Review Article

Microbial Degradation of Indole and Its Derivatives

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Indole and its derivatives, including 3-methylindole and 4-chloroindole, are environmental pollutants that are present worldwide. Microbial degradation of indole and its derivatives can occur in several aerobic and anaerobic pathways; these pathways involve different known and characterized genes. In this minireview, we summarize and explain the microbial degradation of indole, indole-3-acetic acid, 4-chloroindole, and methylindole.

1. Introduction

Indole and its derivatives comprise a major group of heterocyclic aromatic compounds which are widely used for the synthesis of pharmaceuticals, dyes, and industrial solvents [1]. Indole is used as a perfume fixative, a synthetic flavor, and a chemical intermediate for synthesis of a plant growth regulator, indole-3-acetic acid [1, 2]. 2-Methylindole is used for dye manufacturing, including cyanine dyes and cationic diazo dyes [3]. The indole ring is also present as a core building block and key functional group in many pharmaceuticals, alkaloids, and hormones [4].

Indole and its derivatives are also present in many natural products: indole occurs naturally in *Robinia pseudoacacia*, the jasmines, certain citrus plants, and the wood of *Celtis reticulata* [1]. Indole is also present in coal tar [5], fuel oil [6], and cigarette smoke [7, 8]. Indole is one of the main degradation products of microbial metabolism of L-tryptophan, an essential amino acid present in most proteins [9, 10]. More than 85 species of Gram-positive and Gram-negative bacteria can produce indole [11]. 3-Methylindole is commonly found in feces and sewage and is well known for its unpleasant smell [1, 12–14]. Indole-3-acetic acid (auxin) is a naturally occurring plant hormone that has a significant role in plant growth and development.

Indole and its derivatives are discharged into the environment through industrial waste, coal tar waste, and wastewater from coking plants, coal gasification [5, 15, 16] and refineries [6], and cigarette smoke.

Human beings can be exposed to indole via (i) ambient air, (ii) tobacco smoke, (iii) food, and (iv) skin contact with vapors and other products, such as perfumes that contain indole.

Indole and its derivatives are highly toxic to microorganisms and animals and are considered mutagens and carcinogens [17, 18]. Experimental evidences showed that indole caused glomerular sclerosis [19], hemolysis [20–22], improper oviduct functioning [23], and chronic arthritis [24, 25]. Indole inhibits anthraquinone biosynthesis in plants [26]. Furukawa et al. [27] reported that a derivative of indole-3-acetic acid induced neuroepithelial cell apoptosis in rat embryos.

4-Chloroindole irritates the eyes, skin, lungs, and respiratory system and shows antimicrobial activity against several Gram-positive and Gram-negative bacteria [28, 29]. Nitrosated 4-chloroindole and 4-chloro-6-methoxyindole are genotoxic; specifically, they induced sister chromatid exchanges in *Salmonella typhimurium* TA100 [30]. 3-Methylindole causes malabsorption syndrome, anemia, and hepatic coma in human beings [31]. Furthermore, 6-hydroxyskatol,

a metabolite of 3-methylindole generated in the human intestine, has possible psychotropic effects [31].

Indole and its derivatives are considered environmental pollutants due to their toxicity and worldwide occurrence in soils, coastal areas, groundwater, surface waters, and even indoor environments [15, 32]. Several reviews are available for applications and microbial production of indole; however, there are very few reviews on microbial degradation of indole [4, 11]. Recently, rapid progress was made in the study of microbial degradation of indole and its derivatives and a few new pathways were proposed for microbial degradation of indole and its derivatives [28, 33, 34]. The aim of this review is to summarize the microbial degradation of indole, indole-3-acetate, 4-chloroindole, and methylindole and highlight recent developments in the field.

2. Microbial Degradation of Indole

Microbial degradation of indole was investigated under aerobic and anaerobic conditions [12, 13, 15, 33, 34]. Several mechanisms were proposed for indole biodegradation by microorganisms, including bacteria and fungi, under aerobic conditions [12, 35–37, 46]; microorganisms either mineralized indole completely [36, 37, 46] or transformed it into other compounds in the presence of an additional carbon source (cometabolism) [33, 34]. Under aerobic conditions, indole metabolism was generally initiated by oxidation of indole followed by heterocyclic ring cleavage.

2.1. Bacterial Mineralization of Indole. A few indole-mineralizing bacteria have been isolated and characterized for aerobic biodegradation of indole [35–37, 46]. Three major pathways for indole mineralization have been proposed and these pathways are the catechol pathway, the gentisate pathway, and the anthranilate pathway. The catechol pathway was studied in an indole-mineralizing Gram-negative bacterium isolated from tap water [35]. The first step of the catechol pathway was hydroxylation of indole to indoxyl, which was further hydroxylated to 2,3-dihydroxyindole (Figure 1(a)). Further degradation proceeded via isatin, N-formylanthranilic acid, anthranilic acid, salicylic acid, and catechol [35]. The anthranilate pathway of indole degradation was studied in a Gram-positive coccus that utilized indole as its sole source of carbon and energy and degraded it via 2,3-dihydroxyindole, N-carboxyanthranilic acid, and anthranilic acid (Figure 1(b)) [36]. Claus and Kutzner [37] reported the gentisate pathway of indole degradation in an indole-mineralizing bacterium, *Alcaligenes* sp. In 3 isolates from activated sludge. In this pathway, indole degradation occurred via indoxyl, isatin, anthranilic acid, and gentisic acid (Figure 1(c)); the formation of gentisic acid was a key feature of this pathway, formed due to hydroxylation of anthranilic acid. The possibility of new indole degradation pathways, aside from these 3 isolates, has been suggested. Doukyu and Aono [46] reported the mineralization of indole via isatin and isatic acid in *Pseudomonas* sp. strain ST-200. Yin et al. [47] studied indole degradation in an indole-mineralizing bacterium, *Pseudomonas aeruginosa* Gs isolated from mangrove sediments, and detected two major metabolites; however, they could not identify either metabolite.

