

中国多孔菌多样性初探：物种、区系和生态功能

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摘要: 多孔菌是指子实层体呈孔状且质地为革质至木质的一类大型担子菌, 主要生长在各种木材上。我国地域辽阔, 气候带和地形多样, 森林类型和植被组成丰富, 为多孔菌提供了丰富的栖息地。长期的野外资源调查和标本采集, 特别是近年来分子生物学技术的发展, 极大地丰富了对我国多孔菌种类的认识。我国是世界上多孔菌物种多样性最丰富的国家, 现在已知有多孔菌704种, 隶属于11目22科134属, 包括世界广布成分、北温带成分和热带-亚热带成分。多孔菌中的白腐菌是潜在的工业用菌, 褐腐菌在森林的更新过程中起重要作用。

关键词: 木材腐朽菌, 物种多样性, 真菌区系, 生态学

Chinese polypore diversities: species, mycota and ecological functions

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Abstract: Polypores are the group of macro-basidiomycetes with poroid hymenophore and corky basidiocarps that mainly grow on wood. China contains multiple climatic zones and geographic topographies, and thus possesses a variety of forest and vegetation types that provide rich habitats for polypores. Based on extensive collections conducted over a long period of time, a considerable knowledge of Chinese polypore species has been obtained, and this has been enriched further in recent years by using molecular technology. China possesses the highest polypore diversity in the world and 704 polypore species, belonging to 134 genera, 22 families and 11 orders, have been recorded within its borders. These 704 species are composed of cosmopolitan, boreal/temperate and tropical-subtropical elements. White-rot polypores are considered as potential industrial resources, while brown-rot polypores play an essential role in forest renewal.

Key words: Wood-decaying fungi, species diversity, mycota, ecology

多孔菌(polypore)是子实层体呈孔状且质地为革质至木质的一类大型担子菌的统称, 并不是一个自然的分类单元。虽然都有孔状的子实层体, 但不同种类多孔菌的子实体与基物(substrate)的着生方式有所不同, 如平伏、平伏反卷、盖状、具柄、单生或复生等, 表现出宏观形态的多样性。多孔菌主要生长于各种类型的森林中, 与人为干扰较多的地区相比较(Cui *et al.*, 2006; Dai *et al.*, 2006), 在天然林中种类更丰富(Dai *et al.*, 2011, 2012; Cui & Dai, 2012), 然而有些多孔菌也能生长在建筑木和储木上(徐梅卿等, 2006; 戴玉成等, 2008; 曾祥谓等,

2008)。

多孔菌中的许多种类具有重要的经济价值, 包括一些常见的食用菌(戴玉成等, 2010a)、药用菌(戴玉成和杨祝良, 2008; 戴玉成和李玉, 2011)和潜在的工业工程菌(Cohen *et al.*, 2002)。由于多孔菌可以彻底降解植物细胞壁中的木质纤维素, 还可对森林生态系统的天然更新起到重要的促进作用, 使得物质和能量可以在自然界中持续地传递下去(魏玉莲和戴玉成, 2004; 崔宝凯和余长军, 2011)。但另一方面, 还有许多多孔菌种类被报道为木本植物病原菌, 能够侵染活立木, 影响树木的生长, 甚至造成

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树木大面积死亡(戴玉成, 2012)。因此, 对多孔菌的研究既具有科学理论意义, 更具有重要的经济学和生态学意义。

在欧洲和北美洲, 多孔菌的物种多样性研究历史悠久, 发表了多部专著, 其中*European Polypores* (Ryvarden & Gilbertson, 1993, 1994)和*North American Polypores* (Gilbertson & Ryvarden, 1986, 1987)最为经典, 被世界各地的研究者广泛参考。在对种类充分认知的基础上, 欧美地区也进行了一系列关于多孔菌生态学(Junninen & Komonen, 2011)、森林病原学(Asiegbu *et al.*, 2005)以及工业开发和应用(Cohen *et al.*, 2002)方面的研究。中国的多孔菌研究起步较晚, 但在戴芳澜、邓叔群、赵继鼎、臧穆等老一辈真菌学家的积极推动下, 通过几代从业人员的辛勤耕耘, 取得了长足的进步。特别是近年来借助于分子生物学技术, 研究者深入地探讨了一些重要多孔菌类群内的种间系统发育关系, 发表了一批多孔菌的属种新分类单元(Dai, 2010a; Li & Cui, 2013), 并更正了过去的一些错误鉴定(Zhou & Dai, 2012a; Zhou & Kõljalg, 2013), 为充分认识我国多孔菌的物种多样性以及进一步开发利用这类真菌提供了科学依据。对多孔菌与森林生态系统中的植物之间的关系也进行了初步的探索(Zhou *et al.*, 2011; Zhou & Dai, 2012b)。

