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专论与综述

嗜角蛋白真菌的界定、研究方法及其应用价值

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摘　要： 嗜角蛋白真菌(keratinophilic fungi)是指能降解角蛋白并能利用其作为唯一营养源的真菌类群，大部分隶属于爪甲团囊菌目(*Onygenales*)、散囊菌目(*Eurotiales*)和肉座菌目(*Hypocreales*)。由于该类群分布广、种类多、营养方式多样，其研究方法和技术手段也在不断进步，加深了其研究的深度。为了促进对该类群研究现状和研究不足的认识，本文对嗜角蛋白真菌的定义进行了界定，整理了其所包含的主要类群，介绍了 3 种主要研究方法，总结了该类群在饲料、皮革、医药和农业方面及作为生物指标等方面的应用价值，展望了嗜角蛋白真菌的进一步研究方向。

关键词： 丝状真菌；角蛋白；应用领域

Delimitation, research methods and application of keratinophilic fungi

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Abstract: Keratinophilic fungi are those species that can degrade keratin and utilize keratin materials as the only nutrient source most of which belong to *Onygenales*, *Eurotiales* and *Hypocreales*. Since these fungi are widely distributed in various environment or niches, and have many varieties and

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nutritional diversity, more and more methods and techniques have been developed for investigation and characterization of these species. In order to promote the understanding of the current status and research shortage of keratinophilic fungi, this paper defines the keratinophilic fungi, organizes their taxa, introduces three main research methods, summarizes their applications in feed, leather, medicine and agriculture, and as bioindicators. Finally, we summarized research directions of keratinophilic fungi in the future work.

Keywords: filamentous fungi; keratin; application areas

角蛋白是一类广泛分布于人体毛发、指甲及动物爪、角、羽毛的特殊蛋白质，具有保护上皮组织细胞免受机械压力损伤、防止体液流失等功能[1]。在自然界中其含量仅次于纤维素和几丁质[2]。由于角蛋白中存在丰富的二硫键及疏水作用等导致其具有较高的机械强度，不易被普通蛋白水解酶溶解消化，是已知最坚韧的生物材料之一[3]。

近年来，全球畜牧业得到了长足发展，每年可产生数百万吨的角蛋白副产品[4]。目前主要采取焚烧或填埋手段进行处理，而角蛋白中大量的二硫键决定了这些处理极易污染环境[5]。同时，这种初级的处理也导致大量优质生物资源的浪费。目前我国蛋白质饲料较缺乏，约 70%的大豆粕依赖进口[6]。然而来源丰富的角蛋白中富含动物所需的多种必需氨基酸，可作为优质蛋白质饲料来源[7]。研究表明，一些微生物和昆虫能将角蛋白降解为可利用小分子化合物，它们广泛存在于各种生态环境，以温和的方式降解角蛋白并保留各种氨基酸的完整性，是一种环境友好型降解方式[8]。其中一大类微生物为嗜角蛋白真菌(keratinophilic fungi)。

嗜角蛋白真菌的主要类群大部分隶属于子囊菌门的爪甲团囊菌目、散囊菌目和肉座菌目。其中部分成员是潜在的病原体，可引起皮肤癣病(头癣、体癣、手癣、股癣足癣和甲癣)，其慢性复发性感染的特点和不断增加的耐药性严重影响着人们的健康[9]。然而曲霉属、镰刀菌属、木霉属中的某些嗜角蛋白真菌却表现出潜在的应用价值[10-22]。基于张芝元的前期工作和以往的研究[23]，本文为规范嗜角蛋白真菌而给予了明确的定义，简述了目前已知的主要嗜角蛋白真菌类群及传统培养方法和分子生物学分析方法在此方面的研究应用，以期为更好地了解和利用嗜角蛋白真菌提供科学依据。

