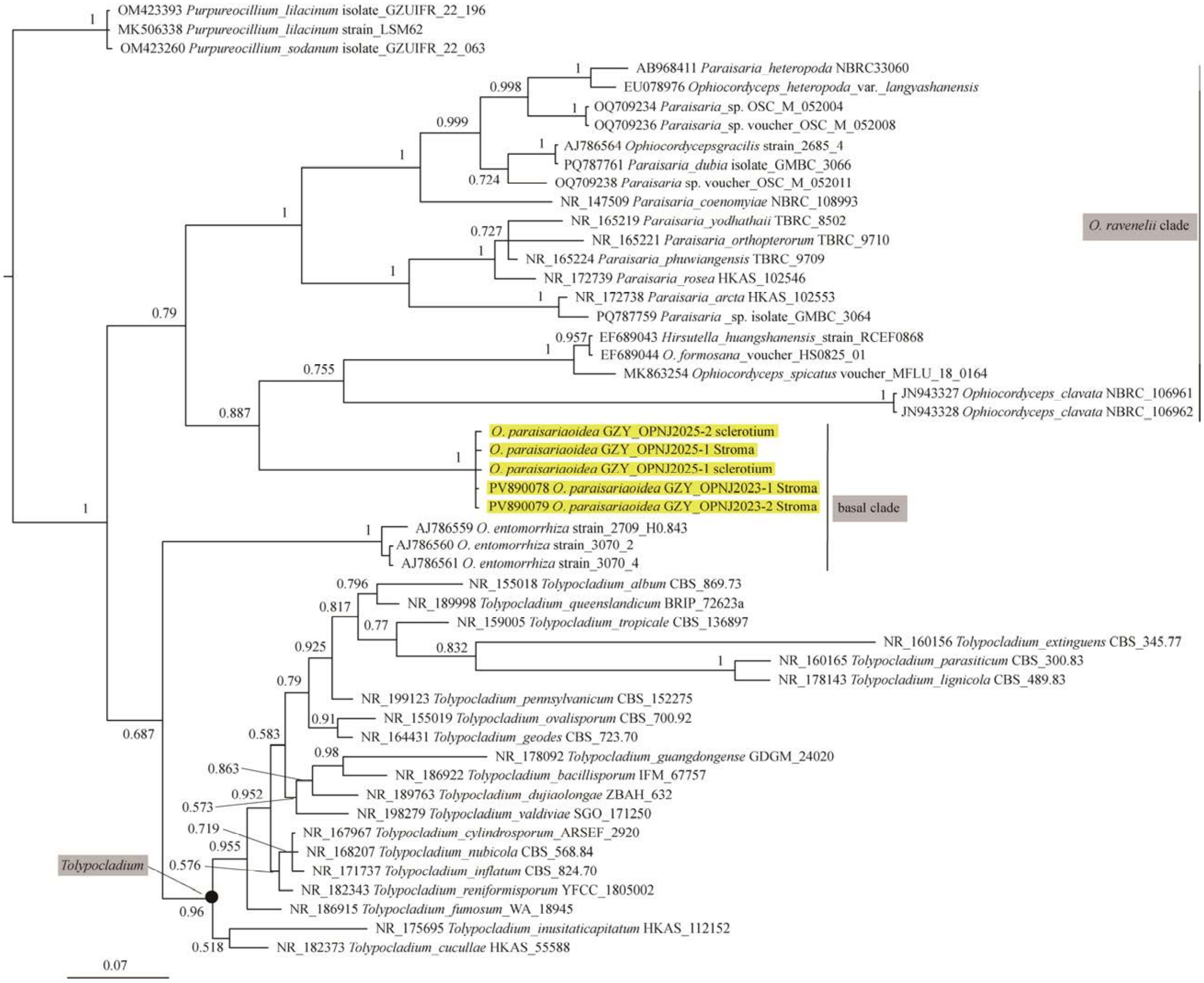

图 2 基于 **ITS** 序列的羽束梗孢状线虫草及其近缘种系统发育树

Fig. 2 Phylogeny of *Ophiocordyceps paraisarioidea* and its related species based on ITS sequences.

Fertile part: The apex of stromata enlarges into a globose fertile part when mature. 0.5–1.0 cm × 0.2–0.5 cm.