本文将从物种、区系和生态功能三个方面介绍中国多孔菌多样性研究的最新进展, 并提出有待深入研究的问题。

1 物种多样性

中国幅员辽阔, 由北至南包括寒温带、温带、暖温带、亚热带、热带等气候区, 从东到西地势逐渐升高, 包括平原、丘陵、盆地、山地和高原等地形。高度多样的自然条件孕育出了丰富的森林类型和植被组成, 也为多孔菌的生长提供了广阔的栖息地。全国各省区及主要的生态区域都有丰富的多孔菌资源(毕志树等, 1994; Li *et al.*, 2007; Wang *et al.*, 2011; Yuan & Dai, 2012)。随着近年调查研究的深入, 中国已知的多孔菌总数增加迅猛, 从2009年报道的604种(戴玉成, 2009)增加到2011年的704种(Dai, 2012), 其中有48种为濒危种类(戴玉成, 2003; 戴玉成等, 2010b)。

我国已知多孔菌物种多样性以东北和东喜马

拉雅地区最为丰富, 这与当地丰富的森林资源有密切关系。东北地区有着中国最重要的森林资源, 也是多孔菌资源调查最为深入的生态区域之一, 已报道多孔菌300种(Dai, 2010b)。相比之下, 东喜马拉雅地区的森林虽然面积稍小但林木树种更为丰富, 通过近10年的逐年调查, 发现多孔菌372种(未发表)。

研究的深入与真菌分类鉴定技术的进步是近年我国多孔菌已知物种迅速增加的重要原因。经典的多孔菌鉴定方法以形态特征为主, 包括子实体在野外新鲜时和烘干之后的宏观形态, 以及在光学显微镜下可观察到的显微形态(Ryvarden, 1991)。经过上百年的发展, 在这种鉴定方法的基础上已经建立起了一个完整的分类学体系, 并沿用至今。但该方法具有一定的主观性和局限性, 如同一形态特征在不同研究者的观察下可能存在差异, 不同学者对各形态特征所具有的分类学意义理解也不同等。在这种情况下, 同一个种甚至被不同研究者划归到不同的属内(Ryvarden, 1991; Reid, 1992)。分子系统学方法为多孔菌分类学研究提供了一个较为可靠的手段, 可将分子序列标记的差异与形态特征的异同相结合作为分类学依据, 对种以及更高级别的分类单元进行划分。近年来, 我国的学者在进行多孔菌资源调查时, 发现了大量的与已知的中国多孔菌形态特征有明显差异的标本, 经现代技术进行详细的分类学研究后, 确认为中国新记录种(Di *et al.*, 2012; He & Li, 2013; Zhao & Cui, 2013); 同时还发现中国有许多虽然形态与欧洲或美洲种类相似但遗传仍有本质差异的标本, 它们应归为不同的种类, 因而将其有效发表为新种(Tian *et al.*, 2013; Zhou & Qin, 2013)。近年的研究成果极大地丰富了中国已知多孔菌的物种多样性, 提高了人类对中国乃至世界多孔菌物种多样性的认识。

然而, 我国多孔菌的物种多样性研究仍需深入, 仍有不少新的物种有待发现, 还有一些种类的真实身份仍有待澄清。灵芝的学名问题就是一个典型的例子: 无论是在中医理论还是民间传说中, 灵芝都是一种极具传奇色彩的“仙草”, 中国的灵芝分类学研究历史可以追溯到100多年前(Patouillard, 1907)。但是早期的分类学研究主要依赖于一些宏观形态特征(Zhao, 1989), 导致灵芝属(*Ganoderma*)的分类异常混乱(Ryvarden, 1994)。长期以来, 欧洲灵芝(*Ganoderma lucidum*)这一描述于英国的种类一直

被用来命名中国的“仙草”。最近有研究表明,“仙草”的学名应是四川灵芝(*Ganoderma sichuanense*) (Wang *et al.*, 2012b), 而并非欧洲灵芝。但Cao等(2012)从四川灵芝的主模式标本中成功获得了ITS序列, 由此发现“仙草”与四川灵芝并非同种, 而是之前未被描述过的新种, 故将其描述为灵芝(*Ganoderma lingzhi*)。尽管如此, “灵芝”的分类仍然还有些问题尚未解决(Yang & Feng, 2013)。

