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Advances in microbial degradation of skatole: A review

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ABSTRACT

In recent years, foul odors have led to widespread public complaints and have become a prominent issue in the field of environmental protection. Skatole, as one of the important components of foul odors, is a decomposition product of tryptophan in the intestines of animals and is mainly found in animal feces. Skatole not only has significant pulmonary toxicity to animals but also poses potential carcinogenic risks to humans. The biological method of removing skatole has the notable advantages of being cost-effective, efficient, and environmentally friendly. However, current research on the microbial degradation of skatole is still insufficient, the metabolic pathways for microbial degradation of skatole are not yet fully elucidated, and there is a lack of research on the functional genes involved in degradation. This review outlines skatole's production and distribution in solid, liquid, and gas media, identifies microorganisms capable of skatole degradation, and examines the microbial degradation mechanisms and influencing factors. Additionally, we summarize the hydroxyindole oxidative ring-opening pathway for skatole degradation in anaerobic conditions and multiple aerobic pathways, including oxidative ring-opening and ring-cleaving. Catechol 1,2-dioxygenase is proposed as a key enzyme in the downstream metabolism of microbial skatole degradation, offering guidance for future research.

1. Introduction

Skatole, known as 3-methylindole (3MI), is one of the key substances causing odor problems and large-scale intensive production has led to massive livestock and poultry manure accumulation, environmental issues like air pollution, threaten human health (Hayes et al., 2014).

Skatole has a low odor threshold, emitting an unpleasant smell even at low concentrations. Studies have shown that the ODT (Odor Detection Threshold) value of skatole in the air of sewage treatment plants is 0.327 ng/L, and the C/ODT ratio of skatole is about 2.8 to 22.5, making it the primary substance responsible for the odor of manure (Zhou et al., 2016a). This compound is a main source of fecal odor in various environments. Currently, numerous studies have found that skatole causes boar taint, induces acute pulmonary edema and emphysema in ruminants, has pulmonary toxicity to humans, and may potentially be a carcinogen for the lungs (Carlson et al., 1972; Yost, 1989; Bray et al., 1990; Walstra et al., 1999). The study by Tittsler et al. (1935) showed that skatole (16–33 mg/L) inhibits the growth of microorganisms like Gram-negative bacteria *Salmonella, Ebuncleia, Shigella*, and *Escherichia*. It also affects the homeostasis of the intestinal microbiota. Moreover, skatole increases endogenous oxidative stress, damaging bacterial cell membranes and reducing bacterial survival rates (Choi et al., 2014).

Skatole, a pervasive pollutant in environmental systems, poses significant challenges due to its malodorous nature and persistent impact on soil and aquatic ecosystems. The presence of skatole not only generates offensive odors that contribute to atmospheric contamination but also induces long-term pollution of soil and water bodies, affecting ecological health and human well-being. Degrading skatole is challenging, particularly at high concentrations. Despite its widespread occurrence and adverse effects, current knowledge on the effective management of skatole remains limited, particularly in terms of sustainable and eco-friendly solutions. Physical approaches, such as

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masking and dilution-diffusion, are commonly used but have the drawback of failing to completely eliminate skatole, leaving its hazards unresolved. Chemical treatments, including burning, oxidation, and absorption, often require substantial energy or incur high costs and carry the risk of secondary pollution. In contrast, biological treatments offer a more sustainable solution. Techniques such as biofilters, bio-scrubbers, bio-drip filters, and activated sludge diffusion reactors utilize microorganisms to biodegrade skatole effectively. These methods are eco-friendly, cost-efficient, safer, and result in less secondary pollution compared to traditional chemical and physical approaches (Lebrero et al., 2011; Talaiekhozani et al., 2016). Microbial degradation of skatole has emerged as a promising strategy to address these challenges. By leveraging the metabolic capabilities of specific microorganisms, skatole can be effectively controlled through dual mechanisms: source inhibition of its biosynthesis and subsequent biodegradation into non-toxic, odorless compounds. This approach offers multifaceted environmental benefits. Firstly, it eliminates malodors while simultaneously enhancing the health of aquatic and soil ecosystems by reducing skatole-related ecological impacts. Notably, microbial degradation exhibits exceptional environmental compatibility, ensuring the complete elimination of skatole contamination without generating secondary pollutants. This not only addresses the immediate issue of odor emission but also establishes an eco-sustainable solution for long-term environmental management.

Despite these potential advantages, several knowledge gaps remain in the field of microbial skatole degradation. These include the limited understanding of the specific microbial taxa and metabolic pathways involved, as well as the lack of optimized strategies for large-scale application. Addressing these gaps is crucial for advancing microbial remediation as a viable and effective solution for skatole pollution.

2. Distribution and production of skatole

Skatole, a nitrogen-containing heterocyclic aromatic compound (C_9H_9 N), is known for its volatility and moderate toxicity (Ma et al., 2021). It dissolves in hot water, alcohol, benzene, chloroform, and ether. Naturally, skatole is found in sugar beet roots, and coal tar. It is also detected in the intestines and feces of animals, activated sludge, municipal wastewater, industrial wastewater, and aquaculture water (Lebrero et al., 2011; Zgarbová and Vrzal, 2023). Low skatole concentrations can be found in plants like jasmine, making it a component in producing essential oils and perfumes (Zgarbová and Vrzal, 2023). The primary source of high concentrations of skatole is the anaerobic fermentation and decomposition of l-tryptophan by microorganisms in the rumen of ruminants and the cecum and colon of monogastric animals (Wesoly and Weiler, 2012).

2.1. Distribution of skatole in the environment

Skatole, predominantly biosynthesized in livestock and human intestines, exhibits significant environmental accumulation linked to intensive farming (Fig. 1). Quantitative analyses reveal species-specific fecal concentrations: 10.0–15.9 mg/kg in humans, 9.9–26.6 mg/kg in pigs, and 0.5–5.1 mg/kg in ruminants (Dehnhard et al., 1991). Anaerobic livestock waste lagoons average 10 mg/L (Szogi et al., 2018), with Korean pig farm manure ponds reaching 100.6 μg/L (Song, 2024). Environmental monitoring demonstrates skatole's pervasive presence across multiple matrices: municipal sludge (373 ± 34 μg/kg, Byliński et al., 2019), alpine sediments (0.9–212 μg/kg, Battaglin et al., 2018), and wastewater (peak 700 mg/L, Zhou et al., 2016a).