1 嗜角蛋白真菌的定义

生长在角蛋白基质上的真菌是否都能被界定为嗜角蛋白真菌？在人类或动物毛发中除含有角蛋白外还含有尿酸、尿素、氨、戊糖、糖原、酚类和氨基酸及其他营养成分，事实上，真菌在摄取非角蛋白物质后，部分角蛋白才被分解利用[24]。Mahariya 等研究发现，毛发上存在非嗜角蛋白真菌和嗜角蛋白真菌连续定殖生长的 4 个演替阶段，即第一阶段(1−30 d)，发现 5 种非嗜角蛋白真菌；第二阶段(31−45 d)，3 种非嗜角蛋白真菌和 3 种嗜角蛋白真菌一起出现；第三阶段(46−60 d)，仅生长 1 种非嗜角蛋白真菌和 4 种嗜角蛋白真菌，第四阶段(75 d 后)，所有非嗜角质真菌完全消失[25]。因此嗜角蛋白真菌的界定一直处于模糊状态。

Rajak 等认为嗜角蛋白真菌与角蛋白降解真菌(keratin-degrading fungi)为同一概念，表示能

降解角蛋白的真菌[26]。在实际应用中，角蛋白降解真菌常指具有角蛋白降解能力的真菌类群，而嗜角蛋白真菌则泛指所有能够以含有角蛋白基质作为天然栖息地的真菌，与角蛋白的亲和力弱于角蛋白降解真菌[27]。Błyskal 则认为角蛋白降解真菌是能够产生角蛋白酶而攻击α-角蛋白的一类微生物，而嗜角蛋白真菌是指仅能利用角蛋白的部分易降解组分及相关物质的真菌[28]。近年来，嗜角蛋白真菌和角蛋白降解真菌的几种定义一直在沿用，甚至被认为是同义词。结合沈鑫等前期工作及前人的相关研究，我们认同 Calin 等的界定，将嗜角蛋白真菌界定为一类偏好各种角质基质，并能降解利用角蛋白作为唯一碳氮源的真菌类群[29-30]。

2 嗜角蛋白真菌的主要类群

嗜角蛋白真菌分布广泛，已从公园、路边、海滩、牧草地、哺乳动物围栏土壤、动物医院及野生动物保护区等土壤中分离出大量类群，大多隶属于金孢霉属(*Chrysosporium* Corda)、假裸囊菌属(*Pseudogymnoascus* Raillo)、地丝霉属(*Geomyces* Traaen)、镰刀菌属(*Fusarium* Link)、曲霉属(*Aspergillus* P. Micheli)、青霉属(*Penicillium* Link)和链格孢属(*Alternaria* Nees)等[23,31-33]。此外，也有关于球托霉属(*Gongronella* Ribaldi)、小克银汉霉属(*Cunninghamella* Matr.)等可降解角蛋白的报道[34-35]。综上，嗜角蛋白真菌大部分隶属于子囊菌门(*Ascomycota* Caval.-Sm.)，其中又以爪甲团囊菌目(*Onygenales* Cif. ex Benny & Kimbr.)、散囊菌目(*Eurotiales* G.W. Martin ex Benny & Kimbr.)和肉座菌目(*Hypocreales* Lindau)为主(表 1)。

2.1 爪甲团囊菌目(*Onygenales*)：金孢霉属(*Chrysosporium*)和皮肤癣菌类群

金孢霉属是一类全球分布的真菌，能够生存于角蛋白腐质、粪便、土壤和食物等环境中，而且部分菌株还是脊椎动物的机会性病原体[67]。研究表明，印度金孢霉(*Chrysosporium indicum* Garg)、嗜角质金孢霉(*C. keratinophilum* D. Frey ex J.W. Carmich.)、刺柄金孢霉(*C. asperatum* J.W. Carmich.)和热带金孢霉(*C. tropicum* J.W. Carmich.)能以人的毛发或禽类羽毛作为底物基质生长[26,36-37,41]。牛、羊及人的毛发不支持乔治金孢霉[*C. georgiae* (Varsavsky & Ajello) Oorschot]生长，但其能以鸡毛为碳氮源[38]。

皮肤癣菌是指能够侵入富含角蛋白的附属器官和皮肤组织，如角质层、角、毛发等引起浅部感染的真菌。由于这类病原菌能侵入角蛋白组织，因此也归为嗜角蛋白真菌。随着分子生物技术的不断发展，更多不确定或已确定物种被重新鉴定并归类。根据最新的分类，皮肤癣菌主要指裸囊菌科(*Arthrodermataceae* Locq. ex Currah)真菌中的部分成员，该科由毛癣菌属(*Trichophyton* Malmsten)、表皮癣菌属(*Epidermophyton* Sabour.)、小孢子菌属(*Microsporum* Gruby)、奈尼兹皮菌属(*Nannizzia* Stockdale)、节皮菌属(*Arthroderma* Curr.)、*Paraphyton* Y. Gräser, Dukik & de Hoog、*Lophophyton* Matr. & Dassonv.、栉霉属(*Ctenomyces* Eidam)、*Guarromyces* Y. Gräser & de Hoog 共 9 个属组成[68-69]。