2.2. Bacterial Cometabolism of Indole. Cometabolism of indole involves bacterial transformation of indole into other compounds in the presence of additional carbon source. These biotransformed products may belong to one or more degradation pathways of indole. Fukuoka et al. [34] studied the biotransformation of indole in *Cupriavidus* sp. strain KK10, isolated from a soil bacterium consortium, and proposed multiple pathways for indole biotransformation based on the identified metabolites. These pathways involve oxidation of indole followed by either N-heterocyclic ring cleavage or carbocyclic aromatic ring cleavage (Figure 2). In the carbocyclic aromatic ring cleavage pathway, indole was oxidized at the 4th and 5th positions to form 4,5-dihydroxyindole via *cis*-4,5-indole-dihydrodiol [34]. The 4,5-dihydroxyindole underwent *ortho*- and *meta*-ring cleavage. The *meta*-ring cleavage product was identified as 4-(3-hydroxy-1*H*-pyrrol-2-yl)-2-oxo-but-3-enoic acid, whereas 3-(2)-formyl-1*H*-pyrrole-2-(3)-carboxylic acid was identified as the *ortho*-ring cleavage product, which was further carboxylated to pyrrole-2,3-dicarboxylic acid [34]. The N-heterocyclic aromatic ring cleavage pathway followed one of the following two mechanisms: (i) monooxygenation of indole at the 2 or 3 positions to form a corresponding indoxyl that further converted to a corresponding oxindole, which was further transformed to isatin or (ii) dioxygenation of indole at the 2 and 3 positions to form 2,3-dihydroxyindole via indole-2,3-dihydrodiol [34]. In the next step, the isatin or 2,3-dihydroxyindole underwent N-heterocyclic *ortho*-ring cleavage to produce N-formylanthranilic acid, which was converted to anthranilic acid. Anthranilic acid was deaminated to produce salicylic acid, which was transformed to gentisic acid via monohydroxylation. The gentisic acid was converted to 1,2,4-trihydroxybenzene which could further produce TCA cycle intermediates [34]. The novel feature of this pathway is the previously unreported formation of 1,2,4-trihydroxybenzene. Indigoids, such as indigo, indirubin, isoindigo, and 2,2-bis(3′-indolyl) indoxyl, were also biotransformation products of indole in *Cupriavidus* sp. KK10 [34].

Another biotransformation pathway of indole was investigated in *Arthrobacter* sp. SPG. Initially, indole was biotransformed into indole-3-acetic acid via a tryptophan-independent pathway [33]. Indole-3-acetic acid was converted to indole-3-glyoxylic acid, which was converted to indole-3-aldehyde (Figure 3(a)). Kim et al. [48] reported that a plant polyphenol stimulated indole biotransformation in *Burkholderia unamae* CK43B isolated from the polyphenol-rich Shorea rhizosphere. Polyphenol-exposed cells of strain CK43B utilized indole as a nitrogen source and degraded it via anthranilic acid and catechol [48].

