•综述•

# 石生真菌研究现状与展望

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**摘要:** 石生真菌是一类生长在裸露岩石上形成紧凑暗色菌落的特殊生命, 在自然界未发现其有性生殖结构, 它们具有丰富的物种多样性。石生真菌是地球上最具耐受力的一种真核生命, 具有独特的适应性, 并进化出各种适应机制以占据严酷的生态位, 它们在细胞结构、代谢方式、抗逆机制等方面具有特殊性。尽管石生真菌很常见,但由于其体积小、生长缓慢并且缺乏明显的形态特征而常常被人们忽视。本文在介绍石生真菌的多样性、研究方法和研究历史的基础上, 重点介绍石生真菌的逆境耐受性和抗逆机制以及石生真菌的应用研究。以期能引起科学工作者对这类特殊生境里的真菌研究的重视, 更好地理解这类真菌在地球上的重要作用。

**关键词:** 石生真菌; 多样性; 抗逆性; 文物保护; 天体生物学

## Research status and prospects of rock-inhabiting fungi

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**Abstract:** Rock-inhabiting fungi (RIF) are peculiar organisms with high diversity that apparently lack sexual reproductive structures and form compact, melanised colonies on bare rock surfaces. These fungi are one of the most stress-tolerant eukaryotic life forms on the earth and have evolved a variety of adaptive mechanisms to occupy harsh niches. They also have special characteristics related to their cell structure, metabolism, and stress tolerance mechanisms. Although RIF are very ubiquitous, they have often been overlooked due to their small size, slow growth and lack of diagnostic features. In this review, we describe the diversity, research approaches, history, adaptive mechanism and applied research of rock-inhabiting fungi, to focus attention on RIF and their importance.

**Key words:** rock-inhabiting fungi; diversity; stress resistance; heritage conservation; astrobiology

石生真菌(rock-inhabiting fungi, RIF)是指生活在岩石表面或伸入岩石内部的一类暗色真菌(Krumbein & Jens, 1981; Friedmann, 1982; Staley et al, 1982)。通常人们认为裸露的岩石表面是地衣、苔藓以及藻类的寄居场所, 然而石生真菌也是一类以石质材料为基质的特殊环境微生物(Urzì et al, 2000)。人们最早在沙漠中发现了石生真菌, 它们以微菌落的形式生长在岩石上。由于它们生长缓慢、部分菌丝与酵母相似, 以前也被称为微菌落真菌(microcolonial fungi)或黑色酵母菌(black yeast) (De Hoog, 1993; Yoshida et al, 1996; Figueras et al, 1996)。石生真菌的表面常覆盖着微小致密的坚硬外壳, 单菌落直径一般不超过1 mm, 在自然界形成一个新菌落一般需要几个月的时间。石生真菌的生长方式大多为等径的分生生长, 产生黑色素化的厚壁细胞, 菌落呈黑色菜花状(Wollenzien et al, 1995; Selbmann et al, 2005, 2013), 菌丝多呈念珠状, 并产生芽殖型分生孢子(图1)。菌落周围常产生胞外聚合物, 这些物质不仅保护真菌细胞, 并且具有疏松岩石表面的作用, 使细胞更容易吸收环境中的营养

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(Sterflinger & Krumbein, 1995)。不同物种的石生真菌形态特点非常相似(Minter, 1987; De Hoog & Mcginnis, 1987), 仅从外观上难以判断微菌落属于什么物种(Friedmann, 1982)。