Skatole contamination is significantly amplified in wastewater treatment systems, with influent concentrations reaching 700 mg/L (Zhou et al., 2016a) and residual levels persisting at 640 μg/L in effluent (Hwang et al., 1995), revealing insufficient removal efficiency. In aquaculture ecosystems, feed modification induces skatole bioaccumulation in fish tissue (Zhou et al., 2016b; Mahmoud et al., 2018), with detectable levels in rainbow trout culture water (Mahmoud and Buettner, 2016). Atmospheric monitoring identifies spatial variability: 0.12–0.3 μg/m^3 in livestock facilities (Trabue et al., 2011; Van Huffel et al., 2012), 0.3–1.5 ppbv near composting plants (Gonzáleza et al., 2018), and 0.06–0.24 μg/m^3 in public restrooms (Chappuis et al., 2015). Anthropogenic sources include tobacco combustion (0.4–16 μg/cigarette, Wynder and Hoffmann, 1968) and food processing byproducts (liquor: 4.4–142.8 μg/L, Dong et al., 2018). Notably, oral microbiota-mediated conversion of indoleacetic acid suggests potential salivary origins (Mishiro et al., 1969; Olsen et al., 1991). This multi-source dissemination pattern necessitates targeted mitigation strategies to address skatole's environmental persistence.

2.2. Mechanisms and contributing factors to skatole production

In addition to naturally occurring in plants, skatole is primarily derived from the microbial decomposition of tryptophan in the intestines of animals. The synthesis of skatole in the intestines involves multiple enzymatic steps, as depicted in Fig. 2 (Deslandes et al., 2001). Initially, tryptophanase converts tryptophan into indole-3-pyruvic acid. Subsequently, decarboxylase catalyzes the conversion of indole 3-pyruvic acid into indole 3-acetaldehyde, which is subsequently transformed into indole-3-acetic acid by indole-3-acetaldehyde dehydrogenase. Ultimately, indole-3-acetic acid undergoes decarboxylation by indole-3-acetic acid decarboxylase, resulting in the formation of skatole (Koga et al., 1992; Deslandes et al., 2001; Whitehead et al., 2008; Russell et al., 2013; Liu et al., 2018a; Roager and Licht, 2018). Moreover, research showed that a strain of *Lactobacillus* sp. isolated from cow

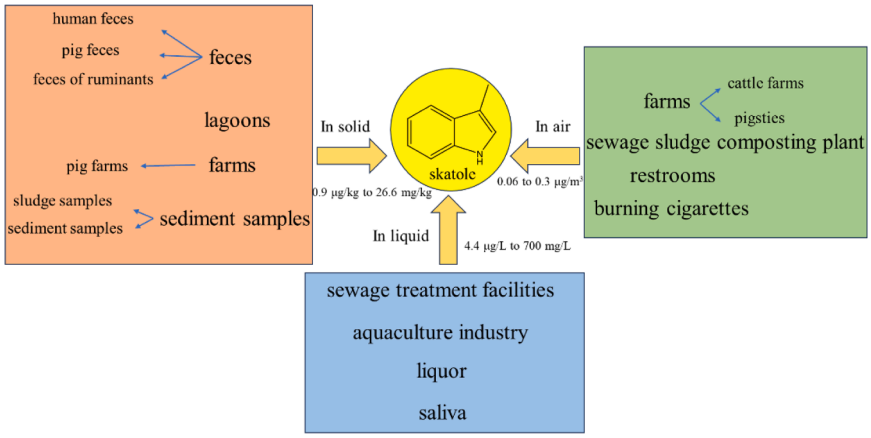

Fig. 1. Distribution of skatole in the environment.

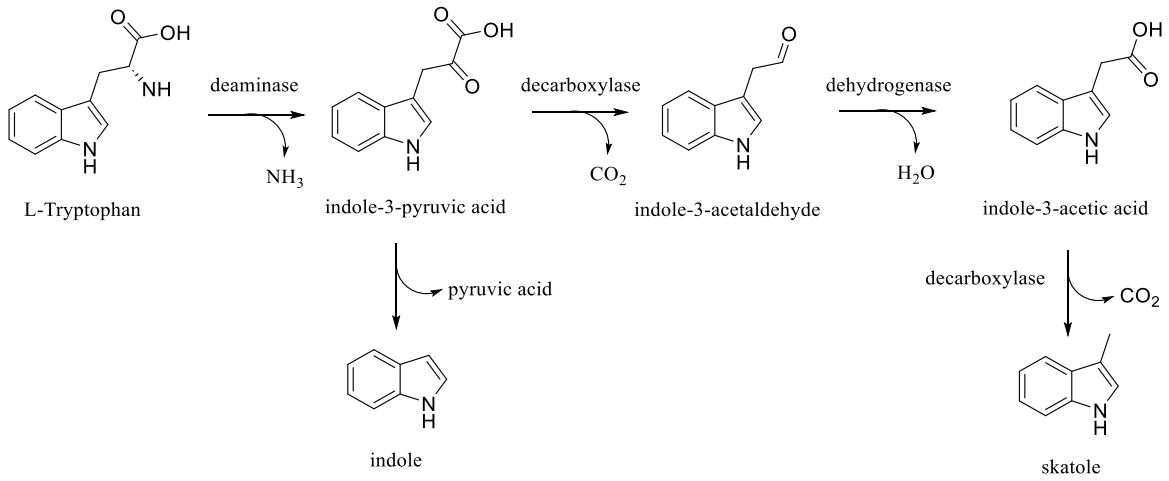

Fig. 2. Pathway of skatole production in the gut (Deslandes et al., 2001).

rumen fluid can decarboxylate indole-3-acetic acid to produce skatole, although it cannot directly utilize tryptophan for skatole production (Yokoyama et al., 1977). *Olsenella scatoligenes* sp. nov., isolated from pig feces, efficiently metabolizes indole-3-acetic acid to generate skatole (Li et al., 2015). Additionally, *Lysinibacillus xylanilyticus*, isolated from contaminated soil, was capable of converting indole to skatole, with the proposed pathway involving the decarboxylation of indole to skatole through intermediates such as indole-3-acetamide and indole-3-acetic acid (Arora et al., 2015). Among four strains isolated from the rumen of sheep and dairy cattle, *Clostridium sporogenes* was found to metabolize tryptophan to skatole, although this process was inhibited by glucose. *Clostridium aminophilum* and M*egasphaera elsdenii* can produce both indole and skatole, while *Actinomyces meyeri* can form indole-3-acetic acid from tryptophan, ultimately leading to skatole production (Attwood et al., 2006).