毛癣菌、表皮癣菌和小孢子菌是最常见的皮肤癣菌。嗜人红色毛癣菌[*T. rubrum* (Castell.) Sabour.]是全球性皮肤病病原菌[70]。然而其复合种 *T. rubrum* complex 的另一分类单元紫色毛癣

表 1　一些常见嗜角蛋白真菌及其偏好基质

Table 1　Some common keratinophilic fungi and their preferred substrates

嗜角蛋白真菌 Keratinophilic fungi	角蛋白基质 Keratin	文献来源 References
爪甲团囊菌目 *Onygenales*		
印度金孢霉 *Chrysosporium indicum*	毛发 Hair	[36]
热带金孢霉 *C. tropicum*	羽毛 Feather	[37]
嗜角质金孢霉 *C. keratinophilum*	毛发 Hair	[37]
刺柄金孢霉 *C. asperatum*	毛发 Hair	[38]
乔治金孢霉 *C. georgiae*	羽毛 Feather	[38]
鸡发癣菌 *Trichophyton gallinae*	羽毛 Feather	[39]
须发癣菌 *T. mentagrophytes*	豚鼠毛发 Guinea pig hair	[40]
T. ajelloi	羽毛 Feather	[41]
T. schoenleinii	毛发 Hair	[42]
T. simii	皮肤 Skin	[43]
红色毛癣菌 *T. rubrum*	毛发，指甲，羽毛 Hair, fingernails, feather	[44]
絮状表皮癣菌 *Epidermophyton floccosum*	皮肤 Skin	[45]
犬小孢子菌 *Microsporum canis*	皮肤 Skin	[46]
石膏样小孢子菌 *M. gypseum*	皮肤 Skin	[47]
粉小孢子菌 *M. fulvum*	羽毛 Feather	[48]
Nannizzia gypsea	皮肤 Skin	[49]
Arthroderma benhamiae	皮肤 Skin	[50]
散囊菌目 *Eurotiales*		
烟曲霉 *Aspergillus fumigatus*	羽毛 Feather	[51]
黑曲霉 *A. niger*	羽毛 Feather	[52]
黄曲霉 *A. flavus*	羽毛 Feather	[53]
寄生曲霉 *A. parasiticus*	羽毛 Feather	[54]
米曲霉 *A. oryzae*	羽毛 Feather	[10]
Aspergillus sp.	羽毛 Feather	[55]
溜曲霉 *A. tamarii*	山羊皮 Goatskin	[13]
产黄青霉 *Penicillium chrysogenum*	羽毛 Feather	[56]
马尔尼菲青霉 *P. marneffei*	羽毛 Feather	[56]
Penicillium spp.	稻草 Straw	[57]
肉座菌目 *Hypocreales*		
哈茨木霉 *Trichoderma harzianum*	羽毛 Feather	[44]
深绿木霉 *T. atroviride*	羽毛 Feather	[58]
绿色木霉 *T. viride*	动物皮肤 Animal skin	[12]
黄色镰刀菌 *Fusarium culmorum*	猪毛 Pig hair	[59]
砖红镰刀菌 *F. lateritium*	猪毛 Pig hair	[59]
Fusarium sp. 1A	动物皮肤 Animal skin	[11]
其他 Others		
Aphanoascus fulvescens	羽毛 Feather	[60]
Absidia sp.	毛发 Hair	[37]
假丝酵母 *Candida parapsilosis*	羽毛 Feather	[61]
Doratomyces microspores	猪表皮 Pig skin epidermis	[62]
Entomophthora coronate	毛发 Hair	[37]
Gymnoascoideus petalosporus	毛发 Hair	[26]
Onygena corvina	羽毛，毛发，角 Feather, hair, corner	[63]
淡紫拟青霉 *Paecilomyces lilacinus*	羽毛 Feather	[64]
马昆德拟青霉 *P. marquandii*	蹄，角 Hoof, corner	[65]
短帚霉 *Scopulariopsis brevicaulis*	羽毛，毛发，山羊皮 Feather, hair, goatskin	[66]

