

•综述•

葡萄座腔菌科真菌的系统学和多样性探讨

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摘要: 葡萄座腔菌科的真菌是子囊菌中重要的代表性类群, 是农林生态系统中重要的组成部分。该类真菌物种资源丰富、全型特征多样, 包括许多具有重要经济价值和生态功能的类群, 隶属于子囊菌门(Ascomycota)果囊菌亚门(Pezizomycotina)座囊菌纲(Dothideomycetes)葡萄座腔菌目(Botryosphaeriales)。本文在概述葡萄座腔科真菌生态功能的基础上, 回顾了一百年来该类真菌目、科、属和种各级分类单元的建立及其系统分类研究历史, 重点评述以 von Arx & Müller 和 Barr 提出的两大分类系统, 总结了基于全型形态特征和多基因序列分析的现代分子系统学研究现状。虽然该类的分类系统日趋完善, 但中国的相关研究存在资源挖掘不够深入、研究的系统性不足等问题。主要针对资源挖掘必要性、分类依据科学性、物种特征全息化等几个方面存在的问题进行了分析和讨论, 并对未来研究方向进行展望, 以期该类真菌的深入研究与开发利用提供科学依据。

关键词: 葡萄座腔菌目; 葡萄座腔菌科; 系统分类学; 生物多样性; 系统发育

Systematics and species diversity of botryosphaeriaceous fungi

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Abstract: Botryosphaeriaceous fungi are an important ascomycete group (Botryosphaeriales, Dothideomycetes, Pezizomycotina, Ascomycota). They play essential roles in economic and ecological environments, especially in agroforestry ecosystems. In this overview, we introduce a wide variety of ecological functions of botryosphaeriaceous fungi. The taxonomic studies of the family Botryosphaeriaceae in its early stages have been reviewed in details since 1823, especially the two major classification systems proposed by von Arx & Müller and Barr. The research status, progress based on holomorphological characteristics and multilocus DNA sequence data are summarized towards updating our understanding of species diversity and classification systems of the group. In addition, the research history, current status and work to be done of the group in China are briefly stated. Problems regarding biodiversity and phylogeny are discussed. Research perspectives are proposed based on taxonomic features, species concepts and exploration of bioresources. This review is expected to provide useful information about effective utilization of fungal resources and control of the harmful effects of botryosphaeriaceous fungi.

Key words: Botryosphaeriales; Botryosphaeriaceae; systematic; biodiversity; phylogeny

葡萄座腔菌科真菌(botryosphaeriaceous fungi) 是子囊菌中重要的代表性类群, 其典型特征为: 子

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囊果和分生孢子果为葡萄状子座型, 子囊双囊壁, 子囊孢子和分生孢子较大, 椭圆形至纺锤形, 许多是具有重要经济价值和生态功能的类群, 隶属于子囊菌门(Ascomycota)果囊菌亚门(Pezizomycotina)座囊菌纲(Dothideomycetes)葡萄座腔菌目(Botryosphaeriales) (Kirk et al, 2008; Phillips et al, 2013)。该类真菌为世界性分布, 寄生或腐生于单子叶植物、双子叶植物或裸子植物等寄主上, 主要生于木本植物的树干和枝条, 也发生于草本植物的叶片或茎秆上, 甚至地衣体上。有些为植物内生菌或腐生菌, 在自然界的生态平衡、物质能量循环中发挥一定作用, 有些则为植物病原菌, 引起许多重要植物病害, 具有重要的经济影响(Barr, 1987; Denman et al, 2000; Slippers & Wingfield, 2007)。

本文在分析葡萄座腔菌科真菌生态功能和回顾分类研究历史的基础上, 总结国内外研究进展, 分析中国研究现状, 并对未来的研究进行展望, 以期该类真菌的深入研究与开发利用提供科学参考。

1 生态功能及经济重要性

葡萄座腔菌科真菌及其相关类群的属和种丰富、形态各异、生态多样, 分布于除极地以外的所有地理和气候区域, 营腐生、寄生或内生生活, 在长势衰弱、濒临死亡或刚刚枯死的木本植物组织上较为常见, 大多数种类可以在人工培养基上生长(Denman et al, 2000; Huang et al, 2008)。它们占据着不同的生态位, 在农林生态系统中行使着各自不同的生态学功能。