Indole can be biologically oxidized to indoxyl and then indoxyl is spontaneously transformed to a dimer, indigo (Figure 3(b)), a blue pigment [49, 50]. Many microorganisms involved in the transformation of indole into indigo have been isolated and characterized [49, 50], including naphthalene-degrading *Pseudomonas putida* PgG7 [51], *m*- and *p*-toluate-degrading *P. putida* mt-2 [52], toluene-degrading
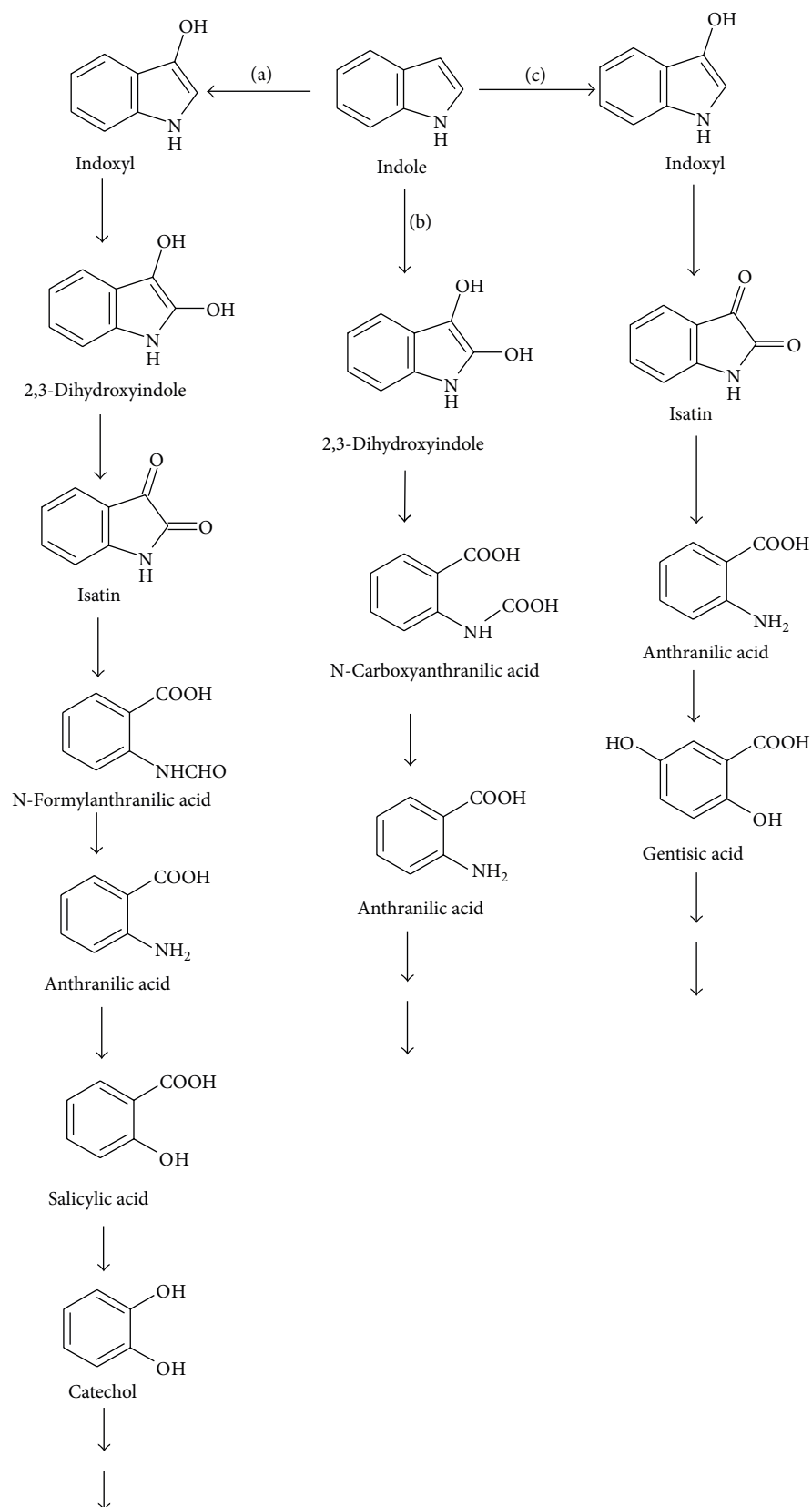
FIGURE 1: Metabolic pathways for mineralization of indole in (a) tap water bacterium [35] and (b) a gram positive coccus [36] and (c) an *Alcaligenes* sp. In 3 [37].
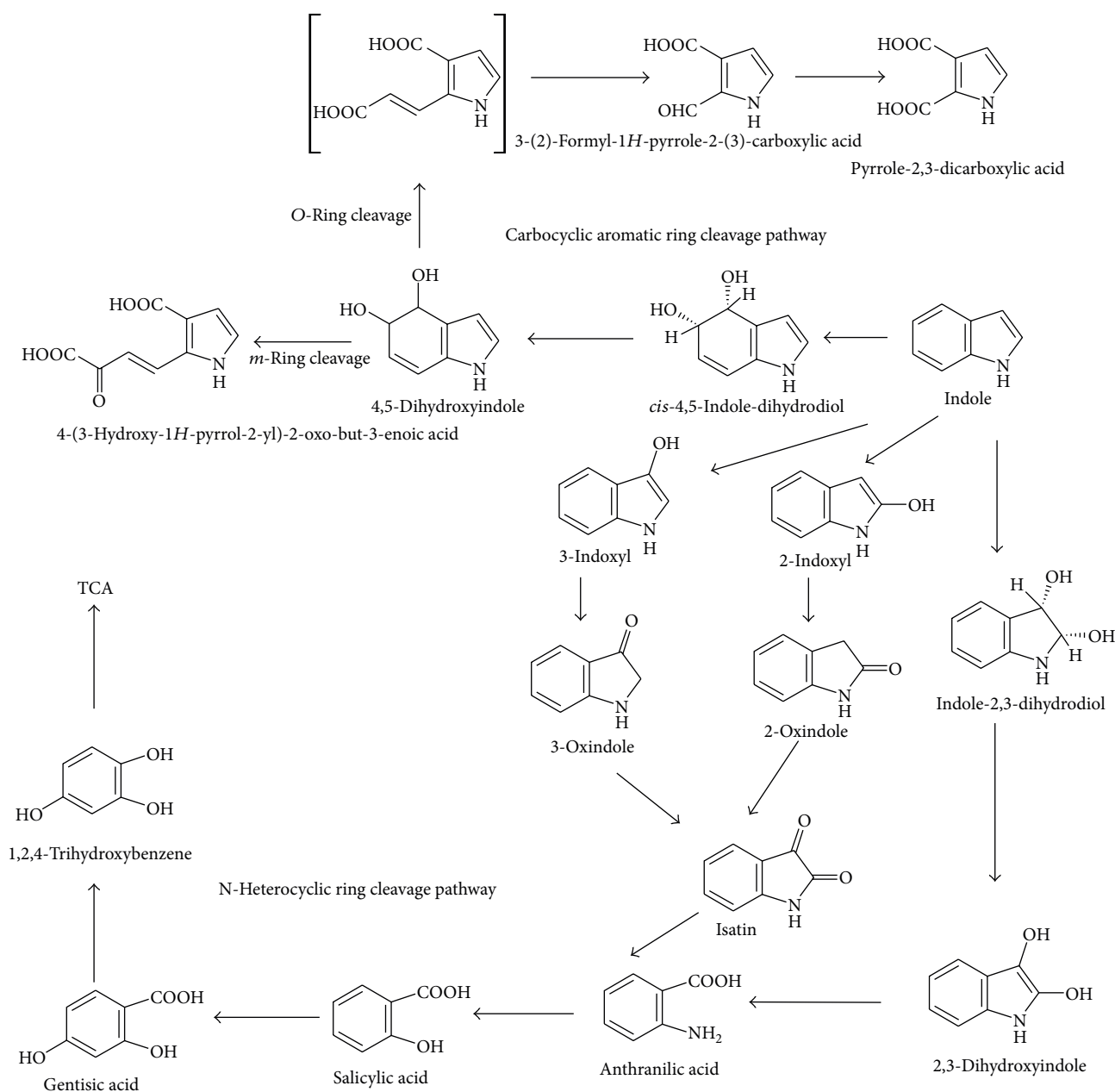
FIGURE 2: Degradation pathways of indole in *Cupriavidus* sp. KK10 [34] via carbocyclic ring cleavage and N-heterocyclic ring cleavage.

P. mendocina KR1 [53], styrene-degrading *P. putida* S12 and CA-3 [54], and tetralin-degrading *Sphingomonas macrogoltabida* [55]. Pathak and Madamwar [56] reported that a naphthalene-degrading strain, *Pseudomonas* sp. HOB1, synthesized indigo and that indigo production increased when naphthalene was used as a growth substrate. Mercadal et al. [57] optimized the conditions of indigo production by a naphthalene-degrading marine strain, *Pseudomonas* sp. J26, and achieved maximum production of indigo (138.1 μM) using 2.5 mM indole at 25°C.