Numerous studies indicate that adding oligosaccharides or beneficial microbes, either alone or in combination, to animal diets can help reduce skatole production. For example, Okrouhlá et al. (2020) reported that incorporating *Helianthus tuberosus* L. into animal feed decreased skatole concentrations in adipose tissues, likely due to a reduction in skatole-producing bacteria in the gastrointestinal tract. In contrast, Doerner et al. (2009) observed that the addition of Fe (III) to the mixed pig lagoon sediments significantly increased skatole concentrations. Ding et al. (2021) revealed that supplementing diets with *Bacillus subtilis* and *xylo-oligosaccharides* significantly reduced intestinal skatole concentrations, primarily affecting *Firmicutes* and *Bacteroidetes*, while increasing *Bifidobacteria* populations. Furthermore, research has shown that the inclusion of a selenized glucose (SeGlu) has the potential to decrease skatole production by modifying the composition and abundance of gut microbiota, promoting the proliferation of advantageous microorganisms, and inhibiting possible pathogenic bacteria (Zeng et al., 2024). SeGlu was found to significantly impact the relative abundance of *Treponema, Bacteroides*, and *Ruminococcus* (Zeng et al., 2024). Additionally, incorporating itaconic acid into diets has been shown to lower the skatole levels in the chicken cecum, with intestinal flora analysis revealing correlations between changes in cecal flora and skatole concentrations. Skatole production was negatively correlated with *Firmicutes, Ruminococcus*, and *Clostridium*, whereas it was positively correlated with *Bacteroidetes* and *Shigella* (Zhu et al., 2023). The investigation by Cook et al. (2007) demonstrated a correlation between increased *Bacteroidetes* levels in swine fecal lagoons and elevated skatole concentrations. Other research highlighted the role of *lactobacilli* in skatole generation within the intestinal microbiota of broiler chickens, with Yang et al. (2019) observing higher skatole concentrations in the cecum compared to the rectum and ileum, which corresponded with higher microbial density in the cecum. This research suggests a strong correlation between skatole levels, gut microbiota composition, and fermentation patterns. The study of Hu et al. (2002) showed that pH influences the degradation of tryptophan into skatole or indole, with low pH favoring indole production and high pH favoring skatole production. Therefore, adjusting pH levels could help control the relative production of indole and skatole. In pig manure lagoons, skatole concentrations were higher at the surface (54 μg/L) compared to deeper layers (38 μg/L at the lowest depth and 24 μg/L in the middle), likely due to differences in oxygen distribution (Loughrin et al., 2008). In summary, skatole production is influenced by intestinal flora composition, pH levels, and oxygen availability, with bacteria such as *Bacteroidetes* playing a key role in this process.

3. Microorganisms and mechanisms for skatole degradation

Since skatole is primarily produced in the intestines, inhibiting its production at the source is challenging. As a result, controlling skatole emissions has traditionally relied on physical and chemical methods. In recent years, biological methods have gained considerable attention due to their cost-effectiveness and environmental benefits. Currently, biological methods for skatole removal include biofilters, bio-scrubbers, bio-drip filters, and activated sludge diffusion reactors. The effectiveness of biological processes in skatole removal largely depends on the microorganisms capable of degrading skatole. Consequently, many studies are focused on identifying efficient skatole-degrading microorganisms.

3.1. Microorganisms capable of degrading skatole in anaerobic conditions

Anaerobic environments, such as those found in anaerobic lagoons and deep soils, provide conditions conducive to the microbial degradation of skatole. However, research on the anaerobic microbial degradation of skatole is relatively limited (Table 1). The earliest study on anaerobic microorganisms degrading skatole dates back to 1986, when a sulfate-reducing bacterium capable of completely degrading 2 mM skatole within four weeks was discovered (Bak and Widdel, 1986). Subsequently, in 1991, a methanogenic consortium isolated from wetland soil was shown to degrade both indole and skatole (Gu and Berry, 1991). The following year, Gu and Berry (1992) confirmed that the methanogenic consortium could completely degrade 0.1 mM skatole within 35 days. In 1997, Kohda et al. (1997) isolated and characterized three strains of skatole-degrading *Clostridium* from animal manure compost. The *Clostridium* strains could degrade 100–300 mg/L of skatole, albeit with a growth lag of 70 h. After four weeks of incubation, *C. aminovalericum* A-4, *C. carnis* A1–6, and *C. malenominatum* A-3 exhibited degradation rates of 6.25 %, 10.24 %, and 32.18 %,

Table 1
Microorganisms that degrade skatole in anaerobic conditions.

Strains		Source	Degradation effect	References
Sulfate-reducing bacteria	G^-	Marine sediments	4 w, 2 mM	(Bak and Widdel, 1986)
Methanogenic complexes	G^-	Wetland soils	35 d, 0.1 mM	(Gu and Berry, 1992)
C. malenominatum A-3	G^+	Animal manure composting	4 w, 100–300 mg/L, degradation rate was 32.18 %	(Kohda et al., 1997)
Facultative anaerobic agent Y		septic tank	48 h, 80 mg/L, degradation rate was 88.52 %	(Ye and Fu, 2023)
Acinetobacter xiamenensis	G^-	Facultative anaerobic agent Y	72 h, 80 mg/L	(Ye and Fu, 2023)

respectively. Recent studies have identified a strain capable of degrading skatole, isolated from a facultative anaerobic agent Y, and identified it as *Acinetobacter*, with 98.29 % homology to *Acinetobacter xiamenensis* (Ye and Fu, 2023). Strain Ya was able to completely degrade 80 mg/L of skatole within 72 h, while agent Y achieved an 88.52 % degradation rate within 48 h. Zhang et al. (2023) isolated a facultative anaerobic strain, *Weissella cibaria* ZWC030, which exhibited the lowest residual skatole levels at a pH of 4.5.