形态学结合分子生物学证据表明, 大多数石生真菌属于子囊菌门的座囊菌纲和散囊菌纲(Reeb et al, 2004; Ruibal et al, 2009; Selbmann et al, 2014)。利用宽松时钟模式和化石二级校准的方法对石生真菌的起源进行的研究指出, 座囊菌纲和散囊菌纲的起源存在差异: 其中, 座囊菌纲的石生真菌起源于泥盆纪后期, 远早于起源于中三叠纪后期的散囊菌纲(Gueidan et al, 2011)。石生真菌具有很强的抗逆能力(Palmer et al, 1990; Sterflinger, 2006; Zakharova et al, 2013), 它们在恶劣的环境中长期进化, 形成了一系列对极端环境的适应性特征(Dadachova & Casadevall, 2008)。石生真菌以无性形态生长在岩石表面, 目前尚未发现产孢或有性繁殖, 这可能是恶劣的环境迫使它们放弃了有性形态, 无性繁殖方式使其更快地完成生命周期, 这样能减少它们生命活动所需的能量, 以适应贫瘠的营养环境(Gorbushina, 2007)。

基于石生真菌独特的生存环境和生物学特征, 本文将详细阐述石生真菌的多样性、逆境耐受性、抗逆机制及应用研究, 并对今后石生真菌的研究进行展望。

## 1　石生真菌的多样性

### 1.1　研究方法

培养性状是目前石生真菌多样性研究的基础。由于石生真菌处于特殊的生境, 需要采取特殊的分离方法。Warscheid (1990)采取破碎岩石的方法分离石生真菌; Gorbushina等(1993)利用牙签或大头针对历史文物上的石生真菌进行分离; 后来, 为了满足大规模的调查研究, Ruibal等(2005)采用稀释平板法对石生真菌进行分离。石生真菌具有普通真菌的共性, 能用PDA、MEA等培养基进行纯培养, 最适生长温度为15–25℃(Selbmann et al, 2008; Egidi et al, 2014)。

Staley等(1982)首次从中国、澳大利亚等地采集岩石样品, 通过电子显微镜观察, 初步描述了石生真菌在岩石表面生长的菌落结构, 并采用细胞亚显微结构观察发现石生真菌具有线粒体、细胞核膜等结构。研究人员还通过设计实验发现它们具有呼吸作用但不能进行光合作用, 明确了石生真菌为异养真核生物。由于形态学观察难以鉴别, 使石生真菌多样性研究进展非常缓慢(Taylor-George et al, 1983; Minter, 1987; De Hoog & Mcginnis, 1987)。随着分子生物学的发展, 单基因分析如18S rDNA(Berbee & Taylor, 1992)、5.8S rDNA与ITS2 (De Hoog et al, 1999)和核酸限制性片段长度多态性技术(DNA RFLP)得以高效应用于石生真菌多样性的研究, 如: mtDNA RFLP (De Cock, 1994)、rDNA RFLP (Uijthof & De Hoog, 1995)。近年来, 多基因(ITS、LSU、nucSSU、mtSSU、RPB1、TUB等)序列分析方法对石生真菌进行多样性研究更是得到业界的认可(Selbmann et al, 2005; Ruibal et al, 2009)。

