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## 白蚁肠道原生动物研究进展

张洁<sup>1,2</sup>, 杜贺<sup>2</sup>, 莫振钻<sup>2</sup>, 张爽<sup>1\*</sup>

(1. 河北农业大学林学院, 河北保定 071000; 2. 广东省科学院动物研究所, 广东省动物保护与资源利用重点实验室, 广东省野生动物保护与利用公共实验室, 广州 510260)

**摘要:** 白蚁的后肠膨大特化, 为肠道微生物提供了栖息地。除了白蚁科的白蚁外, 其它白蚁肠道内都含有原生动物。白蚁肠道原生动物归属于副基体门 Parabasalia 和前轴柱门 Preaxostyla 锐滴虫目 Oxymonadida。白蚁肠道原生动物与多种细菌共生, 二者存在共进化现象。白蚁、原生动物与细菌形成了一个三重共生系统。肠道原生动物在肠道内的分布具有异质性。肠道原生动物的传递机制既保证了肠道微生物群落的稳定性, 也使白蚁肠道微生物群落不断进化。此外, 白蚁肠道原生动物丰度受到白蚁品级和食物等多种因素的影响。肠道原生动物对于白蚁至关重要, 能够进行木质纤维素的分解和固氮作用, 参与肠道内的气体代谢, 并为白蚁提供营养物质。本文对肠道原生动物的分类、原生动物共生细菌、原生动物的空间分布、传递和功能等方面进行了综述, 以期为后续研究提供有益参考。

**关键词:** 鞭毛虫; 原生动物依赖型白蚁; 共生; 协同物种形成; 交哺行为; 产乙酸作用

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### Research progress on protists in termite guts

ZHANG Jie<sup>1,2</sup>, DU He<sup>2</sup>, MO Zhen-Zuan<sup>2</sup>, ZHANG Shuang<sup>1\*</sup> (1. College of Forestry, Hebei Agricultural University, Baoding 071000, Hebei Province, China; 2. Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou 510260, China)

**Abstract:** The hindgut of termites is enlarged and specialized, providing a habitat for intestinal microorganisms. Except for termites belonging to the Termitidae family, all other termite species harbor protists in their guts. The protists in the termite gut belong to the Parabasalia phylum and Preaxostyla phylum Oxymonadida order. The gut protists of termites coexist with various bacteria, exhibiting a coevolutionary relationship. Termites, protists, and bacteria form a triple symbiotic system. The distribution of gut protists within the intestine demonstrates heterogeneity. The transmission mechanism of gut protists not only ensures the stability of the gut microbiota but also facilitates the continuous evolution of the gut microbiota colonies in termites. Additionally, the abundance of gut protists in termites is influenced by various factors, including termite caste and diet. Gut protists are crucial for termites as they contribute to the decomposition of lignocellulose, nitrogen fixation, participation in intestinal gas metabolism, and the provision of nutrients to termites. This article provides a comprehensive review of the

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作者简介: 张洁, 女, 硕士研究生, 研究方向为森林保护, E-mail: 3368104069@qq.com

\*通讯作者 Author for correspondence: 张爽, 女, 博士, 教授, 研究方向为森林保护, E-mail: zhshsuqq@126.com

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classification of gut protists, symbiotic bacteria of protists, spatial distribution, transmission, and functions of protists, aiming to offer a valuable reference for future research.

**Key words:** Flagellates; protist-dependent termites; symbiosis; cospeciation; trophallaxis; acetogenesis

白蚁是世界上最古老的社会性昆虫之一，与蟑螂同属于蜚蠊目 (Inward *et al.*, 2007; Krishna *et al.*, 2013)。与其它昆虫肠道不同的是，白蚁后肠膨大并且存在大量的微生物。传统上将白蚁分为两大类：低等白蚁和高等白蚁，其中低等白蚁肠道内有原生动物、细菌及古菌，而高等白蚁肠道内没有原生动物，只有细菌、古菌等微生物。然而，这种分类方法基于进化的线性发展观，有悖于现代系统发生学的思想，因此白蚁学者主张摒弃“低等”和“高等”术语，使用原生动物依赖型白蚁 (Protist-dependent termite) 或非白蚁科白蚁代替低等白蚁，使用白蚁科白蚁 (Termitidae termite) 代替高等白蚁 (Carrijo *et al.*, 2023)。白蚁肠道共生微生物在白蚁消化过程中扮演着重要角色，在这些微生物的协助下，白蚁能够利用木材中74%~99%的纤维素和65%~87%的半纤维素，这比牛瘤胃降解木质纤维素的效率高很多 (Ohkuma, 2003; Watanabe and Tokuda, 2010)。同时，肠道原生动物与细菌建立了紧密的共生关系 (Zhou *et al.*, 2019)。因此，白蚁、原生动物以及细菌组成了一个三重共生系统 (Triple symbiotic system) (Noda *et al.*, 2007)。本研究从原生动物的分类、原生动物共生细菌、原生动物生态学以及原生动物的代谢及功能等4个方面，对白蚁肠道原生动物研究进展进行综述，以期为未来相关研究提供参考和借鉴。

## 1 白蚁肠道原生动物的分类

白蚁肠道原生动物的研究可追溯到19世纪中期。Lespès (1856) 在暗黑散白蚁 *Reticulitermes lucifugus* 中首次发现了原生动物。随后，Leidy (1877) 对北美散白蚁 *Reticulitermes flavipes* 中肠道原生动物进行了描述，但这些原生动物被认为是对宿主有害的“寄生虫” (Parasite)。随着研究的深入，人们开始认识到原生动物对宿主的有益作用，这促使Imms等 (1920) 提出了共生 (Symbiosis) 的概念。早在100年前，Cleveland (1923) 的研究表明原生动物是白蚁必不可少的一

