Journal of Petroleum & Environmental Biotechnology

Olajire and Essien, J Pet Environ Biotechnol 2014, 5:5
DOI: 10.4172/2157-7463.1000195

Research Article Open Access

Aerobic Degradation of Petroleum Components by Microbial Consortia

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Abstract

This article is a state–of-the-art review on the aerobic degradation of petroleum components that are commonly found in the environment. Numerous microorganisms have been isolated and their phylogeny and metabolic capacity to degrade a variety of aliphatic and aromatic hydrocarbons have been demonstrated. This review focuses on recent progress on how microbes degrade hydrocarbons and heteroaromatic components of petroleum contaminants directed towards better understanding of the aerobic degradation processes and their exploitation for bioremediation. The phylogenetic diversity of the oil-degrading microbes was also discussed.

Keywords: Petroleum components; Aerobic degradation; Microorganisms; Phylogenetic diversity; Environment

Introduction

The biodegradation of petroleum and other hydrocarbons in the environment is a complex process, whose quantitative and qualitative transformations depend on the nature and amount of the oil or hydrocarbons present, the ambient and seasonal environmental conditions, such as free or dissolved oxygen, optimum temperature for oil degradation (20–35°C), physical and/or chemical dispersion of oil, turbulent conditions as opposed to quiescent conditions, and the composition of the autochthonous microbial community [1-7]. Microbial degradation of oil has been shown to occur by attack on aliphatic or light aromatic fractions of the oil, with high-molecular-weight aromatics, resins, and asphaltenes considered to be recalcitrant or exhibiting only very low rates of biodegradation, although some studies have reported their removal at high rates under optimal conditions [8,9].

Biodegradation rates generally increase with increasing temperature such that ecosystems exposed to extremely low temperatures degrade hydrocarbons very slowly. The microbial degradation of petroleum in aquatic environments is limited primarily by nutrients such as nitrogen and phosphorus; salinity and pressure may be important in estuarine and deep-sea regions, respectively. Oxygen, nutrient concentrations, moisture, and pH are predominant factors in determining biodegradation rates in soil.

Petroleum is a complex mixture of different hydrocarbons including aliphatic (linear or branched), cycloalkanes, mono- and polyaromatics, asphaltenes and resins and majority of these compounds are stable, toxic, and carcinogenic [10,11]. Petroleum compounds such as alkanes, benzene, toluene, ethyl benzene, and xylenes (BTEX) and some polycyclic aromatic hydrocarbons (PAHs) are biodegradable under the proper environmental conditions [3,12] and low salinity marine habitats [13-16]. However, higher molecular PAHs, polycyclic aromatic sulphur heterocyclics (PASHs), methyl tertiary butyl ether (MTBE), gasoline additive and other components of petroleum products may be recalcitrant to biodegradation. The non-biodegradable components can still pose a high risk in the immediate vicinity of the area in which they remain. Petroleum hydrocarbons are therefore major contaminants in the environment and they cause damages to the surrounding ecosystems. Oil-contaminated soil, groundwater, and/or wastewater may contain a mixture of contaminant types including salts, organics, alcohols, phenols, acid, radionuclides, PAHs, and trace elements like zinc, cadmium, mercury, copper, chromium, lead etc. at widely varying concentrations [17-19]. The present review was focus on aerobic degradation process of various components of petroleum by microbial consortia. The main petroleum components discussed include aliphatics, alicyclic, and aromatics hydrocarbons as well as the N-, S-and O- heterocyclic aromatic hydrocarbons. Also addressed is the phylogenetic diversity of the oil-degrading microbes.

Biodegradation of Petroleum Compounds

Crude oil is a mixture of hydrocarbons composed of mainly heteroatomic and non-heteroatomic hydrocarbons [11]. To date many studies have reported the ability of microorganisms to utilize crude oil components as the growth substrates (Table 1). Zvyagintseva et al. [20] have reported degradation of isoprenoid and n-alkane fractions of crude oils to a significant extent by an enrichment developed from the brines of the Kalamkass oil fields in Kazakhstan. Diaz et al. [21] have enriched microbial consortia, MPD-7 and MPD-M from Cormorant oil fields in North Sea and sediments associated with mangrove roots, respectively. These cultures degraded aliphatic and aromatic hydrocarbons in crude oil. Total oil degradation by MPD-7 ranged from 20 to 38%, while MPD-M degraded much higher amount of crude oil ranging between 45 and 48%. In a subsequent study, Diaz et al. [22] have immobilized the MPD-M culture on polypropylene fibers and the culture was reported to degrade crude oil. Riis et al. [23] showed the degradation of diesel fuel by microbial communities extracted from Argentinean saline soils. In addition, these authors isolated several halotolerant bacteria of the genera *Cellulomonas*, *Bacillus*, *Dietzia*, and *Halomonas* with the ability to degrade crude oil as the carbon source. Obuekwe et al. [24] reported the isolation of *Fusarium lateritium*, *Drechslera* sp, and *Papulaspora* sp. from a salt marsh in the Kuwaiti desert that are capable of degrading crude oil as the sole carbon source. Similarly, several

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Received June 29, 2014; **Accepted** September 11, 2014; **Published** September 30, 2014

Citation: Olajire AA, Essien JP (2014) Aerobic Degradation of Petroleum Components by Microbial Consortia. J Pet Environ Biotechnol 5: 195. doi:10.4172/2157-7463.1000195

Degrader	References
Streptomyces albiaxialis	Kuznetsov et al. [28]
Enrichment culture, brines of the Kalamkass oil fields,	Zvyagintseva et al. [20]
Kazakhastan	
Marinobacter aquaeolei	Huu et al. [27]
Bacterial consortia MPD-7	Diaz et al. [21]
Rhodococcus erythropolis , Dietzia maris	Zvyagintseva et al. [29]
MPD-M culture immobilized on polypropylene fibers	Diaz et al. [22]
Fusarium lateritium, Drechslera sp.	Obuekwe et al. [24]
Microbial community, Argentinean soil	Riis et al. [23]
Cellulomonas sp. *Bacillus* sp. *Dietzia* sp. *Halomonas* sp.	Riis et al. [23]
Rhodococcus sp. *Gordonia* sp. *Dietzia* sp. *Pseudomonas* sp.	Borzenkov et al. [30]
Actinopolyspora sp. DPD1	Al-Mueini et al. [107]
Bacillus sp. strain DHT	Kumar et al. [31]
Halomonas shengliensis	Wang et al. [25]
Strain C5	Chamkha et al. [33]
Halomonas sp. C2SS100, *Pseudomonas* sp. C450R	Mnif et al. [26,32]
Haloferax sp. *Halobacterium* sp. *Halococcus* sp.	Al-Mailem et al. [111]
Amycolicicoccus subflavus DQS3-9A1	Wang et al. [34]
Marinobacter sedimentalis, *Marinobacter falvimaris*	Al-Mailem et al. [36]

Table 1: Microorganisms having degradation potential for crude oil.

authors have isolated pure cultures including *Halomonas shengliensis* [25], *Halomonas* sp. strain C2SS100 [26], *Marinobacter aquaeolei* [27], *Streptomyces albiaxialis* [28], *Rhodococcus erythropolis,* and *Dietzia maris* [29] from oil fields, production water, and other saline environments that degrade crude oil as the source of carbon. Borzenkov et al. [30] reported the isolation of several strains of hydrocarbon-oxidizing bacteria representing the genera *Rhodococcus, Gordonia, Dietzia*, and *Pseudomonas* from oil and stratal waters of Tatarstan, western Siberia, and Vietnam oil fields. All these strains oxidized *n*-alkane fraction of crude oil. A *Bacillus* sp. strain DHT, isolated from oil contaminated soil, grew and produced biosurfactant when cultured in the presence of variety of hydrocarbons including crude oil, diesel oil, hexadecane, naphthalene, pyrene, dibenzothiophene, salicylate, catechol, and phenanthrene as the sole carbon sources at 30–45°C. However, no growth occurred on toluene, phenol, 2-hydroxyquinoline and carbazole [31]. Similarly, Mnif et al. [32] have reported the isolation of several strains of thermophilic and mesophilic hydrocarbon degrading as well as biosurfactant producing organisms from Tunisian oil fields. Among these, *Pseudomonas* sp. strain C450R and *Halomonas* sp. strain C2SS100 were reported to degrade 93–96% of the aliphatic fraction of crude oil (C_{13}–C_{29}), while producing biosurfactants. Chamkha et al. [33] have isolated a strain C5 closely related to *Geobacillus pallidus* from a tyrosol degrading enrichment developed from production water from a high-temperature oil field in Tunisia. The organism degraded crude oil and diesel as the source of carbon. Wang et al. [34] have isolated a moderate halophilic actinomycete, *Amycolicicoccus subflavus* DQS3-9A1^T from oily sludge at Daqing Oil field, China with the ability to degrade crude oil. Later, Nie et al. [35] studied the genetic capability of the DQS3-9A1^T to metabolize a range of short-chain and long-chain *n*-alkanes such as propane and C_{10}–C_{36} alkanes in crude oil, respectively, as the sole carbon sources. Recently, Al-Mailem et al. [36] have isolated *Marinobacter sedimentalis* and *Marinobacter falvimaris* from soil and pond water collected from hypersaline Sabkhas in Kuwait. Isolation of these organisms was accomplished using agar plates provided with crude oil vapor as the sole source of carbon. These studies also showed that both organisms were capable of fixing atmospheric nitrogen and such potential is beneficial for effective bioremediation of petroleum compounds without the need of providing fertilizer. Biodegradations of crude oil or petroleum usually requires the cooperation of more than one single species. Individual microorganisms can metabolize only a limited range of hydrocarbon substrates, so a consortium composed of many different bacterial species with overall broad enzymatic capacities is required to increase the rate of petroleum biodegradation. Hydrocarbon degradation by microbial communities depends on the composition of the community and its adaptive response to the presence of hydrocarbons. Bacteria and fungi are the key agents of degradation, with bacteria assuming the dominant role in marine ecosystems and fungi becoming more important in freshwater and terrestrial environments. Adapted communities, i.e., those which have been previously exposed to hydrocarbons, exhibit higher biodegradation rates than communities with no history of hydrocarbon contamination. The mechanisms of adaptation which include both selective enrichment and genetic changes result in a net increase in the number of hydrocarbon utilizing organisms and in the pool of hydrocarbon-catabolizing genes within the community. Petroleum compounds differ in their susceptibility to microbial attack and generally degrade in the following order of decreasing susceptibility [37]: n-alkanes > branched alkanes > low molecular weight aromatics >cyclic alkanes, > polycyclic aromatic hydrocarbons > polar compounds. Although many of these compounds can be relatively easily degraded under soil and fresh water environments [3,12] and low salinity marine habitats [13-16]. Biodegradation rates have been shown to be highest for the saturates, followed by the light aromatics, with high-molecular-weight PAHs and polar compounds (resins and asphaltenes) exhibiting extremely low rates of degradation or may not be degraded at all [38-40].