该科真菌有些成员是植物腐生菌, 主要腐生或附生于各种乔木和灌木植物性基质上, 是农林生态系统中的重要组成。如色二孢属(*Diplodia*)真菌的一些种可有效降解木质素和纤维素, 分解枯枝落叶, 对保护生物多样性和维持生态平衡具有重要的意义(Sivanesan, 1984; Barr, 1987)。

还有些成员是熟知的植物内生菌, 可产生生物活性物质, 在生物防治和医药方面具有一定的应用前景。如毛色二孢属(*Lasiodiplodia*)的一些种, 具抗菌活性, 可促进名贵中药沉香的结香过程(韩晓敏等, 2014; Wei et al, 2014), 对羊蹄甲白粉病菌也具有拮抗作用(Kumar & Singh, 2009)。有些种对污染物具有降解或钝化效应, 在污染环境生物修复方面

具有应用前景(张志远等, 2012; Deng et al, 2014)。

葡萄座腔菌科真菌的更多成员为弱寄生菌, 条件适宜时易引起植物病害, 对农林生产具有重要的影响(吴小芹等, 2001; Slippers & Wingfield, 2007; Cunnington et al, 2009)。特别是葡萄座腔菌属(*Botryosphaeria*)、新壳梭孢属(*Neofusicoccum*)、色二孢属、小穴壳孢属(*Dothiorella*)、毛色二孢属等的优势类群会引起流胶、茎枯、梢枯、枝枯、溃疡、蒂腐、根腐、炭腐等多种植物病害(Slippers et al, 2007; Chen et al, 2011; Machado et al, 2014; Xu et al, 2015b), 寄生或腐生于多种作物果实, 引起果腐、环腐、蕉腐、轮纹等果实病害或采后货架期病害(Xu et al, 2015a; Zhou et al, 2015; Huang et al, 2016)。

葡萄座腔菌科及其相关类群的许多成员与人类生活及农林产业紧密相联, 引起了人们对它们的密切关注。由于该类真菌历经葡萄座腔菌属(1863)、葡萄座腔菌科(1918)、葡萄座腔菌目(2006)的分类地位变化, 广义的葡萄座腔菌类真菌囊括了以葡萄座腔菌科为主的葡萄座腔菌目中的相关类群, 许多属和种的归属目前还处于不断修订中。在百余年的研究历程中(1863–2016), 该类真菌分类地位和包含成员虽几经变化, 但主要属于葡萄座腔菌科, 本文仅以狭义的葡萄座腔菌科真菌的系统学和多样性为主线探讨其研究进展及未来展望。

2 经典分类研究

2.1 葡萄座腔菌科的建立及其概述

葡萄座腔菌科由Theissen和Sydow (1918)建立, 当时隶属于子囊菌门盘菌纲(Discomycetes)座囊菌亚纲(Dothideineae)假球壳菌目(Pseudosphaeriales), 囊括葡萄座腔菌属、暗葡腔菌属(*Phaeobotryon*)和双葡腔菌属(*Dibotryon*)等3个属。该科包含形态各异的一类真菌, 分类和命名等方面的变化多样, 曾有3,000多个名称与Botryosphaeriaceae相关(<http://www.indexfungorum.org/Names/names.asp>)。根据最新分类观点, 目前葡萄座腔菌科被处理为子囊菌门座囊菌纲下未定亚纲葡萄座腔菌目的模式科, 普遍认可包括约20属约180种, 其中葡萄座腔菌属为模式属(Phillips et al, 2013; Slippers et al, 2013; Dissanayake et al, 2016; 图1)。

2.2 历史与进展

葡萄座腔菌科真菌及其相关类群最早的研究

可以追溯到Fries在1823年以球壳孢(*Sphaeria dothidea*)为名对葡萄座腔菌(*Botryosphaeria dothidea*)的报道。Cesati和Notaris在1863年建立的葡萄座腔菌属,是指一类具球状、双囊壁子囊、能引起木本植物坏死的子囊菌,但当时没有指定模式种。1877年, Saccardo修订一些前述的种类,较为详细地描述

了该属的形态特征。1909年, Höhnelt曾建议将*B. berengeriana*作为该属的后选模式;而1915年, Theissen和Sydow却建议将*B. quercuum*作为后选模式。由于Cesati和De Notaris建立葡萄座腔菌属时没有包括上述2个种, Barr (1972)否定了他们的建议,提出将葡萄座腔菌作为该属的后选模式种,该提议被后人普遍采纳。Slippers等(2004)根据新指定的模式和附加模式明确了葡萄座腔菌的概念,并给予该属科学的描述。

