微生物学报
Acta Microbiologica Sinica
2024, 64(6): 1922–1935
http://journals.im.ac.cn/actamicrocn
DOI: 10.13343/j.cnki.wsxb.20240287

地球熔岩管道微生物研究对天体生物学的启示

程晓钰[1]，李旻[1,2]，肖龙[3]，刘邓[1,2]，王红梅[1,2*]

1 中国地质大学(武汉) 生物地质与环境地质国家重点实验室，湖北 武汉 430078
2 中国地质大学(武汉)环境学院，湖北 武汉 430078
3 中国地质大学(武汉)地球科学学院，湖北 武汉 430074

程晓钰，李旻，肖龙，刘邓，王红梅. 地球熔岩管道微生物研究对天体生物学的启示[J]. 微生物学报，2024，64(6): 1922-1935.
CHENG Xiaoyu, LI Min, XIAO Long, LIU Deng, WANG Hongmei. Microbial studies in the lava tubes on Earth: overview and implications for astrobiology[J]. Acta Microbiologica Sinica, 2024, 64(6): 1922-1935.

摘　要：天体生物学作为与深空探测相结合的交叉学科，旨在从地球极端环境类比、古代生命载体信息发掘和模拟等方面揭示地外行星体是否适合生命生存和繁衍，其中适宜的环境条件是评价所有天体是否宜居的重要条件。近年来在月球和火星等行星表面发现了大量由火山熔岩流形成的熔岩管道，这些巨型管状地下空间具有稳定的温度和防辐射等环境条件，为生物在地外星体上的生存提供了潜在的庇护场所。基于地球熔岩管道的天体生物学的类比研究可以为探索地外生命痕迹提供重要线索，本文综述了现阶段地球熔岩管道内微生物的研究进展、微生物痕量气体代谢在天体生物学研究中的潜力及天体生物学的研究进展，旨在为后续开展地球及地外熔岩管道的天体生物学研究提供思路。

关键词：天体生物学；熔岩管道；极端微生物；能量代谢方式；月球；火星

资助项目：国家自然科学基金(91951208)；中国博士后科学基金(2023TQ0336)；国家资助博士后研究人员计划(GZB20230678)
This work was supported by the National Natural Science Foundation of China (91951208), the China Postdoctoral Science Foundation (2023TQ0336), and the Postdoctoral Fellowship Program of CPSF (GZB20230678).
*Corresponding author. E-mail: wanghmei04@163.com
Received: 2024-05-08; Accepted: 2024-05-22; Published online: 2024-05-30

Microbial studies in the lava tubes on Earth: overview and implications for astrobiology

CHENG Xiaoyu[1], LI Min[1,2], XIAO Long[3], LIU Deng[1,2], WANG Hongmei[1,2*]

1 State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan 430078, Hubei, China
2 School of Environmental Studies, China University of Geosciences, Wuhan 430078, Hubei, China
3 School of Earth Sciences, China University of Geosciences, Wuhan 430074, Hubei, China

Abstract: As an interdisciplinary subject combined with deep space exploration, astrobiology studies the habitability of extraterrestrial planets by the analogical study of the extreme environments on Earth, the exploration of carrier information of ancient life, and simulation. Notably, suitable environmental conditions are crucial for evaluating the habitability of planets. Recently, a large number of lava landforms suspected of lava tubes have been found on the Moon and planets such as Mars. These giant tube-shaped underground spaces may provide shelters for life to survive in consideration of the relative stable temperature inside and the function of radiation protection. Therefore, the analogical studies based on lava tubes on Earth can provide fundamental clues for exploring the traces of extraterrestrial life. Here, we review the microbial studies about the lava tubes on Earth, the implications of microbial metabolism of trace gas for astrobiology, and the recent progress in astrobiology, aiming to provide ideas for astrobiological research on lava tubes on Earth and other planets.

Keywords: astrobiology; lava tube; extremophiles; energy metabolism pattern; the Moon; Mars

天体生物学是研究宇宙生命的学科，主要采用原位探测技术、太阳系内和太阳系外行星的光谱手段等对地外生命开展研究，以期寻找地外智慧生物[1]。天体生物学作为与深空探测相辅相成的交叉性学科[2]，其主要目标之一便是探究太阳系的行星体，以确定它们是否适合地外生命的生存[3]。地球作为目前已知的唯一存在生命的星球，是天体生物学研究的基石和起点。基于现阶段人们对生命的认识，一般假设地外天体上可能的生命也为碳基生命，研究不同环境碳基生命的种类和适应能力是评价地外环境宜居性的前提[4]。目前基于地球为研究场所的天体生物学的研究分为三部分(图 1)[3]：(1) 研究地球极端环境中生命存在形式及其特殊代谢方式、适应策略和现代生物特征；(2) 通过研究地球上古老的岩石及生物特征来探究灭绝的生命；(3) 将地球样本暴露于模拟的星球环境，进而识别星球极端环境条件如强辐射、极端的温差条件等对矿物、生物和微生物等的潜在影响。与太阳系行星体昂贵的太空任务相比，地球作为研究天体生物学的类似场所具有得天独厚的优势[5]，在天体生物学的研究中发挥着不可替代的作用。

地球上数量最多的生命形式为微生物[10]，而细菌又是微生物中的重要代表，贡献了地球上 3.5−5.5 百亿 t 的生物量[11]。微生物参与的物质循环和能量代谢对已知的生物地球化学循环有直接或间接的贡献[12]，但微生物的生存痕迹现阶段仅被报道于地球，对于“地外星球上是否存

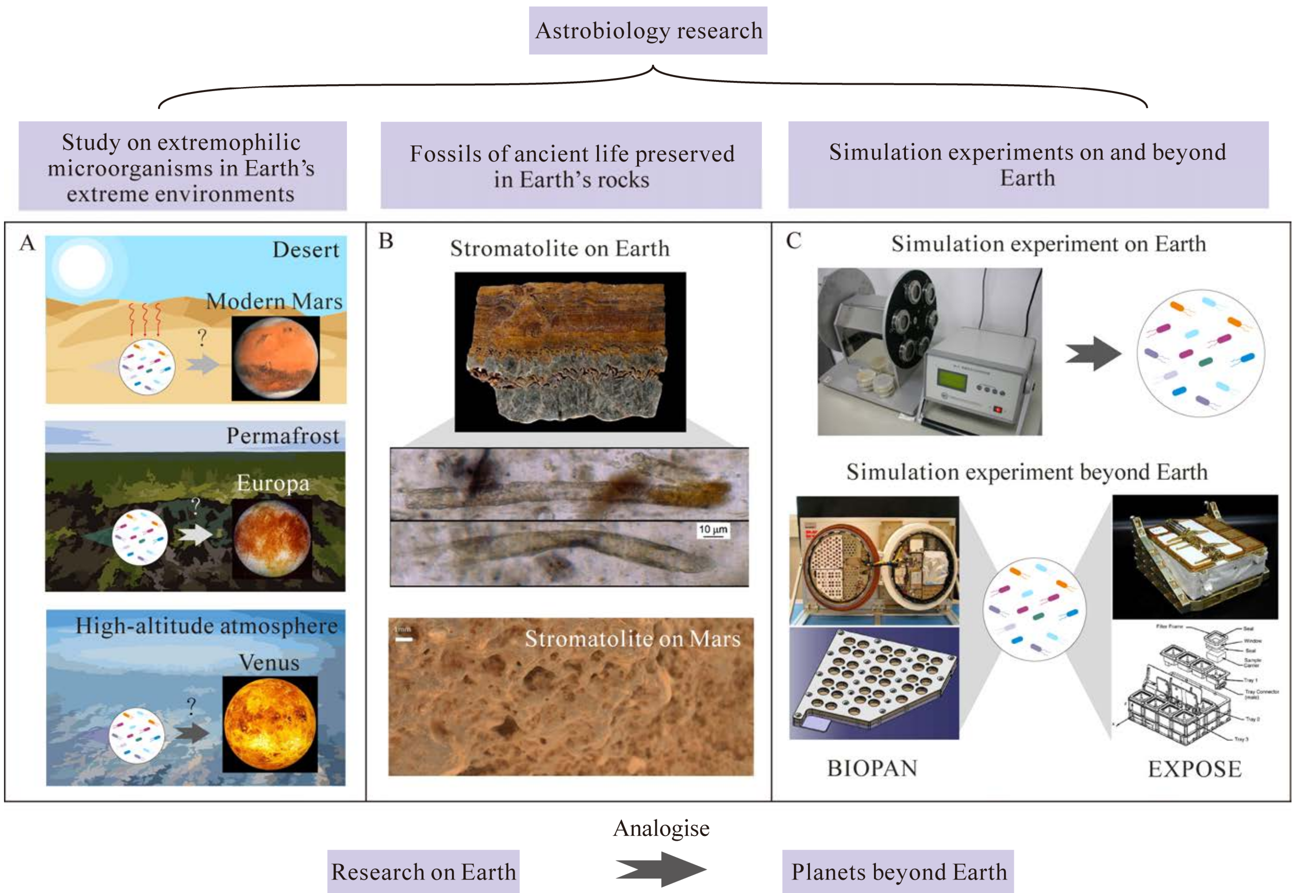

图 1　基于地球类比的天体生物学研究示意图(改编自文献[5-9])

Figure 1　Schematic diagram of researches involved in astrobiology based on the Earth (adapted from references [5-9]).