### 1.2　研究历史

早在一个世纪以前, Muntz (1890)就提出岩石的腐蚀过程有微生物的参与, 并指出这种降解作用不仅发生在岩石表面而且还深入到岩石内部。Gromov (1957)发现俄罗斯北部的原始岩石上有藻类、细菌和真菌的存在。Staley等(1982)首次对石生真菌的菌落大小和生长环境进行了描述。后来, Friedmann和Weed (1987)在南极沙漠岩石内部发现了微生物化石的存在。由于石生真菌种水平上的形态特征差异不明显, 所以相当一段时期内对石生真菌的研究较少。近年来, 分子生物学技术的发展极大地推动了石生真菌多样性的研究。De Hoog和Gueho (1984)利用脱氧核糖核酸碱基成分对*Moniliella*、*Trichosporonoides*和*Hyalodendron*属真菌进行了分类研究。Braams (1992)从德国砂岩纪念碑表面分离鉴定出70多株石生真菌; Sterflinger和Prillinger (2001)利用18S rDNA和ITS1对奥地利维也纳城市建筑物和文物上的石生真菌进行了研究, 发现优势菌群主要为*Coniothyrium*、*Epicoccum*和*Phoma*属; Selbmann等(2005)从南极岩石样品中分离出26株耐冷石生真菌, 并利用2个基因(ITS和SSU)鉴定了1个新属、3个新种; Ruibal等(2005)从西班牙马略卡岛两个不同地点采集岩石样品, 分离出170株石生真菌, 其中只有3个菌株具有特定形态特征。其后, Ruibal等(2008)又从西班牙中部山区分离石生真菌266株, 采用微卫星引物PCR扩增, 鉴定出163个基因型。随后, Ruibal等(2009)分别用3个基因(nucLSU、nucSSU、mtSSU)和5个基因(nucLSU、 nucSSU、mtSSU、RPB1、RPB2)对座囊菌纲的石生真菌进行了系统研究, 发现座囊菌纲的石生真菌主要分布在煤炱目、座囊菌目和多腔菌目; Egidi等(2014)的研究发现石生真菌在座囊菌亚纲具有更高的多样性, 并建立了煤炱目的31个新种和13个新属; Hubka等(2014)利用4个基因(*nuc18S*、*nuc28S*、*ITS*和*B-tubulin*)描述了刺盾炱目Trichomeriaceae科的1个新属(*Bradymyces*)和2个新种; 后来, Su等(2015)从我国的西藏、江西、云南等地采集样品, 分离出石生真菌上千株, 对其中的60多株进行研究, 描述了座囊菌纲的2个新属(*Rupestriomyces*和 *Spissiomyces*)和5个新种。最近, Isola等(2016)从意大利的石质文物上发现了座囊菌纲的2个新属(*Saxophila*和*Lithophila*)和9个新种。研究结果表明, 石生真菌是子囊菌中一个典型的生态类群而非一个系统学类群(Gueidan et al, 2008; Ruibal et al, 2008)。并且这一类群中存在着大量未发现和未明确分类地位的单元。这些石生真菌新属和新种的发现, 极大地丰富了石生真菌的多样性, 为更好地研究石生真菌的群落组成及适应性进化奠定了基础。

## 2 石生真菌的耐受性及其抗逆机制

石生真菌长期暴露在恶劣的环境中, 它们如何适应逆境引起了科学工作者的重视。大量的研究表明石生真菌具有较强的耐高/低温(Friedmann & Weed, 1987)、干旱(Gorbushina et al, 2003, 2008)、渗透压(Sterflinger et al, 1998, 2012)和抗辐射的能力(Dadachova et al, 2007; Onofri et al, 2007, 2008)。在耐受极端温度方面, 研究人员发现石生真菌具有较强的耐冷能力(Nienow & Friedmann, 1993)。而从南极沙漠分离的菌株*Cryomyces* spp.表现出典型的适应温度变化的能力, 它不仅能在南极永冻的条件下长期生存, 而且也能在温度高达90°C下胁迫1小时后正常生长(Onofri et al, 2007, 2008)。在抗温胁迫机制方面, Tesei等(2012)利用二维凝胶电泳对3株不同来源的石生真菌在不同温度下产生的蛋白进行了研究, 结果表明供试菌株在高温和常温下产生的蛋白存在差异, 但一些关键蛋白因子如热休克蛋白的表达并没有变化。

除了温度的胁迫, 往往还有盐胁迫(Van Uden, 1984)。研究发现, 从南极分离的菌株能在25%的NaCl中正常生长(Onofri et al, 2008)。此外, 石生真菌还具有强抗辐射能力, 南极沙漠上空由于臭氧层的空洞, 导致南极生境下的石生真菌受到强辐射胁迫。研究人员把从南极分离的石生真菌和酵母在相同条件进行UV-B辐射, 结果表明, 使酵母失活的辐射强度对石生真菌的生存没有影响(Onofri et al, 2007; Selbmann et al, 2011)。石生真菌不仅能耐受高辐射, 甚至可以利用辐射合成ATP作为能量来源(Dadachova & Casadevall, 2008), 辐射使一些关键基因上调, 一种可诱导的微同源介导的重组途径可能是真核生物适应性进化的潜在机制。