Theissen在1916年曾将假球壳菌科归入多腔菌目(Myriangiales); 1917年, Theissen和Sydow认为假球壳菌科应该与座囊菌科(Dothideaceae)合并; 1918年建立座囊菌亚纲,囊括假球壳目葡萄座腔菌科葡萄座腔菌属。Theissen和Sydow (1918)建立葡萄座腔菌科时,曾将该科处理为假球壳菌科(Pseudosphaeriaceae)的一个亚科; Petrak (1923)否定他们的分类处理,把葡萄座腔菌属归入球壳菌目(Sphaeriales)中格孢腔菌科(Pleiosporaceae)的假球壳菌亚科(Pseudosphaeriaceae)。

Miller (1928, 1938)指出形成子囊果及子囊果包被的细胞组织存在根本的差异,这些不同的组织类型与子囊果中心体特征相关联。球壳菌目具典型子囊壳(perithecial ascomata)和侧丝,而座囊菌目子囊果为子囊座(ascostromatic ascomata),无侧丝。由于葡萄座腔菌属成员缺乏真正的子囊壳包被,所以从假球壳菌科转入座囊菌目。Nannfeldt (1932)将真子囊菌纲真菌分为3类:子囊果为闭囊壳类型(cleistothecial forms),子囊在子囊果内不规则散生,归入闭囊壳菌类(plectascales);子囊座类型(ascostromatic forms),子囊在预先形成的子座空腔内形成,被归入囊腔菌类(Ascoloculares);典型的球壳目,即子囊在子实层内生长发育的类群被归入子囊膜目(Ascohymeniales)。尽管这些术语当时没有被广泛接受,但它们与后来Luttrell(1955)提出的双囊壁(bitunicate)类群和单囊壁(unitunicate)类群的术语内涵基本一致。

Luttrell (1951, 1955)强调子囊果个体发育特性在分类上的重要性,提出核菌类(pyrenomycetous fungi)存在2种主要形态类型:单囊壁类子囊菌和双囊壁类子囊菌(腔子囊菌)。Luttrell (1951)还明确指出8种中心体发育类型,强调子囊间不育丝状体组织的在分类学上的重要性。根据假球壳菌科成员的