在微生物”和“地外星球是否发现微生物的生存痕迹”一直是国际热议话题[13]。1996 年,在 ALH84001 火星陨石中发现了类似于趋磁细菌产生的磁小体，其成分为磁铁矿，磁铁矿的大小、形态及排列方式上均与趋磁细菌体内的磁小体链十分相似，曾被认为火星上存在生命的证据[14-15]。随后利用磁学技术、莫斯科维茨测试和铁磁共振等手段,测试了 ALH84001 陨石中的数百万个磁铁矿晶体的组成及晶体学性质,结果显示，虽然陨石内的磁铁矿异常纯净，并与陆相磁小体化石相似,但全部晶体排列方式并非地球磁小体化石特有的链状排列[16],因此排除了火星陨石磁铁矿的生物成因。然而，目前微生物成因矿物的识别仍是识别地外生命存在的重要途径。

液态水是所有地球生命所必须依赖的,因此地外生命的探寻首先是确定这些星球是否存在(过)液态水。通过卫星及遥感技术探测到多个地外星球上存在(过)液体水、具有适宜微生物生存的温和气候条件等特点,推断地外星球可能和早期的地球一样适合生命的生存[17]。虽然世界各国均致力于在地外星球含水的区域寻找地外星球上生命的生存痕迹及潜在的生物标志物[2,18-20],但目前仍未在“地外星球是否存在生命痕迹”这一领域获得突破性进展,学者认为该项目成功率最

高的生命检测手段是采集火星样本后返回地球进行检测[21]。由于受到探测仪器、地外星球表面采样区的选择、基于地球已知生命的地外生命探索的局限性,以及电离辐射等宇宙射线对生命痕迹的破坏等因素的影响[17,21],极大地限制了人们对地外星球表面生命痕迹的探索及认识。

在前期研究基础上,大量遥感探测数据显示火星上存在与地球类似的熔岩管道[22],并可见大量“天窗”(起源于熔岩管道部分坍塌天花板上的开口)[23]。火星表面恶劣的辐射环境,无法满足生命的生存和保存,但火星的地下环境却可能存在恒温、低辐射等环境条件,是维持生命的挥发物(水等)滞留的庇护场所[24],因此熔岩管道成为最有可能保存火星微生物的场所之一。本文综述了现阶段地球熔岩管道微生物、痕量气体在寡营养和极端环境下的研究潜力及天体生物学研究现状,旨在阐释地球熔岩管道的研究进展和天体生物学研究领域的前景,以期为推进我国天体生物学的发展及深空探测的国家战略需求献计献策。

1 地球熔岩管道内微生物多样性研究

熔岩管道形成于岩浆流动后冷却的过程。熔岩溢出和流动时,熔岩流外表面迅速冷却,形成硬化的壳层,内部岩浆得以保持高温继续流动,随着剩余的熔岩流出管道,便留下一个空洞空间,这是常见的熔岩管道形成机理[17,23]。熔岩管道数据库(Lava Tube Database, https://rgcps.asu.edu/ltdb/)包含来自 6 个大洲 34 个国家的熔岩管道信息,全球已知最长的熔岩管道是夏威夷大岛基拉韦厄的 Kazumura 洞穴,全长 59.3 km,其中基拉韦厄火山的 2/3 被由管道注入的熔岩流覆盖。现阶段火星上熔岩管道的年龄尚不清楚,但其可能发育于地质年龄小的熔岩中。地球上已知的最古老的熔岩管道为发育于 7 百万年前的约旦 AI-Shaam 高原熔岩管道[25]。在古老的地层中,熔岩管道坍塌后被水流或者沉积物覆盖,从而形成蜿蜒的山脊和通道。火星因其寒冷、干燥、风化率低和较弱的构造活动等特点,会使熔岩管道保存更长的时间[17]。目前已经在多个星球表面发现了熔岩管状洞穴,而地球熔岩管道内的微生物研究已经成为天体生物学和比较行星学的重要方向。

地球熔岩管道微生物的研究早期主要集中于夏威夷、亚速尔群岛和美国新墨西哥州的熔岩洞穴内的微生物席[26-28]。地下生态系统中的微生物通过聚集成生物膜来增加其在地下寡营养条件下的生存能力[26,28-30],尤其在熔岩洞穴中富含黄色、白色、粉色和金色的微生物席[26-27,31]。通过分子克隆手段及二代测序技术发现,不同熔岩洞穴内细菌的群落组成不同。夏威夷熔岩洞穴主要以放线菌门(*Actinobacteria*)和变形菌门(*Proteobacteria*)为主[32],而特塞拉岛熔岩洞穴内细菌以酸杆菌门(*Acidobacteria*)为主[27]。通过与外界土壤条件对比,发现熔岩洞穴内放线菌门和硝化螺菌门(*Nitrospirae*)的相对丰度普遍高于土壤环境[31]。熔岩管道中细菌的 α 多样性普遍低于岩溶洞穴和土壤细菌的 α 多样性,这可能与基岩类型及性质不同有关[33-36]。同时,矿物成分的差异及外界环境条件的剧烈变化也使得熔岩管道内微生物结构具有显著性差异[34]。全球洞穴细菌群落分布的研究结果显示,外界温度和降雨量在解释全球洞穴微生物多样性格局差异中发挥着关键作用[37],但以上结论的得出仅基于已发表的洞穴外部环境参数而缺乏洞穴内部温度的实测结果。基于洞穴内实测结果显示,洞穴内部微生物分布主要与样品的 pH 和洞穴内部温度等因素密切相关[35-36],所以对于影响洞穴微生物分布的关键因素至今仍未定论。此外,部分学者认为若火星熔岩管道存在类似环境,微生物可能

会利用次生矿物的颗粒间和颗粒内空间作为微环境来生长并进一步调节矿物沉淀[34,38]，而新生成矿物与微生物间是否存在互利关系(如包裹微生物表面以抵抗外界辐射等)至今仍未知。

冰岛熔岩洞穴的低温更接近火星的环境条件，该熔岩洞穴内细菌类群主要以放线菌门和变形菌门占据主导地位[39-40]，它们在 5 °C 和−5 °C 下均能代谢种类多样的有机碳源[39]。放线菌和变形菌也在岩溶洞穴中广泛分布[35,41-42]，有研究显示变形菌门的微生物与洞穴碳循环(如 CO_2 固定和甲烷氧化)[43-45]和硫循环(如硫氧化)[46-49]存在密切关联。关于熔岩管道微生物潜在的代谢功能研究依然较为匮乏，虽然在熔岩管道中发现了完整的氮代谢途径、多环芳烃降解和碳氢化合物降解相关基因[50]，但并未在富含硫酸盐矿物的熔岩洞穴内发现较高丰度的硫代谢相关基因[38]。分子生物标志物的研究发现，细菌群落是地球火山熔岩管道中生物标志物形成的重要贡献者，其中脂类主要是由低分子量 *n*-烷烃、α-烯烃和支链烯烃组成，说明微生物是熔岩管道内沉积物中有机物的主要来源[34]。地球熔岩管道作为模拟火星地下条件的重要场所，探究其内微生物的群落结构特征、功能信息及控制其内微生物多样性的因素将为后续探索地外生命提供重要科学证据和技术支持。