菌(*T. violaceum* Sabour. ex E. Bodin)可引起仅存于非洲和中东的地方性头癣和体癣[71]。引起皮肤癣病的另一真菌是絮状表皮癣菌[*E. floccosum* (Harz) Langeron & Miloch.][45]。小孢子菌属中研究较多的犬小孢子菌(*M. canis* E. Bodin ex Guég.)是一种亲动物及人的病原真菌，感染力强，容易感染毛发，引起严重的炎症反应[46]。其他一些不常见的皮肤癣菌，如从患者上臂深癣中及刺猬体表分离的石膏样奈尼兹皮真菌[*N. nana* (C.A. Fuentes) Y. Gräser & de Hoog]，是一种罕见的亲人和/或动物的皮肤癣菌，能够引起甲癣、足癣和股癣[49]。*T. benhamiae* (Ajello & S.L. Cheng) Y. Gräser & de Hoog (原 *Arthroderma benhamiae*)可由豚鼠传染至儿童引起炎症性手足癣病[50]。

2.2 散囊菌目(*Eurotiales*)：曲霉属(*Aspergillus*)和青霉属(*Penicillium*)

曲霉属真菌广泛存在于土壤、空气和农作物等环境中，能够引起多种物质腐败变质。曲霉属真菌具有高分泌胞外酶的能力，因此曲霉属嗜角蛋白真菌具有潜在的应用开发潜力[72]。研究发现，烟曲霉(*Aspergillus fumigatus* Fresen.) TKF1 菌株、黑曲霉(*A. niger* Tiegh.)、黄曲霉(*A. flavus* Link) K-03 菌株、米曲霉[*A. oryzae* (Ahlb.) Cohn] nrrl-44 菌株和寄生曲霉(*A. parasiticus* Speare)等具有强大的羽毛降解能力[10,23,29,33,51-56,73]，而且寄生曲霉和米曲霉 nrrl-44 菌株还表现出非致病性的特性[10,54]。

营腐生生活的青霉属真菌在自然界中的分布极其广泛，其主要作用是分解有机质，促进包括 C、N 和 P 等在内的多种元素的循环[74]。然而其中一些菌株可利用角蛋白作为唯一碳氮源，例如产黄青霉(*Penicillium chrysogenum* Thom)和马尔尼菲青霉(*P. marneffei* Segretain, Capponi & Sureau)[56]。

2.3 肉座菌目(*Hypocreales*)：镰刀菌属(*Fusarium*)和木霉属(*Trichoderma*)

镰刀菌属是最大的真菌类群之一[75]。有研究表明，该属成员黄色镰刀菌[*Fusarium culmorum* (Wm.G. Sm.) Sacc.]、砖红镰刀菌(*F. lateritium* Nees)和茄病镰刀菌[*F. solani* (Mart.) Sacc]在含羽毛的基质中表现出较强的角蛋白降解能力[23,29,33,59,76]。Calin 等研究发现镰刀菌菌株对不同类型兽皮均具有降解作用，而且表现出良好的角蛋白酶活性，在对皮革业产生的动物废料的处理中具有一定的应用潜力[11]。

木霉属真菌是常寄生于多种植物的病原真菌类群[77]。哈茨木霉(*Trichoderma harzianum* Rifai) HZN12 菌株和深绿木霉(*T. atroviride* P. Karst.) F6 菌株因能在羽毛基质中快速生长而具有较高的应用潜力[58,78]。此外，绿色木霉(*T. viride* Pers.)能应用于皮革制造过程中的脱毛[12]。