部分：去除白蚁肠道原生动物后，即使白蚁继续取食木材，也会在几周内饥饿而死；但是重新接种正常白蚁的肠道内容物，白蚁不会死亡。因此，肠道原生动物在木材的降解过程中发挥了关键作用。由于白蚁肠道的特殊环境，肠道原生动物很难被培养。目前人工培养出的原生动物有 *Trichomonas termopsidis* (Trager, 1934) 和 *Trichonympha sphaerica* (Yamin, 1978) 等。白蚁原生动物的鉴定很大程度上依赖显微技术。随着高通量测序技术的发展，使得原生动物的鉴定在深度和广度上取得了革新。白蚁肠道原生动物属于单细胞真核生物，但缺乏线粒体，属于2个独立的谱系：副基体门 Parabasalia 和 前轴柱门 Preaxostyla 锐滴虫目 Oxymonadida (Inoue *et al.*, 2000; 杨红等, 2006)。副基体门原生动物细胞内含有氢化酶体，分为 Trichonymphida、Spirotrichonymphida、Cristamonadida 和 Trichomonadida 4个目 (Brugerolle and Patterson, 2001; Adl *et al.*, 2005)。锐滴虫目原生动物细胞内缺乏氢化酶体，关于它的功能研究不多，它包括5个科，其中4个只生活在白蚁和隐尾蠊属蟑螂 *Cryptocercus* 的肠道内 (Brugerolle and Lee, 2000; Hampl, 2017)。

目前鉴定出的白蚁原生动物达数百种 (Yamin, 1979)。不同种类的白蚁共生原生动物的种类和数量差异较大。散白蚁属白蚁肠道中原生动物较多，在北美散白蚁肠道中有20多种原生动物 (Duarte *et al.*, 2017b)；黑胸散白蚁 *Reticulitermes chinensis* 中目前发现有10多种 (Chen *et al.*, 2011; Song *et al.*, 2021)；相比之下，斯奈德楹白蚁 *Incisitermes snyderi* 只有3种原生动物 (Dolan *et al.*, 2000; Gerbod *et al.*, 2002; Harper *et al.*, 2009)。在现代，显微技术在白蚁肠道原生动物的鉴定方面仍然发挥着至关重要的作用，但是在分子生物学技术协助下进行了更精细的分类。例如，台湾乳白蚁 *Coptotermes formosanus* 肠道中，传统上认为有3种原生动物：*Pseudotrichonympha grassii*、*Cononympha leidyi* 和 *Holomastigotoides hartmanni*，但是对肠道原生动物 18S rRNA 基因进

行限制性片段长度多态性分析发现4种带型(Xie et al., 2011);随后根据单细胞转录组发现了台湾乳白蚁肠道原生动物新的物种,即*Holomastigotoides minor*(Nishimura et al., 2020);最新的18S rRNA基因测序结果表明,台湾乳白蚁肠道内有5种原生动物:包括*P. grassii*、*H. hartmanni*、*H. minor*、*Con. leidyi*和*Cononympha koidzumii*(Jasso-Selles et al., 2020)。另外,狭颈动白蚁*Zootermopsis angusticollis*最初鉴定到7种原生动物(Yamin, 1979),基于系统发育聚类和序列分化分析,Tai等(2013)又发现了3个新物种。

## 2 白蚁肠道原生动物共生细菌

白蚁肠道中的原核生物大多是细菌,古菌在后肠共生体中所占比例较低。白蚁具有一个核心的肠道微生物群体(Benamino and Graf, 2016)。例如,在栖北散白蚁*Retculitermes speratus*肠道中,螺旋体门*Spirochaetota*是最占优势的细菌,其次为拟杆菌门*Bacteroidota*、厚壁菌门*Firmicutes*和TG1(Termite group 1)(Hongoh et al., 2003)。在台湾乳白蚁中最优势的细菌来自拟杆菌门(Shinzato et al., 2005)。在白蚁肠道内,存在自由活动的细菌,同时还有一些与原生动物共生。原生动物有自身特异的共生细菌群落(Stephens and Gage, 2020)。这些共生细菌以“外共生体”(Ectosymbionts)的形式附着在原生动物的外表面;或以“内共生体”(Endosymbionts)的形式生活在原生动物的细胞质及细胞核中(Ohkuma et al., 2005)。

白蚁肠道中的细菌具有独特性和新颖性,这些细菌在门水平被划分为TG1、TG2(Termite group 2)和TG3(Termite group 3)(Ohkuma and Kudo, 1996; Hongoh et al., 2003; Hongoh et al., 2005; Hongoh et al., 2006; Ohkuma and Brune, 2011)。TG1门的细菌最初发现于散白蚁属*Retculitermes*肠道中(Ohkuma and Kudo, 1996),是白蚁肠道原生动物的内共生细菌(Stingl et al., 2005; Ikeda-ohtsubo et al., 2007; Ohkuma et al., 2007; Ikeda-ohtsubo and Brune, 2009; Desai et al., 2010)。随着研究深入,在其它环境中也发现有TG1门的细菌,例如蟑螂和牛瘤胃中(Ohkuma et al., 2007)。随后,将TG1门改为难得菌门