Biodegradation of petroleum compounds in different ecosystems

In many ecosystems there is already an adequate indigenous microbial community capable of extensive oil biodegradation, provided that environmental conditions are favorable for oil-degrading metabolic activity. There are several advantages of depending on indigenous microorganisms rather than adding microorganisms to degrade hydrocarbons. First, natural populations must have developed through many years. These microorganisms are adapted for survival and proliferation in that environment. Secondly, the ability to utilize

hydrocarbons is distributed among a diverse microbial population. This population occurs in natural ecosystems and either independently or synergistically metabolizes various hydrocarbons. Many times, when the amount of microorganisms is sufficient in the contaminated environment, microbial seeding may not be required. Microorganisms (bacteria and fungi) have different rates at which they utilize and degrade hydrocarbons in the soil or water. This rate is reflected in the multiplication and colony forming units (cfu) for the isolated organisms. The use of microorganisms to degrade petroleum hydrocarbon resulting from oil spillage has been a subject of extensive research since the first publication of bacterial growth on petroleum hydrocarbons [41,42]. Several petroleum hydrocarbon degrading microorganisms have been isolated from both soil and marine sources, which are the two major environments affected by petroleum hydrocarbon pollution [43,44]. Microorganisms are equipped with metabolic machinery to use petroleum products as a carbon and energy source. The metabolic pathways that hydrocarbon-degrading heterotrophs use can be either aerobic (i.e. they utilize oxygen as the primary electron acceptor) or anaerobic (i.e. they utilize an alternative electron acceptor such as nitrate or sulfate). Aerobic degradation usually proceeds more rapidly and is considered to be more effective than anaerobic degradation because of the less free energy required for initiation and energy yield per reaction. This review mainly focuses on aerobic degradation of petroleum components in different ecosystems.

Soil ecosystem: Petroleum compounds bind to soil components, and they are difficult to be removed or degraded [45]. Petroleum contamination in soil results in an imbalance in the carbon-nitrogen ratio at the spill site, because crude oil is essentially a mixture of carbon and hydrogen. This causes a nitrogen deficiency in oil soaked soil, thus retarding the growth of bacteria and the utilization of carbon sources. Furthermore, large concentrations of biodegradable organics in the top layer soil deplete oxygen reserves in the soil and slow down the rates of oxygen diffusion into deeper layers. Many indigenous microorganisms in water and soil are capable of degrading petroleum contaminants [46,47]. Petroleum hydrocarbons in nature are degraded by diverse groups of microorganisms, which are capable of utilizing hydrocarbons as food [48]. The degradation of complex mixtures of hydrocarbons such as crude oil and metals in soil requires mixedpopulations with overall broad enzymic capacities [43,49]. Bacteria are the most active agents in petroleum degradation and they work as primary degraders of spilled oil in environment [50,51]. Several bacteria are known to feed exclusively on hydrocarbons [52].

Biodegradation of crude petroleum oil from petroleum contaminated soil from North East India was reported by Das and Mukherjee [53]. *Acinetobacter* sp. was reported to be capable of utilizing *n*-alkanes of chain length C_{10}–C_{40} as a sole source of carbon [54]. Bacterial genera, namely, *Gordonia*, *Brevibacterium*, *Aeromicrobium, Dietzia*, *3Burkholderia,* and *Mycobacterium* isolated from petroleum contaminated soil proved to be the potential organisms for hydrocarbon degradation [47,55-59]. The degradation of PAHs by *Sphingomonas* was reported by Daugulis and McCracken [56]. Tang et al [8] reported the degradation process of crude oil by one artificial microalgal-bacteria consortium. The consortium which was constructed by one axenic *Scenedesmus obliquus* named GH2 and four oil component-degrading bacteria with known complementary degradative capabilities, including *Sphingomonas* GY2B, *Burkholderia cepacia* GS3C, *Pseudomonas* GP3A and *Pandoraea pnomenusa* GP3B were reported to completely eliminate alkanes, alkylcycloalkanes and alkylbenzens in 10 and 7 days, respectively. The consortium also preferentially attacked high molecular weight PAHs such as phenanthrene and methylphenanthrenes, a lot of C_2, C_3 naphthalene isomers and some extra lower molecular substances were produced during the PAHs degradation. Chang et al. [9] investigated the extent of biodegradation of non-volatile petroleum hydrocarbons (C_{16}-C_{34}) and the associated microbial activity in predominant aggregate sizes during a pilot-scale biopile experiment conducted at 15°C, with a clayey soil, from a crude oil-impacted site in northern Canada. At the end of 65-d biopile experiment, 42% of the C_{16}-C_{34} hydrocarbons were reported to be degraded in the nutrient-amended macroaggregates, compared to 13% in the mesoaggregates. Higher microbial activity in the macroaggregates of the nutrient-amended biopile was inferred from a larger increase in extractable protein concentrations, compared to the other aggregates. Fungal genera, namely, *Amorphoteca*, *Neosartorya*, *Talaromyces,* and *Graphium* and yeast genera, namely, *Candida, Yarrowia,* and *Pichia* were isolated from petroleum contaminated soil and proved to be the potential organisms for hydrocarbon degradation [55]. Singh [60] also reported a group of terrestrial fungi, namely, *Aspergillus*, *Cephalosporium,* and *Pencillium* which were also found to be the potential degrader of crude oil hydrocarbons. Adenipekun [61] reported that *Pleurotus tuber-regium* have the ability to increase nutrient contents in soils polluted with 1 - 40% engine-oil concentration after six months of incubation and reduction in heavy metals after six months of incubation. Hence, the fungus can be employed in decontaminating environment polluted with engine oil. In a similar study, Adenipekun and Isikhuemhen [62] revealed the ability of white rot fungus, *L. squarrosulus* to improve the nutrient contents of the engine oil contaminated soil and an accumulation of Fe, Zn and Ni to an appreciable extent.

Aquatic ecosystem: In aquatic ecosystems, dispersion and emulsification of oil in slicks appear to be prerequisites for rapid biodegradation. Large masses of mousse, tar balls or high concentrations of oil in quiescent environments tend to persist because of the limited surface areas available for microbial activity. Petroleum fractions containing asphalt components are not degraded quantitatively [63]. Therefore, floating tar globules are encountred in the marine environment in increasing quantities because they are practically oxygenated high molecular weight materials that resist furher microbial degradation. When oil spill occurs, a combination of recovery, disposal and the containment of oil is performed thereafter. The conventional methods to remove oil from aquatic ecosystems include; mechanical clean up, chemical clean up and microbial degradation. Mechanical cleaning of spilled oil and dispersant is nearly impossible in "protected" ecosystems. Microbial degradation is the major mechanism for the elimination of spilled oil and dispersants from aquatic environment [64].

Hamzah et al. [65] reported three bacterial isolates identified as *Pseudomonas aeruginosa* (UKMP-8T), *Rhodococcus* sp. M15-2 (UKMP-5T), and *Rhodococcus* sp. ZH8 (UKMP-7T) isolated from groundwater of a crude oil refinery plant. From these three isolates, they designed four bacterial consortia by mixing the single bacterial cultures in the following ratios: (*P. aeruginosa*: *Rhodococcus* sp. M15-2, 1:1), (*P. aeruginosa*:*Rhodococcus* sp. ZH8, 1:1), (*Rhodococcus* sp. M15-2: *Rhodococcus* sp. ZH8, 1:1), and (*P. aeruginosa*: *Rhodococcus* sp. ZH8:*Rhodococcus* sp. M15-2, 1:1:1), respectively. These bacterial isolates and consortia were reported to show differing preferences for nitrogen source and when fortified with the preferred nitrogen sources and grown in minimal salt medium, within 7 days, all the three single isolates and the four bacterial consortia biodegraded 97.6-99.9% of Tapis Massa oil without any significant differences. Malik and Ahmed [66] investigated the degradation of petroleum hydrocarbons by an oilfield isolated bacterial consortium. They reported that the biotic

removal of alkanes was maximum, 90.96% for tridecane (C_{13}) followed by pentadecane (C_{15}) at 77.95%, octadecane (C_{18}) at 74.1%, while other alkanes showed 56 to 69% after 24 days of incubation. Among the aromatics, the micro aromatics (benzene, toluene and xylene) quickly evaporated after the 4th day of incubation, while the efficiency on polyaromatic fractions (anthracene, phenanthrene and pyrene) was 46.17 to 55.3% after 24 days.

The yeast species, namely, *Candida lipolytica, Rhodotorula mucilaginosa, Geotrichum* sp*, and Trichosporon mucoides* isolated from contaminated water were noted to degrade petroleum compounds [67,68]. Hidayat and Tachibana [69] demonstrated that *Fusarium* sp. F092 have the ability to degrade chrysene and the aliphatic fraction of crude oil contaminating liquid culture with artificial sea water (35%).

Though algae and protozoa are the important members of the microbial community in both aquatic and terrestrial ecosystems, reports on their involvement in hydrocarbon biodegradation are scanty. Walker et al. [70] isolated an alga, *Prototheca zopfi* which was capable of utilizing crude oil and a mixed hydrocarbon substrate and exhibited extensive degradation of *n*-alkanes and isoalkanes as well as aromatic hydrocarbons. Cerniglia et al. [71] also observed nine cyanobacteria, five green algae, one red alga, one brown alga, and two diatoms that could oxidize naphthalene. None of the Protozoa had been reported to utilize hydrocarbons.

The role of fungi in biodegradation process of petroleum products has been extensively studied and the most common fungi which have been recorded as a biodegrades belongs to following genera: *Alternaria, Aspergillus, Candida, Cephalosporium, Cladosporium, Fusarium, Geotrichum, Gliocladium, Mucor, Paecilomyces, Penicillium, Pleurotus, Polyporus, Rhizopus, Rhodotolura, Saccharomyces, Talaromyces and Torulopsis* [72-81].

