

板栗枝枯病相关的壳囊孢属一新种

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摘要: 板栗枝枯病和溃疡病是板栗栽培中的常见病害, 对树木健康和板栗产量造成一定影响。在开展全国板栗栽培区病害调查的基础上, 采集贵州省黔南州望谟县的板栗枝枯标本, 采用组织分离法和单孢分离法获取病原菌菌株, 结合形态学特征和分子系统学分析对分离的菌株进行鉴定。新获得的菌株 CFCC 71068 和 N317B 代表壳囊孢属的 1 个新物种, 命名为微孢壳囊孢 *Cytospora minispora*。研究结果丰富了板栗病原菌的种类, 为后续的分类研究和病害防控提供基础资料。

关键词: 子囊菌; 间座壳目; 分子系统学; 鉴定; 板栗; 壳囊孢属

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A new species of *Cytospora* associated with Chinese chestnut dieback disease

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Abstract: Chinese chestnut (*Castanea mollissima*) dieback and canker diseases are common in plantations, affecting tree health and nut yield. Based on the nationwide disease survey of chestnut cultivation areas, fungal strains associated with diseases were obtained by tissue isolation and single-spore isolation methods from samples collected in Wangmo County, Qiannan Prefecture, Guizhou Province, China. Isolates were identified by combined morphological characteristics and molecular phylogeny. As a result, isolates CFCC 71 068 and N317B represent a new species of the genus *Cytospora*, named *Cytospora. minispora*. The results enrich the category of chestnut pathogens and provide foundational data for subsequent taxonomic studies and disease control.

Key words: Ascomycota; Diaporthales; molecular phylogeny; identification; *Castanea mollissima*; *Cytospora*

板栗 *Castanea mollissima* Blume 是我国重要的经济林树种, 适应性强, 分布广泛, 兼具生态防护、生产栗实和提供木材等功能。然而, 栗疫病、溃疡病、枝枯病、叶斑病和实腐病等多种病害的发生极大地制约了板栗栽培及相关产业的发展(姜宁, 2021)。

板栗枝枯病常见于管理粗放的栗园, 多发生在小枝条上, 很少为害主干。罹病枝条上初见不规则褐色病斑, 随后病斑快速扩展, 蔓延至整个枝条皮层, 一周后小枝即枯死, 病死枝条表皮密生病原菌的黑褐色子实体(谢宝多, 1998; Jiang et al., 2020; 姜宁, 2021)。壳囊孢属 *Cytospora* 的多个病原菌常常引起板栗枝枯病, 包括栗生壳囊孢 *Cytospora castaneicola*、拟角壳囊孢 *C. ceratospermopsis*、宽城壳囊孢 *C. kuanchengensis*、核果壳囊孢 *C. leucostoma*、舒氏壳囊孢 *C. schulzeri* 和兴隆壳囊孢 *C. xinglongensis*(Jiang et

al., 2020; Lin et al., 2024)。其中栗生壳囊孢、宽城壳囊孢和兴隆壳囊孢是我国的特有种。

壳囊孢属隶属间座壳目 Diaporthales 壳囊孢科 Cytosporaceae, 多数种类是木本植物的病原菌、内生菌或腐生菌(Rossman et al. 2007; Abreu et al. 2010; Senanayake et al. 2017, 2018; 姜宁等, 2018)。该属物种的子囊孢子和分生孢子呈腊肠形, 单胞, 透明, 形态特征明显, 易于鉴定到属级阶元(Adams et al. 2006; Lawrence et al., 2018; Pan et al., 2020; Li et al., 2024)。但属内物种数量较多, 而且一个寄主上往往有多种形态相似的壳囊孢真菌, 仅靠形态特征和寄主信息较难鉴定到种级分类阶元(Fan et al., 2020; Lin et al., 2024; Bozorov et al., 2024; Zhao et al., 2024)。目前, 壳囊孢属的分类和鉴定主要依赖于形态特征并结合基于 ITS-*act-rpb2-tefl-tub2* 多基因序列分析(Fan et al., 2020;