Several enzymes, such as monooxygenases, dioxygenases, and cytochrome P450, were characterized for indigo production [50]. Many genes encoding these enzymes were cloned and used to construct engineering bacteria for efficient indigo

production [50]. Ensley et al. [51] cloned and expressed a DNA fragment of a *Pseudomonas* plasmid, containing naphthalene oxidation genes, in *E. coli* and observed that the recombinant *E. coli* synthesized indigo in nutrient-rich medium; indigo production increased in the presence of tryptophan or indole. Wu et al. [58] transferred a plasmid containing naphthalene degrading genes from *Pseudomonas* sp. S13 to *E. coli*. The recombinant *E. coli* was able to synthesize indigo [58]. Qu et al. [59] showed that *E. coli* that expressed biphenyl dioxygenase and biphenyl-2,3-dihydro-diol-2,3-dehydrogenase efficiently transformed indole to indigo. *E. coli* that expressed cytochrome P450 also oxidized indole to indigo. The immobilization of *E. coli* BL21 expressing P450 BM-3 showed better rates of indigo production
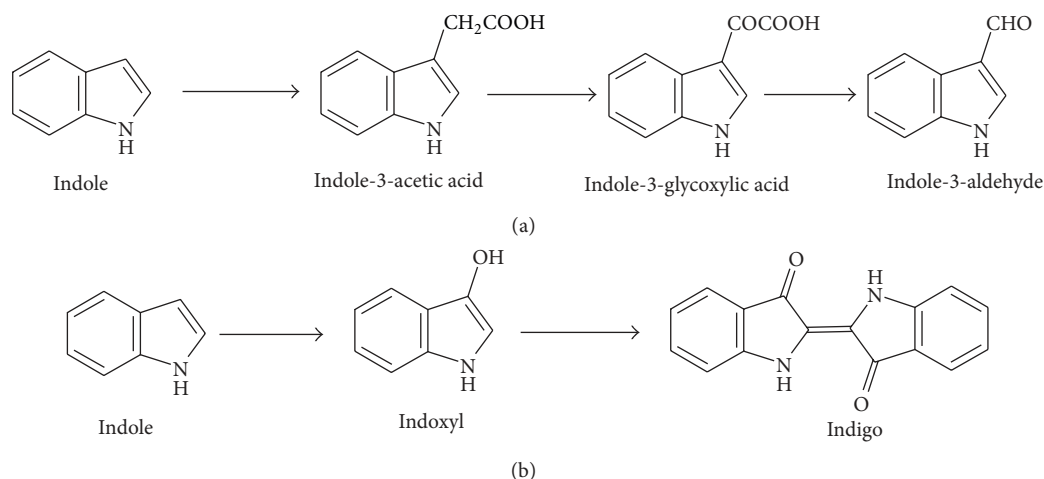
(a)

(b)

FIGURE 3: Biotransformation of indole to indole-3-aldehyde (a) and indoxyl (b).

than nonimmobilized cells [60]. The *xyl*A gene that encodes xylene oxygenase was cloned from the TOL plasmid pWW53 of *P. putida* MT53 and is responsible for indigo production [61]. Nagayama et al. [62] constructed a cosmid library of metagenomic DNA in *E. coli* and introduced it into *P. putida*-derived strains that produced little indigo on indole-containing agar plates. Screening results showed that 29 cosmid clones generated indigo on the indole-containing agar plates [62]. Six representative cosmids were selected for sequencing and *in vitro* transposon mutagenesis, leading to the identification of genes encoding putative classes B and D flavo protein monooxygenases, a multicomponent hydroxylase, and a reductase that were responsible for indigo formation [62].

2.3. Fungal Degradation of Indole. Fungal degradation of indole has also been investigated [12, 38, 63]. Kamath and Vaidyanathan [12] elucidated a metabolic pathway for indole in *Aspergillus niger*. In this pathway, indole was first oxidized to 3-indoxyl (3-hydroxyindole) that was further converted to N-formylanthranilic acid. In the next step, N-formylanthranilic acid was transformed to anthranilic acid by N-formylanthranilate deformylase. The anthranilic acid underwent oxidative deamination and hydroxylation, catalyzed by NADPH-dependent anthranilate hydroxylase, to produce 2,3-dihydroxybenzoic acid that was decarboxylated to catechol by 2,3-dihydroxybenzoate decarboxylase (Figure 4(a)). The further degradation of catechol occurred via ring cleavage by catechol-1,2-dioxygenase.

Another fungal metabolic pathway of indole was studied in an endophytic fungus, *Phomopsis liquidambari*, which utilized indole as its sole source of carbon and nitrogen [38]. In this fungus, indole was initially oxidized to oxindole and isatin. In the next step, isatin was transformed to 2-dioxindole. The 2-dioxindole was further converted to 2-aminobenzoic acid via pyridine ring cleavage (Figure 4(b)) [38]. Katapodis et al. [63] reported indole degradation by a thermophilic fungus, *Sporotrichum thermophile*, using a persolvent fermentation system containing a large amount of indole (the medium contained 20% soybean oil by volume

and up to 2 g/L indole). They reported that most of the indole was partitioned in the organic solvent layer and complete indole degradation was observed after 6 days when the fungus was grown on media containing indole at 1 g/L [63].

2.4. Anaerobic Bacterial Degradation of Indole. Anaerobic degradation of indole has been achieved by pure or mixed culture(s) of bacteria under denitrifying, sulfate-reducing, or methanogenic conditions [64–71]. Mixed microbial populations present in marine sediments [64, 65], freshwater sediments [64, 66, 67], sewage sludge [68–70], and composting pig and chicken manure [13] could anaerobically degrade indole. Wang et al. [71] reported mineralization of indole into carbon dioxide and methane by a consortium of methanogenic bacteria. Berry et al. [72] reported conversion of indole to oxindole under methanogenic conditions. Madsen et al. [66] investigated the effects of physiological and environmental factors on the accumulation of oxindole during anaerobic indole degradation and reported that oxindole was accumulated under methanogenic conditions, but not under denitrifying conditions. Oxindole was also detected as a key intermediate of indole degradation by bacteria consortia under sulfate-reducing conditions, methanogenic conditions [65, 70], and denitrifying conditions [68].