*Elusimicrobia*(Geissinger et al., 2009)。TG2最初也在散白蚁属*Retculitermes*中发现(Hongoh et al., 2003),它还包括从富含硫的泉水中分离到的ZB3分支。后续研究在北极深海、湖泊沉积物和高盐微生物垫中也有发现多种TG2/ZB3分支的细菌,目前TG2/ZB3分支属于候选门*Margulisbacteria*(Utami et al., 2019)。TG3门最初在锯白蚁属*Microcerotermes*中发现,可占肠道内细菌数的10%以上(Hongoh et al., 2005)。在蟑螂、湖泊沉积物、水稻土和深海沉积物中也有发现TG3门细菌(Hongoh et al., 2006)。

### 2.1 白蚁肠道原生动物外共生细菌

在白蚁肠道中,与原生动物外共生的细菌主要包括螺旋体门、拟杆菌门、难得菌门和互氧菌门*Synergistota*等。螺旋体属于螺旋体门,因其形状细长且呈螺旋状卷曲而得名,有些存在于原生动物的外表面,也有很多自由生活于肠液中(Yang et al., 2005)。这些螺旋体通常隶属于密螺旋体属*Treponema*(Iida et al., 2000; Noda et al., 2003; Wenzel et al., 2003; Inoue et al., 2008)。一个原生动物细胞表面可能附着多种螺旋体,同时一种螺旋体可能出现在不同的原生动物上。螺旋体能够通过自身的摆动来推动原生动物的运动。例如,在达尔文澳白蚁*Mastotermes darwiniensis*中的原生动物*Mixotricha paradoxa*细胞表面分布有至少3种螺旋体,它们能够驱动细胞运动(Wenzel et al., 2003)。此外,在*Cryptotermes cavifrons*白蚁肠道中还发现了一种隶属于互氧菌门的运动共生细菌(Hongoh et al., 2007b)。除了推动原生动物游动,外共生细菌在维持原生动物形态方面也发挥了重要作用(Leander and Keeling, 2004)。原生动物的外共生细菌很可能来自于肠液中自由游动的细菌(Hongoh et al., 2007b; Stephens and Gage, 2020)。

拟杆菌目*Bacteroidales*的原生动物也经常作为外共生细菌出现。例如,在栖北散白蚁原生动物*Dinenympha*中发现了一种拟杆菌目外共生细菌*Candidatus Symbiothrix dinenymphae*,该细菌占白蚁肠道中细菌数的2.5%(Hongoh et al., 2007a)。在第二堆砂白蚁*Cryptotermes secundus*、内华达动白蚁*Zootermopsis nevadensis*和食木蟑螂隐尾蠊的肠道发现的拟杆菌目外共生细菌分为3个谱系,并且这些外共生体在形态上有所差异(Noda et al., 2006b)。

虽然大部分的内生微菌属 *Endomicrobium* (属于难得菌门) 作为原生动物的内共生细菌存在, 在维多利亚胃白蚁 *Stolotermes victoriensis* 的 Spirotrichosomid 原生动物和亚当森洞白蚁 *Porotermes adamsoni* 的原生动物 *Trichonympha magna* 上发现内生微菌属的外共生细菌 (Izawa et al., 2017)。

## 2.2 白蚁肠道原生动物内共生细菌

如同外共生细菌一样, 原生动物细胞内的细菌也归属于多个分类单元, 包括拟杆菌目、内生微菌属和密螺旋体属等。这些细菌大部分生活在原生动物的细胞质中, 也有一些被发现存在于原生动物的细胞核内。例如, 在 *Trichonympha agilis* 原生动物中发现 2 种细胞核内细菌 (Sato et al., 2014)。在台湾乳白蚁肠道中, 拟杆菌目的细菌含量极高, 约占所有分析克隆的 70% (Shinzato et al., 2005)。另外, 拟杆菌目细菌作为原生动物 *P. grassii* 的共生体存在, 单个细胞中细菌个数达到  $10^5$  个 (Noda et al., 2005)。通过单细胞基因组扩增技术, 获得了这种细菌 *Candidatus Azobacteroides pseudotrichonymphae* 的完整基因组序列, 基因组大小为 1.1 Mb, 进一步的生物信息学分析表明, 这种细菌不仅具有固氮能力, 还能合成多种氨基酸和辅酶 (Hongoh et al., 2008b)。此外, 内生微菌属的细菌在后肠中占有很高的比例 (Yang et al., 2005)。例如, *Candidatus Endomicrobium trichonymphae* 细胞在 *T. agilis* 原生动物内的数量达 4 000 个/原生动物, 占肠道内细菌总数的 4% (Ohkuma et al., 2007; Hongoh et al., 2008a)。Ca. *Endomicrobium trichonymphae* 的基因组存在缩减演化 (Reductive evolution), 但是它仍具有合成 15 种氨基酸和多种辅酶的能力 (Hongoh et al., 2008a)。另外, 与 *Pseudotrichonympha* 属原生动物有亲缘关系的 *Eucomonympha* 和 *Teranympha* 属原生动物的内共生体属于密螺旋体属 (Ohkuma et al., 2015)。

值得注意的是, 一种原生动物细胞内可能含有多种共生细菌。内华达动白蚁肠道内的原生动物 *Trichonympha collaris* 含有 Ca. *Endomicrobium trichonymphae* 和 *Candidatus Adiutrix intracellularis* 2 种共生细菌。另外, 同属的细菌也可能存在多种原生动物之中。例如, *Pyrsonympha vertens*、*T. agilis* 和 *Dinenympha* 属都有内生微菌属内共生细菌 (Stephens et al., 2022)。梭菌 *Clostridium* 存在于原