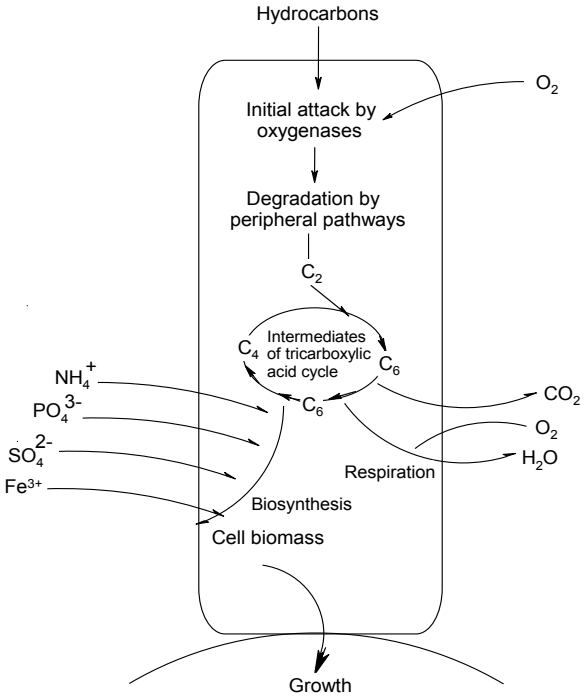


Figure 1: Main principle of aerobic degradation of hydrocarbons by microorganisms.

In the aquatic ecosystems, fungi plays an important role during their ability in removing hazardous compounds from the water, whereas sediment particles contaminated with crude oil from oil spills is one of the desired ecological niche to fungi which inhabits such substrate and use carbon source from hydrocarbons in polluted sediment particles to biodegrade crude oil from the sediments in the beaches. Fungi have been found to be better degraders of petroleum than traditional bioremediation techniques including bacteria, and although hydrocarbon degraders may be expected to be readily isolated from a petroleum oil- associated environment [80,81]. The ability of most fungi to produce extracellular enzymes for the assimilation of complex carbohydrates makes possible the degradation of a wide range of pollutants. They also have dvantage of being relatively easy to grow in fermenters, thus being suited for large scale production. Another advantage is the ease of separation of fungal biomass by filtration due to its filamentous structure. They are also less sensitive to variations in nutrients, aeration, pH, temperature and have a lower nucleic content in the biomass as compared to yeasts.

Marine ecosystem: The microbial response to an oil spill at sea is dependent on numerous factors, including the oil composition and degree of weathering, as well as environmental conditions, particularly temperature and nutrient concentrations [16]. Nevertheless, there are some typical patterns; most notable is the large increase in abundance of *Alcanivorax* spp., which degrade straight-chain and branched alkanes [84-87], followed by *Cycloclasticus* spp., which degrade PAHs [15,52,86,87].

Since the cultivation of *Alcanivorax borkumensis* [88], functional genomic, biochemical and physiological analyses have revealed the underlying basis of its success [52,89-91]. While it lacks catabolic versatility, utilising alkanes almost exclusively as carbon and energy sources, it has multiple alkane-catabolism pathways, with key enzymes including alkane hydoxylases (a non-haem diiron monooxygenase; AlkB1 and AlkB2) and three cytochrome P450-dependent alkane monooxygenases [89]. Their relative expression is influenced by the type of alkane supplied as carbon and energy source and phase of growth [89]. *Alcanivorax borkumensis* also possesses a multitude of other adaptations to access oil (e.g. synthesis of emulsifiers and biofilm formation [89] and to survive in open marine environments [87,89]. *Acinetobacter* spp., which are commonly isolated from oil-contaminated marine environments [92], also have a diverse array of alkane hydroxylase systems enabling them to metabolize both short- and long-chain alkanes [92,93].

Microbial degradation of petroleum hydrocarbons in a polluted tropical stream in Lagos, Nigeria was reported by [94]. Nine bacterial strains, namely, *Pseudomonas fluorescens, P. aeruginosa, Bacillus subtilis, Bacillus* sp., *Alcaligenes* sp., *Acinetobacter lwoffi, Flavobacterium sp., Micrococcus roseus, and Corynebacterium* sp. were isolated from the polluted stream which could be responsible for the degradation of the crude oil.

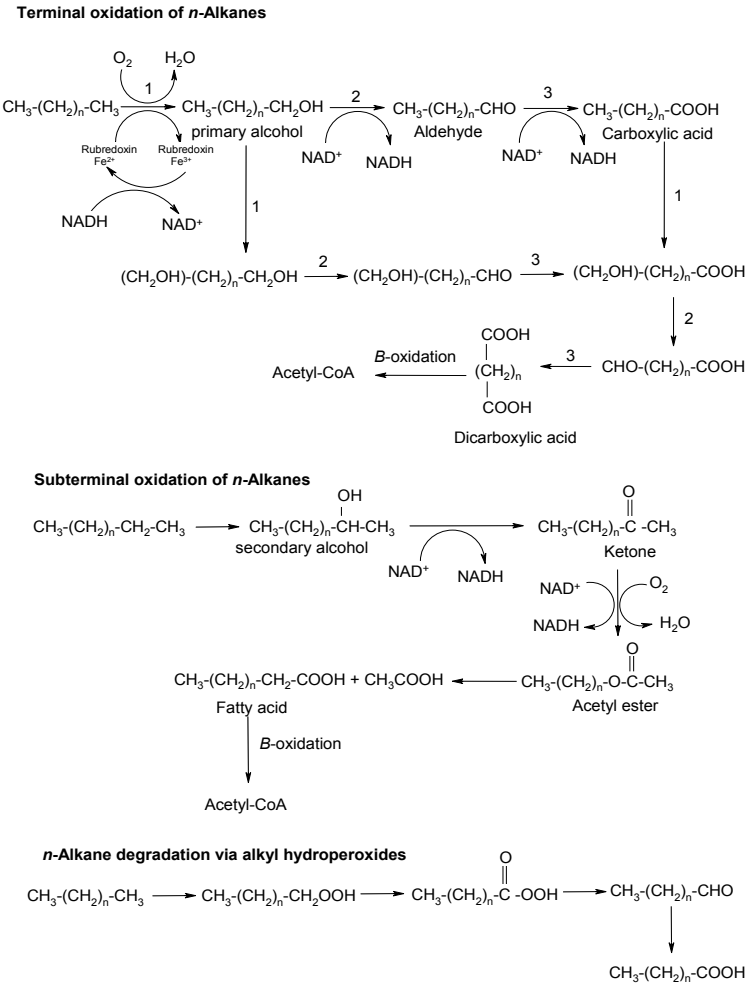
Aerobic degradation of petroleum compounds

The most rapid and complete degradation of the majority of organic pollutants is brought about under aerobic conditions. Figure 1 shows the main principle of aerobic degradation of hydrocarbons [95]. The initial intracellular attack of organic pollutants is an oxidative process and the activation as well as incorporation of oxygen which is the enzymatic key reaction catalyzed by oxygenases and peroxidases. Peripheral degradation pathways convert organic pollutants step by step into intermediates of the central intermediary metabolism, for example,

the tricarboxylic acid cycle. Biosynthesis of cell biomass occurs from the central precursor metabolites, for example, acetyl-CoA, succinate and pyruvate. Sugars required for various biosyntheses and growth are synthesized by gluconeogenesis.

Aliphatic hydrocarbons: Alkanes, a major group in crude oil, are readily biodegraded in the marine and non-marine environments. Oxidation of alkanes is classified as being terminal or sub-terminal. The degradation of alkanes of medium chain length by *Pseudomonas putida* containing the OCT plasmid is initiated by alkane hydroxylase [85,96-98]. This enzyme consists of three components: the membrane-bound oxygenase component and two soluble components called rubredoxin and rubredoxin reductase. The catalytic centre of the oxygenase component contains a dinuclear iron cluster which is also found in other enzymes such as methane monooxygenase and ribonucleotide reductase [96,99]. In *P. putida* (OCT), oxidation of the methyl group of alkanes by alkane hydroxylase yields alkanols that are further oxidized by a membrane-bound alcohol dehydrogenase to alkanals. The alkanals are subsequently transformed to fatty acids and then to acyl CoA by aldehyde dehydrogenase and acyl-CoA synthetase, respectively (Scheme 1) [99]. An alkane degrading pathway yielding secondary alcohols has also been reported. In this pathway, alkanes are oxidized by monooxygenase to secondary alcohols, then to ketones, and finally to fatty acids (Scheme 1) [100,101]. In *Acinetobacter* strain M-1, alkanes are transformed to alkyl peroxides, and these molecules would be further metabolized to the corresponding aldehyde. The first enzyme involved in this pathway contains FAD^+ and Cu^{2+} as prosthetic groups (Scheme 1) [54,102].

Many yeast species, e.g. *Candida maltosa, Candida tropicalis* and *Candida apicola*, were investigated for use with alkanes [103,104]. The first step of alkane degradation (terminal hydroxylation) and of ω- hydroxylation is catalyzed by P450 monooxygenase. The alcohols thus formed are processed by fatty alcohol oxidase and fatty aldehyde dehydrogenase. The P450 enzyme from some yeast strains can catalyze not only the terminal hydroxylation of long-chain alkanes and the ω-hydroxylation of fatty acids, but also the subsequent two steps to yield fatty acids and α, ω-dioic acids (Scheme 1) [104,105]. Catabolic pathways for the degradation of branched alkanes have been elucidated for a few bacteria; for example, *Rhodococcus* strain BPM 1613 degraded phytane (2,6,10,14-tetramethylhexadecane), norpristane (2,6,10-trimethylpentadecane) and farnesane



Scheme 1: Peripheral aerobic pathways of *n*-alkane degradation.
The main pathway is the terminal oxidation to fatty acid. α – and ω – hydroxylation is catalysed by the same set of enzymes. With bacteria, steps 1, 2, 3 are catalysed by alkane monooxygenase, fatty alcohol dehydrogenase and fatty aldehyde dehydrogenase, respectively. With yeast, step 1 is catalysed by P450 monooxygenase, while steps 2 and 3 are catalysed either by fatty alcohol oxidase and fatty aldehyde dehydrogenase, respectively; or by the P450 monooxygenase involved in step 1.