Perithecia: densely arranged on ascocarp, nearly vertically embedded, ellipsoid to cylindrical. 550–710 × 150–230 μm.

Asci: cylindrical, tail slender, some with a narrower neck, thickened in the middle, multi-spored, 150–375 × 3.0–4.75 μm.

Ascus cap: hemispherical, 3.0–4.8 × 1.5–3.4 μm.

Ascospores: filiform, non-disarticulating. 150–278 × 1.8–3.3 μm. Septa fusiform, 6.2–13.8 × 1.8–2.5 μm.

Distribution and Habitat: the forest of Lanping in Henduan Mountains, Yunnan, southwest of China.

Additional specimens examined: GZY_OPNJ2023-2,-3...-8 (7 samples) (Fig. 3A). Yunnan Province: Lanping county, on larva of species of Lepidoptera, burried in soil, July 2023, collected by Yongdong Dai and Dehua Hou. GZY_OPNJ2025-1...-10 (10 samples), collected by Chenxin Chang and Yongdong Dai in Lanping, August 2025.

寄生于鳞翅目昆虫幼虫，寄主体长 2.6–4.0 cm × 0.3–0.4 cm。子座从寄主头部生出，长 5.0–10.0 cm，呈棍棒状，实心，木质化，通常单生，少数自中部分枝 2–5 个，整体深褐色，顶端灰白。成熟时子座顶端膨大形成球形可孕部，大小为 0.5–1.0 cm × 0.2–0.5 cm。子囊壳密集排列于子实体表面，近乎垂直埋生，椭圆至圆柱形，550–710 × 150–230 μm。子囊圆柱形，尾部细长，

部分具细颈，中部稍增厚，内含多个子囊孢子，150–375 × 3.0–4.75 μm，顶端具半球形子囊帽，3.0–4.8 × 1.5–3.4 μm。子囊孢子丝状，分隔不断裂，隔细胞呈梭形，6.2–13.8 × 1.8–2.5 μm。

羽束梗孢状线虫草与虫根线虫草在系统发育位置中接近，二者均产生类似于 *Parisaria*-like 的球形可孕部顶端，且子囊壳均为埋生，在子座形态上与 *Paraisaria* 属物种相似。但 *Paraisaria* 的子座颜色较浅，而羽束梗孢状线虫草与虫根线虫草子座偏深褐色，且在球形可孕部上的子囊壳顶端形成小突起，而 *Paraisaria* 相对平整无明显突起。另一个显著区别在于 *Paraisaria* 属物种子囊孢子断裂成 10 μm 左右的小节，而羽束梗孢状线虫草与虫根线虫草，子囊孢子分隔不断裂(表 3)。