3.2. Microorganisms capable of degrading skatole in aerobic conditions

Research on aerobic microbial degradation of skatole primarily focuses on Gram-negative bacteria such as *Pseudomonadota* and *Proteobacteria* (Table 2). Genera such as *Pseudomonas, Burkholderia*, and *Rhodococcus* have been proven to play significant roles in the degradation of organic pollutants like polycyclic aromatic hydrocarbons. In 2006, Yin et al. (2006) isolated a strain of *Pseudomonas aeruginosa* from mangrove sediment, which could completely degrade skatole at concentrations <2.5 mM within three days, bringing attention to the study of skatole degradation under aerobic conditions. Li et al. (2010) screened a strain of *Pseudomonas putida* LPC24 from a UASB reactor treating piggery wastewater, which could completely degrade 2 mM skatole under microaerobic conditions within 30 days. Subsequently, Meng et al. (2013) studied the degradation of skatole by *Lactobacillus*. They identified four skatole-degrading strains: L*actobacillus brevis* 1.12, L. *plantarum* 102, L. *casei* 6103, and L. *plantarum* ATCC 8014. When the skatole concentration was 1 μg/ml, the degradation rates of the four strains after 24 h were 17.43 %, 0.88 %, 3.48 %, and 5.5 %, respectively, and after 120 h, the degradation rates were 65.35 %, 28.54 %, 52.15 %, and 33.23 %, respectively. Fukuoka et al. (2015) isolated a strain of *Cupriavidus* sp. strain KK10 from the soil, which could completely degrade 100 mg/L skatole within 24 h. The same year, Sharma et al. (2015) screened a strain of purple non-sulfur bacteria, *Rhodopseudomonas palustris* WKU-KDNS3, from an animal manure lagoon, which degraded over 48 % of 1 mM skatole within 72 h and over 93 % after 21 days. Tesso et al. (2019) identified two skatole-degrading strains from activated sludge: *Acinetobacter toweneri* NTA1–2A and *Acinetobacter guillouiae* TAT1–6A. These strains achieved degradation rates of 50 %−85 % when cultured for six days with skatole concentrations <200 mg/L, and degradation rates of 84.32 % and 81.39 % respectively, when cultured for eight days at a skatole concentration of 65 mg/L. Ma et al. (2020a) identified a strain, *Burkholderia* sp. IDO3 could completely degrade 50 mg/L skatole within 24 h at an inoculum level of 1 %. Concurrently, Ma et al. (2020b) examined two strains, *Rhodococcus* DMU1 and DMU2, utilizing an activated sludge system capable of fully decomposing 50 mg/L skatole within 24 h. Wu et al. (2021) screened a strain of *Rhodococcus pyridinivorans* Rp3, which could completely degrade 50 mg/L skatole within 24 h and achieved a degradation rate of 98.4 % for 100 mg/L skatole within 48 h. Hu et al. (2022) discovered

Table 2
Microorganisms degrade skatole in aerobic conditions.

Strains		Source	Degradation effect	References
Pseudomonas aeruginosa Gs	G^-	Mangrove sediments	3 d, <2.5 mM	(Yin et al., 2006)
Pseudomonas putida LPC24	G^-	Pig barn wastewater	30 d, 2 mM	(Li et al., 2010)
L. *brevis* 1.12 (L. *brevis* 1.12)	G^+		1 μg/ml, 24 h, degradation rate was 17.43 %, 120 h, degradation rate was 65.35 %	(Meng et al., 2013)
Cupriavidus sp. Strain KK10	G^-	soil	24 h, 100 mg/L	(Fukuoka et al., 2015)
Rhodopseudomonas palustris WKU-KDNS3	G^-	Animal manure lagoon	1 mM, 72 h, >48 %, 21 d, >93 %	(Sharma et al., 2015)
Acinetobacter toweneri NTA1–2A, *Acinetobacter guillouiae* TAT1–6A	G^-	Chicken manure	<200 mg/L, 6 d, 50–85 % 65 mg/L, 8 d, 84.32 %,81.39 %	(Tesso et al., 2019)
Burkholderia sp. IDO3	G^-	Activated sludge	24 h, 50 mg/L, inoculum amount was 1 %	(Ma et al., 2020a)
Rhodococcus DMU1, DMU2	G^+	Animal manure	24 h, 50 mg/L	(Ma et al., 2020b)
Rhodococcus pyridinophilus Rp3	G^+	Sheep manure composting	24 h, 50 mg/L; 48 h, 100 mg/L, degradation rate was 98.4 %	(Wu et al., 2021)
Acinetobacter oleivorans AO-06	G^-	Pig manure	48 h, 100 mg/L	(Hu et al., 2022)
Rhodococcus gordoniae YKSW-6	G^+		14 h, 100 mg/L	(Zhang et al., 2022)
Lactobacillus casei		intestines	100 mg/L, 168 h, degradation rate was 62.21 %	(Zhuang et al., 2022)
Aerobic agent H		septic tank	48 h, 80 mg/L, degradation rate was 22.39 %	(Ye and Fu, 2023)
Bacillus pallius		chicken manure	10 mg/L, 24 h, degradation rate was 44.5 %	(Xu et al., 2023)
Bacillus subtilis, Pseudomonas toyotomiensis, Priestia aryabhattai, and *Burkholderia contaminans*		sheep rumen fluid	100 mg/L, 48 h, degradation rate was 23.03 %, 20 %, 20 %, and 13.14 %, respectively	(L. Wang et al., 2024)

Acinetobacter oleivorans AO-06, a strain that breaks down skatole, in pig stool, capable of fully decomposing 100 mg/L of skatole in under 48 h. Zhang et al. (2022) examined *Rhodococcus gordoniae* YKSW-6, a strain found in pig manure compost, known for its effectiveness in breaking down 100 mg/L skatole over a span of 14 h. Zhuang et al. (2022) isolated a strain of *Lactobacillus casei* from the intestines of healthy children aged 3–8 years, which could degrade 100 mg/L skatole with a degradation rate of 62.21 % within 168 h. In 2023, research obtained an aerobic agent H, which degraded 80 mg/L skatole with a degradation rate of 22.39 % within 48 h (Ye and Fu, 2023). Xu et al. (2023) screened a strain of *Bacillus pallidus* from chicken manure, which degraded 10 mg/L skatole with a degradation rate of 44.5 % within 24 h. L. Wang et al. (2024) isolated 11 skatole-degrading strains from sheep rumen fluid, including 2 strains of *Bacillus subtilis*, 4 strains of *Priestia aryabhattai*, 2 strains of *Burkholderia contaminans*, and 3 strains of *Pseudomonas toyotomiensis*. These strains degraded 100 mg/L skatole within 48 h, with *Bacillus subtilis* achieving the highest degradation rate of 23.03 %, *Pseudomonas toyotomiensis* and *Priestia aryabhattai* about 20 %, and *Burkholderia contaminans* at 13.14 %. Additionally, Omarini et al. (2022) discovered seven *Basidiomycota* fungal strains capable of degrading 0.3

μg/ml skatole, with <20 % residual skatole after 7 days of cultivation.