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Lin et al., 2024)。

我国栽培和野生板栗上的子囊菌种类较为丰富, 包括一些溃疡病及枝枯病的病原菌类群, 如棒盘孢属 *Coryneum*、壳囊孢属 *Cytospora*、间座壳属 *Diaporthe*、枝腐壳属 *Dendrostoma* 和拟日规壳属 *Gnomoniopsis* 等(姜宁, 2021)。本研究在贵州板栗产区进行病害调查时发现了典型的壳囊孢枝枯病样本, 利用形态学特征和多基因分子系统学分析对菌株进行分类鉴定。

1 材料与方法

1.1 病害调查、采样与分离

于2024年夏季在贵州省进行南方板栗病害种类及分布调查, 观察枝枯病症状并拍照记录(图1)。用枝剪将发病的枝条剪成20 cm长的小段, 放入纸质的标本袋保存, 记录采集地、经纬度、海拔、采集人、寄主、采集日期等信息, 及时带回实验室进行菌株分离和形态学观察。



图1 板栗枝枯病症状

Fig. 1 Symptoms of Chinese chestnut dieback disease

注: A. 受害寄主症状; B. 受害枝条症状。

Notes: A. Symptoms of the diseased host; B. Symptoms of the diseased branches.

选择发病前期的枝条, 采用组织分离法和单孢分离法对真菌菌株进行组织分离, 首先用无菌水冲洗枝条表面后晾干, 削开表皮切取病健交界处约5 mm²的韧皮部组织, 在75%乙醇中消毒1 min后用无菌水漂洗3次, 用无菌脱脂棉吸干组织块水分后移至PDA平板, 每平板均匀放置5个组织块, 置于25℃恒温避光培养箱培养。当组织块周边生出菌丝后在体视显微镜下挑取菌丝尖端移至新PDA平板获得纯净菌落。单孢分离法针对已产生子实体的样本, 从分生孢子器腔室中用无菌针头挑取分生孢子团, 溶于适量无菌水中, 涂布至PDA平板, 待平板上形成肉眼可见的菌落后, 将其转移到新PDA平板获得纯净菌落。模式菌株保藏在中国林业菌种保藏管理中心(CFCC, <https://cfcc.caf.ac.cn/>), 模式标本保存在中国林

业科学研究院标本馆(CAF, <http://museum.caf.ac.cn/>)。

1.2 形态学研究

病原菌及菌株的形态研究主要基于病死枝条上形成的子实体, 包括子实体的着生状态、颜色、尺寸、结构(蔡司体视显微镜 Discovery V8), 产孢结构和分生孢子的形状、颜色和尺寸(奥林巴斯光学显微镜 BX51)。PDA培养基上菌落的生长速度、质地、颜色等也一并观察记录。

1.3 分子系统学分析

采用CTAB法提取菌株的DNA(Doyle, 1991), 利用引物对ITS5/ITS4, ACT512F/ACT728R, RPB2-5f2/RP-B2-7cR, EF1-688F/EF1-1251R和Bt2a/Bt2b扩增rDNA内转录间隔区(the nuclear ribosomal DNA ITS1-5.8S-ITS2, ITS)、肌动蛋白(the partial actin gene, *act*)、RNA合成酶第二亚基(the second largest subunit of RNA polymerase II, *rpb2*)、转录延长因子(the translation elongation factor 1, *tef1*)和微管蛋白(beta tubulin, *tub2*)基因片段(White 1990; O'Donnell and Cigelnik 1997; Carbone and Kohn 1999; Liu et al., 1999)。PCR程序设定参考Fan et al. (2020), 扩增产物经1%琼脂糖凝胶电泳检测, 送至北京睿博兴科生物技术有限公司测序。

本研究获得的序列及参考序列见表1, 设定越橘间座壳(*Diaporthe vaccinii*)为外群。使用MAFFT v. 7进行序列对齐, 并用MEGA7对部分未对齐的碱基进行手动调整(Kumar et al., 2016; Katoh et al., 2019)。利用RAxML v. 8.0进行最大似然法(maximum likelihood)分析, 分子系统树用FigTree v.1.3.1导出并在Adobe Illustrator CS5中进行编辑(Stamatakis, 2014)。