To date, only one pure culture of bacteria capable of utilizing indole as its sole source of carbon and energy, that is, the sulfate reducer *Desulfobacterium indolicum*, has been isolated and characterized. This bacterium was initially isolated from enriched marine sediments by Bak and Widdel [64]. Several studies investigated indole degradation in *Desulfobacterium indolicum*, which degrades indole via oxindole [39, 73], including Johansen et al. [39], who proposed the biodegradation pathway of indole for *D. indolicum*. Initially, indole was hydroxylated at the C-2 position to form oxindole that was further hydroxylated at C-3 to form isatin. Isatin underwent ring cleavage between the C-2 and C-3 atoms on the pyrrole ring of indole to produce isatoic acid, which was decarboxylated to anthranilic acid (Figure 5). The further degradation of anthranilic acid achieved complete
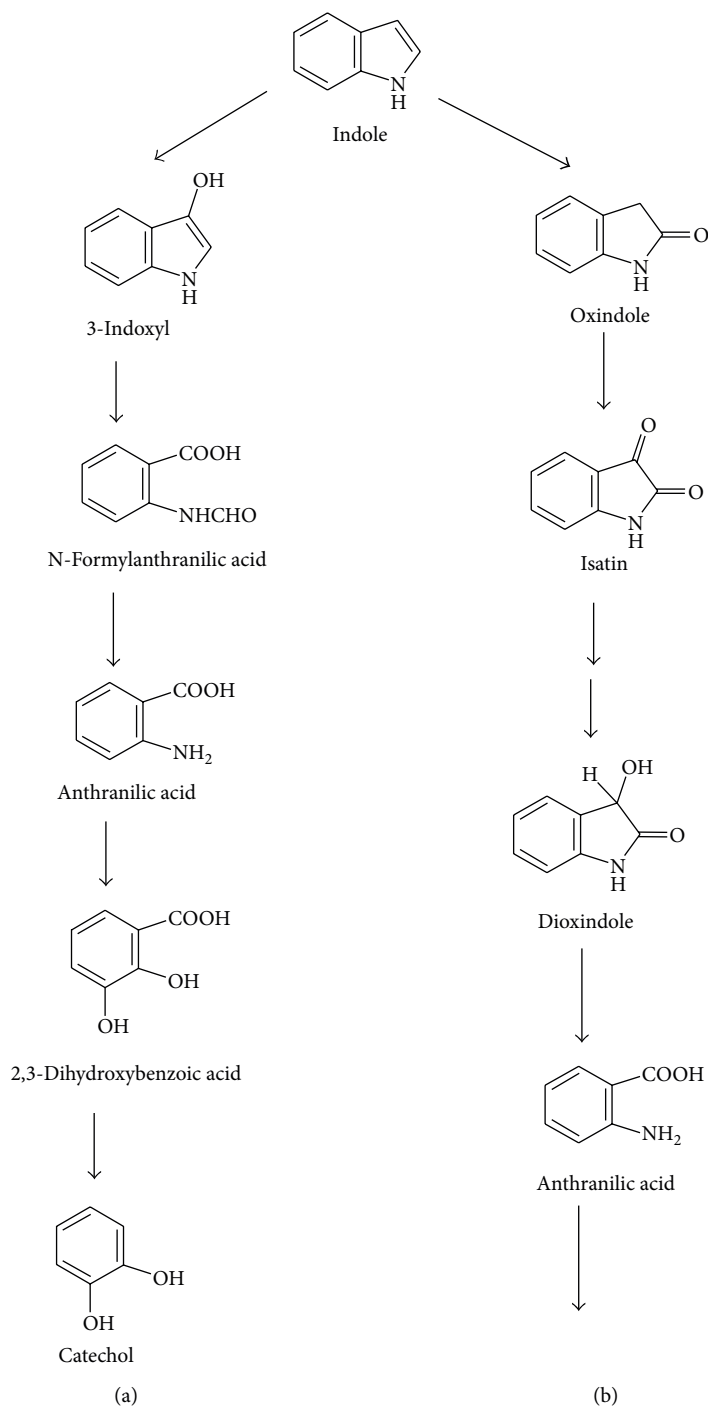
Figure 4: Fungal degradation pathways of indole in (a) *Aspergillus niger* [12] and (b) *Phomopsis liquidambari* [38].
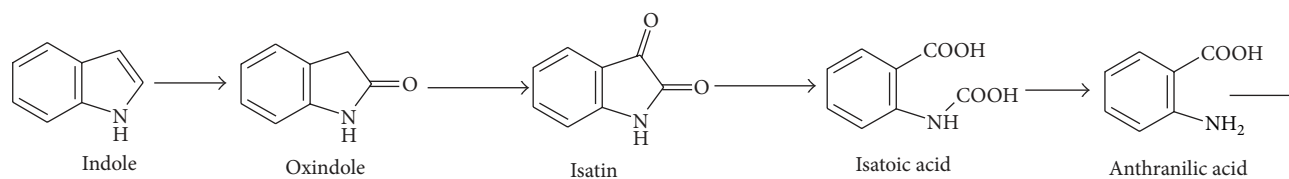

Figure 5: Anaerobic degradation pathway of indole in *Desulfobacterium indolicum* [39].

mineralization. Similar results were reported for indole degradation by a denitrifying microbial community [68].

Hong et al. [74] studied two anaerobic, indole-decomposing microbial communities under both denitrifying and sulfate-reducing conditions. In the denitrifying bioreactor, most of the dominant bacteria were β-proteobacteria, predominantly *Alicycliphilus*, *Alcaligenes*, and *Thauera* genera. In the sulfate-reducing bioreactor, *Clostridia* and *Actinobacteria* were the dominating indole-degrading species [74].

3. Bacterial Degradation of Indole-3-Acetic Acid

Several reports documented the bacterial transformation of indole-3-acetic acid [75–80]. The decarboxylation of indole-3-acetic acid to indole-3-methyl has been reported in many rumen microorganisms, including *Lactobacillus* sp. [75], *Clostridium scatologenes*, and *Clostridium drakei* [76]. Jensen et al. [77] reported the conversion of indole-3-acetic acid to 3-methylindole by a mixed population of pig fecal bacteria. Attwood et al. [78] reported production of 3-methylindole in the presence of indole-3-acetic acid by six rumen microorganisms (similar to *Prevotella* sp., *Clostridium* sp., *Actinomyces* sp., and *Megasphaera* sp.) isolated from grazing ruminants. Ernstsen et al. [79] showed the transformation of indole into indole-3-methanol in *Rhizobium phaseoli*. Tsubokura et al. [80] reported the conversion of indole-3-acetic acid to 2-formaminobenzoylacetic acid by a bacterium isolated from air.