生动物 *T. agilis*、*P. grassii* 和 *Devescovina* sp. 细胞内, 生物信息学分析这些梭菌很可能是寄生在细胞内的 (Takahashi et al., 2023)。

## 2.3 白蚁肠道原生动物与细菌共进化

白蚁肠道原生动物与细菌存在协同物种形成 (Cospeciation) 现象。以 *Trichonympha* 属原生动物为例, 其体内的内生微菌属细菌形成 1 个单系群, 说明二者之间具有共进化关系 (Ikeda-ohtsubo et al., 2007)。*Pseudotrichonympha* 属原生动物只出现在鼻白蚁科 Rhinotermitidae 白蚁中, 二者之间存在共进化现象; 此外, *Pseudotrichonympha* 属原生动物与其内共生细菌之间也展示了类似的共进化模式: 共生细菌的分支模式与原生动物和白蚁的几乎相同 (Noda et al., 2007)。*Trichonympha* 属原生动物形成了 3 个不同的谱系 (Lineage), 而内生微菌属细菌只存在于其中的 1 个顶端谱系 (Apical lineage) —Cluster I, 这个谱系主要包括来自鼻白蚁科和原白蚁科 Termopsidae 白蚁的原生动物; Cluster I 的内共生细菌形成 1 个单系群, 与宿主存在协同物种形成的关系, 这种协同物种形成是由于共生体垂直传播所导致的 (Ikeda-ohtsubo and Brune, 2009)。

虽然原生动物与细菌表现出共进化现象, 但它们之间的关系是复杂的, 在二者的进化历史中存在非共同进化事件 (Non-codivergent evolutionary events) (Noda et al., 2007)。以原生动物 *Devescovina* 为例, *Devescovinids* 与其外共生细菌之间有着明显的共进化现象, 但 *Devescovinids* 的内共生细菌组成复系群, 表明它们是通过水平传播的方式获得 (Desai et al., 2010)。外共生的密螺旋体属、塔梅拉菌属 *Tammella* 和拟杆菌目与自由生活在后肠液体中的亲缘物种形成系统发育簇 (Noda et al., 2003; Noda et al., 2006a, 2006b; Hongoh et al., 2007b)。已有研究表明肠道原生动物能从肠道内自由生活的种群中捕获细菌 (Stephens and Gage, 2020)。另外, *Eucomonympha* 和 *Teranympha* 属的原生动物都含有密螺旋体属的细菌, 其中 *Teranympha* 属原生动物与密螺旋体属的细菌之间存在共进化现象, 而 *Eucomonympha* 属原生动物与密螺旋体属的细菌没有共进化现象, 这可能是共生细菌宿主转移 (Host switches) 导致的 (Noda et al., 2018)。某些木白蚁科 Kalotermitidae 白蚁中的 *Oxymonas* 原生动物的拟杆

菌目外共生细菌亲缘关系较远,这也表明原生动物与细菌之间进化历史的复杂性(Desai *et al.*, 2010)。

### 3 白蚁肠道微生物生态学研究

白蚁肠道包含多种物理化学性质不同的微环境(Brune and Friedrich, 2000)。这种异质性的空间结构为微生物提供了不同的生态位。肠道微生物分布在不同区域,协同分工,形成一个复杂而稳定的内环境体系。在长期的进化过程中,白蚁与肠道内的微生物形成了稳定的共生关系。由于肠道微生物的重要性,微生物的有效传递对白蚁至关重要,垂直传播确保了微生物群落的稳定性和连续性。同时,水平传播模式又能够驱动白蚁肠道微生物群落进化。白蚁肠道原生动物群落的构成不仅受到白蚁品级和食物的影响,还受到激素等多种因素的调控。这些因素共同作用于微生物群落,使其在不断变化中保持着相对的稳定性。

#### 3.1 白蚁肠道原生动物的空间分布

白蚁肠道呈螺旋状,可以分为前肠、中肠以及构造尤为复杂的后肠3部分。后肠进一步可以被划分为5个部分:肠瓣前节(P1)、肠瓣(P2)、囊形胃(P3)、结肠(P4)和直肠(P5)(Tokuda *et al.*, 1997)。白蚁的P3区显著膨大,里面密集分布有大量原生动物。白蚁肠道内的原生动物不是随机散布,而是在肠道的轴向和径向空间上呈现异质性分布的特征。产甲烷细菌主要分布在肠壁区域,而原生动物以及耗氢细菌主要分布在肠腔中心(杨红等, 2006)。有些白蚁后肠肠壁上附着有锐滴虫目的鞭毛虫。例如,原生动物 *Pyrsonympha vertans* 锚定在桑顿散白蚁 *Reticulitermes santonensis* (Yang *et al.*, 2005) 和北美散白蚁的后肠肠壁上(Breznak and Pankratz, 1977)。由于副基体门原生动物在发酵木质纤维过程中产生H<sub>2</sub>,原生动物的径向分布模式对维持肠道内的H<sub>2</sub>分压发挥了重要作用。研究表明,白蚁肠道中的H<sub>2</sub>和O<sub>2</sub>浓度呈辐射状分布,H<sub>2</sub>浓度在肠腔中心最高,向肠壁逐渐降低;O<sub>2</sub>浓度在肠壁处最高,含氧区在肠腔中占的比例很高,厌氧区集中在肠腔中心(Brune, 1998)。原生动物在轴向空间上也呈现异质性的分布。在台湾乳白蚁肠道中, *P. grassii* 主要分布在后肠前部, *Con. leidyi* 主要分布在后肠后部,而