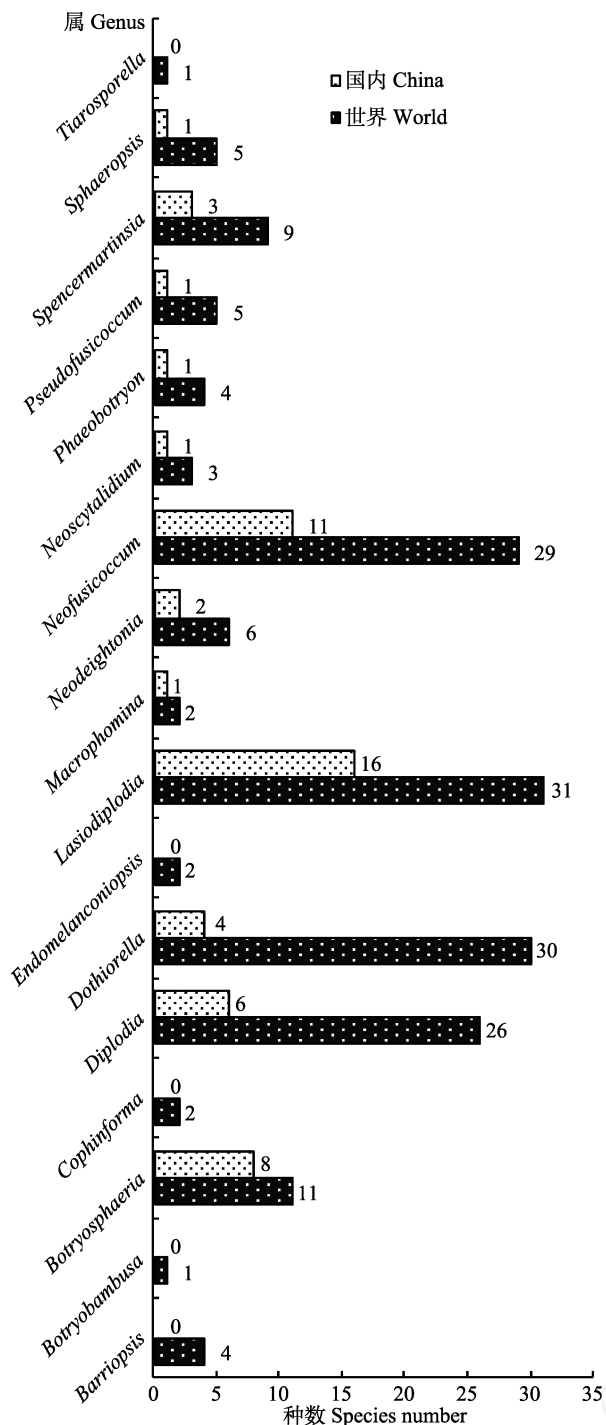


图1 葡萄座腔菌科属种多样性

Fig. 1 Diversity of genera and species in Botryosphaeriaceae

中心体类型将其移入座囊菌目,至此假球壳菌目不复存在。Luttrell (1955)用格孢腔菌目(Pleosporales)取代了假球壳菌目,其中重要类群葡萄腔菌属成员具备格孢腔菌型(Pleospora)中心体发育类型,因此归入格孢腔菌目。尽管Parguey-Leduc (1966)为葡萄座腔菌具备典型的格孢腔菌型中心体特征提供了确凿证据,但Barr (1972)并没有仔细研究子囊间组织清晰可见的该物种标本,在她的早期著作中,仍将葡萄座腔菌属归入座囊菌目。Barr (1979)之后承认葡萄座腔菌科具备典型的格孢腔菌型中心体特征,从而建立了比较成熟的分类系统,确定这类真菌应归入格孢腔菌目,该目中葡萄座腔菌科包括模式属葡萄座腔菌属等9个属(Barr, 1983, 1987)。上述观点得到一些学者的支持,如Eriksson (1981)强调葡萄座腔菌科主要成员中心体具备假囊壳和假侧丝等。

von Arx和Müller (1954, 1975)对葡萄座腔菌科与座囊菌科等相近科之间的区别特征进行了讨论,指出Luttrell (1955, 1973)和Barr (1972)承认的葡萄座腔菌科是由许多没有关联的属组成,对部分类群的归属处理不当,采用的分类学特征存在一些重叠与交叉,如球座菌属(*Guignardia*)和葡萄座腔菌属是近似属,不应该将它们归入座囊菌目和格孢腔菌目两个不同的目中,因此把所具有双囊壁的子囊菌都归入座囊菌目,由两个亚目和包括葡萄座腔菌科在内的34科组成,葡萄座腔菌科内承认14个属。之后的一些学者支持这个观点,如Sivanesan (1984)把葡萄座腔菌属和球座菌属都归入座囊菌目下的葡萄座腔菌科, Hawksworth等(1995)把以葡萄座腔菌属为代表的5个属归入座囊菌目中的葡萄座腔菌科。这种两个主要分类系统分庭抗礼的局面一直持续到20世纪90年代末分子系统学的出现(图2)。

3 基于分子系统学的属和种的多样性研究

DNA序列为探讨真菌界物种、属以至门各级分类阶元的系统发育关系提供了新的依据。Berbee (1996)利用18S rRNA的基因序列研究了腔菌纲(Loculoascomycetes)中各级分类单元之间的系统发育关系,然而,由于所使用的分析方法不同,葡萄座腔菌科2个属即葡萄座腔菌属和球座菌属的分类地位变化很大,在邻接树(neighbour-joining tree)中,大部分物种与座囊菌目中座囊菌属(*Dothidea*)的种

类聚在一起,但在最大似然树(maximum likelihood tree)中,它们则聚在格孢腔菌目中。在随后的18S rDNA序列研究中, Silva-Hanlin和Hanlin (1999)无法确定葡萄座腔菌属、球座菌属等葡萄座腔菌科进化支应归入座囊菌目还是格孢腔菌目。

Denman等(2000)回顾了葡萄座腔菌属及相关类群的分类研究历史,综合形态学和分子系统学的研究结果,重新分析了该类真菌的分类依据:该属真菌子囊和子囊孢子的特征比较稳定,但种间子囊孢子形态相近,大小重叠,很难用于划分种,故主要依据无性型的形态特征和分子证据来划分种, Kirk等(2001)在*Ainsworth & Bisby's Dictionary of the Fungi* (第9版)中记录该科7属69种。鉴于该类真菌的形态多样化,许多物种的概念过于宽泛, Crous等(2006)采用28S rDNA部分序列开展葡萄座腔菌科的分子系统学研究,指出广义的葡萄座腔菌属为多谱系类群,包括约20种,其无性型对应于当时18个腔孢菌类的属。Kirk等(2008)在*Ainsworth & Bisby's Dictionary of the Fungi* (第10版)中记录该科26属1,517种。