2 区系成分多样性

根据真菌词典第十版的分类体系(Kirk *et al.*, 2008), 中国已知的704种多孔菌中, 除分类地位尚

不明确种类外, 其余种类隶属于担子菌门的11目22科134属(图1)。多孔菌目、锈革孔菌目和红菇目包括的多孔菌属、种数目最多(共120属662种), 其他目(伞菌目、阿太菌目、木耳目、牛肝菌目、鸡油菌目、褐褶菌目、革菌目和糙孢菌目)则只有很少的多孔菌。与其他大型真菌类似, 多孔菌中的很多种类具有地区特异性, 特别是以往的“形态种”(morphological species)概念经过分子系统学分析细化为“系统发育种”(phylogenetic species)之后, 人们对其特异性的认识更为清晰。而在属这一分类等级上, 多孔菌的地理成分更具共性, 许多属是世界广布属, 包括中国在内的世界很多地区均有分布, 如小



图1 不同目的多孔菌。(A)木耳目的叶榆孔菌;(B)褐褶菌目的深褐褶菌;(C)锈革孔菌目的肉桂集毛孔菌;(D)多孔菌目的血红密孔菌;(E)红菇目的无壳异担子菌;(F)糙孢孔菌目的袋囊糙孢孔菌。

Fig. 1 Polypores in multiple orders. (A) *Elmerina foliacea* in the Auriculariales; (B) *Gloeophyllum sepiarium* in the Gloeophyllales; (C) *Coltricia cinnamomea* in the Hymenochaetales; (D) *Pycnoporus sanguineus* in the Polyporales; (E) *Heterobasidion ecrustosum* in the Russulales; (F) *Trechispora hymenocystis* in the Trechisporales.

薄孔菌属(*Antrodiella*)、管孔菌属(*Bjerkandera*)、蜡孔菌属(*Ceriporia*)、迷孔菌属(*Daedalea*)、异薄孔菌属(*Datronia*)、灵芝属、纤孔菌属(*Inonotus*)、多年卧孔菌属(*Perenniporia*)、木层孔菌属(*Phellinus*)、多孔菌属(*Polyporus*)、栓孔菌(*Trametes*)、附毛孔菌属(*Trichaptum*)等等。但更多属的分布与地理区域相关(Ryvarden, 1991)。中国地跨北半球的寒温带、温带、暖温带、亚热带和热带, 因此汇集了这些气候带所具有的大部分多孔菌属。如北温带成分的薄孔菌属(*Antrodia*)、齿毛菌属(*Cerrena*)、层孔菌属(*Fomes*)、拟层孔菌属(*Fomitopsis*)、全缘孔菌属(*Haploporus*)、异担子菌属(*Heterobasidion*)、褐腐干酪孔菌属(*Oligoporus*)、剥管孔菌属(*Piptoporus*)、毡被孔菌属(*Spongipellis*)等, 热带-亚热带成分的假芝属(*Amauroderma*)、黄肉孔菌属(*Aurificaria*)、小集毛孔菌属(*Coltriciella*)、环褶孔菌属(*Cyclomyces*)、俄氏孔菌属(*Earliella*)、浅孔菌属(*Grammothele*)、小孔菌属(*Microporus*)等。

3 功能多样性

作为森林生态系统中的重要组成部分, 绝大多数的多孔菌以腐生(图2A、B)或寄生(图2C)为主, 但也有少数种类与树木形成外生菌根(图2D), 如地花孔菌属(*Albatrellus*)的绝大部分种类(Ryvarden, 1991)以及集毛孔菌属(*Coltricia*)和小集毛孔菌属的一些种类(Tedersoo *et al.*, 2007; Cui *et al.*, 2008)。

根据对木材造成的腐朽类型, 可将这类多孔菌分成白腐菌和褐腐菌两大类(图3)。白腐菌是唯一可以完全降解木质素的生物, 如果没有白腐菌, 那么倒木不会被彻底分解, 其中所含的能量和物质也不会被完全还原出来, 白腐菌也因此被视为潜在的工业染料和生物降解材料(司静等, 2011a, b, c, 2012; Si *et al.*, 2013)。在我国大兴安岭地区的野外调查发现, 落叶松的幼苗常生长于木材被褐腐菌降解后的残留物上(崔宝凯和余长军, 2011), 表明褐腐菌在落叶松天然更新过程中起着重要作用, 主要体现在这



图2 不同营养方式的多孔菌。(A)腐生于腐朽木上的黄白变孔菌;(B)腐生于倒木上的东方栓孔菌;(C)寄生于活树上的红贝俄氏孔菌;(D)形成外生菌根的绵地花孔菌。

Fig. 2 Polypores of different trophic types. (A) *Anomoporia albolutescens* saprotrophic on rotten wood; (B) *Trametes orientalis* saprophytic on fallen wood; (C) *Earliella scabrosa* parasitic on living tree; (D) *Albatrellus ovinus* forming ectomycorrhizae with trees.