(2,6,10-trimethyldodecane) via ß-oxidation [96,106]. β-Oxidation of the fatty acids results in the formation of acetyl-CoA. Alkanes with an uneven number of carbon atoms are degraded to propionyl-CoA, which is in turn carboxylated to methylmalonyl-CoA and further converted to succinyl-CoA. The sub-terminal oxidation occurs with lower (C_3 - C_6) and longer alkanes with the formation of a secondary alcohol and subsequent ketone (Scheme 1) [95]. Branching, in general, reduces the rate of biodegradation. Methyl side groups do not drastically decrease the biodegradability, whereas complex branching chains, e.g., the tertiary butyl group, hinder the action of the degradative enzymes [95]. Al-Mueini et al. [107] have reported the isolation of an extremely halophilic actino- mycete, *Actinopolysporasp.* DPD1 from an oil production site in the Sultanate of Oman and was shown to degrade *n*-alkanes (pentadecane, eicosane, pentacoase) and fluorine. The organism efficiently degraded pentadecane (100% in 4 days) and eicosane (80% in 10 days). Degradation of longer chain alkanes such as pentacosane ($C_{25}H_{52}$) proceeded at much slower rate resulting in only 15% degradation in 2 weeks and no triacontane ($C_{30}H_{62}$) was degraded even after 20 days of incubation. Sass et al. [108] isolated a strain DS-1, closely related to *Bacillus aquimaris* from Discovery deep-sea hypersaline anoxic sediment that grew using *n*-alkanes (*n*-dodecane and *n*-hexadecane) as the sole sources of carbon. Mnif et al. [26,32] isolated *Halomonas sp*. strain C2SS100 and *Pseudomonas* sp.strain C450R on the basis of their ability to degrade crude oil also degraded hexadecane as the sole carbon source. Dastgheib et al. [109] have isolated a halotolerant *Alcanivorax* sp. strain Qtet3 from tetracosane degrading enrichments obtained from a hydrocarbon contaminated soils from Qom location in Iran. Strain Qtet3 degrades a wide range of *n*-alkanes (from C_{10} to C_{34}) with considerable growth on C_{14} and C_{16}. Strain Qtet3 completely degraded tetracosane ($C_{24}H_{50}$) as the sole carbon source in 20 days. In addition, the organism also degrades phytane and pristine, but not aromatic hydrocarbons such as naphthalene, phenanthrene, pyrene, and anthracene. Also, two Marinobacters, *M. sedimentalis* and *M. falvimaris* isolated on the basis of their ability to grow on crude oil from hypersaline Sabkhas in Kuwait also utilized Tween 80 and a wide range of individual aliphatic hydrocarbons (C_9–C_{40}) as carbon sources [36]. Tapilatu et al. [110] have reported the isolation of several strains of archaea that degrade *n*-alkanes (heptadecane and eicosane) from a shallow crystallizer pond (Camargue, France) with no known contamination history. Of these isolates, strain, MSNC2 was closely

Hydrocarbon	Structure	Degrader	References
Octane	C_8H_{18}	*Rhodococcus* sp. *Arthrobacter* sp. *Bacillus* sp.	Plotnikova et al. [139,140]
Decane	$C_{10}H_{22}$	*Bacillus* sp strain *DHT*	Kumar et al. [31]
Tetradecane	$C_{14}H_{30}$	EH4 (*Haloarcula vallismortis*)	Bertrand et al. [227]
Pentadecane	$C_{15}H_{32}$	*Actinopolyspora* sp.	Al-Mueini et al. [107]
		Marinobacter aquaeolei	Huu et al. [27]
Hexadecane	$C_{16}H_{34}$	Enrichment, Great Salt Lake, Utah	Ward and Brock [228]
		EH4 (*Haloarcula vallismortis*)	Bertrand et al. [227]
		Marinobacter hydrocarbonoclasticus	Gauthier et al. [229]
		Marinobacter aquaeolei	Huu et al. [27]
		Bacillus sp strain DHT	Kumar et al. [31]
		Strain DS1	Sass et al. [108]
		Halomonas sp C2SS100 *Pseudomonas* sp. C450R	Mnif et al. [26]
Octadecane	$C_{18}H_{38}$	Microbial mats	Abed et al. [230]
		Haloferax sp. *Halobacterium* sp.	Al-Mailem et al. [111]
		Halococcus sp.	
Heptadecane	$C_{17}H_{36}$	*Haloarcula* sp. *Haloferax* sp.	Tapilatu et al. [110]
Pristane	$C_{19}H_{40}$	EH4 (*Haloarcula vallismortis*)	Bertrand et al. [227]
		Marinobacter hydrocarbonoclasticus	Gauthier et al. [229]
		Marinobacter aquaeolei	Huu et al. [27]
		Microbial mats, Arabian Gulf coast, Saudi Arabia	Abed et al. [230]
		Alcanivorax sp. Qtet3	Dastgheib et al. [109]
Eicosane	$C_{20}H_{42}$	EH4 (*Haloarcula vallismortis*)	Bertrand et al. [227]
		Marinobacter hydrocarbonoclasticus	Fernandez-Linares et al. [231]
		Actinopolyspora sp. DPD1	Al-Mueini et al. [107]
		Haloarcula sp. *Haloferax* sp.	Tapilatu et al. [110]
Phytane	$C_{20}H_{42}$	*Alcanivorax* sp. strain Qtet3	Dastgheib et al. [109]
Heneicosane	$C_{21}H_{44}$	EH4 (*Haloarcula vallismortis*)	Bertrand et al. [227]
		Marinobacter hydrocarbonoclasticus	Gauthier et al. [229]
Tetracosane	$C_{24}H_{50}$	*Alcanivorax* sp. strain Qtet3	Dastgheib et al. [109]
Pentacosane	$C_{25}H_{52}$	*Actinopolyspora* sp. DPD1	Al-Mueini et al. [107]
n-Alkane	C_{10}–C_{30}	*Halobacterium* sp	Kulichevskaya et al. [232]
	C_{10}–C_{34}	*Haloferax* sp. *Halobacterium* sp. *Halococcus* sp.	Al-Mailem et al. [111]
	C_{10}–C_{34}	*Alcanivorax* sp. strain Qtet3	Dastgheib et al. [109]
	C_9–C_{40}	*Marinobacter sedimentalis*	Al-Mailem et al. [36]
		Marinobacter falvimaris	

Table 2: Microorganisms having degradation potential for aliphatic hydrocarbons.

related to *Haloarcula* and strains, MSNC4, MSNC14, and MSNC16 to *Haloferax*. In addition, strain MSNC14 also degraded phenanthrene. Three extremely halophilic archaeal strains, *Haloferax*, *Halobacterium* and *Halococcus* isolated on the basis of crude oil utilization also degraded *n*-alkanes and mono and polyaromatic compounds as the sole sources of carbon and energy [111]. Overall, studies reveal that both bacteria and archaea have the capacity to metabolize *n*-alkanes with varying chain lengths (Table 2).

Alicyclic hydrocarbons: Cycloalkanes representing minor components of mineral oil are relatively recalcitrant to microbial attack [95]. The absence of an exposed terminal methyl group as in *n*-alkanes complicates the primary attack. A few species are able to use cyclohexane as sole carbon source. Cycloalkanes, including condensed cycloalkanes are degraded by a co-oxidation mechanism [96,101,112]. The mechanism of cyclohexane degradation is shown in Scheme 2. The formation of a cyclic alcohol and a ketone has been observed [101]. A monooxygenase introduces an oxygen into the cyclic ketone, and the cyclic ring is cleaved (Scheme 2).

Aromatic compounds: A multitude of catabolic pathways for the degradation of aromatic compounds have been elucidated; for example, toluene is degraded by bacteria along five different pathways. On the pathway encoded by the TOL plasmid, toluene is successively degraded to benzyl alcohol, benzaldehyde and benzoate, which is further transformed to the TCA cycle intermediates [13]. The first step of toluene degradation with *P. putida* F1 is the introduction of two hydroxyl groups to toluene, forming *cis*-toluene dihydrodiol. This intermediate is then converted to 3-methylcatechol [113]. With *Pseudomonas mendocina* KR1, toluene is converted by toluene 4-monooxygenase to *p*-cresol, this being followed by *p*-hydroxybenzoate formation through oxidation of the methyl side chain [13,114]. With *Pseudomonas pickettii* PKO1, toluene is oxidized by toluene 3-monooxygenase to *m*-cresol, which is further oxidized to 3-methylcatechol by another monooxygenase [13,114]. With *Bukholderia cepacia* G4, toluene is metabolized to *o*-cresol by toluene 2-monooxygenase, this intermediate being transformed by another monooxygenase to 3-methylcatechol [13].

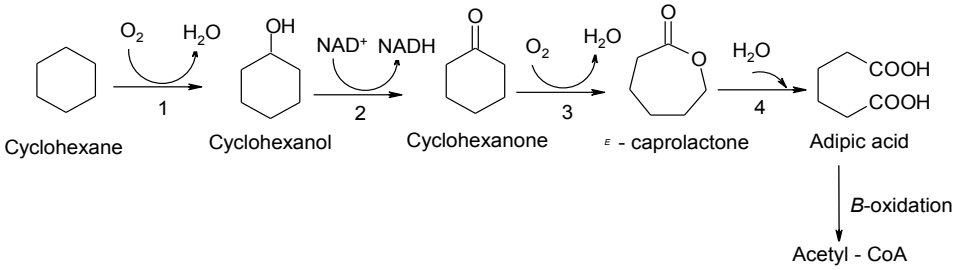
Burkholderia sp. strain JS150 is unique in using multiple pathways for the metabolism of toluene (Scheme 3) [115].

The oxygenolytic cleavage of the aromatic ring occurs via *o*- or *m*-cleavage [116]. The metabolism of a wide spectrum of aromatic compounds by one species requires the metabolic isolation of intermediates into distinct pathways. The key enzymes of the degradation of aromatic substrates are induced and synthesized in appreciable amounts only when the substrate or structurally related compounds are present. Scheme 4 shows the pathways of the oxygenolytic ring cleavage of phenol to intermediates of the central metabolism. At the branch-point, catechol is either oxidized by the intradiol *o*-cleavage, or the extradiol *m*-cleavage. Both ring cleavage reactions are catalyzed by specific dioxygenases. The product of the *o*-cleavage – *cis, cis*-muconate – is transferred to the unstable enollactone, which is in turn hydrolyzed to oxoadipate. This dicarboxylic acid is activated by transfer to CoA, followed by the thiolytic cleavage to acetyl-CoA and succinate. Protocatechuate is metabolized by a homologous set of enzymes. The additional carboxylic group is decarboxylated and, simultaneously, the double bond is shifted to form oxoadipate enollactone [95].