2 结果与分析

2.1 分子系统学分析

基于ITS-*act-rpb2-tef1-tub2*多基因序列构建的壳囊孢属的分子系统发育树如图2所示, 共包含44个菌株, 其中越橘间座壳 *Diaporthe vaccinii* 为外群。本研究从板栗病枝上分离获得的菌株CFCC 71068和N317B形成1个单独的分枝, 邻近槭生壳囊孢 *Cytospora acericola*、榄李生壳囊孢 *C. lumnitzericola*、屏边壳囊孢 *C. pingbianensis* 和侧柏壳囊孢 *C. platycladi*。因此, CFCC 71068和N317B代表壳囊孢属潜在的新物种, 经形态学和序列分析鉴定为微孢壳囊孢(*Cytospora minispora*)。

2.2 分类学

微孢壳囊孢(新种)

Cytospora minispora Ning Jiang, sp. nov. (Fig. 3)

表1 分子系统学研究中使用的菌株及序列号

Tab. 1 Isolates and GenBank accession numbers used in the molecular phylogenetic analyses.

种名 Species	菌株号 Isolates	国家 Country	序列号 GenBank accession numbers				
			ITS	<i>act</i>	<i>rpb2</i>	<i>tefl</i>	<i>tub2</i>
阿比西尼亚壳囊孢 <i>Cytospora abyssinica</i>	CBS 116 819*	埃塞俄比亚	PP988703	PQ074579	PQ074884	PQ074244	PQ075201
	CBS 117 004	埃塞俄比亚	PP988702	PQ074578	PQ074883	PQ074243	PQ075200
槭生壳囊孢 <i>Cytospora acericola</i>	CFCC 55 994*	中国	PP988705	PQ074581	PQ074886	PQ074246	PQ075203
	CFCC 55 995*	中国	PP988706	PQ074582	PQ074887	PQ074247	PQ075204
	CFCC 58 486	中国	PP988704	PQ074580	PQ074885	PQ074245	PQ075202
清迈壳囊孢 <i>Cytospora Chiangmaiensis</i>	MFLUCC 21-0049*	泰国	MZ356514	MZ451157	MZ451165	MZ451161	NA
素贴壳囊孢 <i>Cytospora diopuiensis</i>	CFCC 55 884	中国	OK316819	NA	OK358569	OK358471	OK358473
	CFCC 55 885	中国	OK316820	NA	OK358470	OK358472	OK358474
	MFLUCC 18-1 419*	泰国	MK912137	MN685819	NA	NA	NA
意大利壳囊孢 <i>Cytospora italica</i>	CBS 112 156	未知	PP988864	NA	NA	PQ074389	NA
	MFLUCC 14-0440*	意大利	KU900329	NA	NA	NA	NA
榄李生壳囊孢 <i>Cytospora lumnitzericola</i>	MFLUCC 17-0508*	泰国	MG975778	MH253457	NA	NA	NA
绿心壳囊孢 <i>Cytospora lxviniensis</i>	CFCC 56 780*	中国	PP988909	PQ074739	PQ075058	PQ074432	PQ075371
	CFCC 56 803*	中国	PP988910	PQ074740	PQ075059	PQ074433	PQ075372
微孢壳囊孢 <i>Cytospora minispora</i>	CFCC 71 068*	中国	PQ623380	PQ619110	PQ619112	PQ619114	PQ619116
	N317B	中国	PQ623381	PQ619111	PQ619113	PQ619115	PQ619117
尼什克壳囊孢 <i>Cytospora nitschkei</i>	CBS 116 854*	埃塞俄比亚	PP988927	PQ074755	PQ075074	PQ074448	PQ075388
掌状壳囊孢 <i>Cytospora palmoides</i>	CFCC 58 443	中国	PP988930	PQ074758	PQ075077	PQ074451	PQ075391
	CFCC 58 445	中国	PP988931	PQ074759	PQ075078	PQ074452	PQ075392