*Holomastigotoides* 在白蚁后肠中几乎均匀分布,这些原生动物的空间差异分布说明它们存在功能上的分工(Nishimura *et al.*, 2020)。对北美散白蚁的研究还表明,原生动物的比例在后肠前部最高(Cook and Gold, 1998)。

#### 3.2 白蚁肠道原生动物的传递

蚁巢内的个体可以通过交哺(Trophallaxis)传递营养物质,白蚁通过交哺行为获得食物的同时,也得到肠道内的微生物。当白蚁蜕皮时,肠道被清空,白蚁通过交哺作用重新获得肠道微生物。有翅生殖蚁肠道内携带微生物,在建立新蚁巢并孵化出首批工蚁后,生殖蚁会将肠道内的微生物传递给蚁巢内的工蚁。这种传播模式导致白蚁与肠道微生物具有共进化现象(Hongoh *et al.*, 2005; Noda *et al.*, 2007; Husseneder, 2010)。垂直传播是形成白蚁肠道群落的主要因素,保证了肠道微生物群落在白蚁种群中的稳定性和连续性(Abdul Rahman *et al.*, 2015)。统计模型推演显示,食木白蚁肠道原生动物的传播率非常高,传播率与原生动物在群体中的比例呈正相关,但仅用传播率不能解释原生动物在群体中的丰度(Michaud *et al.*, 2020)。原生动物在不同世代之间的传递并不是完美的,因为有翅成虫仅含有该物种的部分原生动物;通过双亲传递(Biparental transmission),能够使后代群体获得几乎全部的原生动物群落,从而保证原生动物群落在不同世代之间的稳定性(Velenovsky *et al.*, 2023)。

除了垂直传播模式,白蚁肠道微生物的传播也存在水平传播方式。当不同物种的个体相遇时,体弱的个体可能会被强者捕食,从而导致其体内的原生动物等微生物被传递(Thorne and Haverty, 1991)。此外,水平传播也可能通过取食土壤或者白蚁粪便完成,这种方式也有助于微生物在不同白蚁个体或种群之间传播(Bourguignon *et al.*, 2018)。水平传播在白蚁肠道微生物群落形成中的作用常被忽视(Tai *et al.*, 2015)。混合模式传播(Mixed-mode transmission)被认为是白蚁肠道微生物群落形成的主要驱动力。这种传播方式结合了垂直传播和水平传播两种模式,既保证了微生物群落从亲代到子代的稳定传递,又为新微生物的引入提供了可能性,从而增加了群落的多样性和适应性(Bourguignon *et al.*, 2018)。

### 3.3 影响白蚁肠道微生物群落的因素

虽然白蚁的肠道内存在一个核心的微生物群落，但这个群落会因白蚁品级的不同而有所差异。北美散白蚁工蚁肠道内的密螺旋体属和内生微菌属细菌以及原生动物比有翅成虫肠道内的丰度高(Benjamino and Graf, 2016)。在幼龄蚁巢中，蚁王体内含有的原生动物数量通常比蚁后多；此外，成熟蚁巢的兵蚁肠道内也含有大量的原生动物，而补充型生殖蚁中则缺少原生动物(Shimada et al., 2013)。另外，白蚁的保幼激素和蜕皮激素对原生动物生命活动存在影响(Scharf and Peterson, 2021)。例如，保幼激素会导致原生动物数量减少及基因表达下调(Sen et al., 2013)。原生动物群落的聚类与白蚁的系统发育紧密相关，而肠道细菌的聚类与白蚁的蚁巢类型相对应，这表明细菌在进化过程中展现了对宿主生态变化的高度适应性(Waidele et al., 2017)。

除了品级和激素，食物也是肠道微生物群落构成的关键因素。通过喂食北美散白蚁不同类型的木质纤维，其肠道微生物的群落结构发生了改变，这表明食物对白蚁肠道微生物生态具有一定选择性，可能促使某些微生物的增长，同时抑制其它微生物的生存(Huang et al., 2013; Tarayre et al., 2015)。当白蚁食物来源发生变化时，低丰度的细菌可能会成为影响肠道微生物群落变化的关键因素(Benjamino et al., 2018)。此外，研究还发现木质素对维持特定原生动物种群，如台湾乳白蚁肠道中的*P. grassi* 和 *H. hartmanni*，具有积极作用(Tarmadi et al., 2017)。当白蚁摄入缺乏木质素的食物时，其肠道内螺旋体细菌的相对丰度降低，变形杆菌和拟杆菌的相对丰度增加(Su et al., 2017)。另外，喂食热处理的木材也会改变肠道原生动物的群落结构(Duarte et al., 2017a)。这些发现证明了食物在维持白蚁肠道微生物群落结构中的重要角色。但是也有研究表明食物改变并不能解释所有的肠道微生物改变，环境因素以及白蚁自身的遗传因素在白蚁肠道群落结构中发挥了重要作用(Boucias et al., 2013)。