3 嗜角蛋白真菌的研究方法

3.1 调节培养基法

微生物所生存的自然环境通常为寡营养环境，而且自然环境中温度、氧气和 pH 会随着时间季节的变化而改变。然而人工培养基中营养丰富且物理环境恒定，为生长较快的微生物提供了良好的生长条件，导致了生长缓慢的微生物难以被分离和培养；此外，不同的微生物类群所需要的营养物质有所差异，有些类群具有特殊的营养偏好，因而目前自然环境中还存在大量真菌“暗物质”[79-80]。目前已被描述的真菌仅约 12 万种[81]。基于此，人们提出了调节培养基法。调节培养基法是通过调节培养基中不同营养物质或浓度比探究未培养微生物的培养条件。如通过毛发诱饵的富集培养，其中人发、羽毛、羊毛常用于对嗜角蛋白真菌的富集(表 1)。然而，研究表明，某些嗜角蛋白真菌不

能被某些角蛋白基质富集，如牛、羊及人类毛发不能富集乔治金孢(*C. georgiae*)，鸡发癣菌(*T. gallinae*)不能利用人或豚鼠毛发中的角蛋白[38-39]。究其原因，可能是因为一些真菌对角蛋白成分的偏好性利用所致，如不同来源的角质中 α-角蛋白(富含半胱氨酸残基)和 β-角蛋白(富含小侧链甘氨酸、丙氨酸和丝氨酸残基)组成成分及结构不同。Ulfig 通过在不同温度下设置的毛发诱饵法，确定了温度等因素对污泥中嗜角蛋白真菌组成的影响[82]。

3.2 群体培养法

生物间互作，包括互利共生、偏利共生、竞争、寄生或捕食，是影响嗜角蛋白真菌可培养的重要生物因素。传统纯培养方法忽略了生物间的互作。群体培养法是指通过保存微生物群体间的互作实现微生物培养，如原位培养和共培养。原位培养法是将样品置于模拟的自然环境条件下分离培养微生物。此法并不了解微生物生长的全部因素条件，人们只是通过模拟自然条件进行培养。基于原位培养原理，现已发展起来扩散室、分离芯片、Trap 技术、I-Tip 技术及胶囊包埋等技术，将难培养微生物转变成易培养微生物[83]。周士越等设计了适用于真菌的分离芯片原位培养装置，此法比传统培养方法获得了更高的真菌多样性[84]。混合菌株协作生长的共培养法在降解角蛋白方面表现出了复杂性低、可控性强、稳定性好等优点[85]。结合传统培养法及生态学理念的新途径，将对嗜角蛋白新资源的发现及筛选高效降解角蛋白菌株产生积极影响。

3.3 分子生物学方法

近年来，各种分子生物学技术及高通量测序(high-throughput sequencing)技术的应用，对嗜角蛋白真菌各方面的研究也产生了深远的影响。分子生物学方法应用于嗜角蛋白真菌的研究起步较晚，起初主要用于证明一些病原菌的关系[86-89]，后续逐渐应用于嗜角蛋白真菌系统学及物种鉴定中[32,34-35]。随着分子技术的发展，高通量测序技术因其能够直接提取样本中微生物群落的核酸并测定其核酸序列，不再受限于对样本微生物的培养而备受关注。Hamm 等[90]使用 Illumina 测序与依赖培养的方法相结合，对干旱生态系统中不同类型生物土壤结皮和根际土壤中嗜角蛋白真菌多样性、时空分布及季节波动性进行了研究，证实了该地区皮肤癣菌丰度低，而链格孢属真菌丰度较高。随着组学技术应用于嗜角蛋白真菌的研究，该类真菌降解角蛋白的机制将会更加明晰。Kang 等基于宏基因组分析预测了假定的角蛋白酶和氨基酸代谢、二硫键还原及尿素循环与角蛋白降解相关的代谢通路，揭示了角蛋白降解相关的潜在代谢关系[91]。

随着嗜角蛋白真菌研究方法的逐步发展，该类群的成员也将发生变化，越来越多新的嗜角蛋白真菌将被发现。然而随着分子生物学方法的发展，嗜角蛋白真菌的作用机制也将逐渐明晰，将在人们的生活中扮演更为重要的角色。

4 嗜角蛋白真菌的应用

通过总结以往研究发现，各嗜角蛋白真菌类群所涉及的应用领域极其广泛。如肉座菌目镰刀菌属真菌(*Fusarium* sp. 1A)能产生对动物皮肤具有良好活性的角蛋白酶[11]，因而在皮革行业展现出较好的应用潜力。木霉属真菌中棘孢木霉对植物种子的萌发及幼苗的生长有促进作用[11]；哈茨木霉已广泛用于生物防治[14-15]；也有将该属真菌应用于皮革行业的报道，表明木霉属真菌在农业、工业上都有较大的应用潜力[12,16]。爪甲团囊菌目金孢霉属真菌代谢产物表现出极