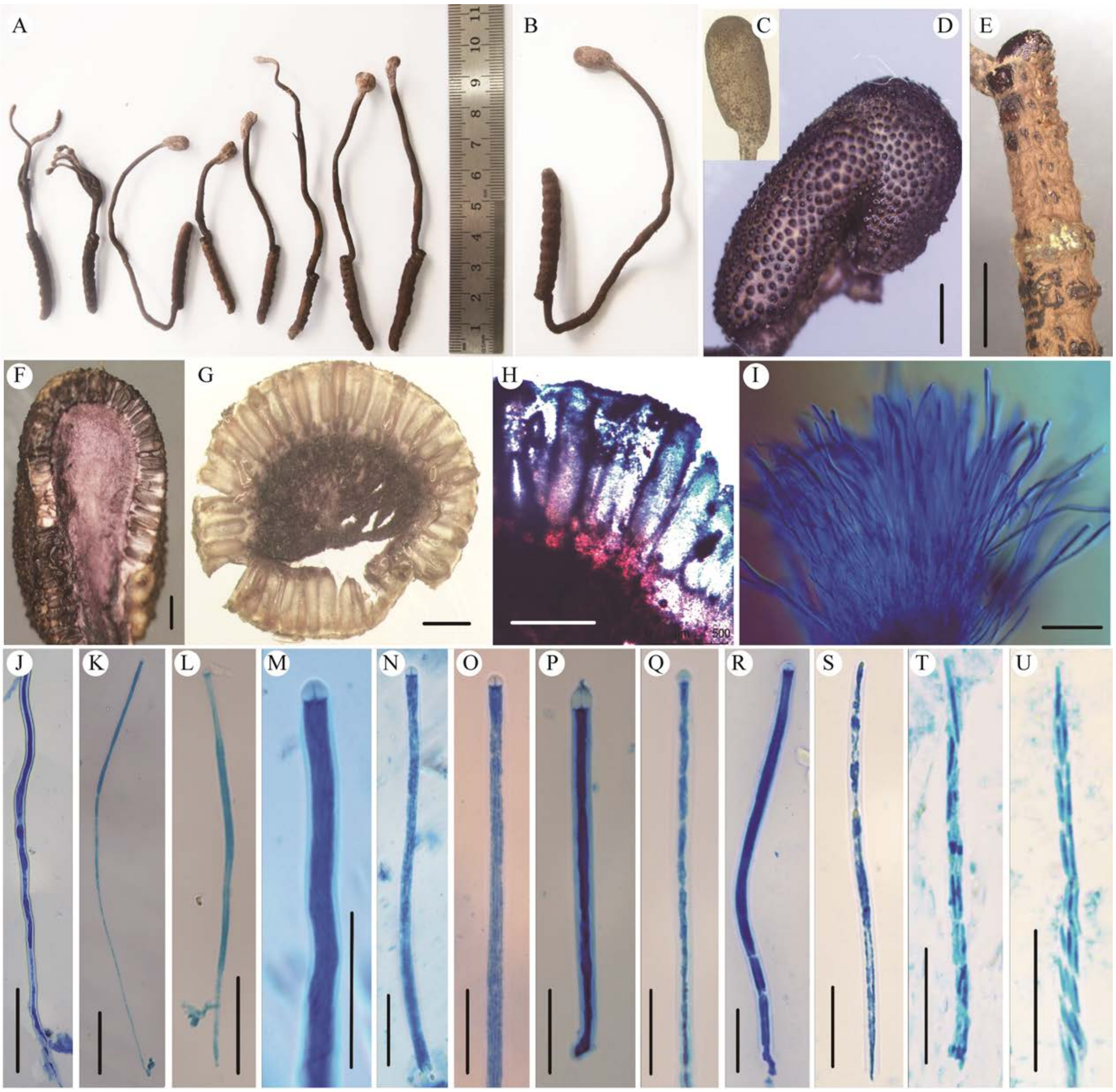

图 3 羽束梗孢状线虫草形态特征 A：标本形态特征；B：模式标本 GZY_OPNJ2023-1 形态特征；C, D：球状可孕部特征(不同标本)；E：寄主形态特征；F–H：埋生子囊壳特征；I–S：单个子囊、子囊帽结构特征；T, U：分隔不断裂的子囊孢子结构特征；标尺：D=1 mm；E=1 cm；F–H=500 μm；I=100 μm；O–Q=50 μm；J–N, R–U=20 μm

Fig. 3 Morphological characteristics of *Ophiocordyceps paraisarioidea*. A: Morphological characteristics; B: Holotype: GZY_OPNJ2023-1; C, D: The globose fertile part; E: Host morphological characteristics; F–H: Perithecia; I–S: Filiform ascus and ascospore; T, U: Non-disarticulating ascospores. Scale bars: D=1 mm, E=1 cm, F–H=500 μm; I=100 μm; O–Q=50 μm; J–N, R–U=20 μm.

表 3 羽束梗孢状线虫草与其近缘种的形态及显微形态特征比较

Table 3 Comparison of macro- and micromorphological characteristics of *Ophiocordyceps paraisarioidea* and its closely related species