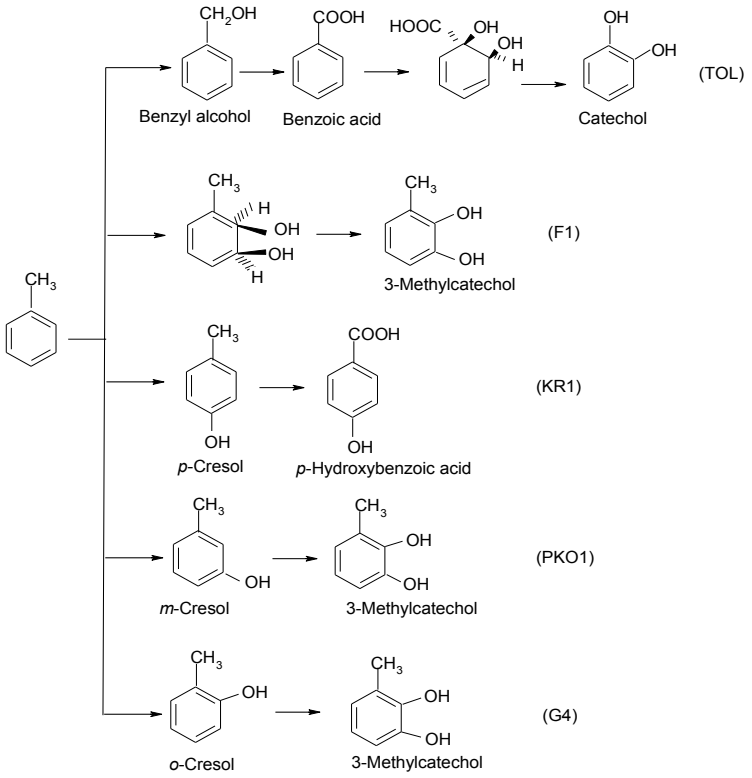
The oxygenolytic *m*-cleavage yields 2- hydroxymuconic semialdehyde, which is metabolized by the hydrolytic enzymes to formate, acetaldehyde, and pyruvate (Scheme 4). These are then utilized in the central metabolism. In general, a wealth of aromatic substrates is degraded by a limited number of reactions, which include hydroxylation, oxygenolytic ring cleavage, isomerization, and hydrolysis [117-120]. The inducible nature of the enzymes and their substrate specificity enable bacteria with a high degradation potential, e.g., *Pseudomonads* and *Rhodococci*, to adapt their metabolism to the effective utilization of substrate mixtures in polluted soils and to grow at a high rate.

Several studies have successfully isolated bacteria and archaea that degrade oxygenated aromatics. Table 3 lists organisms that degrade oxygenated hydrocarbons. Woolard and Irvine [121] showed that a halophile isolated from a mixed culture obtained from a saltern at GSL Utah readily degraded phenol. Alva and Peyton [122] isolated a haloalkaliphile, *Halomonas campisalis* near Soap Lake in central Washington and showed that this organism degraded phenol and catechol as the sole sources of carbon at pH 8–11. A Gram-positive halophilic bacterium, *Thalassobacillus devorans* isolated from an enrichment culture developed from saline habitats in southern Spain was shown to degrade phenol [123]. The strain C5, closely related to *Geobacillus pallidus* isolated from a tyrosol-utilizing enrichment also degrades a variety of other oxygenated aromatic compounds including benzoic, *p*-hydroxybenzoic, protocatechuic, vanillic, *p*-hydroxyphenylacetic, 3,4-dihydroxyphenylacetic, cinnamic, ferulic, phenol, and *m*-cresol. However, no degradation of non-oxygenated hydrocarbons such as toluene, naphthalene, and phenanthrene was observed [33]. Recently, Bonfá et al. [124] have shown the degradation of phenol as the sole source of carbon by *Halomonas organivorans*, *Arhodomonas aquaeolei*, and *Modicisalibacter tunisiensis* isolated from different hypersaline environments.

Many reports also exist on the ability of halophilic and halotolerant organisms to degrade benzoates. The halotolerant, *Pseudomonas*



Scheme 2: Peripheric metabolic pathway for the aerobic degradation of cyclohexane.
1, cyclohexane monooxygenase; 2, cyclohexanol dehydrogenase; 3, cyclohexanone monooxygenase; 4, ε-caprolactone hydrolase.

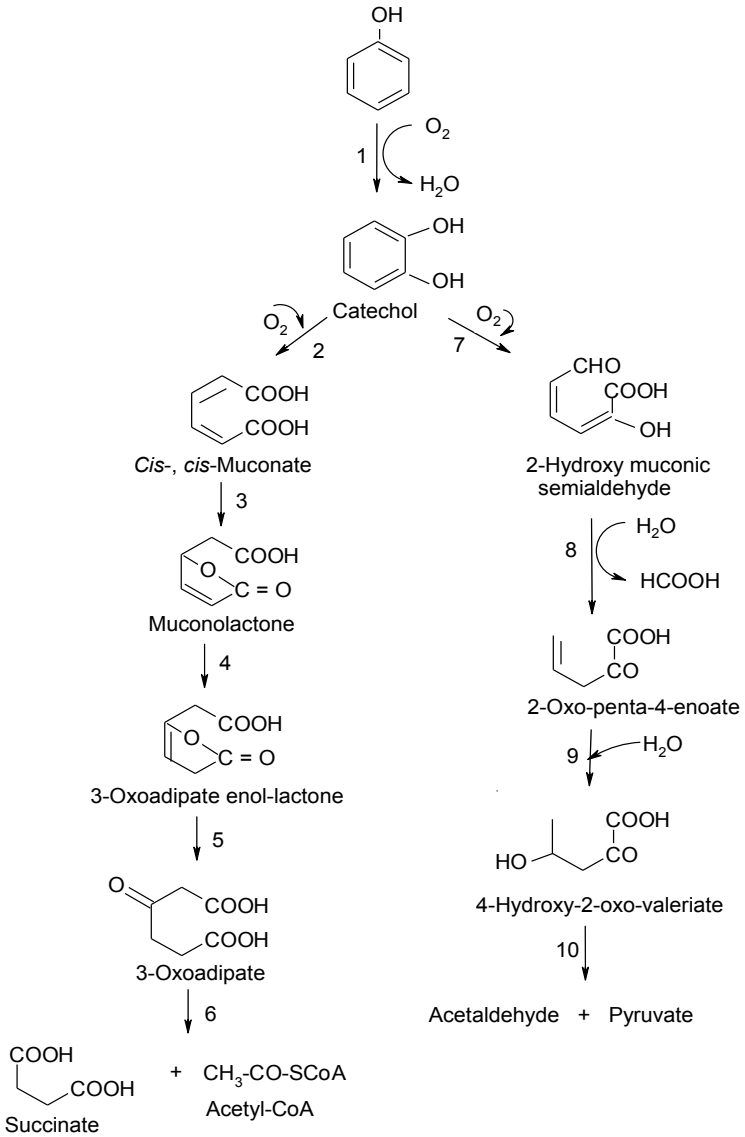


Scheme 3: Divergent pathways for aerobic degradation of toluene.
The pathways from top to bottom are found with *P. putida* (TOL), *P. putida* (F1), *P. mendocina* (KR1), *P. pickettii* (PKO1) and *B. cepacia* (G4), respectively.

halodurans (re-classified as *Halomonas halodurans*) degrades benzoic acid [125]. Garcia et al. [126,127] have isolated several strains of *Halomonas* spp. including the *Halomonas organivorans* from water and sediment of salterns and hypersalines oils collected in different part of the Southern Spain. These isolates degraded a wide range of aromatic compounds including benzoic acid, *p*-hydroxy benzoic acid, phenol, salicylic acid, *p*-aminosalicylic acid, phenylacetic acid, phenylpropionic acid, cinnamic acid, ferulic acid, and *p*-coumaric acid as the sole sources of carbon. Abdelkafi et al. [128] have reported the isolation of a *p*-coumaric acid degrading *Halomonas* strain IMPC from a *p*-coumaric acid degrading enrichment culture obtained from a Table-olive fermentation rich in aromatic compounds. This strain converted *p*-coumaric acid to *p*-hydroxybenzaldehyde, *p*-hydroxybenzoic acid, and then to protocatechuic acid prior to ring cleavage. In addition, the strain also degraded other lignin-related compounds such as cinnamic acid, *m*-coumaric acid, *m*- and *p*-methoxy cinnamic acid, *m*- and *p*- methylcinnamic acid, and ferulic acid to their corresponding benzoic acid derivatives. Oie et al. [129] have studied the degradation of benzoate and salicylate by *Halomonas campisalis* isolated from an alkaline Soap Lake. This study showed that the organism degraded benzoate and salicylate to catechol and then to *cis*, *cis*-muconate thus indicating degradation *via* the *ortho*-cleavage pathway. Kim et al. [130] have isolated a *Chromohalobacter* sp. strain HS-2 from salted fermented clams that degrades benzoate and *p*-hydroxybenzoate as the sole carbon and energy sources.

Cuadros-Orellana et al. [131] have reported the isolation of 10 halophilic archaea from Dead Sea that degrades *p*-hydroxybenzoic acid as the sole carbon and energy source. In addition, strain L1, a member of the unclassified Halobacteriaceae family of the phylum, *Euryarchaeota* also degrades benzoic acid to gentisate. Erdogmus et al. [132] reported the ability of many archaeal strains belonging to *Halobacterium*, *Haloferax*, *Halorubrum*, and *Haloarcula* group to degrade *p*-hydroxybenzoic acid. These studies clearly demonstrate that archaea that metabolize *p*-hydroxybenzoic are wide spread in the environment. Among bacteria, *Halomonas* spp. has been frequently reported for their ability to degrade phenolics and benzoates and only few reports exist on their potential to degrade non-oxygenated hydrocarbons.