2 痕量气体对地球熔岩管道微生物的潜在作用

地球上某些微生物可以直接利用大气中的痕量气体(如一氧化碳、氢气和甲烷等)获得能量[51]，如在洞穴中报道的一株来自分枝杆菌属(*Mycobacterium*)的放线菌能够利用甲烷作为唯一碳源进行能量代谢(图 2)[52]。“好奇号”火星探测器检测到火星气体中二氧化碳(CO_2)所占的比例最高(约为 96.00%)，其次为占比约 1.93%的氩气、1.90%的氮气、0.15%的氧气和低于 0.10%的一氧化碳(CO)[53]。CO_2 作为长期滞留大气可能会导致温室效应加剧的气体之一，其在地球上的“源”和“汇”研究一直都是关注热点[54]。地球岩溶地区溶蚀作用产生的碳汇量约为 6.08×10^8 t-C/a，占总遗失碳汇的 1/3[55]。洞穴作为来自不同过程 CO_2 的实时储存库，地下 CO_2 存储可能占大气 CO_2 总含量的一半以上[56]。洞穴内黑暗和寡营养的环境条件使得洞穴内微生物具有独特的碳源获取(如 CO_2 固定)途径[44,57-59]。其中岩溶洞穴内参与 CO_2 固定(卡尔文循环)的 1,5-二磷酸核酮糖羧化酶/加氧酶 (ribulose-1,5-bisphosphate carboxylase/oxygenase，RuBisCO)和氨透性酶蛋白显著高于其他生境(图 2)，说明洞穴内微生物是潜在的 CO_2 固定活性单元[44]。

除 CO_2 外，地球大气中存在的微量气体如氢气(H_2)和 CO 等，它们能够作为微生物氧化的底物，为微生物生长提供能量。研究证明，火星上也存在微量的 H_2 和 CO，它们可能为寻找火星等地外生命的存在提供新的必需条件[60-61]。利用 H_2 和 CO 的无机营养型微生物主要利用两种核心酶：氢化酶(hydrogenases)和一氧化碳脱氢酶(carbon monoxide dehydrogenases)[51]。对于异养微生物和化能自养微生物而言，大气 H_2 可对其生长起到辅助作用，如 H_2 代谢生成的 ATP 可用于将 CO_2 固定为生物质，而有些化能自养型微生物能够利用 CO 作为单一能源进行代谢(图 2)[60]。现有研究表明，生活在南极洲沙漠土壤中的优势微生物群落能编码并表达利用大气中痕量气体的氢化酶和一氧化碳脱氢酶，同时也能进行 CO_2 固定(图 2)[61]。以上结果说明，大气中的痕量气体在一定程度上能够为微生物提供能源，从而维持寡营养的极端条件下生态系统的运转。

此外，微生物产甲烷被认为是火星生命的潜在代谢途径[62-63]。1997 年首次在火星上发现可

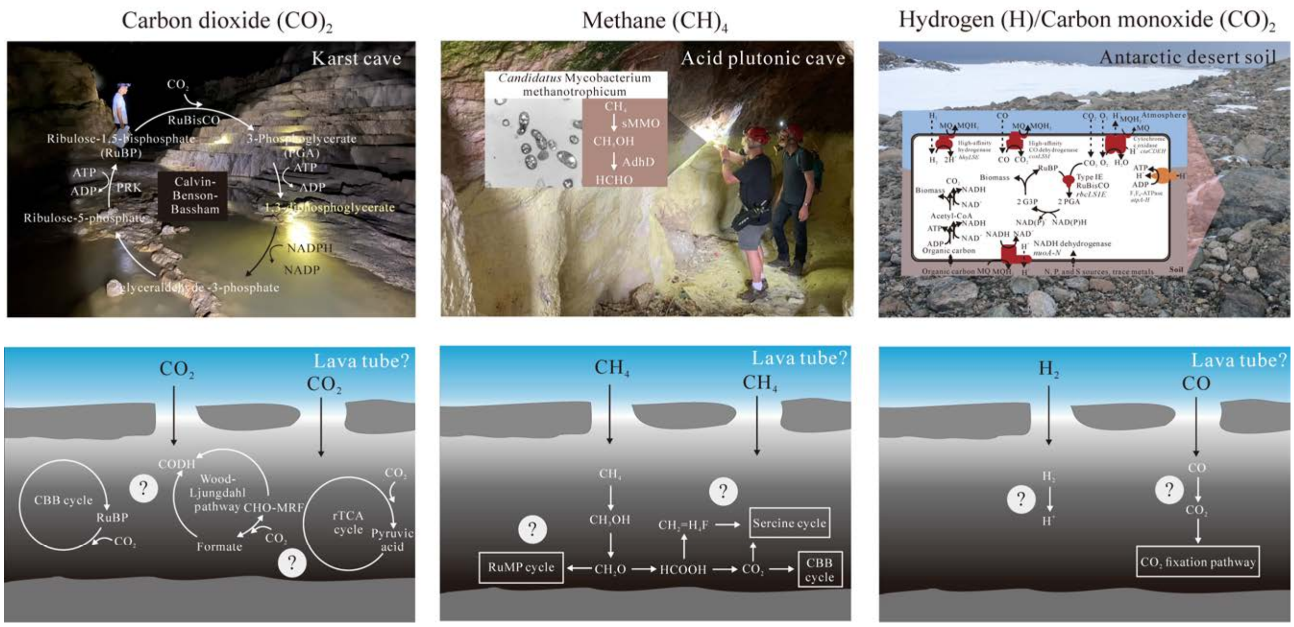

图 2 微生物对大气痕量气体消耗研究进展及对天体生物学的启示示意图(改编自文献[52,61])

Figure 2 Schematic diagram of research progress on the microbial consumption of trace gases in the atmosphere and its implications for astrology (adapted from references [52,61]).

能存在甲烷(CH_4)[64]，进一步研究发现火星上 CH_4 浓度存在季节性波动，但 CH_4 浓度变化幅度大于紫外线对地表有机物降解产甲烷的幅度，这意味着火星大气中的甲烷可能与火星表面或地下甲烷的局部释放密切相关[65]。与地球 CH_4 的生存时间相比，火星上的 CH_4 光化学周期短，为维持火星上 CH_4 的现有浓度则需要极大的 CH_4 通量补充；但非生物过程不易产生富含 CH_4、CO_2 且低 CO 含量的大气，因此有学者提出在特定条件下甲烷是由生物产生，大气甲烷是检测系外星球生命存在与否的关键因素[66]，但对于火星上是否具备产甲烷微生物能够行使产甲烷功能所需的底物及环境条件目前仍未知。

CH_4 作为重要的温室气体，在地质历史时期与 CO_2 共同补偿早期太阳的热量不足，维持类星球温度，该过程可能有助于生命的形成，因此 CH_4 也被认为是生命存在的标志气体[67-69]。地球上 CH_4 参与了许多重大的地质事件，如通过升温间接导致了生物危机[70-71]。大气 CH_4 浓度自工业革命以来逐年递增，基于自上而下的大气反演方法进行全球 CH_4 通量估算结果显示，2008−2017 年全球 CH_4 总排放量约为 576 t-CH_4/a，CH_4 总消耗量约为 556 t-CH_4/a，地球系统中甲烷源和汇的不平衡导致大气平均温度的逐年升高，但模型中甲烷排放导致的温度上升幅度与现实监测结果不匹配，使得研究热点多集中于探究地球陆地生态系统中被忽略的甲烷汇[72-74]。

地球上好氧甲烷氧化菌的甲烷氧化在两个不同浓度下由两种不同的同工酶来完成[75-77]：含有传统 pMMO1 的甲烷氧化菌类群偏好大于 0.43 mg/dm^3 的 CH_4 浓度，而当 CH_4 浓度低于 0.07 mg/dm^3 时，主要是含有 pMMO2 的甲烷氧化菌类群发挥作用。作为黑暗、寡营养的代表研究生境之一的洞穴近年来被确认为潜在的陆地甲烷汇，其中微生物在痕量甲烷(0.001 4 mg/dm^3)消耗中发挥着至关重要的作用[78-82]。这类能够利用