3.3. Bacterial communities involved in skatole degradation

A study found that microorganisms extracted from chicken and pig manure compost fermentation systems could degrade 30 mg/L skatole by 9.0–20.4 % (Nakai et al., 1999). Facultative anaerobic Gram-positive cocci, aerobic Gram-positive cocci, and facultative anaerobic Gram-positive endospore-forming rods were detected in these compost systems. Ma et al. (2020b) collected manure samples from cattle and geese, enriched skatole-degrading bacteria in a bioreactor, and found that these microbial communities had the capability to decompose skatole within 70 days. Through an analysis of community diversity and abundance, the researcher observed a notable decrease in *Lactococcus, Pseudomonas*, and *Flavobacterium* levels, with *Arthrobacter* becoming the prevalent species. Furthermore, Qu et al. (2020) established a skatole-degrading activated sludge system from porcine slurry and divided the incubation process into two separate phases. During the initial phase (1–20 days) with a skatole concentration of 10 mg/L, the activated sludge system completely degraded the skatole within 5 days. During the second phase (21–40 days) with a skatole concentration of 50 mg/L, skatole degradation occurred within 3 days. At the end of the incubation, *Arthrobacter* and *Fusicolla* emerged as the primary genera within the system. Macro-genomic and macro-transcriptomic analyses by Ma et al. (2023) revealed that *Rhodococcus* and *Pseudomonas* were the dominant active genera in the skatole-degrading community. Ma et al. (2020a) added *Burkholderia* sp. IDO3, a strain proficient in skatole degradation, to an activated sludge system lacking skatole-degrading capacity. This integration facilitated the complete removal of 100 mg/L of skatole within 12 h. The system maintained its efficient skatole degradation capacity throughout the following 24 days. Ye and Fu (2023) isolated skatole-degrading microorganisms by screening cultures of microbial agents H and Y. The microbial agents H, Y, *Lactobacillus rhamnosus*, and *Saccharomyces cerevisiae* were combined into a deodorizer with a 1:1:1:1 vol ratio. The composite deodorizer was added to aged and fresh human feces for anaerobic fermentation, resulting in significant skatole reduction in aged feces. After fermentation, *Acinetobacter* levels significantly increased in aged feces, while *Lactobacillus* became the dominant genus in fresh feces. Ma et al. (2023) also conducted metagenomic and metatranscriptomic analyses, confirming that *Rhodococcus* and *Pseudomonas* were the main active genera in skatole-degrading microbial communities. The study of Nakai et al. (1999) suggested that skatole-degrading microorganisms are primarily present in mesophilic microbial communities during composting. However, they did not detect Gram-negative bacteria, actinomycetes, or fungi at any stage in chicken and pig manure composting systems, despite currently known skatole-degrading bacteria being Gram-negative. According to microbial metabolomics research, most literature indicated that after the complete degradation of skatole, *Actinobacteria* became the predominant species, potentially involved in the degradation process.

4. Microbial pathways for skatole degradation

4.1. Anaerobic metabolic pathways

Research on anaerobic fermentation of indole-degrading methanogenic consortia identified 3-methyloxindole as a metabolite (Gu and Berry, 1992). Their findings confirmed that skatole cannot serve as a carbon and energy source for methanogens, indicating that the degradation pathway of skatole does not involve the hydroxy indole-indigo pathway. In a related study, Gu et al. (2002) examined methane-producing and sulfate-reducing bacteria isolated from marine sediments. Under methanogenic conditions, skatole was oxidized exclusively at the 2-position to yield 3-methyloxindole. Conversely, under sulfate-reducing conditions, the pyrrole ring of 3-methyloxindole was cleaved between the heterocyclic nitrogen atom and the adjacent 2-position carbon, leading to the formation of α-methyl-2--aminobenzeneacetic acid. This intermediate was eventually fully degraded to CO_2 and H_2S. The proposed anaerobic degradation pathway of skatole is depicted in Fig. 3 (Gu et al., 2002).

4.2. Aerobic metabolic pathways

Yin et al. (2006) identified indole-3-carboxylic acid and indole-3-ol as intermediates in skatole degradation by *Pseudomonas aeruginosa*. Subsequent studies revealed diverse degradation pathways: Li et al. (2010) proposed a 3-methylindole metabolic pathway involving formyl anthranilic acid and anthranilic acid in *Pseudomonas putida* LPC24, while observing C2/C3 hydroxylation and pyrrole ring cleavage. Fukuoka et al. (2015) confirmed pyrrole ring cleavage in *Cupriavidus* sp. KK10, excluding the indigo degradation pathway. Tesso et al. (2019) reported novel metabolites including β-alanine betaine from *Acinetobacter* strains. Mechanistic analyses showed skatole inhibits ATP synthesis but induces 192 oxidoreductases in *Burkholderia* sp. IDO3, suggesting catechol pathway involvement (Ma et al., 2020a). Multiple strains exhibited distinct intermediates: *Acinetobacter oleivorans* AO-06 produced phenylacetic acid derivatives (Hu et al., 2022), while *Rhodococcus gordoniae* YKSW-6 generated phenylacetaldehyde and N-(2-acetylphenyl) formamide via sequential C2 oxidation (Zhang et al., 2022). Genetic studies on *Rhodococcus* DMU1 revealed skatole metabolism employs flavoprotein monooxygenases upstream and catechol 1,2-dioxygenase downstream, with enzymatic confirmation of ortho-cleavage pathways (Li et al., 2023a; Ma et al., 2023). This catechol cleavage mechanism appears conserved across species, including *Burkholderia* sp. IDO3 (Li et al., 2023b).

The results of the above studies collectively demonstrated that microbial degradation of skatole typically follows a specific metabolic pathway. Typically, this process begins with oxidation at the C2 position and undergoes various transformations, including hydroxylation, carboxylation, and decarboxylation. Furthermore, steps such as oxidative ring-opening or splitting can lead to the removal of the pyrrole ring, ultimately producing CO2 through a multi-stage oxidation process that feeds into the tricarboxylic acid cycle. Studies have suggested that skatole's initial metabolic route likely involves the oxygenase pathway, while its subsequent metabolism proceeds via the catechol pathway, involving catechol 1,2-dioxygenase, which facilitates further oxidation of the pyrrole ring and a series of complex oxidative breakdowns feeding into the tricarboxylic acid cycle. Interestingly, the findings for *Cupriavidus* sp. diverged from earlier research. Fukuoka et al. (2015) found that when glycerol was the only carbon source, skatole co-metabolism predominantly followed a carbocyclic aromatic ring fission pathway. This discrepancy may be attributed to KK10′s inability to utilize 3-methylindole as a carbon source for growth, as the study did not detect the expected downstream product, salicylic acid. This finding suggests that variations in available carbon sources can lead to divergent degradation pathways in different strains. In conclusion, the aerobic degradation pathway of skatole is hypothesized to align with the proposed pathway illustrated in Fig. 4 (Yin et al., 2006; Li et al., 2010; Fukuoka et al., 2015; Hu et al., 2022; Zhang et al., 2022).