## 4 白蚁肠道原生动物的代谢与功能

原生动物以及共生细菌在白蚁肠道中扮演着至关重要的角色。肠道原生动物最重要的功能是

进行木质纤维的分解。此外，这些微生物还参与多种代谢活动，在木质纤维发酵过程中会产生乙酸、甲烷和H<sub>2</sub>等中间产物，这些物质对于白蚁的生理机能和能量供应都至关重要。肠道细菌参与了对原生动物发酵产物的进一步代谢，从而提高了对食物资源的利用效率。原生动物及其共生细菌在白蚁营养供给方面发挥着重要作用(Hongoh, 2011; Alom et al., 2023)。原生动物共生细菌能够进行固氮作用，并合成白蚁必须的某些氨基酸和辅因子，从而弥补食物中的氮元素的不足(Peterson and Scharf, 2016)。除此之外，白蚁肠道微生物还参与白蚁品级分化的调节和免疫调控等(Cleveland, 1957; Lüscher, 1972)。

### 4.1 降解纤维素功能

白蚁高效降解木质纤维素的能力归结于白蚁与肠道微生物建立的协同作用(Ohkuma, 2008)。白蚁能够产生糖苷水解酶(Glycoside hydrolases, GHs)和辅助性的氧化还原酶(Lo et al., 2011; Geng et al., 2018; Wu et al., 2019)。白蚁产生的GHs主要包括GH9、GH1和GH22(Li et al., 2006; Watanabe and Tokuda, 2010; Ni and Tokuda, 2013; Geng et al., 2018)。内源性纤维素酶基因最初由Watanabe等(1998)从栖北散白蚁中分离。纤维素酶属于GH的一种，包括内切-β-1,4-葡聚糖酶(Endo-β-1,4-glucanases, EGs)、外切纤维二糖水解酶(Exo-cellulobiohydrolases, CBHs)以及β-葡萄糖苷酶(β-glucosidases, BGs)。在台湾乳白蚁中，BGs主要在唾液腺中表达(Wu and Li, 2018)。白蚁分解木材的能力很大程度上依赖于肠道共生微生物群(Watanabe and Tokuda, 2010)。白蚁肠道原生动物以及共生细菌也分泌多种酶。这些酶与白蚁的内源性酶协同作用，使得白蚁可以去除木质纤维素中的大多数中性多糖和一半以上的酸性糖(Hyodo et al., 1999; Katsumata et al., 2007)。因此，白蚁是一个高效的天然生物反应器。

#### 4.1.1 白蚁肠道原生动物降解木质纤维

原生动物降解木质纤维最直接的证据来自体外培养实验，实验表明原生动物*Trichomitopsis termopsidis*消化木材粉末、淀粉、微晶纤维素和木聚糖(Odelson and Breznak, 1985)。利用分子克隆技术，分离到多种原生动物来源的纤维素酶，包括CBHs和EGs，这些酶隶属于GH45、GH7和

GH5 等家族 (Brune and Ohkuma, 2011)。例如, 在台湾乳白蚁肠道原生动物中分离出多种 EGs 酶基因 (Watanabe *et al.*, 2002)。从栖北散白蚁后肠原生动物中分离到多种糖基水解酶, 包括纤维素酶、木聚糖酶 (Xylanases)、阿拉伯糖苷酶 (Arabinosidase)、甘露糖苷酶 (Mannosidase) 和阿拉伯呋喃糖苷酶 (Arabinofuranosidase) (Todaka *et al.*, 2007)。在栖北散白蚁后肠的原生动物中成功分离出木糖异构酶 (Xylose isomerase) 基因 (Katahira *et al.*, 2017)。此外, 利用色谱技术, 从 *Coptotermes lacteus* 白蚁肠道中分离出原生动物来源的 EGs 酶, 它们属于 GH7 家族 (Watanabe *et al.*, 2002)。

在白蚁肠道内, 不同的原生动物在木质纤维素降解过程中起着不同的作用。例如, 台湾乳白蚁肠道内的 *P. grassii* 和 *H. hartmanni* 都能吞噬纤维素, 其中 *P. grassii* 主要降解高度聚合的纤维素, *H. hartmanni* 主要消化低分子量的纤维素; *Con. leidyi* 完成纤维素降解最后阶段的工作 (Yoshimura *et al.*, 1996)。这些原生动物有序地降解木质纤维, 呈现出显著的功能分工 (Nishimura *et al.*, 2020)。木材颗粒在进入后肠后, 首先被栖息在后肠前部的 *P. grassii* 所分解 (Yoshimura, 1992)。其中, 纤维二糖水解酶 (Cellulohydrolase) 基因在原生动物 *P. grassii* 转录组中表达极高, 表明 *P. grassii* 能够高效地降解纤维素 (Nishimura *et al.*, 2020)。通过 RNA 干扰技术, 进一步验证了纤维二糖水解酶基因在白蚁纤维素降解过程中的关键作用 (Liu *et al.*, 2017)。此外, 木聚糖主要由原生动物 *H. hartmanni* 产生的木聚糖酶进行降解 (Arakawa *et al.*, 2009)。另一种原生动物 *Con. leidyi* 则具有降解壳聚糖功能, 能够将其转化为氨基酸, 为宿主提供营养 (Nishimura *et al.*, 2020)。

#### 4.1.2 白蚁肠道原生动物共生细菌降解木质纤维

白蚁肠道细菌参与木质纤维的降解。通过宏基因组技术, 发现肠道内多种参与木质纤维降解的细菌 (Liu *et al.*, 2019)。目前, 已经从白蚁肠道分离出多株能够进行木质纤维降解的细菌 (羊桂英等, 2020)。原生动物共生细菌参与木质纤维降解的最直接证据来自基因组测序。通过分离单个细菌或原生动物, 进行基因组扩增和测序, 研究表明, 外共生细菌 *Candidatus Symbiothrix dinnympphae* (属于拟杆菌目) 锚定在原生动物