痕量甲烷作为碳源和能源的微生物被称为高亲和性大气甲烷氧化菌 USC (upland soil cluster)类群，该类群被广泛分布于碳酸盐洞穴和玄武岩洞穴中，其与氮循环间的潜在耦联关系可能驱动了洞穴内元素循环[43,83-87]。此外，基于土壤高亲和性甲烷氧化菌的甲烷氧化动力学研究结果显示，大气浓度的 CH_4 并不足以维持这类微生物的生长[88]，说明这类微生物拥有其他能量利用形式以满足其在痕量 CH_4 条件下的正常生长发育。USCα 唯一的纯培养菌株甲基荚膜菌属(*Methylocapsa gorgona*) MG08 的完整基因组验证了这一结果：该菌株不仅能够利用大气浓度的 CH_4，而且能够利用痕量 H_2 和 CO 作为能量[89]。虽然目前仍缺乏对地球熔岩管道内微生物与痕量气体间作用关系的研究，但是基于已有的地球洞穴研究手段和技术方法有望突破地球熔岩管道内微生物生态及潜在功能等方面的瓶颈。此外，厘清已知的地球上熔岩管道内微生物与痕量气体间的关联及相互作用关系，将有助于后续开展地外生命的探索任务。

3 天体生物学研究进展与展望

如前文所述，天体生物学现阶段研究的开展主要聚焦于 3 个方面(图 1)[3]。首先，在极端环境生命挖掘方面通常从地球生命极限着手，即通过研究地球上的极端条件下，如温度(低温和高温)、pH 值(酸性或者碱性)、极度干燥、高盐度、高压和寡营养条件下微生物的生存策略[5,90-91]，为在地外极端环境下探索生命提供线索。熔岩洞穴中的放线菌门(如假诺卡氏菌科)、硝化螺菌门(如磁螺菌属和类固醇杆菌属)和拟杆菌门(如噬几丁质菌科)被发现在低温(5 ℃)条件仍具有活性，其中放线菌门能够原位固定碳以供给自身能量[39,92]。地球微生物具有极强的生存耐受潜能且能够独立生存于熔岩表面进行生长代谢活动，这为后期探究火星熔岩洞穴内是否存在生命提供了参考。熔岩洞穴作为在火星上寻找生命和未来人类居住的优先候选生境，可能具有恒温、大气压强略高于火星表面、一定的水条件，以及大气主要成分为 CO_2，同时也含有 CO、H_2 和 CH_4 等稀有气体，加之与火星表面相比，地下的熔岩管道能够抵挡宇宙射线和太阳风辐射等条件，为火星生命存在提供可能[93]。截至目前，火星侦查轨道飞行器已在火星表面发现超过 1 000 个熔岩洞穴，为未来探测火星熔岩洞穴中是否存在生命提供了候选着陆地点[94]。

其次，微生物活动形成的沉积构造以及活动后造成的同位素分馏等现象均可为生命存在提供证据。地球上关于早期生命痕迹最有力的记录之一就是 34−33 亿年的澳大利亚斯特雷利池地层中保存的叠层石，它们具有特殊的三维凸起结构，大多呈波浪状、分枝状或圆锥形，层状结构厚度不等，横向由层状碳酸盐岩连接[95-97]。叠层石中保存的有机层状物的碳同位素结果进一步证实了多种微生物的参与。因此，将叠层石的形态特征与同位素特征相结合，可为叠层石的微生物成因提供确凿的证据。目前，人们除了致力于新型生物标志物的开发外，也将目光聚焦于适用于地外探测器的仪器研发[98]，以探测外行星熔岩洞穴中是否存在生物。

与前两个方面相比，第三部分研究则基于模拟研究，即直接在地球场所中模拟地外极端条件或将样本置于空间站，探讨地球样本中微生物和矿物特征等的变化[3]。例如，研究者通过模拟地外微重力和空间辐射等条件来研究其对微生物的影响[8,99]。能够抗辐射的不动杆菌属(*Acinetobacter*)对过氧化氢和地外极端条件(干燥、蒸汽和紫外线照射等)表现出抗性。奇异球菌属(*Deinococcus*)能够通过激活 DNA 修复机制、活性氧解毒系统和相容介质的积累等在电离

辐射的致命作用下存活[8]。对于太空实验站的研究,根据暴露在太空环境的时长分为短期实验与长期实验[9],短期暴露设备的代表是欧洲航天局(European Space Agency, ESA)开发的 BIOPAN,该设备可将实验样本暴露于低轨道环境中至少两周,目的是极大程度下地回收实验材料[100-101]。已有研究结果显示,黏土、岩石和陨石对微生物孢子具有保护作用[102-103],该结果为开展地外熔岩洞穴内生命存在研究提供了理论基础。长期暴露装置则是基于国际空间站设计,代表性装置为 ESA 研发的 EXPOSE[9]。在 EXPOSE-E 任务中发现,若不受太阳辐射的影响,细菌孢子在火星任务中存活的概率较大[104]。被称为地球“先锋物种”的蓝细菌对极端条件的耐受性一直是学者们关注的重点,在 EXPOSE-R2 任务中便选择了来自沙漠的蓝细菌 *Chroococcidiopsis* 开展研究,结果显示高 UVC 辐射下,与火星矿物类似的矿物能够保护 *Chroococcidiopsis* 细胞完整性[105]。2014−2016 年的任务结果也显示,生命以生物膜形式存在比以浮游生活形式生存更能长期抵抗太空和火星上的恶劣环境条件[106]。以上结果说明,生物膜作为地球上最古老的生命迹象之一,使得微生物能够抵抗太空恶劣环境条件,因此生物膜也可能成为探索地外生命的新线索。地球洞穴中存在着大量不同色泽的生物膜,除保护微生物功能外,生物膜颜色的差异与微生物群落组成密切相关,不同的生物膜在洞穴中发挥的功能具有差异[107],如参与矿物沉积和溶解[108]。地球熔岩管道作为研究地外熔岩管道内生命的突破口,采用现代分子生物学研究手段结合地外环境模拟的方法,将有助于揭示其内特殊能量代谢方式,为后续探索地外生命提供指导思路。

总之,通过卫星和遥感等方法发现地外星球存在大量与熔岩管道类似的洞穴环境,这些地下熔岩管道具有屏蔽外界辐射、潜在水环境和维持恒定温度等特点,从而为生命的存在提供潜在的环境条件。然而,目前地球上熔岩管道微生物研究仍停留在群落组成及基础代谢功能的探索阶段,亟须利用在岩溶洞穴中已成形的研究手段进行深度解析,未来关于天体生物学的研究方向及采用技术可集中于以下三方面。(1) 地球熔岩管道内微生物多样性和微生物对 CH_4、CO 和 H_2 等痕量气体的利用效率及代谢途径。该研究领域可利用稳定同位素探针技术定向破译具有代谢活性的微生物利用特定代谢底物的物质流,进一步结合单细胞拉曼筛选和培养技术定向获得目的菌群,从而揭示能够利用痕量气体的微生物的特殊能量代谢方式。(2) 基于太空模拟仓,探究太空极端条件对熔岩管道微生物的影响,如细胞膜的完整性、ATP 的含量、DNA 完整性和细胞内酯酶活性等,以获得太空极端条件影响下潜在的微生物变化指示信息,为后续地外生命探索提供理论支持。(3) 基于地球熔岩洞穴,探索微生物膜中微生物之间的相互作用、能量代谢以及抵抗不良环境的机制,以期明晰微生物生存极限及微生物对太空恶劣环境条件的耐受程度。上述三方面的研究成果都将服务于探索地外生命的人类发展目标,为寻找并打造地外新家园的生命蓝图建立坚实的生物学理论及实践基础。

参考文献

[1] CHYBA CF, HAND KP. Astrobiology: the study of the living universe[J]. Annual Review of Astronomy and Astrophysics, 2005, 43: 31-74.

[2] 林巍, 李一良, 王高鸿, 潘永信. 天体生物学研究进展和发展趋势[J]. 科学通报, 2020, 65(5): 380-391.
LIN W, LI YL, WANG GH, PAN YX. Overview and perspectives of astrobiology[J]. Chinese Science Bulletin, 2020, 65(5): 380-391 (in Chinese).