The complete mineralization of indole-3-acetic acid has also been studied [40]; four metabolic pathways for aerobic degradation of indole-3-acetic acid were proposed and these pathways involve two catechol pathways, a gentisate pathway, and an anthranilate pathway. The catechol pathway of indole-3-acetic acid degradation was initially studied in a *Pseudomonas* sp. that degraded indole-3-acetic acid via 3-methylindole, 3-indoxyl, salicylic acid, and catechol [40]. In this pathway, indole-3-acetic acid was initially decarboxylated to 3-methylindole, which was converted to 3-hydroxyindole via hydroxylation and removal of methyl group (Figure 6(a)). Subsequent hydroxylation and reduction gave 2,3-dihydroxy-dihydroindole, which underwent ring cleavage and hydrolysis to produce salicylic acid, which was then metabolized via catechol [40]. Catechol is also detected as a metabolite of indole-3-acetic acid degradation by *Pseudomonas putida* 1290 [81], *Pseudomonas* sp. LD2 [82], and *Arthrobacter* sp. [83]. Another catechol pathway of indole-3-acetic acid degradation was studied in *Pseudomonas putida* 1290, which utilized indole-3-acetic acid as its sole source of carbon and energy and degraded indole-3-acetic acid with 2-hydroxy-indoleacetic acid, dioxindole-3-acetic acid, and catechol as intermediates (Figure 6(b)) [41, 84, 85]. The genes and enzymes involved in this pathway were characterized; an 8994-bp DNA fragment containing ten *iac* genes (*iacABCDEFG*, *iacHI*, and *iac*R) was responsible for indole-3-acetic acid degradation in *Pseudomonas putida* 1290 [84, 85]. Scott et al. [41] confirmed the role of *iac*A, *iac*E, and *iac*C in the degradation of indole-3-acetic acid: the *iacA* gene product was involved in the first step of indole-3-acetic acid degradation and catalyzed hydroxylation of the indole ring of indole-3-acetic acid; the *iacE* gene product catalyzed the hydroxylation of 2-hydroxy-indole-3-acetic acid at position 3 of the indole ring to produce dioxindole-3-acetic acid, which is the substrate of the *iacC* gene product [41]; the *iacR* gene product is a transcriptional regulator controlling repression or induction of the *iac* operons [41]; the roles of the other *iac* genes (*iacB*, *iacD*, *iacE*, *iacF*, *iacG*, *iacH*, and *iacI*) in these steps remain unknown.

The gentisate pathway of indole-3-acetic acid degradation was studied in *Alcaligenes* sp. In 3, which degraded indole-3-acetic acid via isatin, anthranilic acid, and gentisic acid (Figure 6(c)). Similar metabolites were detected during the degradation of indole by the same bacterium. These data suggest that *Alcaligenes* sp. In 3 degraded both indole and indole-3-acetic acid via the gentisate pathway. Jensen et al. [42] reported the anthranilate pathway of indole-3-acetic acid degradation in *Bradyrhizobium japonicum*, which degraded indole-3-acetic acid via dioxindole-3-acetic acid, dioxindole, isatin, 2-aminophenyl glyoxylic acid (isatinic acid), and anthranilic acid (Figure 6(d)).

The anaerobic degradation pathway of indole-3-acetic acid was studied in the denitrifying betaproteobacterium, *Azoarcus evansii* [43]. The first step of this pathway is production of the enol and keto forms of 2-oxo-indole-3-acetic acid. Initially, a molybdenum cofactor-containing dehydrogenase catalyzed the hydroxylation of the N-heterocyclic pyrrole ring to produce the enol form of 2-oxo-indole-3-acetic acid [43]. In the next step, a hydantoinase-like enzyme catalyzed the hydrolytic ring opening of the keto form to form 2($2'$-aminophenyl)succinate (Figure 6(e)). The next step involves formation of 2($2'$-aminophenyl)succinyl-CoA, catalyzed by the CoA ligase or the CoA transferase. The 2($2'$-aminophenyl)succinyl-CoA was rearranged to produce 2-aminobenzylmalonyl-CoA, catalyzed by a coenzyme B_{12}-dependent mutase. Further degradation of 2-aminobenzylmalonyl-CoA leads to the formation of 2-aminobenzoyl-CoA or benzoyl-CoA [43]. The 14 genes encoding proteins similar to indole-3-acetic acid-induced proteins in *Azoarcus evansii* were identified in the genome of *Aromatoleum aromaticum*, strain EbN1 [43].

Some bacteria promote plant growth by degrading exogenous indole-3-acetic acid in plant roots [86]; for example, Zúñiga et al. [86] reported that bacterial degradation of indole-3-acetic acid plays a key role in plant growth-promoting traits and is necessary for efficient rhizosphere colonization. They reported that wild-type *Burkholderia phytofirmans* promotes the growth of *Arabidopsis* plant roots in the presence of exogenously added indole-3-acetic acid; however, a mutant strain with destructed *iacC* was unable to promote the growth of the plant root [86].