	CFCC 58 451	中国	PP988932	PQ074760	PQ075079	PQ074453	PQ075393
	CXY 1 280*	中国	JN411939	NA	NA	KJ781297	NA
大沙叶壳囊孢 <i>Cytospora pavettae</i>	CBS 145 562*	南非	MK876386	MK876457	MK876483	MK876497	MK876503
彭世洛壳囊孢 <i>Cytospora phitsanulokensis</i>	MFLUCC 21-0046*	泰国	MZ356517	MZ451160	MZ451168	MZ451164	MZ451172
屏边壳囊孢 <i>Cytospora pingbianensis</i>	MFLUCC 18-1 204*	中国	MK912135	MN685817	MN685826	NA	NA
侧柏壳囊孢 <i>Cytospora platycladi</i>	CFCC 50 504*	中国	MH933645	MH933552	MH933610	MH933516	MH933581
	CFCC 50 505	中国	MH933646	MH933553	MH933611	MH933517	MH933582
	CFCC 50 506	中国	MH933647	MH933554	MH933612	MH933518	MH933583
甘蔗壳囊孢 <i>Cytospora sacchari</i>	CBS 160.33	印度	PP988977	PQ074800	PQ075118	NA	NA
娑罗双壳囊孢 <i>Cytospora shoreae</i>	MFLUCC 21-0047*	泰国	MZ356515	MZ451158	MZ451166	MZ451162	MZ451170
	MFLUCC 21-0048	泰国	MZ356516	MZ451159	MZ451167	MZ451163	MZ451171
桧柳生壳囊孢 <i>Cytospora tamaricicola</i>	CFCC 50 507	中国	MH933651	MH933559	MH933616	MH933525	MH933587
	CFCC 50 508*	中国	MH933652	MH933560	MH933617	MH933523	MH933588
	CFCC 58 268	中国	PP989016	PQ074835	PQ075157	PQ074531	PQ075468
	CFCC 58 482	中国	PP989017	PQ074836	PQ075158	PQ074532	PQ075469
	CFCC 59 052	中国	PP989018	PQ074837	PQ075159	PQ074533	PQ075470
泰国壳囊孢 <i>Cytospora thailandica</i>	MFLUCC 17-0262*	泰国	MG975776	MH253459	NA	NA	NA
	MFLUCC 17-0263	泰国	MG975777	MH253460	NA	NA	NA
绿座壳囊孢 <i>Cytospora viridistroma</i>	CBS 116 811*	刚果	PP989051	NA	NA	NA	NA
	CBS 116 812	刚果	PP989052	PQ074864	PQ075182	PQ074558	PQ075494
	CBS 116 813	委内瑞拉	PP989053	PQ074865	PQ075183	PQ074559	PQ075495
	CBS 117 011	哥伦比亚	PP989056	PQ074866	NA	PQ074560	PQ075496
兴隆壳囊孢 <i>Cytospora xinglongensis</i>	CFCC 52 458*	中国	MK432622	MK442946	MK578082	NA	NA
	CFCC 52 459	中国	MK432623	MK442947	MK578083	NA	NA
木果棟壳囊孢 <i>Cytospora xylocarpi</i>	CBS 116 861	泰国	PP989069	PQ074878	PQ075195	PQ074573	PQ075506
	MFLUCC 17-0251*	泰国	MG975775	MH253458	NA	NA	NA
越橘间座壳 <i>Diaporthe vaccinii</i>	CBS 160.32	美国	KC343228	JQ807297	NA	KC343954	KC344196

注: NA表示序列缺失, *表示模式菌株, 本研究中的菌株及序列加粗标示。

Note: NA means not applicable and * represents the ex-type isolates. Isolates from the present study are marked in bold.