高的应用价值，如嗜角质金孢霉的分泌物能够有效抑制皮肤癣菌的活性，可用于生物制药；热带金孢霉代谢物能有效杀死致倦库蚊幼虫，因此可用于生物防治[92-93]。散囊菌目曲霉属真菌应用最为广泛，在饲料业、皮革业、医药、农业、生物修复、功能性食品方面都具有应用价值[10,13,17-22]。如米曲霉将羽毛进行生物转化后所产生的粗蛋白中存在动物体中最缺乏的必需氨基酸——赖氨酸[10]。溜曲霉(*A. tamarii*)去除山羊皮毛的同时提高了皮革的强度性能[13]。黑曲霉的羽毛水解产物对植物的产量和生长发育也表现出显著影响，还可防治植株疾病[20]。一些其他嗜角蛋白真菌还可作为生物指标[94]。通过总结嗜角蛋白真菌在各方面的应用，其表现出环境友好性及应用的广泛性，证明了嗜角蛋白真菌具有极高的实用价值(表 2)。

5 展望

截至目前，嗜角蛋白真菌在不同地理区域不同生境的土壤中均有报道，而且多为病原或潜在病原真菌。为了人类的健康卫生，它们的研究应该引起人们的重视。目前嗜角蛋白真菌的研究主要集中于三方面：(1) 该类真菌资源的分布和新分类单元的报道；(2) 产角蛋白酶发酵条件优化；(3) 角蛋白酶破坏角蛋白结构机制的探索[23,33]。然而对嗜角蛋白真菌类群中爪甲团囊菌科和众多皮肤癣菌的裸囊菌科、粘丝裸囊菌科等阶元及以下阶元的系统发育研究深度不够,在应用中大多采用传统的单菌发酵且角蛋白的降解机制尚未探明。今后的研究中可基于扩大菌株数量及物种范围的基础上,在目、科及属水平上进行系统发育研究，明确这类资源各个类群的系统发育地位，结合所产代谢产物角蛋白酶的基因分析，建立一个完整而自然的现代分类系统，为病原菌的正确诊断和治疗提供科学依据。

虽然嗜角蛋白真菌单菌种降解的研究已取得了一定的成果，但随着生态理念的加入，在共生互作的框架下探索综合、稳定提高嗜角蛋白真菌降解角蛋白基质的潜能，将使之发挥更

表 2 嗜角蛋白真菌的应用实例

Table 2 Examples of the application of keratinophilic fungi

应用 Application		嗜角蛋白真菌 Keratinophilic fungi	参考文献 References
饲料行业 Feed production	对羽毛进行生物转化成羽毛粉，作为动物饲料替代蛋白质来源 Biotransformation of feathers into feather meal as an alternative protein source for animal feed	米曲霉、粉小孢子菌 *Aspergillus oryzae*, *Microsporum fulvum*	[10]
皮革行业 Leather industry	对动物皮肤具有良好活性 Good activity on animal skin	*Fusarium* sp.	[11]
	产生的角蛋白酶使山羊皮脂肪腺体完全降解 Complete degradation of goat skin fat glands by the production of keratinase	短帚霉 *Scopulariopsis brevicaulis*	[95]
	脱毛后显示出干净的颗粒表面，没有颗粒受损 After hair removal shows clean particle surface with no particle damage	哈茨木霉 *Trichoderma harzianum*	[16]
	兽皮标本脱毛 Dehairing of animal skin specimens	绿色木霉 *Trichoderma viride*	[12]

(待续)

(续表 2)