图3 白腐菌、褐腐菌及其引起的木材腐朽。(A)木蹄层孔菌及其引起的白色腐朽;(B)盖波斯特孔菌及其引起的褐色腐朽。

Fig. 3 White-rot and brown-rot polypores and their causing rot in wood. (A) *Fomes fomentarius* causing a white rot; (B) *Postia pileata* causing a brown rot.

些褐腐残留物能够改善土壤的理化性质,促进外生菌根的形成和非共生微生物的固氮作用等。此外,褐腐菌与白腐菌的比例在大兴安岭林区的火烧迹地中明显升高,表明褐腐菌在过火林恢复过程中具有重要意义(余长军等,2004)。

外生菌根菌和植物之间的共生关系一直受到菌物学家和植物学家的高度重视(Hibbett *et al.*, 2000; Taylor & Alexander, 2005),但是,对于形成外生菌根的多孔菌却少有研究,仅仅停留在初步认识阶段(Ryvarden, 1991; Tedersoo *et al.*, 2007)。中国的外生菌根菌研究主要集中在伞菌类群(Ge *et al.*, 2012; Wang *et al.*, 2012a),尚无针对多孔菌的相关报道。

4 展望

经过长期的系统调查和采集,发现了一批中国新记录种,丰富了我国已知的多孔菌种类。分子生物学技术为担子菌物种多样性研究带来了深刻的变革(Yang, 2011),使得一些原以欧洲和北美洲多孔菌种类概念鉴定的中国标本亦被更准确地描述

为新种。但是,在分子系统学研究中,分子标记的使用以参考国外研究为主,且研究的类群基本集中在属和属下的分类单元。在今后的研究中,除继续发现和描述新种外,更应使用多基因序列组合的方法对科或目等更高级别分类单元进行系统发育分析。近年来,我国研究者在对羊肚菌(*Morchella*)和狭义牛肝菌(*Boletus sensu stricto*)的研究中,通过多基因系统发育分析,推断出它们的起源中心、演化时间以及地理分布等信息(Du *et al.*, 2012; Feng *et al.*, 2012)。这种研究方式值得借鉴到多孔菌的研究之中。

虽然通过近10余年来对中国全境特别是生态热点区域的长期、多次调查,积累了大量关于多孔菌在中国不同气候带和多种林型中的种类、群落结构、出现频次与寄主关系等数据,但相关的区系报道较少,下一步需要在总结现有调查结果的基础上,对主要生态区域内的多孔菌区系进行系统的分析。在多孔菌生态分布模式方面,我国虽然已经进行了一些研究,但往往将多孔菌与其他类型的真菌一起分析(魏玉莲等, 2010; Zhang *et al.*, 2010),专门针对多孔菌的研究还不够系统和深入,仅仅比较了多孔菌在阔叶树和针叶树寄主间(Zhou & Dai, 2012b)以及不同纬度地区间的区系多样性(Zhou *et al.*, 2011)。为了更准确地认识多孔菌的生态分布模式,需要对更多的生物多样性热点地区的多孔菌进行专门的资源调查,并积累长期的野外数据,以揭示多孔菌在不同时间和空间尺度下的分布规律。现阶段的生态学研究对纬度梯度水平变化的研究已经较深入,开始针对不同海拔梯度之间的差异进行比较(Sanders & Rahbek, 2011),这也是中国多孔菌区系研究进一步发展的方向之一。长白山自然保护区内的植被垂直分布特征明显,且具有超过15年的调查积累,为这方面的研究提供了充足的数据基础。我们已经着手分析这些数据,以期早日填补多孔菌在不同海拔梯度间分布模式研究的空白。

国内对多孔菌生态功能的研究相对较少,国外有研究表明多孔菌可为昆虫提供食物和栖息地(Hoebeke *et al.*, 1987; Martin, 1987),但相关研究仅停留在对现象的简单描述和推断上,对于一些在野外工作中经常观察到的现象仍无系统的理论研究,如为什么腐朽程度不同的木材上生长的多孔菌种类不同,某些种类的多孔菌在处于腐朽初始阶段的

木材上占主导,而另一些在腐朽后期的木材上占主导?我们准备使用高通量测序技术研究不同腐朽阶段木材上的多孔菌(包括子实体和木材中的菌丝体)的群落组成,揭示其动态变化及内在的驱动因素,以加深人们对多孔菌在森林生态系统中功能和重要性的认识。

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