石生真菌不仅菌落呈黑色, 而且还产生不同类型的天然黑色素, 主要包括DOPA型和DHN型(Kogej et al, 2003, 2004), 黑色素对石生真菌抗逆具有重要作用(Gadd & de Rome, 1988; Gunde-Cimerman et al, 2000; Zhdanova et al, 2000; Dadachova et al, 2007)。研究表明, 石生真菌细胞壁的黑化现象表明黑色素聚酮化合物的生物合成途径是可诱导的(Dadachova & Casadevall, 2008)。另外, 研究人员通过人工气候箱模拟干旱环境, 对供试菌株进行干旱胁迫, 经过二维凝胶电泳分析蛋白的表达差异, 结果显示干旱胁迫使一些关键因子下调, 但该研究并没有揭示相应蛋白的变化情况(Hofmann et al, 2000; Zakharova et al, 2013, 2014a)。岩石表面营养物质贫乏, 石生真菌主要通过放慢生长速度节省能量。

在抗氧化和渗透压方面, 研究发现石生真菌产生的次生代谢产物类菌孢素能够吸收最大波长在310 nm左右的紫外线, 这不仅可以保护真菌免受UV辐射的侵害, 同时也是真菌抗氧化和渗透压的保护剂(Volkman et al, 2003)。通过对菌株*Cryomyces antarcticus*的基因组解析发现, 实验菌株的聚酮合酶和漆酶表达量低, 但未能挖掘到相关目标基因(Sterflinger et al, 2014)。研究石生真菌的抗逆特性不仅有利于抗逆基因的挖掘, 而且对明确逆境相关生物学代谢途径具有重大意义。