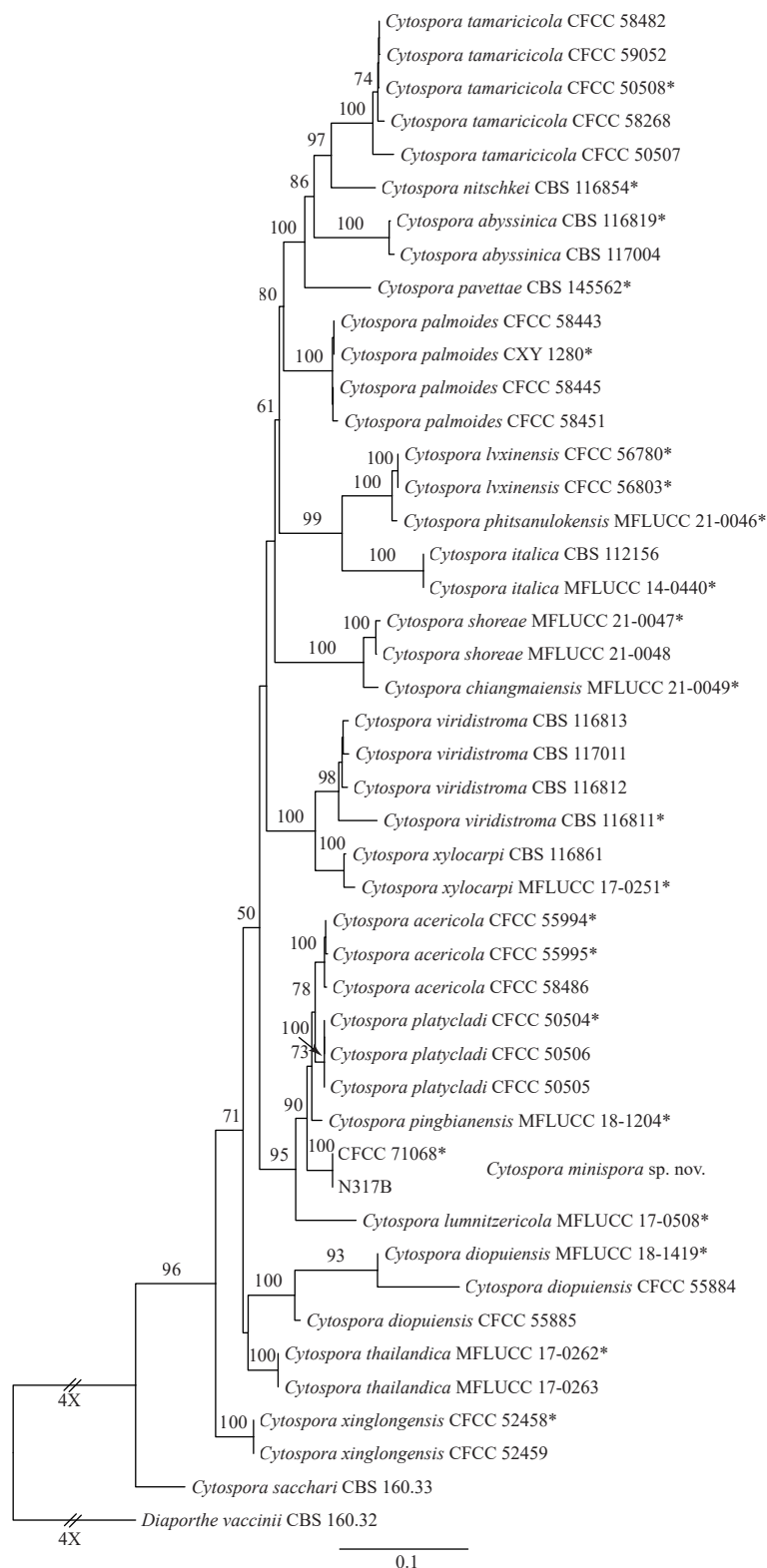


图 2 基于 ITS, *act*, *rpb2*, *tef1* 和 *tub2* 序列的壳囊孢属分子系统学分析

Fig. 2 Phylogenetical tree of *Cytospora* of ML analysis on basis of combined ITS, *act*, *rpb2*, *tef1* and *tub2* sequences

Mycobank: MB856576

Etymology: Referring to its small conidia.