*Dinnymppha* spp. 的表面, 通过对对其进行全基因组测序, 发现该细菌包含多个糖苷水解酶基因, 能够将单糖转化成乙酸盐 (Yuki *et al.*, 2015)。原生动物 *Streblomastix strix* 可能不直接参与纤维素消化, 但其表面的细菌群落却能分泌一系列复杂的糖基水解酶, 这些酶使它们能够将纤维素降解为单体, 并进一步促进 *S. strix* 的代谢过程 (Treitli *et al.*, 2019)。

#### 4.2 H<sub>2</sub>的产生与利用

H<sub>2</sub>是白蚁代谢的关键中间产物。白蚁肠道产氢的速率比牛胃高 (Pester and Brune, 2007)。虽然不同白蚁 H<sub>2</sub> 积累程度有差异, 但白蚁体内的 H<sub>2</sub> 都会被迅速转化。H<sub>2</sub> 的转化占白蚁呼吸活动的 22%~26% (Pester and Brune, 2007)。肠道内的大部分 H<sub>2</sub> 通过细菌的乙酸形成作用 (Acetogenesis) 被利用, 还有一小部分通过甲烷生成被去除。另外, 还有极少量的 H<sub>2</sub> 被释放到体外。白蚁的 H<sub>2</sub> 排放特性在其它微生物生态系统中并不常见, 这使其成为一个引人注目的研究焦点 (Sugimoto *et al.*, 1998)。虽然白蚁能够释放 H<sub>2</sub>, 但是不同种类的白蚁在 H<sub>2</sub> 释放量上存在显著差异 (Sugimoto *et al.*, 1998)。肠道内 H<sub>2</sub> 的生产和利用之间总体上是平衡的 (Pester and Brune, 2007)。

##### 4.2.1 H<sub>2</sub>的产生

白蚁肠道原生动物吞噬木材或纤维素颗粒, 通过发酵作用产生乙酸、CO<sub>2</sub> 和 H<sub>2</sub> (Hungate, 1943; Yamin, 1981)。因此, 这些纤维素分解原生动物被认为是肠道中 H<sub>2</sub> 的主要产生者 (Ebert and Brune, 1997; Inoue *et al.*, 2007)。氢化酶体是产生 H<sub>2</sub> 的细胞器, 在厌氧能量产生中起核心作用 (Müer, 1993)。副基体门的原生动物, 由于含有氢化酶体, 因此能够产生 H<sub>2</sub>; 而锐滴虫目原生动物的发酵产物尚不清楚 (Hongoh, 2011)。除了原生动物, 白蚁肠道中的细菌也可以将糖发酵产生 H<sub>2</sub>。例如, *Treponema azotonutricium* ZAS-9 是一种可人工培养的厌氧细菌, 具有固氮活性, 能够将麦芽糖发酵成乙酸盐、乙醇、CO<sub>2</sub> 和 H<sub>2</sub> (Leadbetter *et al.*, 1999; Gruber *et al.*, 2004; Lilburn *et al.*, 2011)。全基因组测序表明, *T. agilis* 细胞内的属于难得菌门的 Rs-D17 细菌能够产生 H<sub>2</sub> 和乙酸盐 (Hongoh *et al.*, 2008a)。

氢化酶催化 H<sub>2</sub> 的可逆氧化反应, 在 H<sub>2</sub> 的产生过程中起到重要作用。大部分氢化酶存在于古菌

和细菌中，也有一小部分存在于真核生物。氢化酶分为3类：[Fe]氢化酶、[NiFe]氢化酶和不含金属的氢化酶（Vignais *et al.*, 2001）。氢化酶与电子分岔亚基结合成一个大的复合体，这个大的复合体能够进行吸能的电子载体铁氧还蛋白的还原，也能从NADH产生H<sub>2</sub>（Schuchmann *et al.*, 2018）。Inoue等（2007）在台湾乳白蚁的原生动物*P. grassii*中鉴定到2个编码Fe氢化酶的基因，它们催化H<sub>2</sub>的生成。通过生物信息学分析，在*T. azotonutricium* ZAS-9中发现多个[Fe]氢化酶样蛋白（Ballor *et al.*, 2012）。这些结果表明，白蚁肠道共生体是一个丰富的新型[Fe]氢化酶库。

#### 4.2.2 H<sub>2</sub>的利用

在白蚁体内，存在着多种进行产乙酸作用的细菌，能够将H<sub>2</sub>和CO<sub>2</sub>转化为乙酸盐，它们主要隶属于螺旋体门、厚壁菌门和δ-变形菌纲Deltaproteobacteria（Rosenthal *et al.*, 2013）。一氧化碳脱氢酶（Carbon monoxide dehydrogenase）是同型产乙酸细菌Wood-Ljungdahl途径的关键酶，*cooS*基因编码一氧化碳脱氢酶复合物的催化（β）亚基，通过对肠道细菌的*cooS*基因进行分析，发现了151种不同的*cooS*基因，这些基因分为3个系统发育分支（Phylogenetic clades）（Matson *et al.*, 2011）。结合单细胞技术在内的多种手段，在内华达白蚁肠道中发现了2种同型产乙酸菌：δ-变形菌和螺旋体，其中δ-变形菌和原生动物共生，而螺旋体自由生活在肠液中（Rosenthal *et al.*, 2013）。此外，*Treponema primitia* ZAS-1和ZAS-2两个菌株通过乙酸形成作用利用H<sub>2</sub>（Leadbetter *et al.*, 1999；Graber *et al.*, 2004）。生物信息学分析表明，*Treponema primitia* ZAS-1和ZAS-2编码多个[Fe]氢化酶样蛋白，在其中发现1个新型的[Fe]氢化酶家族，可与甲酸脱氢酶形成复合体，参与乙酸形成作用（Ballor *et al.*, 2012）。