## 3 石生真菌的应用

### 3.1 石生真菌对石质文物的影响

石质文物主要包括石雕、石窟、壁画等。石生真菌定殖在石质文物表面, 对古建筑物和历史遗迹

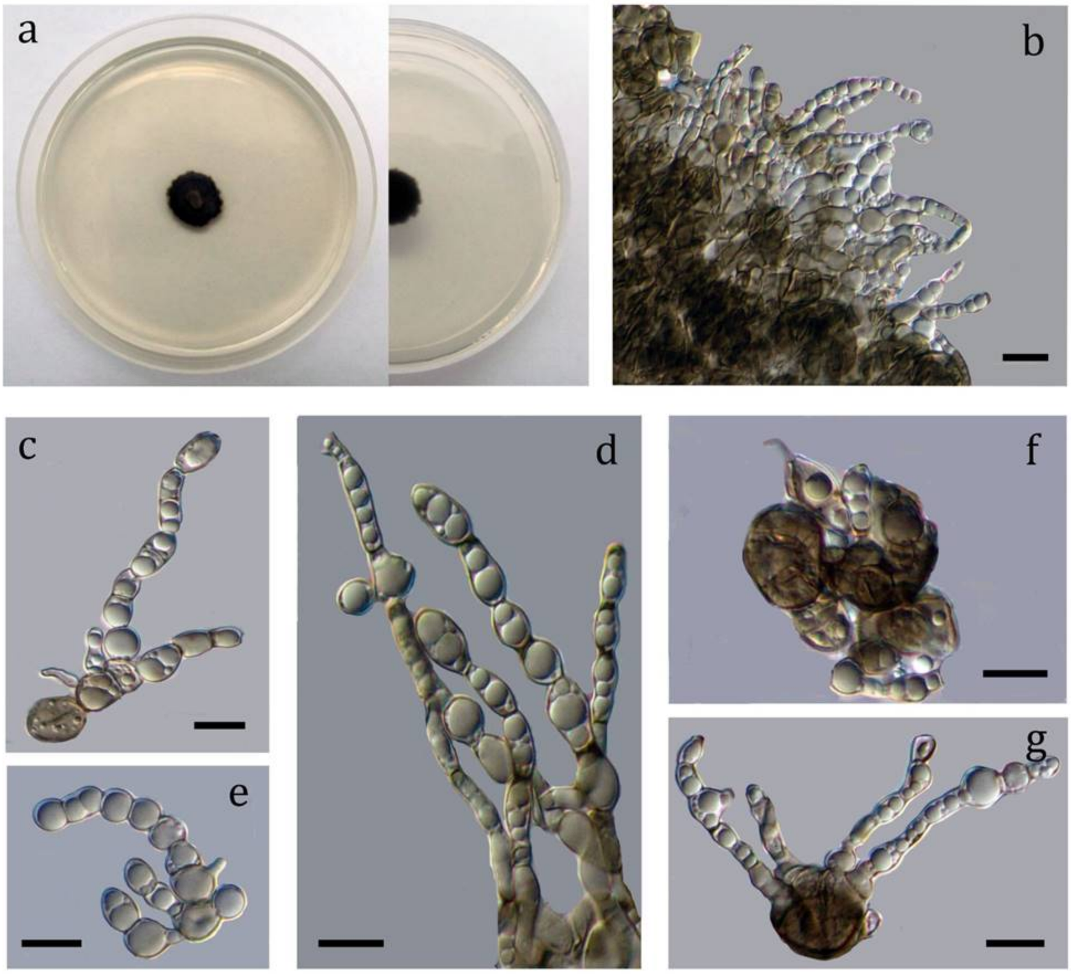


**图1　一株散囊菌纲石生真菌纯培养图。(a) MEA培养基上培养6周的菌落结构; (b)链状,念珠状菌丝; (c, d, e)不同菌丝上的分生孢子; (f, g)单独的芽殖型孢子, 标尺 = 10 μm。**

Fig. 1　Pure culture of rock-inhabiting fungi (Chaetothyriales). (a) Colony after 6 weeks on MEA; (b) Catenated, moniliform hyphae; (c, d, e) holoblastic conidia in undifferentiated hyphae; (f, g) Solitary, enlarged, darkly pigmented multicellular body with enteroblastic proliferations and budding cells. Scale bars = 10 μm.

甚至宝石具有显著的破坏作用(Wollenzien et al, 1997; Tretiach et al, 2012; Onofri et al, 2014)。黑色的石生真菌菌落定殖在岩石上, 使岩石表面的颜色发生变化, 这一特点较早地引起了文物工作者的重视(Urzi et al, 1993)。Diakumaku等(1995)发现大理石和石灰岩材质纪念碑的黑化现象是由于真菌引起的, 并且是通过物理过程而不是化学作用(如产酸)来腐蚀的, 否定了人们长期认为石质文物的黑化是空气污染导致的说法。近年来, 古建筑上的石生真菌研究得到越来越多的关注(Ascaso et al, 2004; Cámara et al, 2011)。Gravesen等(1994)的研究表明真菌对建筑材料有破坏作用; Dornieden等(1997)指出石生真菌造成岩石表面选择性吸收太阳的辐射, 导致岩石晶体局部的延伸, 进而破坏建筑物的完整结构; Daghino等(2009)发现石生真菌*Verticillium leptobactrum*可以风化纤维蛇纹石并可用于石棉的生物降解。Gadd (2007)报道石生真菌通过生物力学和生物化学风化岩石, 认为石生真菌和蓝细菌、地衣在全球生物地球化学循环中起着重要的作用。由于国外石质文物较为丰富, 主要包括意大利(Zucconi et al, 2012; Marvasi et al, 2012)、希腊(Sterflinger et al, 1997)、乌克兰(Bogomolova & Minter, 2003)、土耳

其(Sert et al, 2007a, b, c)等地的历史文物上的石生真菌得到了越来越多的研究(De Leo et al, 1999, 2003; Sterflinger et al, 1999)。石生真菌定殖在历史文物表面不仅对文物的美观具有影响，而且腐蚀文物(Marvasi et al, 2012)。研究石生真菌对石质文物的保护具有重要的理论及实践意义。