Conidiomata pycnidial, immersed in bark, erumpent when mature, discoid to conical, (650~900) μm diam, with

multi-locule. *Ectostromatic disc* grey to brown, (250~350) μm diam, with single ostiole per disc in the centre. *Ostiole* circular, black, (50~75) μm diam. *Locules* independent, sharing one ostiole. *Conidiophores* hyaline, branched,

(9~21.5) × (1~2) μm. *Conidiogenous cells* phialidic, subcylindrical to cylindrical, (7~9.5) × (1~2) μm. *Conidia* hyaline, unicellular, allantoid, (3~4) × (1~1.5) μm (av = (3.7 × 1.4) μm). *Colonies* on PDA initially white, growing fast and covering the 9-cm-diam Petri dish after 5 d, with flocculent aerial mycelium and turning grey after 15 d.

Material examined: CHINA, Guizhou Province, Qiannan Buyei and Miao Autonomous Prefecture, Wangmo County, Chinese chestnut plantation, from diseased branches of *Castanea mollissima*, Ning Jiang, Shuji Li & Yingying Wu, 23 Jul. 2024 (holotype CAF800099; ex-type culture CFCC 71 086); Guizhou Province, Qiannan Buyei

and Miao Autonomous Prefecture, Wangmo County, Chinese chestnut plantation, from diseased branches of *C. mollissima*, Ning Jiang, Shuji Li & Yingying Wu, 23 Jul. 2024 (culture N317B).

Notes: *Cytospora minispora* proposed in this study is phylogenetically close to *C. acericola*, *C. lumnitzericola*, *C. pingbianensis* and *C. platycladi* (Fig. 2). *C. acericola*, *C. lumnitzericola*, and *C. platycladi* were described with their asexual morphs, while *C. lumnitzericola* was only described with its sexual morph, hence we can compare *C. minispora* with *C. acericola*, *C. lumnitzericola*, and *C. platycladi* in their asexual morph (Norphanphoun et al.,