	去除山羊皮毛的同时提高了皮革的强度性能 Removal of goat fur and improving the strength of the leather	溜曲霉 *Aspergillus tamarii*	[13]
医药 Medicine	分泌物能够有效抑制皮肤癣菌的活性 The secretion can effectively inhibit the activity of dermatophytes	嗜角质金孢霉 *Chrysosporium keratinophilum*	[92]
	乙醇提取物能够抑制蛋白质变性 Ethanol extract can inhibit protein denaturation	黑曲霉、米曲霉 *Aspergillus niger*, *Aspergillus oryzae*	[17]
	分泌的棘白菌素能有效抑制真菌活性 Secreted echinocandins can effectively inhibit fungal activity	*Aspergillus delacroxii*	[18]
农业 Agriculture	有益于植物种子的萌发以及幼苗的生长 Beneficial to the germination of plant seeds and the growth of seedlings	棘孢木霉 *Trichoderma asperellum*	[11]
	生物除草剂 Biological herbicides	淡紫紫孢菌 *Purpureocillium lilacinum*	[96]
	大蒜白腐病生物杀菌剂 Garlic white rot biofungicide	哈茨木霉 *Trichoderma harzianum*	[14]
	对油棕灵芝基腐病的防治 Control of basal rot of *Ganoderma lucidum* in oil palm	哈茨木霉 *Trichoderma harzianum*	[15]
	作为生物防治菌减少玉米粒中毒素浓度 Reduction of toxin concentration in corn kernels as a biocontrol bacterium	黄曲霉 *Aspergillus flavus*	[19]
	羽毛水解产物对植物的产量及产量构成因素和生长发育表现出显著影响，还可防止植株疾病 Feather hydrolysis products showed significant effects on plant yield and yield components and growth and development, and also prevented plant diseases	黑曲霉 *Aspergillus niger*	[20]
	代谢物对致倦库蚊幼虫的杀虫效果 Insecticidal effect of metabolites on the larvae of the burned-out *Culex quinquefasciatus*	热带金孢霉 *Chrysosporium tropicum*	[93]
	抗线虫害虫综合治理的候选菌株 Candidate strains for integrated nematode-resistant pest management	淡紫拟青霉 *Paecilomyces lilacinus*	[97]
生物修复 Bioremediation	作为生物吸附剂对重金属的去除 Removal of heavy metals as biosorbents	黑曲霉 *Aspergillus niger*	[21]
	多环芳烃污染土壤生物修复的候选菌株 Candidate strains for bioremediation of PAH-contaminated soil	短帚霉 *Scopulariopsis brevicaulis*	[98]
其他 Others	产生发酵物质应用于功能性食品方面 Production of fermented substances for functional food applications	米曲霉 *Aspergillus oryzae*	[22]
	基于其基因序列获得西伯利亚东北部古环境的重要信息 Obtaining important information on the palaeoenvironment of northeastern Siberia based on its gene sequences	*Phialophora* sp., *Geomyces pannorum*	[94]

大的作用。杜东霞等人工合成了一种高效降解猪毛的菌群组合[85]；Nasipuri 等构建的细菌生理功能群，其角蛋白降解能力比单培养物平均提高了 30%，不同菌株互作极大地提高了对角蛋白的降解效果[99]。然而生理功能群的充分利用仍有诸多难题。一般认为随着微生物的生长和代谢，嗜角蛋白菌通过变性、分解和转氨基作用将角蛋白基质降解为氨基酸、肽和能量等物质[100-101]，但机制尚未明确。角蛋白降解的生理功能群优于单一菌株的潜在机制可能涉及基因沉默或过表达，也可能是生物膜的形成[102]。因而可从宏基因组的角度对生理功能群成员之间的潜在互作(交叉喂养和成员之间的劳动分工)进行探索，进而为今后规模化发酵条件的优化及全面解析降解机制提供帮助。此外，研究者开发了更先进的计算分析工具预测嗜角蛋白生理功能群，不局限于生物技术和培养策略。例如，Minty 等设计的参数方程模型描述并预测了大肠杆菌(*Escherichia coli*)和里氏木霉(*Trichoderma reesei*)共生菌群的行为[103]；Kong 等构建了一个通用框架(方程和参数可重复使用)以反映生态系统的模块化结构，发现能从双菌株生态系统衍生的模型成功预测更复杂的四菌株生态系统的动力学[104]。此外，计算分析工具也被应用于许多天然微生物菌群模型的互作机制中，如微生物燃料电极上的群落、产甲烷群落、土壤和根际生态系统等，这将进一步为构建微生物生理功能菌群提供理论指导[105-107]。

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