[3] MARTINS Z, COTTIN H, KOTLER JM, CARRASCO N, COCKELL CS, de la TORRE NOETZEL R, DEMETS R, de VERA JP, D'HENDECOURT L,

EHRENFREUND P, ELSAESSER A, FOING B, ONOFRI S, QUINN R, RABBOW E, RETTBERG P, RICCO AJ, SLENZKA K, STALPORT F, TEN KATE IL, et al. Earth as a tool for astrobiology: a European perspective[J]. Space Science Reviews, 2017, 209(1): 43-81.

[4] WESTALL F, BRACK A. The importance of water for life[J]. Space Science Reviews, 2018, 214(2): 50.

[5] COLEINE C, DELGADO-BAQUERIZO M. Unearthing terrestrial extreme microbiomes for searching terrestrial-like life in the Solar System[J]. Trends in Microbiology, 2022, 30(11): 1101-1115.

[6] SCHOPF JW, KUDRYAVTSEV AB, CZAJA AD, TRIPATHI AB. Evidence of Archean life: stromatolites and microfossils[J]. Precambrian Research, 2007, 158(3/4): 141-155.

[7] JOSEPH RG, PLANCHON O, DUXBURY NS, LATIF K, KIDRON GJ, CONSORTI L, ARMSTRONG RA, GIBSON C, SCHILD R. Oceans, lakes, and stromatolites on Mars[J]. Advances in Astronomy, 2020, 2020: 6959532.

[8] HUANG B, LI DG, HUANG Y, LIU CT. Effects of spaceflight and simulated microgravity on microbial growth and secondary metabolism[J]. Military Medical Research, 2018, 5(1): 18.

[9] OLSSON-FRANCIS K, COCKELL CS. Experimental methods for studying microbial survival in extraterrestrial environments[J]. Journal of Microbiological Methods, 2010, 80(1): 1-13.

[10] LARSEN P, HAMADA Y, GILBERT J. Modeling microbial communities: current, developing, and future technologies for predicting microbial community interaction[J]. Journal of Biotechnology, 2012, 160(1/2): 17-24.

[11] WHITMAN WB, COLEMAN DC, WIEBE WJ. Prokaryotes: the unseen majority[J]. Proceedings of the National Academy of Sciences of the United States of America, 1998, 95(12): 6578-6583.

[12] BARDGETT RD, FREEMAN C, OSTLE NJ. Microbial contributions to climate change through carbon cycle feedbacks[J]. The ISME Journal, 2008, 2(8): 805-814.

[13] CLELAND CE, COPLEY SD. The possibility of alternative microbial life on Earth[J]. International Journal of Astrobiology, 2005, 4(3/4): 165-173.

[14] McKAY DS, GIBSON EK Jr, THOMAS-KEPRTA KL, VALI H, ROMANEK CS, CLEMETT SJ, CHILLIER XDF, MAECHLING CR, ZARE RN. Search for past life on Mars: possible relic biogenic activity in Martian meteorite ALH84001[J]. Science, 1996, 273(5277): 924-930.

[15] THOMAS-KEPRTA KL, CLEMETT SJ, BAZYLINSKI DA, KIRSCHVINK JL, McKAY DS, WENTWORTH SJ, VALI H, GIBSON EK Jr, McKAY MF, ROMANEK CS. Truncated hexa-octahedral magnetite crystals in ALH84001: presumptive biosignatures[J]. Proceedings of the National Academy of Sciences of the United States of America, 2001, 98(5): 2164-2169.

[16] WEISS BP, KIM SS, KIRSCHVINK JL, KOPP RE, SANKARAN M, KOBAYASHI A, KOMEILI A. Magnetic tests for magnetosome chains in Martian meteorite ALH84001[J]. Proceedings of the National Academy of Sciences of the United States of America, 2004, 101(22): 8281-8284.

[17] LÉVEILLÉ RJ, DATTA S. Lava tubes and basaltic caves as astrobiological targets on Earth and Mars: a review[J]. Planetary and Space Science, 2010, 58(4): 592-598.

[18] SCHWIETERMAN EW, KIANG NY, PARENTEAU MN, HARMAN CE, DasSARMA S, FISHER TM, ARNEY GN, HARTNETT HE, REINHARD CT, OLSON SL, MEADOWS VS, COCKELL CS, WALKER SI, GRENFELL JL, HEGDE S, RUGHEIMER S, HU RY, LYONS TW. Exoplanet biosignatures: a review of remotely detectable signs of life[J]. Astrobiology, 2018, 18(6): 663-708.

[19] NORDHEIM TA, HAND KP, PARANICAS C. Preservation of potential biosignatures in the shallow subsurface of Europa[J]. Nature Astronomy, 2018, 2: 673-679.

[20] HORNECK G, WALTER N, WESTALL F, GRENFELL JL, MARTIN WF, GOMEZ F, LEUKO S, LEE N, ONOFRI S, TSIGANIS K, SALADINO R, PILAT-LOHINGER E, PALOMBA E, HARRISON J, RULL F, MULLER C, STRAZZULLA G, BRUCATO JR, RETTBERG P, CAPRIA MT. AstRoMap European astrobiology roadmap[J]. Astrobiology, 2016, 16(3): 201-243.

[21] IMPEY C. Life beyond Earth: how will it first be detected?[J]. Acta Astronautica, 2022, 197: 387-398.

[22] KESZTHELYI L, JAEGER W, McEWEN A, TORNABENE L, BEYER RA, DUNDAS C, MILAZZO M. High Resolution Imaging Science Experiment (HiRISE) images of volcanic terrains from the first 6 months of the Mars Reconnaissance Orbiter Primary Science Phase[J]. Journal of Geophysical Research: Planets, 2008, 113(E4005): 1-25.

[23] 肖龙, 黄俊, 赵佳伟, 赵健楠. 月面熔岩管洞穴探测的意义与初步设想[J]. 中国科学: 物理学 力学 天文学, 2018, 48(11): 87-100.
XIAO L, HUANG J, ZHAO JW, ZHAO JN. Significance and preliminary proposal for exploring the lunar lava tubes[J]. Scientia Sinica Physica, Mechanica & Astronomica, 2018, 48(11): 87-100 (in Chinese).

[24] 宋靖华, 张杨姝禾, 袁焕鑫. 利用熔岩管道建设月球基地的规划设想[J]. 城市建筑, 2019, 16(7): 44-51.
SONG JH, ZHANG YSH, YUAN HX. A tentative plan of lunar base under lava tubes[J]. Urbanism and Architecture, 2019, 16(7): 44-51 (in Chinese).

[25] KEMPE S, AL-MALABEH A. Newly discovered lava tunnels of the AI-Shaam Plateau basalts, Jordan[J]. Geophysical Research Abstracts, 2005, 7(03204): 1-3.

[26] NORTHUP DE, MELIM LA, SPILDE MN, HATHAWAY JJM, GARCIA MG, MOYA M, STONE FD, BOSTON PJ, DAPKEVICIUS MLNE, RIQUELME C. Lava cave microbial communities within mats and secondary mineral deposits: implications for life detection on other planets[J]. Astrobiology, 2011, 11(7): 601-618.

[27] MARSHALL HATHAWAY JJ, GARCIA MG, BALASCH MM, SPILDE MN, STONE FD, DAPKEVICIUS ML, AMORIM IR, GABRIEL R, BORGES PAV, NORTHUP DE. Comparison of bacterial diversity in azorean and hawai'ian lava cave microbial mats[J]. Geomicrobiology Journal, 2014, 31(3): 205-220.

[28] RIQUELME C, RIGAL F, HATHAWAY JJM, NORTHUP DE, SPILDE MN, BORGES PAV, GABRIEL R, AMORIM IR, de LURDES NE, DAPKEVICIUS M. Cave microbial community composition in oceanic islands: disentangling the effect of different colored mats in diversity patterns of Azorean lava caves[J]. FEMS Microbiology Ecology, 2015, 91(12): fiv141.

[29] NORTHUP DE, BARNS SM, YU LE, SPILDE MN, SCHELBLE RT, DANO KE, CROSSEY LJ, CONNOLLY CA, BOSTON PJ, NATVIG DO, DAHM CN. Diverse microbial communities inhabiting ferromanganese deposits in Lechuguilla and Spider Caves[J]. Environmental Microbiology, 2003, 5(11): 1071-1086.