物种 Species	寄主 Host	分布 Distribution	子座 Stromata	可孕部 Fertile part	子囊壳 Perithecium/μm	子囊 Asci	子囊孢子 Ascospore	文献引证 Reference
O. paraisarioidea	Larva of Lepidoptera	Yunnan, China	5.0–9.0 cm	Globose to ellipsoidal, at the tip of stromata, 5–8 mm × 2–4 mm	Immersed, ellipsoid to cylindrical, 550–710 × 150–230 μm	150–375 × 3.0–4.75 μm	Filiform, non-disarticulating, 150–178 × 1.8–3.3 μm	本研究 This study
O. entomorrhiza	Tenebrionidae, Lampyridae (Coleoptera)	Asia, Europe	3.5–6.2 cm	Globose, at the tip of stromata, 2–3 mm × 2 mm	Immersed, 600–950 × 230–400 μm	300–600 × 4–6 μm	Filiform, non-disarticulating septa, 6–8 (10) × 1.5–2 μm	Kiyoshi 2000
Paraisaria dubia (=*O. gracilis*)	Larva of Hepialidae (Lepidoptera)	Africa, America, Asia, Europe	4.0–9.0 cm	Globose to ellipsoidal, red ochreous to pale orange, 4–9 mm × 4–7 mm	Immersed, elongate to oviform, (320–)560–840 × 200–360 μm	(200–)400–530 × 5–8 μm	Filiform, disarticulating, second ascospore, 5–9 × 1.5–2 μm	梁宗琦等 1995 Liang *et al.* 1995
Par. gracilioides	Larva of Elateridae (Coleoptera)	Bolivia, China, Colombia, Japan and Mexico	2.0–9.0 cm	Spherical, pale rufous, 4–5.5 mm	Immersed, ellipsoidal to naviform, 680–900 × 200–280 μm	450–700 × 5–6.5 μm	Filiform, disarticulating, second ascospore, 7–12 × 1–2 μm	樊美珍等 2001 Fan *et al.* 2001
Par. arcta	Larva of Lepidoptera	Guizhou, China	1.6 cm	Subglobose with constriction at center, white, 2 mm× 3 mm	Immersed, ampulliform to ellipsoidal, 230–530 × 70–180 μm	100–180 × 2–4 μm	Filiform, disarticulating, second ascospore, 2.6–4.2 ×0.5–1.3 μm	Wei *et al.* 2021

羽束梗孢状线虫草与虫根线虫草相比，最显著的差异是前者寄主为鳞翅目一种蛾类幼虫，而后者寄主为鞘翅目幼虫及成虫。此外，*O. entomorrhiza* 子座偏黑，且容易产生 *Tilachlidiopsis*-like 孢梗束(Kobayasi 1937；Bałazy 1982)，而 *O. paraisarioidea* 子座偏褐色，未观察到 *Tilachlidiopsis*-like 孢梗束(表 3)。

3 讨论

本文报道了一个线虫草属新物种，命名为羽束梗孢状线虫草，其与虫根线虫草在子座形态上均与 *Paraisaria* 属物种相似，均在子座顶端产生球形可孕部，且子囊壳均为埋生(表 3)，容易误将羽束梗孢类群错误当成虫根线虫草(Kobayasi 1937；Pérez-Villamares *et al*. 2017)。从形态特征来看，*Paraisaria* 属物种子座颜色较浅，而羽束梗孢状线虫草与虫根线虫草通常子座偏深褐色，在球形可孕部上的子囊壳顶端通常形成小突起，而 *Paraisaria* 相对平整。本物种与虫根线虫草相比，寄主类型、子座颜色和质地等均有显著区别。从 5 基因系统发育树看，*O. paraisarioidea*、*O. entomorrhiza* 与 *Tilachlidiopsis nigra* 位于线虫草属基部，形成一个独立的分支(basal clade)。另外，ITS 序列的系统发育结果也显示 *O. paraisarioidea* 和 *O. entomorrhiza* 与 *O.ravenelii* clade 有紧密的亲缘关系。我们的研究较好地补充了线虫草属基部分支类群的物种多样性。该类群可能代表了线虫草属早期演化过程中一类形态与寄主特征多样、系统位置关键类型，对深入理解线虫草属的起源与早期辐射具有重要意义。从地理分布看，*O. entomorrhiza* 分布于日本和欧洲，而本文报道的 *O. paraisarioidea* 目前仅见分布于中国西南生物多样性热点地区——横断山区，可能横断山区复杂的地形地貌和多样的生态环境为线虫草属基部类群的分化和 *O. paraisarioidea* 的物种形成提供了生态位基础，显示该区域在物种形成与适应中的重要作用。