### 3.2 石生真菌与天体生物学

地球上的极端环境包括高温、低温、寡营养、极高/极低pH值、高盐、高辐射等，在这些环境中都能发现微生物，这给研究外太空是否存在生命提供了新线索(Miller, 2005)。微生物学家希望通过分子生物学和生理学方面的研究了解生命生存和适应环境的策略(Ma et al, 2004; Wang et al, 2007)。科学家早期在沙漠环境的岩石内部发现了大量微生物化石，提出如果生命起源于火星，则类似的微生物化石同样可能在火星上找到(Friedmann & Weed, 1987)。石生真菌是地球上耐胁迫能力最强的生物之一，这激发了人们对真菌生存极限以及太空生物学的研究兴趣(Gorbushina, 2003; Onofri et al, 2008, 2009)。欧洲航天局和意大利航天中心合作，首次对石生真菌进行外太空实验，研究人员于2008年2月7日通过宇宙飞船把采自南极的两株石生真菌*Cryomyces antarcticus*和*C. minteri*送入国际空间站，并使其暴露在太空条件下(Rabbow et al, 2009, 2012)；经过565天的外太空处理，存活率为12.5% (Onofri et al, 2012)。Onofri等(2008, 2009)的研究结果表明，石生真菌能在模拟太空和火星的条件下生存，可以耐受90℃的高温。为了更进一步研究石生真菌耐受太空的能力，菌株*C. antarcticus*再次被欧洲航天局选作研究天体生物学的材料，于2014年7月被送入国际空间站进行了为期两年的实验(Selbmann et al, 2015)。石生真菌作为一种能够适应寡营养和恶劣自然环境条件的特殊生命类群，有望作为研究天体生物学的模式材料，这对于我们更好地理解生命本质和探索生命极限有非常重要的意义。

## 4 展望

据估计，全世界的真菌种类约为150万(Hawksworth, 1991)，但至今正式描述的物种只有7% (Hawksworth, 2004)，绝大多数真菌是未知的。其原因一方面在于没有合适的分离培养方法，缺少对许多真菌类群适应的培养条件和培养基；另一方面在于对真菌生活环境特别是对极端环境缺乏了解，不能准确地评价不同地域中真菌群落的结构组成(Hawksworth & Rossman, 1997)。最近几年，意大利特殊环境保藏中心的生物学家开展了对南极真菌的系统调查，他们发现南极荒漠蕴含着大量的石生真菌(Selbmann et al, 2014; Egidi et al, 2014; Hubka et al, 2014)，未来对特殊环境中石生真菌的调查是丰富其生物多样性的有效途径。

近年来，随着测序技术的发展，宏基因组测序克服了传统纯培养微生物技术的不足，为人们调查微生物的群落组成和多样性以及开发利用未培养微生物资源、发现新的基因提供了便利(Schloss & Handelsman, 2005)，也给研究特殊环境中石生真菌的多样性、群落组成和功能提供了新方法。在过去的几年中，研究人员希望通过蛋白质组和基因组测序的方法找到石生真菌的抗逆机制，遗憾的是，目前结果并不清晰(Zakharova et al, 2014a, b; Sterflinger et al, 2014)。随着测序成本的降低，对石生真菌进行全基因组测序以及不同胁迫条件下的转录组研究对于揭示石生真菌的抗逆性机制具有重要　意义。

尽管Staley等(1982)从我国戈壁环境采集石头样品对石生真菌进行了调查，但一直以来，我国对于石生真菌的研究极为缺乏。作者所在的实验室过去几年对国内的石生真菌资源进行了初步调查，发现我国的石生真菌分布十分广泛。我国不仅拥有丰富的地理生态类型(如新疆的戈壁、西南地区的喀斯特地貌以及有着“地球第三极”之称的青藏高原荒漠地区)，而且有着不可计量的石质文物(如重庆的大足石刻千手观音、山西的云冈石窟以及不同地区的纪念碑和宝石)，这些特殊的生境蕴藏着大量未被调查的石生真菌资源。开展系统的石生真菌研究不仅能极大地丰富物种多样性，而且对于阐明真菌的生存极限、起源、进化以及对逆境的适应性机制具有重要的意义。

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