4. Bacterial Degradation of 4-Chloroindole

Only one bacterium is known for biodegradation of 4-chloroindole: Arora and Bae [28] studied the degradation pathway of 4-chloroindole in *Exiguobacterium* sp. PMA, which utilized 4-chloroindole as its sole source of carbon and energy. 4-Chloroindole was initially dehalogenated and
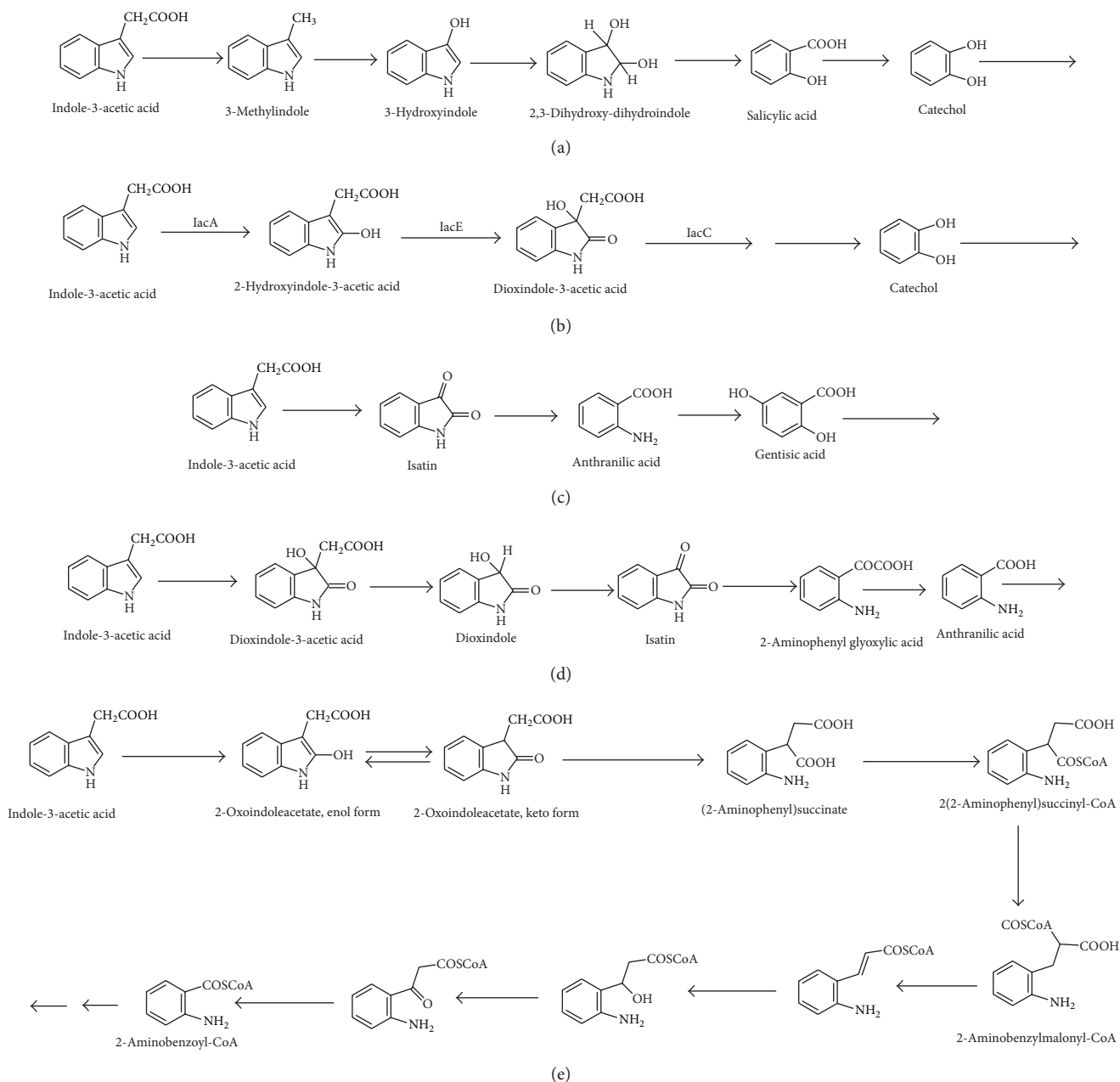
FIGURE 6: Degradation pathways of indole-3-acetic acid in (a) a *Pseudomonas* sp. [40]; (b) *Pseudomonas putida* 1290 [41]; (c) *Alcaligenes* sp. In 3 [37]; (d) *Bradyrhizobium japonicum* [42]; (e) *Azoarcus evansii* [43].

further degradation of indole proceeded via isatin, anthranilic acid, and salicylic acid (Figure 7(a)). The enzyme activities for 4-chloroindole dehalogenase and anthranilic acid deaminase were detected in the crude extract of the 4-chloroindoles-induced cells of *Exiguobacterium* sp. PMA, confirming indole and salicylic acid formation in the degradation pathway of 4-chloroindole. *Exiguobacterium* sp. PMA also degraded 4-chloroindole in sterile and nonsterile soil [28]. The degradation rate was faster in sterile soil than in nonsterile soil [28].

5. Bacterial Degradation of Methylindole

The degradation of 3-methylindole, which is commonly known as skatole, was studied in several bacteria [13]. Kohda et al. [13] isolated three species of skatole-degrading *Clostridium* (*C. aminovalericum*, *C. carnis*, and *C. malenominatum*) from pig and chicken manure composting processes which degraded skatole from 300 to 800 mg/L. Yin et al. [87] reported biodegradation of 1-methylindole and 3-methylindole using enrichment cultures derived from mangrove
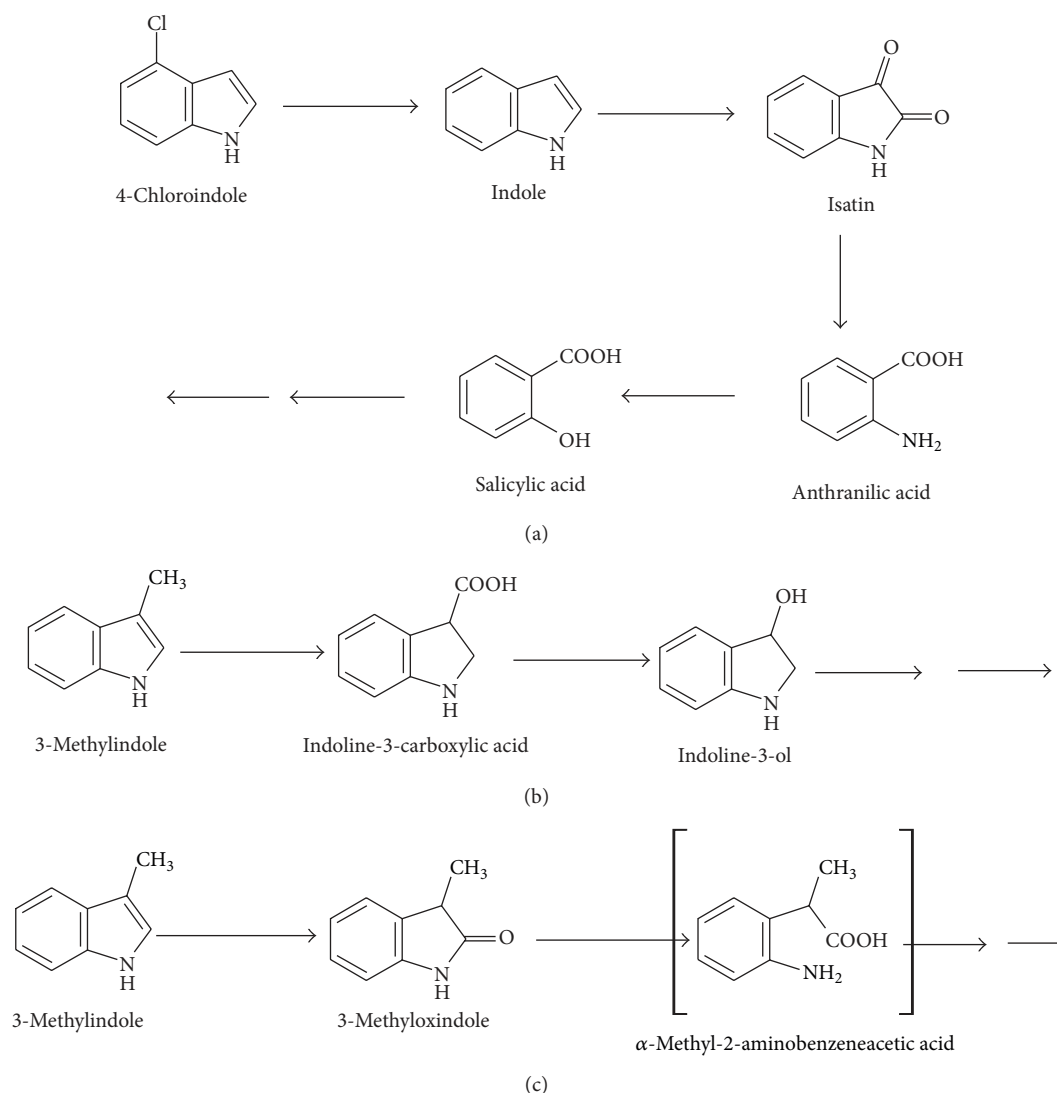
FIGURE 7: Degradation pathway of (a) 4-chloroindole in *Exiguobacterium* sp. PMA [28], (b) 3-methylindole in *Pseudomonas* sp. GS [44], and (c) 3-methylindole by a sulfate reducing consortium [45].