Schoch等(2006)基于座囊菌纲的96个分类单位的18S rRNA、28S rRNA、翻译延长因子1- α (EF1- α)和RNA聚合酶第二大亚基(RPB2)的基因序列数据构建了多基因系统树。结果表明,葡萄座腔菌属和球座菌属的所有成员聚类于一个进化分支,而与其他目关系疏远。为此建立一个新目,即葡萄座腔菌目,当时仅含葡萄座腔菌科。

近年来,分子证据大量用于子囊菌的系统分类,对葡萄座腔菌科及相关类群提出了许多不同的分类学观点(图2),承认了葡萄座腔科真菌的10–20个属不等(Lumbsch & Huhndorf, 2010; Hyde et al, 2011; Wijayawardene et al, 2012)。根据国际植物分类学会墨尔本会议修订的《国际藻类真菌及植物命名法规》和阿姆斯特丹宣言 (Hawksworth et al, 2011; McNeill et al, 2012),采用“一种真菌,一个名称”分类命名原则,无性阶段形态和培养特性纳入真菌系统分类研究,葡萄座腔菌科的概念及相关类群归属不断进行相应的清理与订正 (Kirk et al, 2013)。依据各属模式标本及相关分子证据特征, Liu等(2012)列出葡萄座腔科真菌27属, Hyde等(2013, 2014)列出该科28属,并对该科重要植物病原类群的系统分类和分子系统学研究进展进行了归纳总