The most abundant hydrocarbons in produced water are the one-ring aromatic hydrocarbons, benzene, toluene, ethyl benzene, and xylenes (BTEX) and low molecular weight saturated hydrocarbons [133]. Benzene is a category A carcinogen. Leakage from produced water storage tanks, pipelines, spills, and seepage from surface contaminated sites can cause major BTEX contamination [10]. BTEX are relatively highly soluble in water and hence can contaminate large volumes of ground water. Although there have been many recent reports on the biodegradation of non-oxygenated hydrocarbons, only few reports exist on the biodegradation of BTEX compounds (Table 4). Nicholson and Fathepure [134,135] have reported the degradation of BTEX in microcosms established with soil samples from an oilfield and from an uncontaminated salt flat in Oklahoma. Hassan et al. [136] have reported the isolation of *Alcanivorax* sp. HA03 from soda lakes in Wadi E1Natrun capable of degrading benzene, toluene, and chlorobenzene as the sole sources of carbon. This observation that Alcanivorax can also degrade aromatic compounds expands the metabolic capability of this group of organisms because Alcanivorax



Scheme 4: The two alternative pathways of aerobic degradation of phenol: *o*- and *m*- cleavage. *1, phenol monoxygenase; 2, catechol 1,2-dioxygenase; 3, muconate lactonizing enzyme; 4, muconolactone isomerase; 5, oxoadipate enol-lactone hydrolase; 6, oxoadipate succinyl- CoA transferase; 7, catechol 2,3-dioxygenase; 8, hydroxymuconic semialdehyde hydrolase; 9, 2-oxopent-4- enoic acid hydrolase; 10, 4-hydroxy-2- oxovalerate aldolase*.

are primarily known for their ability to degrade aliphatic hydrocarbons. Degradation of benzene was also reported in archaea. For example, the crude oil degrading *Haloferax*, *Halobacterium*, and *Halococcus* isolated from a hypersaline Arabian Gulf coast degraded benzene as the sole source of carbon [111].The complete degradation of PAHs requires a community of microorganisms. PAHs are taken up by microorganisms and are activated in aerobic metabolism by insertion of two oxygen atoms by bacteria and green algae to produce either cis-dihydrodiols or phenols [137]. Simple PAHs such as naphthalene, biphenyl and phenanthrene are readily degraded aerobically. The degradation of these compounds is generally initiated by dihydroxylation of one of the PAH rings, this being followed by cleavage of the dihydroxylated ring. Ring hydroxylation is catalyzed by a multi-component dioxygenase which consists of a reductase, a ferredoxin, and an iron sulphur protein, while ring cleavage is generally catalyzed by an iron-containing meta-cleavage enzyme. The carbon skeleton produced by the ring-cleavage reaction is then dismantled, before cleavage of the second aromatic ring (Scheme 5) [138].

Plotnikova et al. [139,140] have isolated *Pseudomonas* sp., *Rhodococcus* sp., *Arthrobacter* sp., and *Bacillus* sp. from soil and sediment contaminated with waste generated by chemical and salt-producing plants. All these isolates degraded naphthalene and salicylate as the sole carbon sources. In addition, some of these organisms also grew on phenanthrene, biphenyl, *o*-phthalate, gentisate, octane, and phenol as the sole sources of carbon. Zhao et al. [141] have shown the degradation of phenanthrene by a halophilic bacterial consortium developed from soil samples collected from the Shengli Oilfield in China. Phenanthrene was completely degraded by the enrichment in 8 days. Molecular analysis of the enrichment culture indicated the presence of *alpha* and *gamma-proteobacteria* including members of the genus *Halomonas*, *Chromohalobacter, Alcanivorax, Marinobacter,*

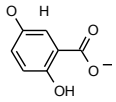
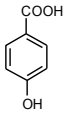
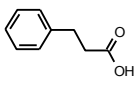
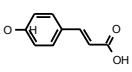
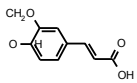
Hydrocarbon	Structure	Degrader	References
Phenol		Halophilic isolate *Halomonas* sp. *Candida tropicals Halomonas campisalis Halomonas organivorans Thelassobacillusdevorans Arthrobacter* sp. Strain C5 *Halomonas organivorans*, *Arhodomonas aquaeolei*, *Modicisalibacter tunisiensis*	Woolard and Irvine [121] Hinteregger and Streischsberg [233] Bastos et al. [234] Alva and Peyton [122] Garcia et al. [126,127] Garcia et al. [123] Plotnikova et al. [140] Chamkha et al. [33] Bonfá et al. [124]
Benzoate		*Halomonas halodurans* *Haloferax* sp. D1227 *Halomonas* sp. *Halomonas organivorans Halomonas campisalis Chromohalobacter* sp. strainHS-2 *Haloferax* sp. Strain C5 *Halomonas elongate Halomonas eurihalina Marinobacter lipolyticus*	Rosenberg [125] Emerson et al. [235] Kleinsteuber et al. [236] Garcia et al. [126,127] Oie et al. [129] Kim et al. [130] Bonfá et al. [144] Chamkha et al. [33] Garcia et al. [123]
		*Pseudomonas* sp. *Rhodococcus* sp. *Arthrobacter* sp. *Bacillus* sp. *Halomonas organivorans Halomonas organivorans, Salinicoccus roseus Halomonas venusta Halomonas alimentaria Halomonas campisalis Bacillus* sp. strainDHT *Haloferax* sp.	Plotnikova et al. [139] Garcia et al. [126] Garcia et al. [127] Oie et al. [129] Kumar et al. [31] Bonfá et al. [144]
o-Phthalate		*Rhodococcus* sp. *Arthrobacter* sp. *Bacillus* sp.	Plotnikova et al. [139,140]
Gentisate		*Rhodococcus* sp. *Arthrobacter* sp. *Bacillus* sp.	Plotnikova et al. [139]
4-Hydroxy-benzoate		*Haloarcula* sp. strainD1, *Halomonas organivorans Halomonas elongate* Halophilic archaeal strains *Chromohalobacter* sp. strainHS-2 Strain C5 *Haloferax* sp. *Halobacterium* sp. *Haloferax* sp. *Halorubrum* sp. *Haloarcula* sp.	Fairley et al. [237] Garcia et al. [126] Garcia et al. [127] Cuadros-Orellana et al. [131,238] Kim et al. [130] Chamkha et al. [33] Bonfá et al. [144] Erdogmus et al. [132]
Phenyl propionic acid		*Haloferax* sp. D1227 *Halomonas organivorans Halomonas elongata Halomonas glaciei Halomonas organivorans*	Emerson et al. [235]; Fu and Oriel [239] Garcia et al. [123] Garcia et al. [126,127]
Cinnamic acid		*Haloferax* sp. D1227 *Halomonas organivorans Halomonas organivorans Halomonas salina/Halomonashalophila Halomonas elongate Halomonas* strain IMPC Strain C5	Emerson et al. [219] Garcia et al. [114] Garcia et al. [115] Abdelkafi et al. [128] Chamkha et al. [32]
p-Coumaric acid		*Halomonas organivorans* *Halomonas organivorans Halomonas salina Chromohalobacter israelensis Halomonas* strain IMPC Strain C5	Garcia et al. [112] Garcia et al. [113] Abdelkafi et al. [128] Chamkha et al. [33]
Ferulic acid		*Halomonas organivorans* *Halomonas* strain IMPC *Halomonas elongate* Strain C5	Garcia et al. [126] Abdelkafi et al. [128] Garcia et al. [123] Chamkha et al. [33]

Table 3: Microorganisms having degradation potential for phenolics and benzoates.