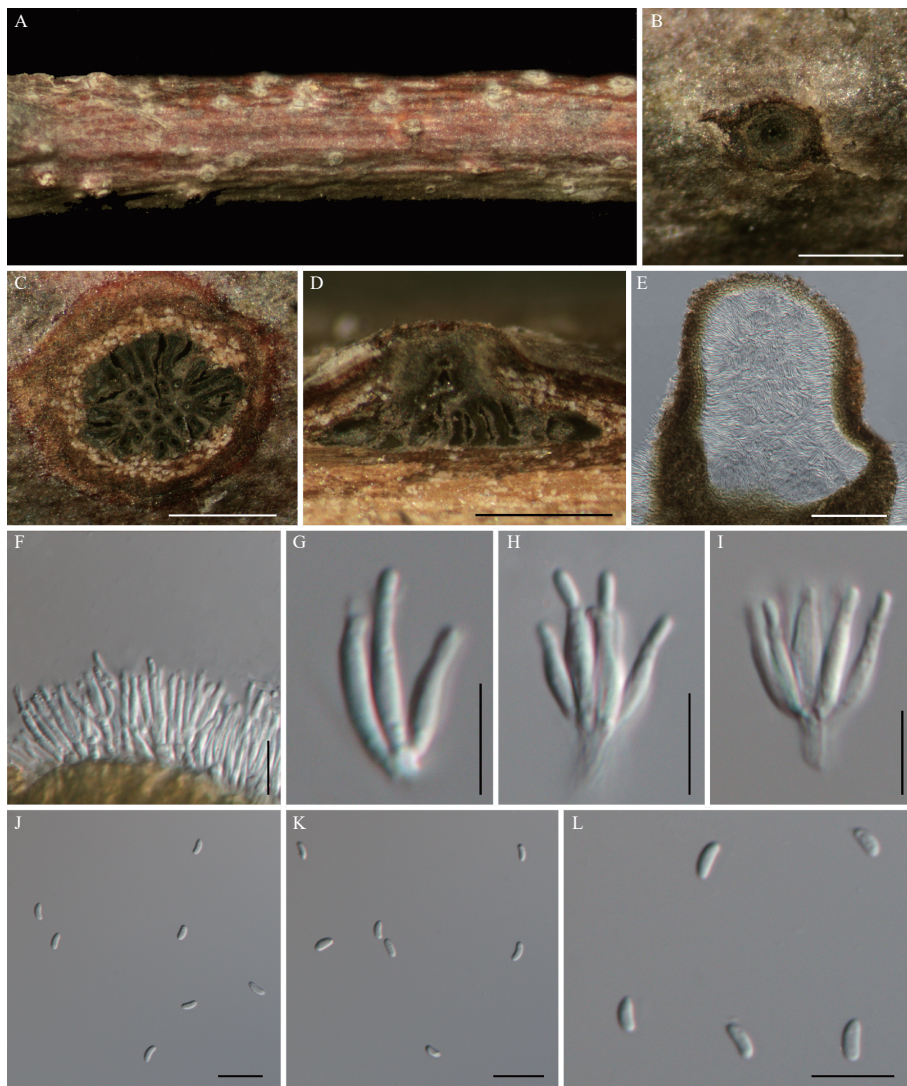


图3 微孢壳囊孢的形态特征 (CAF800099)

Fig. 3 Morphology of *Cytospora minispora* (CAF800099)

注: A, B: 病死板栗枝条上的分生孢子器; C, E: 分生孢子器横切面; D: 分生孢子器纵切面; F: 分生孢子梗及产孢细胞; G, H, I: 产孢细胞及初生的分生孢子; J, K, L: 分生孢子。

Notes: A, B: Habit of conidiomata on the cankered branches of *Castanea mollissima*; C, E: Transverse section through conidiomata; D: Longitudinal section through conidiomata; F: Conidiophores and conidiogenous cells; G, H, I: Conidiogenous cells giving rise to conidia; J, K, L: Conidia. Scale bars: B–D = 500 μm; E = 300 μm; F–L = 10 μm.

2018; Fan et al., 2020; Shang et al., 2020; Lin et al., 2024). *C. minispora* can be distinguished from *C. acericola* by smaller ostiole (50~75) μm vs. (130~220) μm , from *C. lumnitzericola* and *C. platycladi* by shorter conidia (3~4) \times (1~1.5) μm vs. (4~4.5) \times (1~3) μm in *C. lumnitzericola* vs. (4.5~5) \times (1~1.5) μm in *C. platycladi* (Norphanphoun et al., 2018; Fan et al., 2020; Lin et al., 2024).

词源学: 种加词指该种较小的分生孢子。

分生孢子体为分生孢子器型, 初埋生, 成熟后突出寄主表皮, 盘状至圆锥状, 直径(650~900) μm , 内含多腔室。顶盘灰褐色, 直径(250~350) μm , 中间生1小孔。小孔圆形, 黑色, 直径(50~75) μm 。各腔室独立, 不共用腔室壁, 共用孔口。分生孢子梗透明, 分枝(9~21.5) \times (1~2) μm 。产孢细胞瓶梗式, 近圆柱形至圆柱形, (7~9.5) \times (1~2) μm 。分生孢子透明, 单胞, 腊肠形, (3~4) \times (1~1.5) μm , $av = (3.7 \times 1.4)\mu\text{m}$ 。菌落在PDA培养基上初为白色, 生长迅速, 5 d后长满9 cm培养皿, 气生菌丝羊毛状, 15 d后转为灰色。

微孢壳囊孢与槭生壳囊孢、榄李生壳囊孢、屏边壳囊孢和侧柏壳囊孢的分子系统学亲缘关系较近(图2)。槭生壳囊孢、榄李生壳囊孢和侧柏壳囊孢仅被描述了无性型特征, 而屏边壳囊孢仅见有性型描述, 因此可通过无性特征型比较微孢壳囊孢与槭生壳囊孢、榄李生壳囊孢和侧柏壳囊孢(Norphanphoun et al., 2018; Fan et al., 2020; Shang et al., 2020; Lin et al., 2024)。微孢壳囊孢较槭生壳囊孢孔口小(50~75) μm vs. (130~220) μm ; 较榄李生壳囊孢和侧柏壳囊孢分生孢子短(3~4) \times (1~1.5) μm vs. (4~4.5) \times (1~3) μm vs. (4.5~5) \times (1~1.5) μm (Norphanphoun et al., 2018; Fan et al., 2020; Lin et al., 2024)。