[30] SCHABEREITER-GURTNER C, SAIZ-JIMENEZ C, PIÑAR G, LUBITZ W, RÖLLEKE S. Phylogenetic diversity of bacteria associated with Paleolithic paintings and surrounding rock walls in two Spanish caves (Llonín and La Garma)[J]. FEMS Microbiology Ecology, 2004, 47(2): 235-247.

[31] LAVOIE KH, WINTER AS, READ KJH, HUGHES EM, SPILDE MN, NORTHUP DE. Comparison of bacterial communities from lava cave microbial mats to overlying surface soils from Lava Beds National Monument, USA[J]. PLoS One, 2017, 12(2): e0169339.

[32] TEEHERA KB, JUNGBLUTH SP, ONAC BP, ACOSTA-MAEDA TE, HELLEBRAND E, MISRA AK, PFLITSCH A, RAPPÉ MS, SMITH SM, TELUS M, SCHORGHOFER N. Cryogenic minerals in Hawaiian lava tubes: a geochemical and microbiological exploration[J]. Geomicrobiology Journal, 2018, 35(3): 227-241.

[33] GUTIERREZ-PATRICIO S, OSMAN JR, GONZALEZ-PIMENTEL JL, JURADO V, LAIZ L, CONCEPCIÓN AL, SAIZ-JIMENEZ C, MILLER AZ. Microbiological exploration of the Cueva del Viento lava tube system in Tenerife, Canary Islands[J]. Environmental Microbiology Reports, 2024, 16(2): e13245.

[34] PALMA V, GONZÁLEZ-PIMENTEL JL, JIMENEZ-MORILLO NT, SAURO F, GUTIÉRREZ-PATRICIO S, deLa ROSA JM, TOMASI I, MASSIRONI M, ONAC BP, TIAGO I, GONZÁLEZ-PÉREZ JA, LAIZ L, CALDEIRA AT, CUBERO B, MILLER AZ. Connecting molecular biomarkers, mineralogical composition, and microbial diversity from Mars analog lava tubes[J]. The Science of the Total Environment, 2024, 913: 169583.

[35] ZHU HZ, ZHANG ZF, ZHOU N, JIANG CY, WANG BJ, CAI L, LIU SJ. Diversity, distribution and co-occurrence patterns of bacterial communities in a Karst cave system[J]. Frontiers in Microbiology, 2019, 10: 1726.

[36] YUN Y, WANG HM, MAN BY, XIANG X, ZHOU JP, QIU X, DUAN Y, ENGEL AS. The relationship between pH and bacterial communities in a single Karst ecosystem and its implication for soil acidification[J]. Frontiers in Microbiology, 2016, 7: 1955.

[37] BIAGIOLI F, COLEINE C, DELGADO-BAQUERIZO M, FENG YZ, SAIZ-JIMENEZ C, SELBMANN L. Outdoor climate drives diversity patterns of dominant microbial taxa in caves worldwide[J]. The Science of the Total Environment, 2024, 906: 167674.

[38] FISHMAN CB, BEVILACQUA JG, HAHN AS, MORGAN-LANG C, WAGNER N, GADSON O,

McADAM AC, BLEACHER J, ACHILLES C, KNUDSON C, MILLAN MM, BOWER DM, MUSILOVA M, JOHNSON SS. Extreme niche partitioning and microbial dark matter in a *Mauna loa* lava tube[J]. Journal of Geophysical Research: Planets, 2023, 128(6): e2022JE007283.

[39] O'CONNOR BRW, FERNÁNDEZ-MARTÍNEZ MÁ, LÉVEILLÉ RJ, WHYTE LG. Taxonomic characterization and microbial activity determination of cold-adapted microbial communities in lava tube ice caves from lava beds national monument, a high-fidelity Mars analogue environment[J]. Astrobiology, 2021, 21(5): 613-627.

[40] KOPACZ N, CSUKA J, BAQUÉ M, IAKUBIVSKYI I, GUÐLAUGARDÓTTIR H, KLARENBERG IJ, AHMED M, ZETTERLIND A, SINGH A, TEN KATE IL, HELLEBRAND E, STOCKWELL BR, STEFÁNSSON ÁB, VILHELMSSON O, NEUBECK A, SCHNÜRER A, GEPPERT W. A study in blue: secondary copper-rich minerals and their associated bacterial diversity in Icelandic lava tubes[J]. Earth and Space Science, 2022, 9(5): e02234.

[41] TOMCZYK-ŻAK K, ZIELENKIEWICZ U. Microbial diversity in caves[J]. Geomicrobiology Journal, 2016, 33(1): 20-38.

[42] de MANDAL S, CHATTERJEE R, KUMAR NS. Dominant bacterial phyla in caves and their predicted functional roles in C and N cycle[J]. BMC Microbiology, 2017, 17(1): 90.

[43] CHENG XY, LIU XY, WANG HM, SU CT, ZHAO R, BODELIER PLE, WANG WQ, MA LY, LU XL. USC γ dominated community composition and cooccurrence network of methanotrophs and bacteria in subterranean Karst caves[J]. Microbiology Spectrum, 2021, 9(1): e0082021.

[44] ORTIZ M, LEGATZKI A, NEILSON JW, FRYSLIE B, NELSON WM, WING RA, SODERLUND CA, PRYOR BM, MAIER RM. Making a living while starving in the dark: metagenomic insights into the energy dynamics of a carbonate cave[J]. The ISME Journal, 2014, 8(2): 478-491.

[45] CHEN Y, WU LQ, BODEN R, HILLEBRAND A, KUMARESAN D, MOUSSARD H, BACIU M, LU YH, COLIN MURRELL J. Life without light: microbial diversity and evidence of sulfur- and ammonium-based chemolithotrophy in Movile Cave[J]. The ISME Journal, 2009, 3(9): 1093-1104.

[46] HOSE LD, PALMER AN, PALMER MV, NORTHUP DE, BOSTON PJ, DuCHENE HR. Microbiology and geochemistry in a hydrogen-sulphide-rich Karst environment[J]. Chemical Geology, 2000, 169(3/4): 399-423.

[47] ENGEL AS, MEISINGER DB, PORTER ML, PAYN RA, SCHMID M, STERN LA, SCHLEIFER KH, LEE NM. Linking phylogenetic and functional diversity to nutrient spiraling in microbial mats from Lower Kane Cave (USA)[J]. The ISME Journal, 2010, 4(1): 98-110.

[48] MACALADY JL, JONES DS, LYON EH. Extremely acidic, pendulous cave wall biofilms from the Frasassi cave system, Italy[J]. Environmental Microbiology, 2007, 9(6): 1402-1414.

[49] ENGEL AS, LEE N, PORTER ML, STERN LA, BENNETT PC, WAGNER M. Filamentous "Epsilonproteobacteria" dominate microbial mats from sulfidic cave springs[J]. Applied and Environmental Microbiology, 2003, 69(9): 5503-5511.

[50] WENG MM, ZAIKOVA E, MILLAN M, WILLIAMS AJ, McADAM AC, KNUDSON CA, FUQUA SR, WAGNER NY, CRAFT K, KOBS NAWOTNIAK S, SHIELDS A, BEVILACQUA J, BAI Y, HUGHES SS, GARRY WB, HELDMANN JL, LIM DSS, BUCKNER D, GANT P, JOHNSON SS. Life underground: investigating microbial communities and their biomarkers in Mars-analog lava tubes at craters of the moon national monument and preserve[J]. Journal of Geophysical Research: Planets, 2022, 127(11): 1-30.

[51] GREENING C, GRINTER R. Microbial oxidation of atmospheric trace gases[J]. Nature Reviews Microbiology, 2022, 20: 513-528.

[52] van SPANNING RJM, GUAN QT, MELKONIAN C, GALLANT J, POLERECKY L, FLOT JF, BRANDT BW, BRASTER M, ITURBE ESPINOZA P, AERTS JW, MEIMA-FRANKE MM, PIERSMA SR, BUNDUC CM, UMMELS R, PAIN A, FLEMING EJ, van der WEL NN, GHERMAN VD, SARBU SM, BODELIER PLE, et al. Methanotrophy by a *Mycobacterium* species that dominates a cave microbial ecosystem[J]. Nature Microbiology, 2022, 7: 2089-2100.