分子系统发育已成为当下物种识别鉴定及系统发育重要的研究手段(James *et al*. 2006；Spatafora *et al*. 2006；Sung *et al*. 2007a；Yang & Rannala 2012)，因此序列的有效性和完整性尤为关键。近年来，多基因系统发育逐渐取代单基因分析，成为线虫草属分类与系统发育研究的主流方法(Chen *et al*. 2013；Sanjuan *et al*. 2015；代永东 2018；Araújo & Hughes 2019；邹维秋 2022；Tang *et al*. 2023；杨涛 2023；Dai *et al*. 2024；周云 2024；Xu *et al*. 2025)。与单基因相比，多基因系统发育具备一定的容错能力，即允许部分基因缺失而不显著影响结果。本研究对多系统发育分析所用 5 个基因的序列情况进行统计发现，不同基因存在不同程度的缺失(有效数据量：*nr*SSU 337、*nr*LSU 388、*tef-1α* 426、*rpb1* 401、*rpb2* 257)，其中 *rpb2* 缺失最为严重，达到 46% (202/439)。本研究在开展 *O. paraisarioidea* 的分子测序过程中，成功扩增了 ITS、*nr*SSU、*nr*LSU、*tef-1α* 和 *rpb1* 基因，但 *rpb2* 基因可能由于引物特异性不足或与目标物种序列匹配度较低等原因，经过多标本多次扩增，仍未获得目标序列。在系统树构建过程中，我们将 *O. paraisarioidea* 的 *rpb2* 基因标注为“missing data”，所得结果在主要分支上的支持度依然较高，且 ML 和 BI 两种分析方法所得拓扑结构一致，能够有效解析 *O. paraisarioidea* 的系统发育位置，并为其分类地位提供可靠的分子证据。但是需要注意的是，数据缺失不可避免地会对系统发育分析结果产生影响，应尽量减少此类情况的发生。后续应该设计更具有针对性的特异性引物，以补充相关数据。

本研究在构建线虫草属系统发育关系时，将寄主类型映射至线虫草属系统发育树上(图 1A)，发现 *O. paraisarioidea* 所属的线虫草属基部分支(Basel clade)及其近缘的 *O. ravenelii* clade 的已知寄主均为鞘翅目昆虫[虽 *O. variabilis* 寄主为双翅目食木虻幼虫，但与鞘翅目幼虫习性相似(Hodge *et al*. 1998)]，而本研究报道的 *O. paraisarioidea* 却以鳞翅目为寄主。这一“特例”打破了该分支对寄主类型的传统一致性，为 Araújo & Hughes (2019)提出的“线虫草属以鞘翅目为祖先寄主”的假说提供了新的视角，提示这

一观点或需进一步探讨。这一发现暗示线虫草属在早期演化过程中可能存在更为复杂或多次发生的寄主转换事件，或在特定生态环境下形成了对非典型寄主的适应能力。尤其是在中国横断山区这一生态多样性极高的区域，宿主可获得性和环境选择压力可能促成了物种对鳞翅目等其他昆虫类群的利用，进而推动其生态位扩展和系统发育分化。

Paraisaria 是 Samson & Brady (1983)根据 *Ophiocordyceps gracilis* 的无性阶段特征即白色松散的束状孢梗束，轮生分枝的分生孢子梗，梗上具瓶状、以顶端增生方式繁殖的瓶梗，形成易聚集成孢子头状的单个透明的分生孢子而建立。Sung *et al*. (2007a)基于多基因系统发育研究将该属并入 *Ophiocordyceps* 属中。随后，Mongkolsamrit *et al*. (2019)认为 *Paraisaria* 在形态学上具有明显区别，且系统发育上形成一个相对独立且支持率较高的单系类群，因而将其从 *Ophiocordyceps* 中恢复为独立属。然而，尽管 *Paraisaria* 的形态特征具有较强的识别性，其属级地位在系统发育上仍缺乏充分支持，从本研究的结果来看，该类群位于 *O. ravenelii* clade 分支内，且嵌套于 *Ophiocordyceps* 属的系统发育框架之中(非单独分支)。因此目前尚不足以支持其作为一个独立属。当前 *Ophiocordyceps* 属内界限与谱系关系仍存在争议，亟须依托更全面深入的数据、形态特征及生态信息进行综合解析，以推动该属系统分类的进一步厘清和优化。

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