Currently, research on the microbial degradation of skatole is still in its nascent stages, with most studies focusing primarily on the structural dynamics and diversity of microbial communities. The specific regulatory mechanisms, including the roles of transcriptional regulators or operons, remain largely unexplored. Several studies have identified key genes and enzymes associated with skatole degradation in *Burkholderia* and *Rhodococcus* species. These microorganisms exhibit significant upregulation of genes involved in oxidative stress response, ribosomal functions, transporter activity, oxidative phosphorylation, and oxidoreductase activity (Ma et al., 2020a; Li et al., 2023a). The inducibility of these enzymes suggests that the functional genes linked to skatole degradation are tightly regulated, with metabolic pathways being

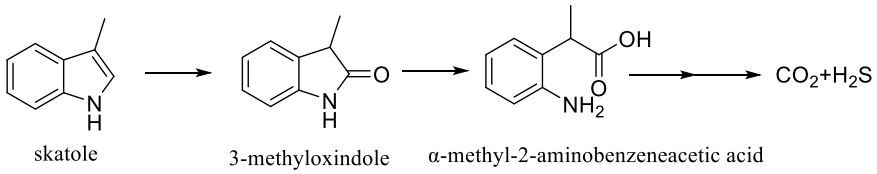

Fig. 3. Anaerobic degradation pathway of skatole (Gu et al., 2002).

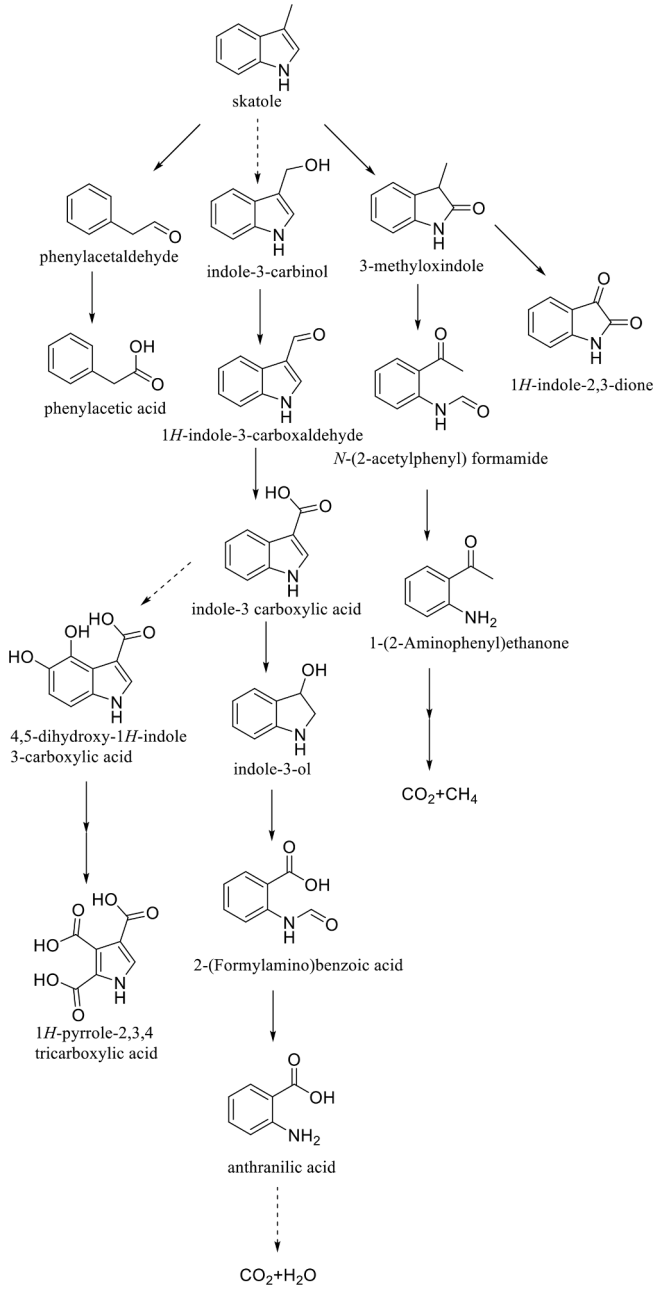

Fig. 4. Aerobic degradation pathway of skatole (Yin et al., 2006; Li et al., 2010; Fukuoka et al., 2015; Hu et al., 2022; Zhang et al., 2022).

activated in response to skatole exposure (Li et al., 2023a). In *Burkholderia*, elevated expression levels have been observed in genes encoding indole oxygenase, phenol hydroxylase, and catechol 1,2-dioxygenase, highlighting their critical roles in skatole catabolism (Ma et al., 2020a). Similarly, a gene cluster in *Rhodococcus* containing novel flavoprotein monooxygenase and cyclohexanol oxidase genes was found to be upregulated during skatole degradation (Li et al., 2023a). Notably, a specific catechol 1,2-dioxygenase gene has been identified as a key functional determinant in skatole degradation, further underscoring its importance in the metabolic pathway (Li et al., 2023a). A study is the identification of specific genes in *Acinetobacter piscicola* p38, such as styrene monooxygenase (ACDW34_08180) and flavin reductase (ACDW34_08185), which are capable of degrading skatole (Z. Wang et al., 2024). These findings suggest that the degradation process may involve complex biochemical pathways requiring specific enzymes and cofactors.

5. Factors influencing microbial degradation of skatole

5.1. Initial skatole concentration

Several studies have demonstrated the detrimental effects of skatole on bacterial biofilm development and its ability to inhibit the growth of a wide range of Gram-negative bacteria. Skatole, at a concentration of 330 mg/L, can effectively inhibit the growth of 25 Gram-negative bacteria isolated from the intestines (Tittsler et al., 1935). Additionally, skatole has the potential to form specific adducts with DNA and is considered a possible carcinogenic and mutagenic compound (Yokoyama and Carlson, 1979; Regal et al., 2001). As such, the initial concentration of skatole imposes certain limitations on the growth of skatole-degrading bacteria (Table 3). For instance, research has shown that a concentration of 400 mg/L of skatole can completely inhibit the growth of L*actobacillus acidophilus*, whereas growth can resume when the concentration is reduced to 100 mg/L (Dreizen and Spies, 1948). Kohda et al. (1997) identified three strains of *Clostridium* that could only grow in a medium with initial skatole concentrations between 100 and 300 mg/L. Yin et al. (2006) found that a strain of *Pseudomonas aeruginosa* could not grow when the initial concentration of skatole exceeded 524 mg/L, underscoring the toxicity of high skatole concentrations to bacteria. At initial concentrations below 327 mg/L, *Pseudomonas putida* LPC24 effectively reduced skatole, but the degradation rate significantly decreased at 458 mg/L, and growth was inhibited at 524 mg/L (Li et al., 2010). Research by Tesso et al. (2019) revealed that increasing skatole

Table 3
Bacterial species capable of tolerating skatole.