[53] MAHAFFY PR, WEBSTER CR, ATREYA SK, FRANZ H, WONG M, CONRAD PG, HARPOLD D, JONES JJ, LESHIN LA, MANNING H, OWEN T, PEPIN RO, SQUYRES S, TRAINER M, TEAM MS, KEMPPINEN O, BRIDGES N, JOHNSON JR, MINITTI M, CREMERS D, et al. Abundance and isotopic composition of gases in the martian atmosphere from the Curiosity rover[J]. Science, 2013, 341(6143): 263-266.

[54] TANS PP, FUNG IY, TAKAHASHI T. Observational contrains on the global atmospheric CO_2 budget[J]. Science, 1990, 247(4949): 1431-1438.

[55] 袁道先. "岩溶作用与碳循环"研究进展[J]. 地球科学进展, 1999, 14(5): 425-432.
YUAN DX. Progress in the study on Karst processes and carbon cycle[J]. Advance in Earth Sciences, 1999, 14(5): 425-432 (in Chinese).

[56] SERRANO-ORTIZ P, ROLAND M, SANCHEZ-MORAL S, JANSSENS IA, DOMINGO F, GODDÉRIS Y, KOWALSKI AS. Hidden, abiotic CO_2 flows and gaseous reservoirs in the terrestrial carbon cycle: review and perspectives[J]. Agricultural and Forest Meteorology, 2010, 150(3): 321-329.

[57] HE ZL, XU MY, DENG Y, KANG S, KELLOGG L, WU LY, van NOSTRAND JD, HOBBIE SE, REICH PB, ZHOU JZ. Metagenomic analysis reveals a marked divergence in the structure of belowground microbial communities at elevated CO_2[J]. Ecology Letters, 2010, 13(5): 564-575.

[58] JONES DS, ALBRECHT HL, DAWSON KS, SCHAPERDOTH I, FREEMAN KH, PI YD, PEARSON A, MACALADY JL. Community genomic analysis of an extremely acidophilic sulfur-oxidizing biofilm[J]. The ISME Journal, 2012, 6(1): 158-170.

[59] 云媛. 喀斯特洞穴系统微生物群落对环境变化的响应：以和尚洞为例[D]. 武汉：中国地质大学博士学位论文, 2018.
YUN Y. The response of microbial community in Karst cave system to environmental changes[D]. Wuhan: Doctoral Dissertation of China University of Geosciences, 2018 (in Chinese).

[60] COWAN DA, FERRARI BC, McKAY CP. Out of thin air? Astrobiology and atmospheric chemotrophy[J]. Astrobiology, 2022, 22(2): 225-232.

[61] JI MK, GREENING C, VANWONTERGHEM I, CARERE CR, BAY SK, STEEN JA, MONTGOMERY K, LINES T, BEARDALL J, van DORST J, SNAPE I, STOTT MB, HUGENHOLTZ P, FERRARI BC. Atmospheric trace gases support primary production in Antarctic Desert surface soil[J]. Nature, 2017, 552: 400-403.

[62] JAKOSKY BM, NEALSON KH, BAKERMANS C, LEY RE, MELLON MT. Subfreezing activity of microorganisms and the potential habitability of Mars' polar regions[J]. Astrobiology, 2003, 3(2): 343-350.

[63] VARNES ES, JAKOSKY BM, McCOLLOM TM. Biological potential of Martian hydrothermal systems[J]. Astrobiology, 2003, 3(2): 407-414.

[64] MAGUIRE WC. Martian isotopic ratios and upper limits for possible minor constituents as derived from Mariner 9 infrared spectrometer data[J]. Icarus, 1977, 32(1): 85-97.

[65] WEBSTER CR, MAHAFFY PR, ATREYA SK, MOORES JE, FLESCH GJ, MALESPIN C, McKAY CP, MARTINEZ G, SMITH CL, MARTIN-TORRES J, GOMEZ-ELVIRA J, ZORZANO MP, WONG MH, TRAINER MG, STEELE A, ARCHER D Jr, SUTTER B, COLL PJ, FREISSINET C, MESLIN PY, et al. Background levels of methane in Mars' atmosphere show strong seasonal variations[J]. Science, 2018, 360(6393): 1093-1096.

[66] THOMPSON MA, KRISSANSEN-TOTTON J, WOGAN N, TELUS M, FORTNEY JJ. The case and context for atmospheric methane as an exoplanet biosignature[J]. Proceedings of the National Academy of Sciences of the United States of America, 2022, 119(14): e2117933119.

[67] KRESS ME, McKAY CP. Formation of methane in comet impacts: implications for Earth, Mars, and Titan[J]. Icarus, 2004, 168(2): 475-483.

[68] SCHINDLER TL, KASTING JF. Synthetic spectra of simulated terrestrial atmospheres containing possible biomarker gases[J]. Icarus, 2000, 145(1): 262-271.

[69] CATLING DC, ZAHNLE KJ, McKAY C. Biogenic methane, hydrogen escape, and the irreversible oxidation of early Earth[J]. Science, 2001, 293(5531): 839-843.

[70] SUN YD, JOACHIMSKI MM, WIGNALL PB, YAN CB, CHEN YL, JIANG HS, WANG LN, LAI XL. Lethally hot temperatures during the Early Triassic greenhouse[J]. Science, 2012, 338(6105): 366-370.

[71] CHEN CS, QIN SF, WANG YP, HOLLAND G, WYNN P, ZHONG WX, ZHOU Z. High temperature methane emissions from Large Igneous Provinces as contributors to Late Permian mass extinctions[J]. Nature Communications, 2022, 13: 6893.

[72] SAUNOIS M, STAVERT A, POULTER B, BOUSQUET P, CANADELL J, JACKSON R, RAYMOND P, DLUGOKENCKY E, HOUWELING S, PATRA P, CIAIS P, ARORA V, BASTVIKEN D, BERGAMASCHI P, BLAKE D, BRAILSFORD G, BRUHWILER L, CARLSON K, CARROL M, CASTALDI S, et al. The global methane budget 2000–2017[J]. Earth System Science Data, 2020, 12(3): 1561-1623.

[73] STAVERT AR, SAUNOIS M, CANADELL JG, POULTER B, JACKSON RB, REGNIER P, LAUERWALD R, RAYMOND PA, ALLEN GH, PATRA PK, BERGAMASCHI P, BOUSQUET P, CHANDRA N, CIAIS P, GUSTAFSON A, ISHIZAWA M, ITO A, KLEINEN T, MAKSYUTOV S, McNORTON J, et al. Regional trends and drivers of the global methane budget[J]. Global Change Biology, 2022, 28(1): 182-200.

[74] TURNER AJ, FRANKENBERG C, KORT EA. Interpreting contemporary trends in atmospheric methane[J]. Proceedings of the National Academy of Sciences of the United States of America, 2019, 116(8): 2805-2813.

[75] BAANI M, LIESACK W. Two isozymes of particulate methane monooxygenase with different methane oxidation kinetics are found in *Methylocystis* sp. strain SC2[J]. Proceedings of the National Academy of Sciences of the United States of America, 2008, 105(29): 10203-10208.

[76] HO A, KERCKHOF FM, LUKE C, REIM A, KRAUSE S, BOON N, BODELIER PLE. Conceptualizing functional traits and ecological characteristics of methane-oxidizing bacteria as life strategies[J]. Environmental Microbiology Reports, 2013, 5(3): 335-345.

[77] TCHAWA YIMGA M, DUNFIELD PF, RICKE P, HEYER J, LIESACK W. Wide distribution of a novel *pmoA*-like gene copy among type II methanotrophs, and its expression in *Methylocystis* strain SC2[J]. Applied and Environmental Microbiology, 2003, 69(9): 5593-5602.

[78] MATTEY DP, FISHER R, ATKINSON TC, LATIN JP, DURRELL R, AINSWORTH M, LOWRY D, FAIRCHILD IJ. Methane in underground air in Gibraltar Karst[J]. Earth and Planetary Science Letters, 2013, 374: 71-80.

[79] FERNANDEZ-CORTES A, CUEZVA S, ALVAREZ-GALLEGO M, GARCIA-ANTON E, PLA C, BENAVENTE D, JURADO V, SAIZ-JIMENEZ C, SANCHEZ-MORAL S. Subterranean atmospheres may act as daily methane sinks[J]. Nature Communications, 2015, 6: 7003.