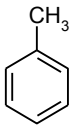
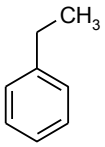
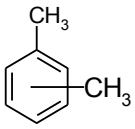
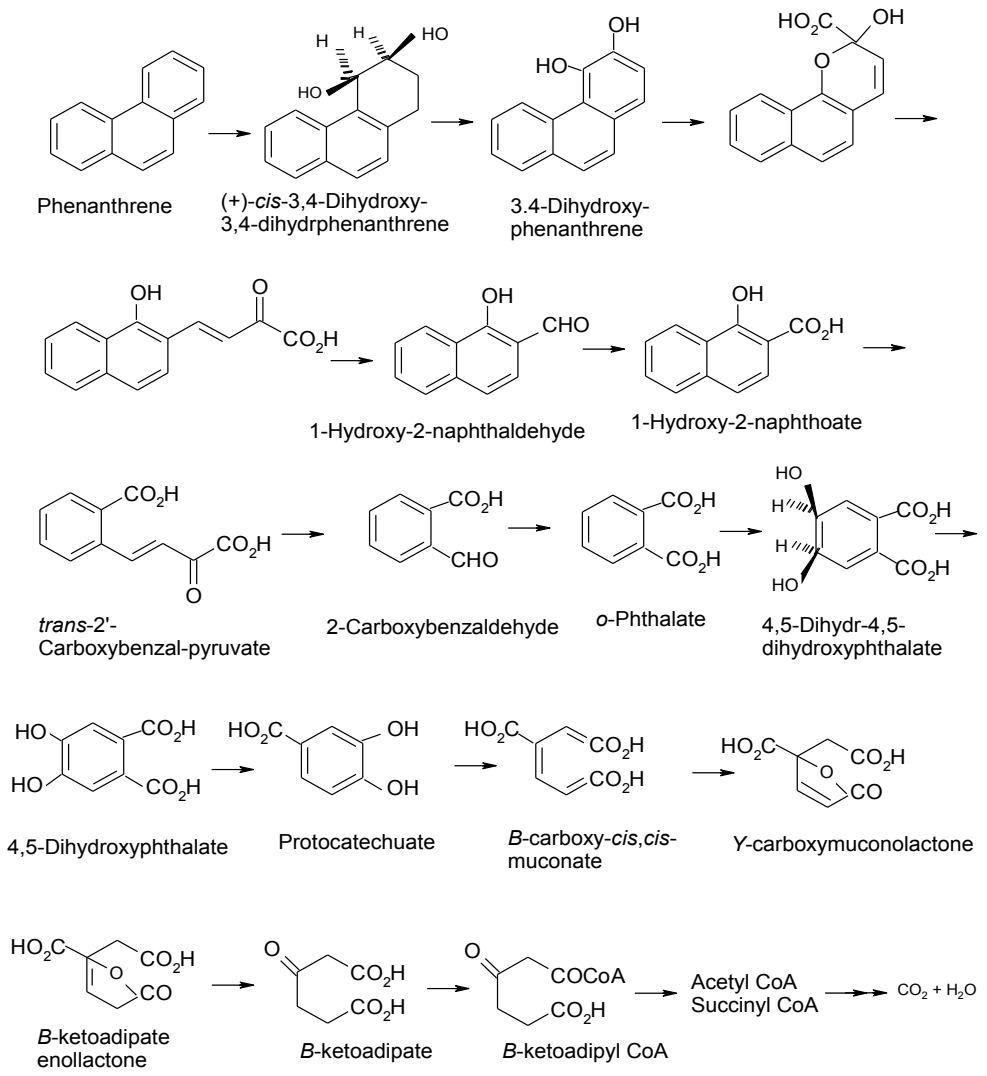
Hydrocarbon	Structure	Degrader	References
Benzene		Enrichment, Oilfield Oklahoma Enrichment, Great Salt Plains, Oklahoma *Planococcus* sp. strainZD22 *Arhodomonas* sp. strainSeminole Enrichment, Rozel Point, Great Salt Lake, Utah *Arhodomonas* sp. strainRozel *Marinobacter vinifirmus, M. hydrocarbonoclasticus Haloferax* sp.*Halobacterium* sp. *Halococcus* sp. *Alcanivorax* sp.HA03 *Marinobacter sedimentalis*, *Marinobacter falvimaris*	Nicholson and Fathepure [134] Nicholson and Fathepure [135] Li et al. [240] Nicholson and Fathepure [241], Dalvi et al. [242] Sei and Fathepure [243] Azetsu et al. [244], Dalvi et al. [242] Berlendis et al. [245] Al-Mailem et al. [111] Hassan et al. [136] Al-Mailem et al. [36]
Toluene		Enrichment, oilfield soil, Oklahoma Enrichment, Great Salt Plains, Oklahoma *Planococcus* sp. strainZD22 *Arhodomonas* sp. strainSeminole Enrichment, Rozel Point, Great Salt Plains, Utah *Arhodomonas* sp. strainRozel *Marinobacter vinifirmus, M.hydrocarbonoclasticus Haloferax* sp. *Halobacterium* sp. *Halococcus sp.* *Alcanivorax* sp.HA03 3–15	Nicholson and Fathepure [134] Nicholson and Fathepure [135] Li et al. [240] Nicholson and Fathepure [241], Dalvi et al. [242] Sei and Fathepure [243] Azetsu et al. [244], Dalvi et al. [242] Berlendis et al. [245] Al-Mailem et al. [111] Hassan et al. [136]
Ethylbenzene		Enrichment, oilfield soil, Oklahoma *Planococcus* sp. strainZD22 *Marinobacter vinifirmus, M.hydrocarbonoclasticus*	Nicholson and Fathepure [134] Li et al. [240] Berlendis et al. [245]
Xylene		Enrichment, oilfield soil, Oklahoma *Planococcus* sp. strainZD22 *Marinobacter vinifirmus, M.hydrocarbonoclasticus*	Nicholson and Fathepure [134] Li et al. [240] Berlendis et al. [245]

Table 4: Microorganisms having degradation potential for benzene, toluene, ethylbenzene and xylenes (BTEX).

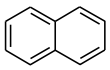
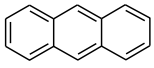
Idiomarina, and Thalassospira. Dastgheib et al. [142] have obtained a mixed culture (Qphe-SubIV) consisting of *Halomonas* sp. and *Marinobacter* sp. from hydrocarbon contaminated saline soil collected from five different regions in Iran. These organisms degraded several PAHs including naphthalene, phenanthrene, anthracene, fluoranthene, fluorine, pyrene, benz[a]anthracene, and benzo[a]pyrene as the sole carbon sources. Recently, Al-Mailem et al. [36] have reported the ability of *Marinobacter sedimentalis* and *Marinobacter falvimaris* isolated from hypersaline sabkhas to degrade biphenyl, phenanthrene, anthracene and naphthalene as the sole sources of carbon and energy. More recently, Gao et al. [143] have isolated

Marinobacter nanhaiticus strain D15-8W from a phenanthrene-degrading enrichment obtained from sediment from the South China Sea. The strain D15-8W degrades naphthalene, phenanthrene or anthracene as the sole source of carbon. Bonfá et al. [144] have isolated several strains of *Haloferax* that degrade a mixture of the PAHs including naphthalene, anthracene, phenanthrene, pyrene and benzo[a] anthracene. Extremely halophilic archaeal strains of *Haloferax*, *Halobacterium*, and *Halococcus* isolated from a hypersaline coastal area of the Arabian Gulf not only degraded crude oil and *n*-octadecane as the carbon sources, but also grew on phenanthrene [111]. Erdogmu¸s et al. [132] showed the degradation of naphthalene, phenanthrene and pyrene as the sole carbon sources by several archaeal strains including *Halobacterium piscisalsi*, *Halorubrum ezzemoulense*, *Halobacterium salinarium*, *Haloarcula hispanica*, *Haloferax* sp. *Halorubrum* sp. and *Haloarcula* sp. isolated from brine samples of Camalt Saltern in Turkey. All these studies demonstrate the potential of bacteria and archaea to degrade PAHs (Table 5).

Numerous works have been done on the use of fungi for biodegradation of petroleum hydrocarbons [38,44,78,116,145]. Most filamentous fungi is unable to totally mineralize aromatic hydrocarbons; but only transform them into indirect products of lowered toxicity and increased susceptibility to decomposition with the use of bactetria. Among the filamentous fungi capable of aliphatic hydrocarbon biodegradation include *Cladophialophoria* and *Aspergillus*, whereas fungi belonging to *Cunninghamella*, *Penicillimum*, *Fusarium* and *Aspergillus* are capable of degrading aromatic hydrocarbons. Prenafela-Boldu et al. [2,116] have reported the use of *Cladophialophoria sp.* fungi in monoaromatic hydrocarbons (BTEX) mineralization. Their results showed that the decomposition is more dynamic for toluene, ethylbenzene and m-xylene than for benzene. Common fungi with ability of biodegradation of aromatic compounds (BTEX, PAH) include *Phanerochaete chrysosporum*. This fungus produces extracellular enzymes (lignic peroxydase) that participate in decomposition of a lignic cell –wall in plants and in oxygenation of various xenobiotics. The microorganism transforms PAH into chinone derivative and later splits the aromatic ring of chinones with their complete mineralization in consecutive stages. Flayyih and AI- Jawhari [146] investigated the abilities of four fungi isolated from indigenously polluted soil to utilize petroleum hydrocarbon as their source. Of all the fungal isolates obtained in their study *Aspergillus niger*, *Aspergillus fumigatus*, *Fusarium solani*



Scheme 5: Catabolic pathway for the aerobic degradation of phenanthrene with *Nocardioides sp.* KP7.

Hydrocarbon	Structure	Degrader	References
Naphthalene		*Micrococcus* sp. *Pseudomonas* sp. *Alcaligenes* sp. *Pseudomonas* sp. *Rhodococcus* sp. *Arthrobacter* sp. *Bacillus* sp. *Bacillus* sp strainDHT *Haloferax* sp. *Halobacterium* sp. *Halococcus* sp. *Haloferax* spp. *Arthrobacter* spp. SN17 Mixed culture (Qphe-SubIV) *Marinobacter sedimentalis Marinobacter falvimaris Marinobacter nanhaiticus* *Halobacterium piscisalsi*, *Halorubrum ezzemoulense*, *Halobacterium salinarium*, *Haloarcula hispanica Haloferax* sp. *Halorubrum* sp. *Haloarcula* sp.	Ashok et al. [246] Plotnikova et al. [139,140] Kumar et al. [31] Al-Mailem et al. [111] Bonfá et al. [144] Plotnikova et al. [140] Dastgheib et al. [142] Al-Mailem et al. [36] Gao et al. [143] Erdogmus et al. [132]
Anthracene		EH4 (*Haloarcula vallismortis)* *Micrococcus* sp. *Pseudomonas* sp. *Alcaligenes* sp. *Haloferax* spp Mixed culture (Qphe-SubIV) *Marinobacter sedimentalis* *Marinobacter falvimaris* *Marinobacter nanhaiticus*	Bertrand et al. [227] Ashok et al. [246] Bonfá et al. [144] Dastgheib et al. [142] Dastgheib et al. [142] Gao et al. [143]

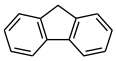
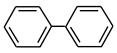
Phenanthrene		EH4 *(Haloarcula vallismortis)* *Micrococcus* sp. *Pseudomonas* sp. *Alcaligenes* sp. *Pseudomonas* sp. *Arthrobacter* sp. Microbial consortium, Shengli Oilfield, China *Haloferax* sp *Haloferax* sp. *Halobacterium* sp.	Bertrand et al. [227] Ashok et al. [246] Plotnikova et al. [139,140] Zhao et al. [141] Tapilatu et al. [110] Al-Mailem et al. [111] Bonfá et al. [144]
		Halococcus sp. *Haloferax* spp. Mixedculture(Qphe-SubIV) *Marinobacter sedimentalis Marinobacter falvimaris Marinobacter nanhaiticus* *Halobacterium piscisalsi*, *Halorubrum ezzemoulense*, *Halobacterium salinarium*, *Haloarcula hispanica Haloferax* sp. *Halorubrum* sp. *Haloarcula* sp.	Dastgheib et al. [142] Al-Mailem et al. [36] Gao et al. [143] Erdogmus et al. [132]
Acenaphthene		EH4 (*Haloarcula vallismortis)*	Bertrand et al. [227]
Fluorene		*Actinopolyspora* sp. DPD Mixed culture(Qphe-SubIV)	Al-Mueini et al. [107] Dastgheib et al. [142]
Pyrene		*Bacillus* sp strainDHT *Haloferax* spp. Mixedculture(Qphe-SubIV) *Halobacterium piscisalsi*, *Halorubrum ezzemoulense*, *Halobacterium salinarium*, *Haloarcula hispanica Haloferax* sp. *Halorubrum* sp. *Haloarcula* sp.	Kumar et al. [31] Bonfá et al. [144] Dastgheib et al. [142] Erdogmu¸s et al. [132]
Biphenyl		*Rhodococcus* sp. *Arthrobacter* sp. *Haloferax* sp. *Halobacterium* sp. *Halococcus Marinobacter sedimentalis Marinobacter falvimaris*	Plotnikova et al. [139,140] Al-Mailem et al. [111] Al-Mailem et al. [36]