Strains	Tolerable skatole concentrations		References
25 Gram-negative bacteria	330 mg/L	Moderately tolerant	(Tittsler et al, 1935)
L. *acidophilus*	100–400 mg/L	Moderately tolerant	(Dreizen and Spies, 1948)
Clostridium	100–300 mg/L	Moderately tolerant	(Kohda et al., 1997)
Pseudomonas aeruginosa	< 524 mg/L	Advanced Tolerance	(Yin et al., 2006)
Pseudomonas putida LPC24	327–524 mg/L	Advanced Tolerance	(Li et al., 2010)
Burkholderia sp. IDO3	< 180 mg/L	sensitive bacteria	(Ma et al., 2020a)
Rhodococcus DMU1	< 200 mg/L	sensitive bacteria	(Li et al., 2023a)
Rhodococcus gordoniae YKSW-6	100–150 mg/L	sensitive bacteria	(Zhang et al., 2022)

concentrations correlated with a reduced degradation rate in two *Acinetobacter* strains. *Burkholderia* sp. IDO3 demonstrated enhanced degradation capabilities at higher skatole concentrations, however, growth was progressively impeded as skatole concentrations increased, ultimately ceasing at 180 mg/L (Ma et al., 2020a). At concentrations higher than 200 mg/L, *Rhodococcus* DMU1′s growth and skatole degradation abilities were compromised (Li et al., 2023a). *Rhodococcus gordoniae* YKSW-6 achieved complete skatole degradation at concentrations below 100 mg/L but experienced a significant reduction to <40 % degradation as concentrations exceeded 150 mg/L, significantly impacting strain growth (Zhang et al., 2022).

5.2. pH levels

pH plays a crucial role in microbial growth, significantly affecting cell membrane permeability, intracellular enzyme activity, and nutrient absorption (Zhang et al., 2022). The research has shown that the optimum pH for the degradation of skatole by *Pseudomonas aeruginosa* Gs is 7.0, with a decline in degradation rate when pH falls below 6.5 or rises above 7.5; growth is completely inhibited below 4.5 (Yin et al., 2006). *Acinetobacter* sp. NTA1–2A and TAT1–6A expressed optimal growth at pH 6.0, with a gradual decrease in degradation rate observed outside this range (Tesso et al., 2019). *Burkholderia* sp. IDO3 efficiently degraded skatole and grew normally between pH 4.0 and 9.0, but growth ceased and degradation rates significantly decreased at pH levels below 3.0 or above 10.0 (Ma et al., 2020a). The activity of *Acinetobacter oleivorans* AO-06 was inhibited under extremely acidic or alkaline conditions (Hu et al., 2022). *Rhodococcus gordoniae* YKSW-6 demonstrated effective skatole degradation under neutral and alkaline conditions but experienced significantly inhibited degradation activity at pH values below 6.0 (Zhang et al., 2022). A study found that aerobic bacteria are more significantly inhibited under acidic conditions for skatole degradation, whereas anaerobic bacteria are more significantly inhibited under alkaline conditions (Ye and Fu, 2023).

5.3. Nutrition requirements

The availability of various carbon and nitrogen sources significantly influences the growth and degradation capabilities of bacterial strains. According to the research, *Rhodococcus pyridinophilus* Rp3 can effectively degrade skatole under other suitable exogenous nutrient conditions and utilize it as its sole carbon source (Wu et al., 2022). Kohda et al. (1997) discovered that peptones, glucose, and yeast powder in the PYG medium facilitated the degradation of skatole by *C. malenominatum* A-3. Conversely, *Cupriavidus* sp. strain KK10, as identified by Fukuoka et al. (2015), could not use skatole as a carbon source but could completely degrade 100 mg/L skatole within 24 h when provided with glycerol. Xu et al. (2002) demonstrated that adding 0.5 %, 1.0 %, and 1.5 % oligofructose to the culture medium reduced skatole concentration by 22.3 %, 45.8 %, and 54.4 %, respectively, promoting the growth of *Bifidobacterium* while inhibiting the growth of *Clostridium* and *Escherichia coli*. Similarly, Liu et al. (2018b) observed that inulin and soya oligosaccharides significantly reduced skatole concentration in chicken manure, leading to a notable increase in *Bifidobacterium* levels. Furthermore, Li et al. (2009) incorporated beet pulp, ryegrass hay, alfalfa hay, and oligofructose into swine manure slurry for anaerobic fermentation. The study revealed that beet pulp and oligofructose reduced skatole yield, while ryegrass hay and alfalfa hay increased skatole yield.

5.4. Role of metal ions

The activity of intracellular enzymes can be influenced by the presence of metal ions in microbial cultures. Some metal ions can serve as enzyme activators, while others may act as enzyme inhibitors. Several studies have investigated the impact of different metal ions on the degradation processes carried out by various bacterial strains. For instance, *Burkholderia* sp. IDO3 showed no significant changes in its degradation rate in the presence of Fe^{2+}, Zn^{2+}, Mg^{2+}, and Mn^{2+}; however, the degradation of skatole was almost completely inhibited by Ni^{2+} and Cu^{2+} (Ma et al., 2020a). Additionally, Fe^{2+} and Mn^{2+} initially inhibited the degradation ability of *Burkholderia* sp. IDO3 within 12 h, but the strain was still able to degrade 50 mg/L of skatole within 24 h completely (Ma et al., 2020a). Moreover, the addition of Cu^{2+}, Zn^{2+}, and Ni^{2+} significantly inhibited skatole degradation by *Rhodococcus* DMU1, whereas Mg^{2+} and Fe^{2+} had no noticeable impact on the degradation rate (Li et al., 2023a). Subsequent research indicated that a concentration of 1 mmol/L, Zn^{2+} and Mn^{2+} led to a decrease in the degradation rate of *Rhodococcus* DMU1, while Cu^{2+} completely hindered the strain's ability to degrade skatole (Li et al., 2023a). Interestingly, Wu et al. (2022) discovered that Mg^{2+} played a crucial role as an essential metal ion for skatole degradation by the *Rhodococcus pyridinophilus* Rp3 strain. Conversely, Fe^{2+}, Mn^{2+}, and Zn^{2+} exerted inhibitory effects on the growth of the strain, resulting in a notable reduction in the degradation rate.