sediment obtained from the Mai Po Nature Reserve of Hong Kong; a pure culture of *Pseudomonas aeruginosa* Gs isolated from this enrichment utilized 1-methylindole and 3-methylindole as its sole source of carbon and energy and completely degraded 1-methylindole and 3-methylindole after more than 40 days and 24 days, respectively, when the concentration of 3-methylindole or 1-methylindole was 2.0 mM in the culture [87]. Indoline-3-carboxylic acid and indoline-3-ol were identified as metabolites of 3-methylindole in *P. aeruginosa* Gs (Figure 7(b)) [44]. Gu and Berry [32] reported the degradation of 3-methylindole via 3-methyloxindole using a methanogenic consortium derived from enrichment of wetland soil. The removal of 3-methylindole was monitored by the four strains of lactic acid bacteria (*Lactobacillus brevis* 1.12 (*L. brevis* 1.12), *L. plantarum* 102, *L. casei* 6103, and *L. plantarum* ATCC8014); *L. brevis* 1.12 was the best at removing 3-methylindole [88]. Gu et al. [45] reported that a methanogenic bacterial consortia derived from marine sediment

from Victoria Harbour transformed 3-methylindole to 3-methyloxindole, whereas a sulfate-reducing consortium mineralized 3-methylindole completely via 3-methyloxindole and α–methyl-2-aminobenzeneacetic acid (Figure 7(c)).

Sharma et al. [89] isolated a new 3-methylindole-degrading purple nonsulfur bacterium, *Rhodopseudomonas palustris* WKU-KDNS3, from a swine waste lagoon using an enrichment technique. This bacterium could remove >93% of the total 3-methylindole in the medium by 21 days.

6. Conclusions and Future Perspectives

(i) Microbes degrade indole either by mineralization or cometabolism (biotransformation). In mineralization, microbes utilized indole as the sole source of carbon and energy and degraded it completely via a series of chemical reactions; however, in the process of biotransformation, indole was transformed to other

compounds in the presence of an additional carbon source. These biotransformed products may be more or less toxic than indole and sometimes used as useful products; for example, several bacteria convert indole to indigo, a compound of industrial value. Similarly, *Arthrobacter* sp. SPG biotransformed indole to indole-3-acetic acid (a plant growth-promoting hormone), indole-3-glyoxylic acid, and indole-3-aldehyde. A few microbes adopt detoxification mechanisms via biotransformation and convert indole to less toxic or nontoxic compounds; for example, *Cupriavidus* sp. strain KK10 transformed indole to less toxic or nontoxic products via N-heterocyclic ring cleavage or carbocyclic aromatic ring cleavage.

(ii) Three major pathways for aerobic bacterial mineralization of indole have been proposed. However, the genes and the enzymes involved in these pathways could not yet be characterized.

(iii) Anaerobic degradation of indole has been studied under methanogenic, sulfate-reducing and denitrifying conditions. However, a few indole-mineralizing bacteria are known for anaerobic degradation of indole. More indole degrading anaerobic bacteria should be isolated to understand the mechanism of anaerobic degradation of indole.

(iv) More biochemical studies should be carried out to elucidate the metabolic pathways of degradation of 4-chloroindole and methylindole.

(v) Four major pathways of aerobic bacterial degradation of indole-3-acetic acid have been elucidated. However, the genetics of bacterial degradation pathway of indole-3-acetic acid was studied in *Pseudomonas putida* 1290 that contains *iac* gene cluster for indole-3-acetic acid degradation. Furthermore, complete characterization of *iac* genes would be very helpful to understand the mechanism of biodegradation of indole-3-acetic acid.

Conflict of Interests

The authors declare that they have no conflict of interests.

Authors' Contribution

Pankaj Kumar Arora collected all the relevant publications, arranged the general structure of the review, drafted the paper, and produced figures. Hanhong Bae and Ashutosh Shrama revised the paper.

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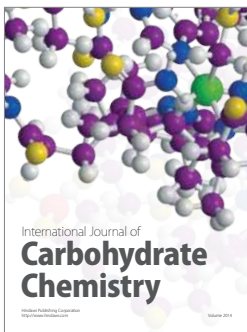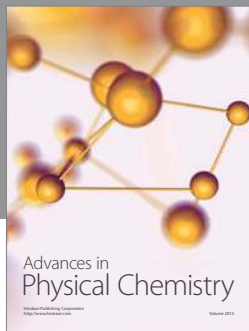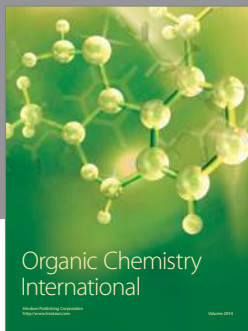## References

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