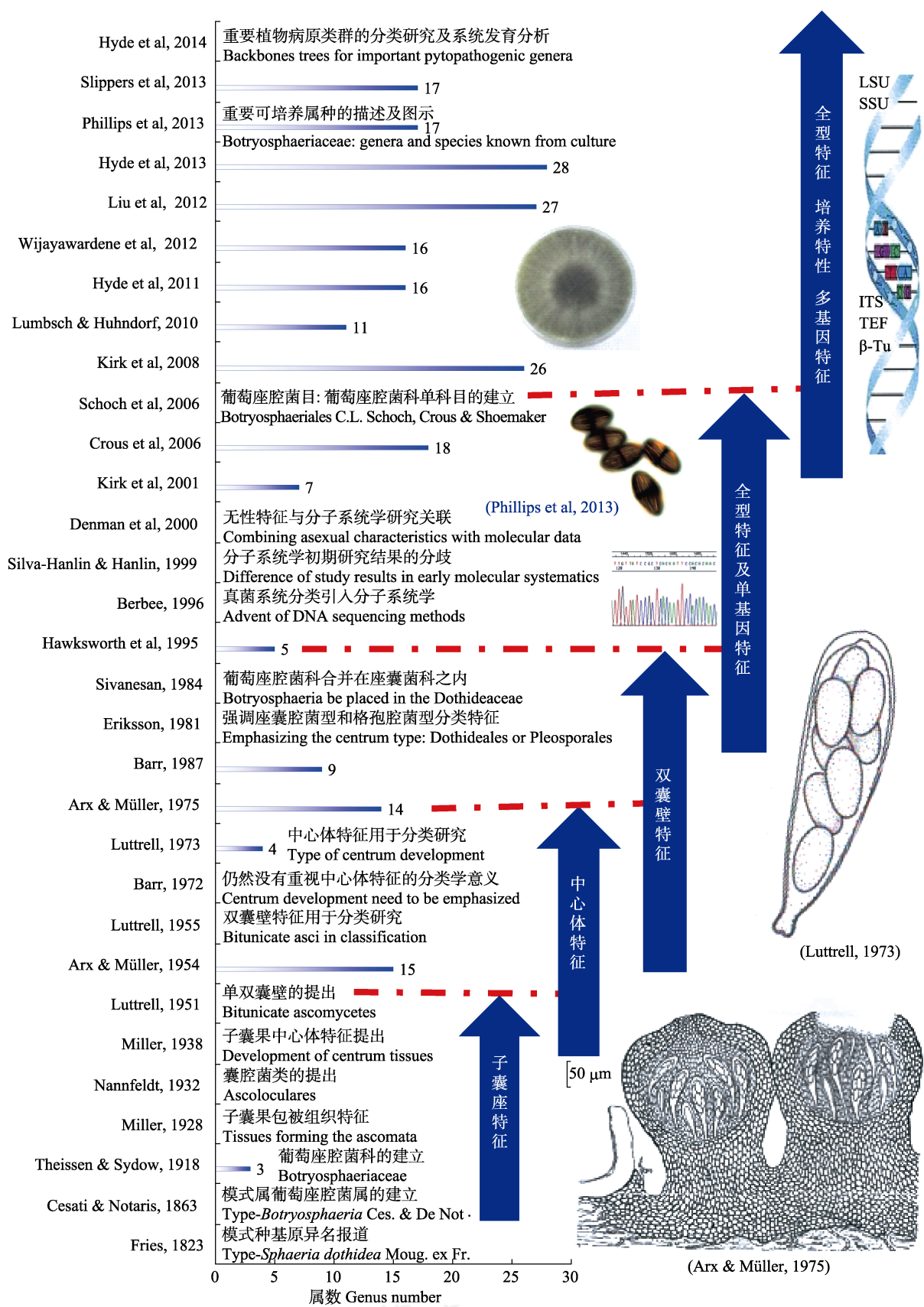


图2 葡萄座腔菌科研究进展年代记事表
Fig. 2 The chronicle table on research progresses in Botryosphaeriaceae

表1 葡萄座腔菌科及其各属研究进展和存在问题
Table 1 Research progresses and comments of genera in Botryosphaeriaceae

	存在的问题 Comments	主要文献 References
葡萄座腔菌科 Botryosphaeriaceae	模式科; 属种的分类与名称需要修订 Type family, many genera and species need to be corrected	Crous et al, 2006; Liu et al, 2012; Slippers et al, 2013; Phillips et al, 2013
<i>Barriopsis</i> A. J. L. Phillips et al, 2008	具分子证据, 但标本材料较少 A few molecular data, lack of fresh collections	Phillips et al, 2008; Abdollahzadeh et al, 2009; Doilom et al, 2014
<i>Botryobambusa</i> R. Phookamsak et al, 2012	单种属; 竹生, 具分子证据和全型特征 Monotypic genus on bamboo, some molecular data and holomorph characteristics	Liu et al, 2012; Hyde et al, 2013
葡萄座腔菌属 <i>Botryosphaeria</i> Ces. & De Not, 1863	模式属; 存在复合种, 大量记录名称仍需订正 Type genus, remaining species complex, lots of epithets need to be corrected	Denman et al, 2000; Slippers et al, 2004; Abdollahzadeh et al, 2013; Phillips et al, 2013
棺孢腔菌属 <i>Cophinforma</i> Doilom et al, 2012	具分子证据及全型特征, 需更多材料 A few molecular data and holomorph characteristics, lack of more fresh collections	Mehl et al, 2011; Liu et al, 2012; Phillips et al, 2013
色二孢属 <i>Diplodia</i> Fr, 1834	常见属; 大量记录名称需要清理与订正 Common genus, lots of epithets need to be corrected	Alves et al, 2004, 2014; Phillips et al, 2012, 2013
小穴壳孢属 <i>Dothiorella</i> Sacc, 1880	常见属; 大量记录名称需要订正, 缺乏有性材料 Common genus, lots of epithets need to be corrected, lack of teleomorph collections	Crous et al, 2006; Phillips et al, 2008; Phillips et al, 2013; Abdollahzadeh et al, 2014
<i>Endomelanconiopsis</i> E. I. Rojas & Samuels, 2008	具分子证据, 缺少有性特征材料 A few molecular data, lack of teleomorph collections	Rojas et al, 2008; Hyde et al, 2013
毛色二孢属 <i>Lasiodiplodia</i> Ellis & Everh, 1896	常见属; 具分子证据, 但有性特征材料较少 Common genus, some molecular data, but lack of fresh teleomorph collections	Alves et al, 2008; Abdollahzadeh et al, 2010; Phillips et al, 2008, 2013
亚大茎点菌属 <i>Macrophomina</i> Petr, 1923	较小属; 缺少更多分子证据及有性特征材料 Minor genus, lack of more molecular data and fresh teleomorph collections	Crous et al, 2006; Liu et al, 2012; Sarr et al, 2014
<i>Neodeightonia</i> C. Booth, 1970	新修订属; 具全型特征及分子证据 Revised genus, a few molecular data and holomorph characteristics	Punithalingam, 1969; Phillips et al, 2008, 2013; Liu et al, 2010, 2012; Hyde et al, 2013
新壳梭孢属 <i>Neofusicoccum</i> Crous, 2006	常见属; 具分子证据及全型特征 Common genus, a few molecular data and holomorph characteristics	Crous et al, 2006; Abdollahzadeh et al, 2013; Phillips et al, 2013; Hyde et al, 2014
新暗色柱节孢属 <i>Neoscytalidium</i> Crous & Slippers, 2006	具分子证据, 缺少有性特征材料 A few molecular data, lack of fresh teleomorph collections	Crous et al, 2006; Chuang et al, 2012; Lan et al, 2012; Phillips et al, 2013
暗葡萄腔菌属 <i>Phaeobotryon</i> Theiss. & Syd, 1915	新修订属; 具分子证据, 缺少全型特征材料 Revised genus, a few molecular data, lack of fresh holomorph collections	Phillips et al, 2008; Abdollahzadeh et al, 2009; Fan et al, 2015
拟壳梭孢属 <i>Pseudofusicoccum</i> Mohali, Slippers & M. J. Wingf, 2006	具分子证据, 缺少有性特征材料 A few molecular data, lack of fresh teleomorph collections	Crous et al, 2006; Pavlic et al, 2008; Mehl et al, 2011
斯潘氏菌属 <i>Spencermartinsia</i> A. J. L. Phillips et al, 2008	具较多分子证据, 缺乏有型特征材料 Some molecular data, lack of fresh teleomorph collections	Phillips et al, 2008; Abdollahzadeh et al, 2014
拟球壳霉属 <i>Sphaeropsis</i> Sacc, 1880	常见属; 大量记录名称需要清理与订正 Common genus, lots of epithets need to be corrected	Palmer et al, 1987; Phillips et al, 2008, 2013; Liu et al, 2012; Slippers et al, 2013
<i>Tiarosporella</i> Höhn, 1919	具分子证据, 属内成员需进一步清理与订正 A few molecular data, lots of members need to be corrected	Liu et al, 2012; Jami et al, 2012