[80] WEBSTER KD, MIRZA A, DELI JM, SAUER PE, SCHIMMELMANN A. Consumption of atmospheric methane in a limestone cave in Indiana, USA[J]. Chemical Geology, 2016, 443: 1-9.

[81] WEBSTER K, LAGARDE LR, SAUER P, SCHIMMELMANN A, LENNON J, BOSTON P. Isotopic evidence for the migration of thermogenic methane into a sulfidic cave, Cueva de Villa Luz, Tabasco, Mexico[J]. Journal of Cave and Karst Studies, 2017, 79(1): 24-34.

[82] LENNON JT, NGUYỄN-THÙY D, PHẠM TM, DROBNIAK A, TẠ PH, STREIL T, WEBSTER KD, SCHIMMELMANN A. Microbial contributions to subterranean methane sinks[J]. Geobiology, 2017, 15(2): 254-258.

[83] ZHAO R, WANG HM, CHENG XY, YUN Y, QIU X. Upland soil cluster γ dominates the methanotroph communities in the Karst Heshang Cave[J]. FEMS Microbiology Ecology, 2018, 94(12): fiy192.

[84] CHENG XY, WANG HM, ZENG ZL, LI L, ZHAO R, BODELIER PLE, WANG YH, LIU XY, SU CT, LIU SJ. Niche differentiation of atmospheric methane-oxidizing bacteria and their community assembly in subsurface Karst caves[J]. Environmental Microbiology Reports, 2022, 14(6): 886-896.

[85] CHENG XY, ZENG ZL, LIU XY, LI L, WANG HM, ZHAO R, BODELIER PLE, WANG WQ, WANG YH, TUOVINEN OH. Methanotrophs dominate methanogens and act as a methane sink in a subterranean Karst cave[J]. The Science of the Total Environment, 2023, 892: 164562.

[86] WEBSTER KD, SCHIMMELMANN A, DROBNIAK A, MASTALERZ M, ROSALES LAGARDE L, BOSTON PJ, LENNON JT. Diversity and composition of methanotroph communities in caves[J]. Microbiology Spectrum, 2022, 10(4): e0156621.

[87] PRATSCHER J, VOLLMERS J, WIEGAND S, DUMONT MG, KASTER AK. Unravelling the identity, metabolic potential and global biogeography of the atmospheric methane-oxidizing upland soil cluster A[J]. Environmental Microbiology, 2018, 20(3): 1016-1029.

[88] KNIEF C, DUNFIELD PF. Response and adaptation of different methanotrophic bacteria to low methane mixing ratios[J]. Environmental Microbiology, 2005, 7(9): 1307-1317.

[89] TVEIT AT, HESTNES AG, ROBINSON SL, SCHINTLMEISTER A, DEDYSH SN, JEHMLICH N, von BERGEN M, HERBOLD C, WAGNER M, RICHTER A, SVENNING MM. Widespread soil bacterium that oxidizes atmospheric methane[J]. Proceedings of the National Academy of Sciences of the United States of America, 2019, 116(17): 8515-8524.

[90] SCHMID AK, ALLERS T, DiRUGGIERO J. SnapShot: microbial extremophiles[J]. Cell, 2020, 180(4): 818-818.e1.

[91] MERINO N, ARONSON HS, BOJANOVA DP, FEYHL-BUSKA J, WONG ML, ZHANG S, GIOVANNELLI D. Living at the extremes: extremophiles and the limits of life in a planetary context[J]. Frontiers in Microbiology, 2019, 10: 780.

[92] SELENSKY MJ, MASTERSON AL, BLANK JG, LEE SC, OSBURN MR. Stable carbon isotope depletions in lipid biomarkers suggest subsurface carbon fixation in lava caves[J]. Journal of Geophysical Research: Biogeosciences, 2021, 126(7): e2021JG006430.

[93] PERKINS S. Core concept: lava tubes may be havens for ancient alien life and future human explorers[J]. Proceedings of the National Academy of Sciences of the United States of America, 2020, 117(30): 17461-17464.

[94] CARRIER BL, BEATY DW, MEYER MA, BLANK JG, CHOU L, DasSARMA S, des MARAIS DJ, EIGENBRODE JL, GREFENSTETTE N, LANZA NL, SCHUERGER AC, SCHWENDNER P, SMITH HD, STOKER CR, TARNAS JD, WEBSTER KD, BAKERMANS C, BAXTER BK, BELL MS, BENNER SA, et al. Mars extant life: what’s next? conference report[J]. Astrobiology, 2020, 20(6): 785-814.

[95] ALLWOOD AC, GROTZINGER JP, KNOLL AH, BURCH IW, ANDERSON MS, COLEMAN ML, KANIK I. Controls on development and diversity of Early Archean stromatolites[J]. Proceedings of the National Academy of Sciences of the United States of America, 2009, 106(24): 9548-9555.

[96] HOFMANN HJ, GREY K, HICKMAN AH, THORPE RI. Origin of 3.45 Ga coniform stromatolites in warrawoona group, western Australia[J]. Geological Society of America Bulletin, 1999, 111(8): 1256-1262.

[97] WALTER MR, BUICK R, DUNLOP JSR. Stromatolites 3 400–3 500 Myr old from the North Pole area, Western Australia[J]. Nature, 1980, 284(5755): 443-445.

[98] UCKERT K, CHANOVER NJ, GETTY S, VOELZ DG, BRINCKERHOFF WB, MCMILLAN N, XIAO XF, BOSTON PJ, LI X, McADAM A, GLENAR DA, CHAVEZ A. The characterization of biosignatures in caves using an instrument suite[J]. Astrobiology, 2017, 17(12): 1203-1218.

[99] SENATORE G, MASTROLEO F, LEYS N, MAURIELLO G. Effect of microgravity & space radiation on microbes[J]. Future Microbiology, 2018, 13: 831-847.

[100] DEMETS R, SCHULTE W, BAGLIONI P. The past, present and future of Biopan[J]. Advances in Space Research, 2005, 36(2): 311-316.

[101] HARBOE-SORENSEN R, MEIJER H, RONNET JC, DEMETS R, ADAMS L, HEINRICH W, ROCHER H. BIOPAN-flight experiment “card”[J]. IEEE Transactions on Nuclear Science, 1994, 41(6): 2340-2345.

[102] RETTBERG P, RABBOW E, PANITZ C, HORNECK G. Biological space experiments for the simulation of Martian conditions: UV radiation and Martian soil analogues[J]. Advances in Space Research, 2004, 33(8): 1294-1301.

[103] HORNECK G, RETTBERG P, REITZ G, WEHNER J, ESCHWEILER U, STRAUCH K, PANITZ C, STARKE V, BAUMSTARK-KHAN C. Protection of bacterial spores in space, a contribution to the discussion on panspermia[J]. Origins of Life and Evolution of the Biosphere, 2001, 31(6): 527-547.

[104] HORNECK G, MOELLER R, CADET J, DOUKI T, MANCINELLI RL, NICHOLSON WL, PANITZ C, RABBOW E, RETTBERG P, SPRY A, STACKEBRANDT E, VAISHAMPAYAN P, VENKATESWARAN KJ. Resistance of bacterial endospores to outer space for planetary protection purposes: experiment PROTECT of the EXPOSE-E mission[J]. Astrobiology, 2012, 12(5): 445-456.

[105] BAQUÉ M, de VERA JP, RETTBERG P, BILLI D. The BOSS and BIOMEX space experiments on the EXPOSE-R2 mission: endurance of the desert cyanobacterium *Chroococcidiopsis* under simulated space vacuum, Martian atmosphere, UVC radiation and temperature extremes[J]. Acta Astronautica, 2013, 91: 180-186.

[106] COTTIN H, RETTBERG P. EXPOSE-R2 on the international space station (2014-2016): results from the PSS and BOSS astrobiology experiments[J]. Astrobiology, 2019, 19(8): 975-978.

[107] BANERJEE S, JOSHI SR. Insights into cave architecture and the role of bacterial biofilm[J]. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences, 2013, 83(3): 277-290.

[108] PORTILLO MC, GONZALEZ JM. Differential effects of distinct bacterial biofilms in a cave environment[J]. Current Microbiology, 2010, 60(6): 435-438.