3 讨论

本研究描述了与板栗枝枯病相关的壳囊孢属真菌的1个新物种——微孢壳囊孢 *Cytospora minispora*。截至目前, 中国板栗壳囊孢枝枯病相关真菌已发现7种, 分别是栗生壳囊孢、拟角质壳囊孢、宽城壳囊孢、核果壳囊孢、微孢壳囊孢、舒氏壳囊孢和兴隆壳囊孢(Jiang et al., 2020; Lin et al., 2024)。其中宽城壳囊孢的单腔室分生孢子器明显区别于其余6种壳囊孢的多腔室分生孢子器(Jiang et al., 2020; Lin et al., 2024)。此外, 产孢结构和分生孢子作为稳定的形态特征, 可用于区分物种。板栗上的7种壳囊孢中, 分生孢子长度这一指标可以用于区分多个物种。本文中新发表的微孢壳囊孢的长度明显小于拟角质壳囊

孢、宽城壳囊孢、核果壳囊孢、微孢壳囊孢、舒氏壳囊孢和兴隆壳囊孢; 但与栗生壳囊孢的分生孢子长度存在部分重叠(表2)。因此, 在区分板栗上的壳囊孢类群时, 基于多基因片段的系统发育学分析必不可少。

表2 板栗生壳囊孢的形态差异
Tab. 2 Difference of *Cytospora* species from *Castanea mollissima*.

壳囊孢物种 Species of <i>Cytospora</i>	产孢细胞尺寸/ μm Size of conidiogenous cells	分生孢子尺寸/ μm Size of conidia
栗生壳囊孢 <i>C. castaneicola</i>	(8.4~12.5) \times (0.9~1.4)	(3.4~5.4) \times (1~1.5)
拟角质壳囊孢 <i>C. ceratospermopsis</i>	(8.5~15.5) \times (1.5~2.5)	(5~6.5) \times (1~1.5)
宽城壳囊孢 <i>C. kuanchengensis</i>	(8.5~11) \times (1~1.5)	(6~7.5) \times (1~2)
微孢壳囊孢 <i>C. minispora</i>	(7~9.5) \times (1~2)	(3~4) \times (1~1.5)
核果壳囊孢 <i>C. leucostoma</i>	(9.5~21) \times (1~1.5)	(4.5~5.5) \times (1~1.5)
舒氏壳囊孢 <i>C. schulzeri</i>	(8.5~18.5) \times (1~2)	(4.5~6.5) \times (1~1.5)
兴隆壳囊孢 <i>C. xinglongensis</i>	(6.5~8.5) \times (1~1.5)	(8.5~9.5) \times (1~1.5)

壳囊孢属真菌可导致多种重要林木的腐烂病、溃疡病和枝枯病, 比如杨树 *Populus* spp. 腐烂病(Lin et al. 2023)、苹果 *Malus pumila* Mill. 溃疡病(Zhao et al. 2024)和柳树 *Salix* spp. 溃疡病(Fan et al. 2015; Lin et al. 2022)等。板栗上壳囊孢导致的溃疡病和枝枯病早在20世纪就有报道(谢宝多, 1998), 但由于板栗病害的普遍发生, 很多枯死枝条往往被当作其它病害处理, 从而掩盖了壳囊孢属真菌导致的枝枯病的存在。近年来, 有研究揭示了板栗上壳囊孢的多样性(姜宁, 2021), 但病原菌的区系及致病力尚待进一步深入研究。

4 结论

本研究结合形态学特征和多基因分子系统学分析, 从贵州板栗经济林枝枯病样本中分离鉴定一个真菌新物种——微孢壳囊孢 *Cytospora minispora*; 通过比较板栗上7种壳囊孢真菌的形态特征, 为病害的识别诊断奠定理论基础。

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