结。根据真菌全型形态特征、培养特性、分子证据, 结合各类群的分类研究及经济重要性等文献资料, Phillips等(2013)提供了该科可培养17属110种的特征描述、图示及分种检索表, Slippers等(2013)重新

构建了葡萄座腔菌目系统树, 列出该科28属, 其中17属提供了分子证据, 其余11属还需要对全型特征和分子证据进行深入研究。Wijayawardene等(2014)提出座囊菌纲最新分类系统, 其中葡萄座腔菌科为

葡萄座腔菌目中最大的科, 包括29属, Dissanayake等(2016)列出该科23属187种的名录并简要讨论, 在此汇总Phillips等(2013)对具培养特性和分子证据的17属的分类学处理(表1, 图1, 2)。

4 中国葡萄座腔菌类真菌多样性研究

中国葡萄座腔菌类真菌的研究最早可以追溯到对贝伦格葡萄座腔菌的报道(Teng, 1934)。早期分类学研究主要依据有性阶段的形态特征, 20世纪50–60年代, 戴芳澜、邓叔群、姜广正、余永年等学界前辈在全国进行了广泛的真菌资源和植物病害调查, 收集到许多标本材料, 研究结果收录在真菌分类研究的文献中。20世纪80年代后的很长一段时期, 中国葡萄座腔菌类真菌的分类研究工作一直未受到重视, 仅有零星报道(黄天章, 1977; 尚衍重, 1987; Sivanesan & Hsieh, 1989; Hsieh et al, 1994, 1996; Teng, 1996), 缺乏专门研究。《中国的真菌》中收录葡萄座腔菌类真菌2属3种(邓叔群, 1963), 《中国真菌总汇》收录2属14种(戴芳澜, 1979), Eriksson和Yue (1988)清理订正并记录2属12种, 《台湾真菌名录》中收录了分布在台湾省的2属28种(王也珍等, 1999), *Checklist of Hong Kong Fungi*中收录2属9种(Lu et al, 2000)。截至2006年, 按照现代分类学观点, 我国已知葡萄座腔菌类真菌1科5属26种。