在山林原白蚁*Hodotermopsis sjostedti*中，60%的还原性产乙酸作用和全部的固氮作用是由原生动物*Eucomonympha*属的内共生细菌产生的（Ohkuma *et al.*, 2015）。与*T. agilis*细胞共生的2种细菌：Ca. *Endomicrobium trichonymphae*和*Candidatus Desulfovibrio trichonymphae*，Ca. *Endomicrobium trichonymphae*属于内共生，而Ca. *Desulfovibrio trichonymphae*嵌入细胞内，只通过一个小孔与外界相连，基因组测序表明Ca.

*Desulfovibrio trichonymphae*具有氧化H<sub>2</sub>的功能（Kuwahara *et al.*, 2017）。虽然产甲烷作用也可以利用部分H<sub>2</sub>，但这只占H<sub>2</sub>消耗的极小部分（Brune, 2018）。

#### 4.3 固氮功能

白蚁可以长期仅依靠纤维素生存（Cleveland, 1925），这一现象促使Hungate推测白蚁可以固定大气中的N<sub>2</sub>（Hungate, 1941）。随后，通过乙炔还原法，证明白蚁具有固氮作用（Benemann, 1973；Breznak *et al.*, 1973）。研究还发现，当喂食白蚁抗生素后，其固氮活性消失，这表明白蚁的固氮活性来自肠道细菌（Breznak *et al.*, 1973）。虽然从白蚁后肠中分离出多株固氮细菌（French *et al.*, 1976；Potrikus and Breznak, 1977；Lilburn *et al.*, 2011），但大部分的固氮细菌不能被人工培养。随着分子生物学技术的发展，通过功能基因（*nifH*）和宏基因组测序技术，发现白蚁肠道固氮微生物的多样性远超预期（Ohkuma *et al.*, 1996；Noda *et al.*, 1999；Ohkuma *et al.*, 1999；Noda *et al.*, 2002；Lilburn *et al.*, 2001）。*nifH*基因分为4个分支（Clusters I - IV）（Zehr *et al.*, 2003）。目前分离到的*nifH*基因大多归属于Cluster II和Cluster III，归属于Cluster I的细菌非常少（Brune and Ohkuma, 2011）。例如，在黑胸散白蚁肠道中只发现归属于Cluster II和Cluster III的*nifH*序列（Du *et al.*, 2012）。通过对19种白蚁和*Cryptocercus punctulatus*中的*nifH*研究表明，白蚁的蚁巢类型比白蚁的系统发育能更好地解释固氮菌的群落结构（Yamada *et al.*, 2007）。

在白蚁肠道内，固氮菌可自由生活于肠液中，同时，也存在与原生动物共生的固氮菌。例如，干木白蚁的固氮活性主要来自原生动物的拟杆菌目外共生细菌（Desai and Brune, 2012）。在山林原白蚁中，几乎所有的固氮作用是原生动物*Eucomonympha*的内共生细菌完成，这个细菌属于密螺旋体属Cluster II的成员（Ohkuma *et al.*, 2015）。另外，与台湾乳白蚁肠道原生动物*P. grassii*共生的细菌Ca. *Azobacteroides pseudotrichonymphae*也具有固氮活性，它能够将N<sub>2</sub>转化为NH<sub>3</sub>（Hongoh *et al.*, 2008b）。但固氮活性在台湾乳白蚁幼龄巢中非常微弱，白蚁主要通过有机土壤获得氮源（Mullins *et al.*, 2021）。而木白蚁科肠道内的固氮活性比土木两栖的台湾乳白蚁

要高 (Mullins and Su, 2023)。台湾乳白蚁固氮活性的高低受食物成分和白蚁生理状态的影响 (梅建凤等, 2002)。因此, 固氮细菌在白蚁营养中的作用仍有待深入研究。

## 5 展望

白蚁肠道原生动物与共生细菌形成了一个复杂的共生体, 对维持白蚁的生命活动发挥了重要作用。由于白蚁肠道微环境的复杂性, 很多原生动物和共生细菌都不能被人工培养。利用现代分子生物学技术, 包括扩增子测序、宏基因组以及单细胞技术, 极大地深化了我们对于原生动物分类、共生细菌群落结构、原生动物-共生细菌进化关系及原生动物功能等方面的认识。尽管生物信息学手段已经对肠道细菌的功能进行解析, 但许多基因的功能仍未进行验证。针对白蚁肠道特殊的理化特性创新分离培养技术和策略将有助于肠道原生动物的功能研究。同时, 利用多组学联合手段, 能够更深入地解析肠道原生动物的生理功能。将研究聚焦于宿主与原生动物的相互作用, 将有助于能更全面地揭示肠道原生动物的作用, 深化对其生物特性的认识。通过对原生动物降解木质纤维机制的深入研究, 有望为应对相关的生态和环境问题提供新的应用策略。

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