5.5. Impact of exogenous aromatic compounds

Li et al. (2023a) demonstrated that phenol, m-cresol, o-cresol, gentianic acid, salicylic acid, and indole had no significant impact on skatole degradation by *Rhodococcus* DMU1. Similarly, Ma et al. (2020a) found that after 24 h of incubation with various exogenous aromatic compounds, quinoline notably inhibited the growth of *Burkholderia* sp. IDO3, thereby hindering skatole degradation. In contrast, indole, phenol, o-cresol, gentianic acid, and salicylic acid enhanced the growth of *Burkholderia* sp. IDO3, resulting in complete skatole degradation. Consequently, it can be inferred that while quinoline exerts an inhibitory effect on skatole degradation, indole may facilitate the degradation process.

6. Conclusion

The large-scale intensive development of livestock farming has led to the widespread presence of skatole in environments such as anaerobic lagoons, municipal wastewater, sewage treatment plants. This extensive presence significantly impacts residents' quality of life and poses a threat to public health. Biological deodorization, as a green, safe, and economically efficient technology, has emerged as a research hotspot, especially in addressing odor problems. Currently, biological methods for treating odorous compounds primarily include bioaugmentation and bioremediation. Compared to individual microorganisms, microbial consortia exhibit higher degradation efficiency. However, in large-scale wastewater treatment, it is necessary to establish usage frequencies based on the scale of deodorization to ensure long-term effective deodorization. Moreover, incorporating skatole-degrading bacteria into non-degrading systems can enhance their ability to degrade skatole, which is particularly advantageous in large-scale fermentation environments requiring sustained degradation. Notably, the efficiency of skatole-degrading bacteria may not match that of composite microbial consortia in removing odorous compounds.

While the manuscript presents a comprehensive list of skatole-degrading strains, we recognize the importance of critically assessing their relative effectiveness. The majority of anaerobic bacteria exhibit relatively low degradation rates and prolonged processing durations for skatole decomposition. In contrast, certain aerobic and facultative anaerobic strains demonstrate superior performance. Notably, *Acinetobacter* stands out for its high degradation efficiency and significantly reduced processing time, making it a highly effective candidate for skatole bioremediation. Among aerobic bacteria, *Pseudomonas* displays strong tolerance toward skatole, although it requires extended degradation periods to achieve complete breakdown. In comparison, *Lactobacillus* and *Bacillus* exhibit limited degradation efficiencies, suggesting that they may be less suitable for large-scale applications. Conversely,

Cupriavidus and *Acinetobacter* combine elevated skatole tolerance with enhanced degradation capabilities, positioning them as strong contenders for practical use. Particularly, *Burkholderia, Rhodococcus*, and *Acinetobacter*, exhibit exceptional multifunctional advantages. These strains possess high tolerance to skatole, remarkable degradation efficiency, and rapid processing kinetics. Their combined attributes make them highly promising candidates for efficient environmental bioremediation applications.

While current research has identified aerobic bacteria as the primary microbial agents capable of skatole degradation, several limitations and knowledge gaps remain. These bacteria demonstrate measurable degradation capacities under standard pH and temperature conditions, with enhanced efficacy observed at pH 6 and 30 °C. Given that wastewater sludge typically maintains a pH close to 6, these findings suggest the potential applicability of microbial inoculants for deodorization in sludge treatment systems. However, significant challenges persist in translating these laboratory findings into practical applications. Critical limitations include the absence of optimized inoculant formulations and insufficient empirical data validating their performance in large-scale operational environments. Additionally, the efficiency of specific bacterial species under varying conditions (e.g., pH, oxygen availability) is not yet fully understood, highlighting the need for further research. To advance this bioremediation approach toward industrial feasibility, systematic investigations into microbial consortia engineering and field-scale validation are essential. Future studies should focus on optimizing microbial inoculants, exploring the synergistic effects of different bacterial species, and evaluating their performance under diverse environmental conditions. Addressing these limitations will be crucial for the successful implementation of microbial degradation strategies in real-world applications.

Although considerable research has focused on screening microorganisms capable of degrading skatole, specific mechanisms and key enzymes involved in skatole degradation remain underexplored. A comprehensive understanding of the transcriptional regulators or operons involved in skatole degradation is still lacking. The regulatory mechanisms that enable different microbial taxa to degrade skatole efficiently under varying environmental conditions remain to be elucidated. This gap in knowledge underscores the need for further systematic investigation into the genetic and regulatory aspects of skatole degradation. In summary, while some progress has been made in identifying key genes and enzymes involved in skatole degradation, the broader regulatory framework remains underexplored. Future research should focus on uncovering the transcriptional regulators and operons that govern this process, as well as exploring the environmental factors that influence microbial degradation efficiency. This would be a critical direction for advancing the understanding and application of skatole bioremediation strategies.

Furthermore, most studies on skatole-degrading bacteria have predominantly concentrated on Gram-negative bacteria, with fewer reports on fungi. Some evidence suggests that Gram-positive bacteria such as *Lactobacillus* may play a significant role in skatole degradation, but further validation and research are needed. Moreover, some studies indicate that following complete skatole degradation, *Actinobacteria* and fungi from the *Ascomycota* family may become dominant. Further research should aim to screen and identify additional fungi capable of degrading skatole, investigate the underlying degradation mechanisms, and identify functional genes involved. To gain a comprehensive understanding of skatole degradation, several crucial aspects need to be explored. First, it is imperative to identify the functional genes responsible for skatole degradation in various bacterial species. Simultaneously, validating the correlation between the skatole catabolic pathways across different genera and the catechol 1,2 - dioxygenase - mediated degradation route is essential. Gene knockout and other advanced molecular techniques should be systematically employed to validate gene functions and pinpoint the key enzymatic determinants that are crucial for skatole catabolism. Moreover, the regulatory role of Mg^{2+} in modulating enzymatic activity during the skatole degradation process requires in - depth mechanistic exploration. Understanding how Mg^{2+} influences the activity of relevant enzymes can provide insights into optimizing the degradation efficiency. In addition, future research should focus on the complex microbial community dynamics involved in skatole degradation. This includes investigating the interspecies modulatory interactions and the underlying regulatory mechanisms that govern catabolic efficiency. Adopting such a multidimensional approach will significantly contribute to the development of targeted microbial consortia, which are essential for optimizing skatole bioremediation strategies.

In conclusion, future research efforts should deeply delve into the microbial degradation pathways of skatole, closely monitor the changes in microbial communities to understand the impact of skatole on these communities. Ultimately, the goal is to develop effective strategies for treating skatole - contaminated agricultural waste and sewage through bioremediation or bioaugmentation, thereby reducing the environmental and health risks associated with skatole pollution.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The data that has been used is confidential.

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