近10年来, 笔者与合作者对我国葡萄座腔菌科开展了系统分类研究, 对保存于中国科学院微生物研究所真菌标本馆(HMAS)的所有葡萄座腔菌属及相关类群标本进行了重新鉴定, 按照现代分类学观点清理和修订了15个种, 发表6个新种, 2个中国新记录种(Li & Zhuang, 2007)。根据Ainsworth & Bisby's *Dictionary of the Fungi* (第10版) (Kirk et al, 2008)的分类观点, 李文英和庄文颖(2013)简述了中国葡萄座腔菌属的研究进展。结合近年来我国报道的一些新种和新记录种(李文英, 2008; Zhao, 2010; Chen et al, 2011; Zhou et al, 2016), 对采自全国各地的1,000余份标本材料进行了分类鉴定, 按照现代分类观点(Liu et al, 2012; Hyde et al, 2013; Phillips et al, 2013; Slippers et al, 2013; Dissanayake et al, 2016), 澄清并确认中国葡萄座腔菌科真菌12属55种(表1, 图1)。可以预见, 随着研究的深入, 对该类群在我国分布范围和物种数量将不断刷新。

我国对葡萄座腔菌科真菌的分子生物学研究

起步于对林木溃疡病、果树轮纹病、流胶病等重要植物病害病原菌的分类地位订正及重要病原菌之间的系统发育关系等(王金利等, 2007; 赵嘉平等, 2007; 余仲东等, 2010; 李夏等, 2015), 利用我国材料对葡萄座腔菌科及相关类群的系统学关系进行了初步探讨, 为建立趋于自然的分类系统提供了有力佐证(程燕林等, 2011; 王庆灵, 2013^①; Fan et al, 2015; Zhou et al, 2016), 如李文英和庄文颖(2009)采用18S 和28S nrDNA序列片段对部分葡萄座腔菌科及相关类群进行了系统发育分析, 提出当时分类地位不确定的双壁子囊菌大聚颈腔菌属(*Macrovalsaria*)与葡萄座腔菌属的关系比较接近, 应归于葡萄座腔菌科, 这一结果也得到后来学者的进一步证实和支持(Liu et al, 2012; Hyde et al, 2013; Wijayawardene et al, 2014)。上述研究为进一步探讨葡萄座腔菌科的属间关系以及深入开展该类真菌的分子系统学研究提供了科学依据。

5 存在问题及研究展望

近年来, 真菌分子系统学的研究进展与菌物命名法规的变革引起真菌分类系统的巨大变化, Wijayawardene等(2014)对葡萄座腔菌类真菌提出新分类系统, 但学者们普遍认为Phillips等(2013)和Dissanayake等(2016)提出的分类学处理得到了分子证据的支持, 更趋于合理。目前该类真菌的研究仍存在许多悬而未决的问题, 如有些属的分类地位和命名存在疑问, 有些属中大量名称有待清理与订正, 有些属种缺乏对全型特征的认识, 有些属和种之间的关系缺乏分子证据等(表1)。因此, 进一步加强资源挖掘, 深入开展该类真菌的系统分类和物种多样性研究十分必要。以物种全型的形态特征、培养特性及多基因序列佐证等作为重要分类依据, 是该类群分类学和系统发育研究的必然趋势。

我国葡萄座腔菌科的分类研究走过了80余年历程, 经过从有性特征分类至全型特征分类、从形态分类到分子系统研究的发展过程。近年来虽然陆续报道了一些新种和中国新记录种(表1, 图1), 但已知种数仅占全球物种数量的30%左右, 其中许多种类仍需清理与订正, 物种多样性和地理分布规律、生态功能和经济重要性等方面尚缺乏全面的研究。

①王庆灵 (2013) 葡萄座腔菌科真菌的系统分类研究. 硕士学位论文, 河北农业大学, 河北保定。

中国具有多样化的气候与地理类型以及丰富的植被资源, 葡萄座腔菌科真菌丰富的物种多样性取决于多样化的生境。由于该类群生活史的不同阶段特征多样, 需要进一步扩大采集范围, 加强培养特性的研究, 以便获得更多、更全面的信息。在我国开展葡萄座腔菌科的资源多样性调查、标本采集、菌株分离培养和系统分类研究, 将进一步加深我国对该科物种多样性的认识, 为建立趋于自然的正确属、种概念和明确属间与种间的系统发育关系及其在具有双囊壁子囊的真菌中的分类地位提供更加充分的科学依据, 为有益真菌资源的储备及持续利用奠定基础, 为控制有害真菌的影响提供基础信息, 将对科学地认识我国生物多样性和生物资源保护利用起到积极的推动作用。

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