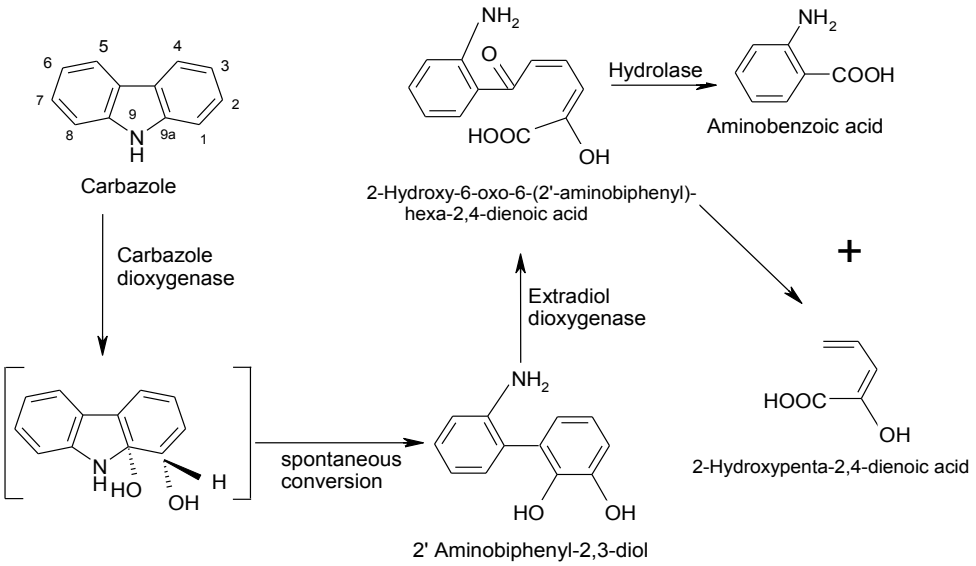
Table 5: Microorganisms having degradation potential for polycyclic aromatic hydrocarbons (PAHs).

and *Penicllium funiculosum* were found to be more predominant in the polluted soil. The highest percentage loss of petroleum hydrocarbon concentration by the mixed cultures of fungi were 90% with *A. niger* and *A. fumigatus*, but the lowest loss of petroleum hydrocarbon calculated in mixed four fungal strains (*A. niger*, *A. fumigatus*, *P. funiculosum* and *F. solani*) to 70%. Vanishree et al. [147] used fungus *Penicillium sp.* for biodegradation of petrol. The efficiency of the fungal strain on the degradation of different concentrations of petrol was studied. The ability of *Penicillium sp.* to tolerateoil pollutant and grow on them suggest that it can be employed as bioremediation agent and used for restoration of ecosystem contaminated by oil.

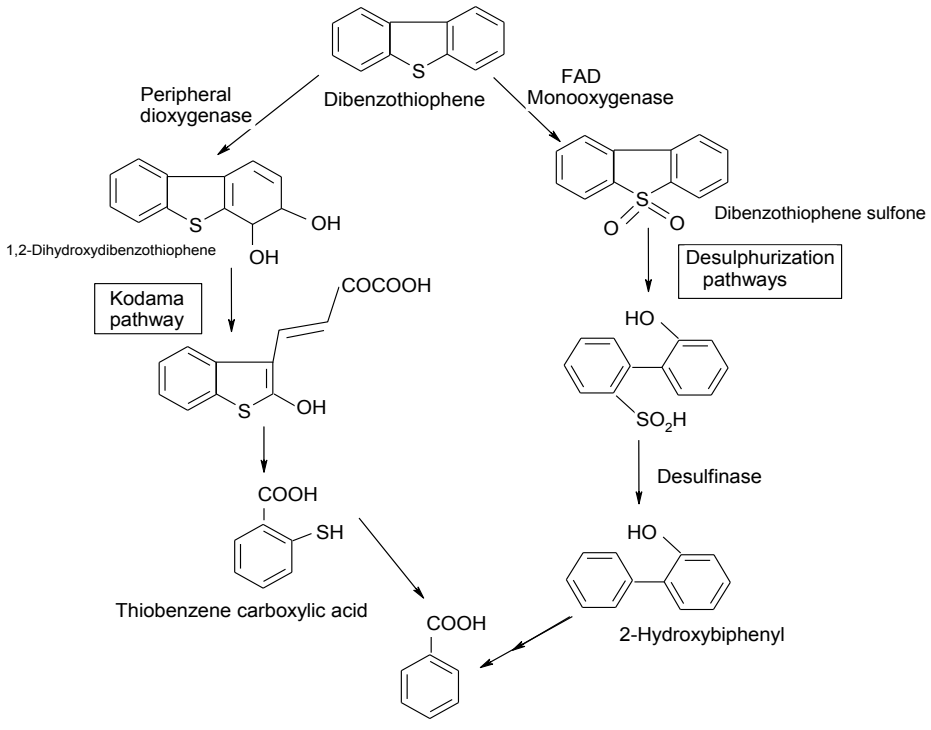
Four fungi strains viz. *Aspergillus niger, Aspergillus terreus, Rhizopus sp* and *Penicillium sp* were also isolated from soil and tarball samples collected from mangrove forest of Alibaug and Akshi coastal area, Maharashtra, India [148]. These strains were assessed for their degradation capability of petroleum hydrocarbons measuring growth diameter in Potato Dextrose Agar (PDA) solid media for different concentrations of kerosene. *Rhizopus sp* showed the highest growth diameter in 5% kerosene and *Aspergillus niger* showed the highest growth diameter in 20% kerosene while, *penicillium sp* showed the lowest growth diameter at all the concentrations of kerosene as compared to other three strains. A mixed culture consisting of *penicillium sp*, *Rhizopus sp* and *Aspergillus terreus was reported to* show highest growth diameter.

Heteroaromatic compounds: Many bacterial species have been reported to decompose dibenzofurans and carbazole, a structural analogue with nitrogen instead of oxygen [149-153]. Guo et al. [151] isolated a stable carbazole-degrading microbial consortium consisting of *Chryseobacterium* sp. NCY and *Achromobacter* sp. NCW. The initial reactions of dibenzofuran and carbazole can be classified into angular and lateral dioxygenation, which may be catalyzed by different enzymes. These enzymes were found in Gram-positive and negative bacteria [138,152,154-156]. Many bacterial strains have the ability to use carbazole as the sole carbon, nitrogen and energy source [150,157]. Most isolates degraded carbazole by following the so-called angular pathway, in which carbazole is initially attacked at the 1 and 9a positions by carbazole dioxygenase, followed by the spontaneous conversion of the dihydroxylated intermediate to 2'-aminobiphenyl-2,3-diol (Scheme 6). An extradiol dioxygenase then attacks the hydroxylated ring at the meta position to give 2-hydroxy-6-(2'-aminophenyl)-6-oxo-2,4-hexadienoic acid, which is hydrolysed to produce anthranilic acid and 2-hydroxypenta-2,4-dienoic acid [150,154-157].

Benzothiophene (BT) and its derivatives are the major sulfur heteroaromatic compounds that are commonly found in higher molecular weight fractions of petroleum. However, no bacterial strain has been found to grow on benzothiophenes as the sole carbon source, and all reported biotransformations of benzothiophenes are based on cometabolism. Attacks on the thiophene ring of benzothiophenes lead to the formation of sulfoxides and sulfones, or to ring opening and the formation of 2-mercaptomandelaldehyde and 2-mercaptophenylglyoxalate [158-160]. Catabolism of dibenzothiophene is catalyzed by distinct enzymes in two pathways (Scheme 7). The catabolic branch of initial sulfur oxidation, also called 4S pathway, through which rapid desulfurization can be obtained. Consecutive desulfurization is achieved by desulfinase. These monooxygenases require FAD as a co-factor, accompanied by a specific flavin reductase [161]. FAD containing monooxygenases are very common in all biota and catalyze various detoxification

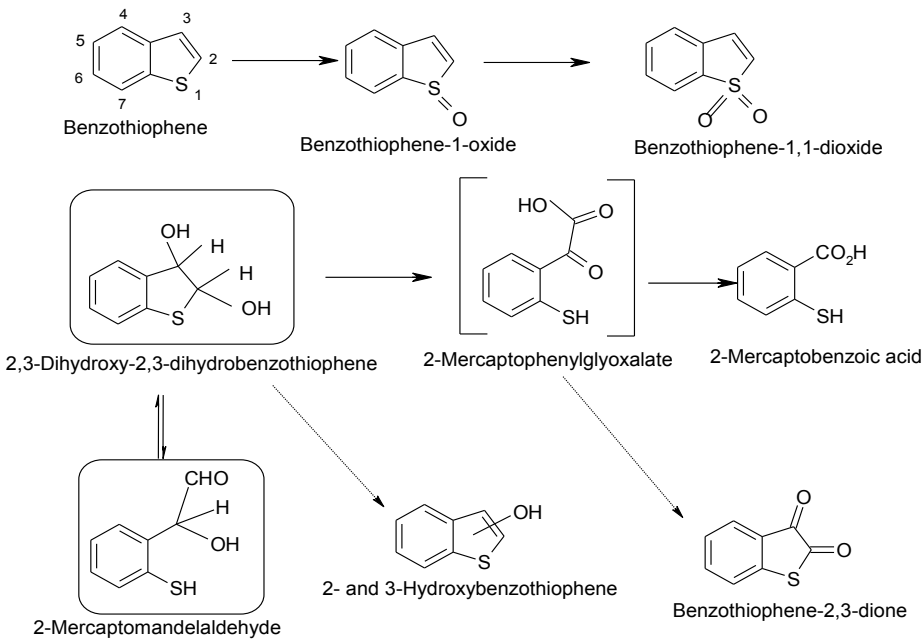


Scheme 6: Aerobic degradation of carbazole via the angular pathway by various carbazole-utilizing bacteria.



Scheme 7: Bacterial catabolic pathways for the aerobic degradation of dibenzothiophene.

steps. For example, Sutherland et al. [162] reported a FAD containing monooxygenase of high sequence homology with dibenzothiophene desulfurization enzymes. In general, all bacterial species with high-desulfurization activities have the enzymes and broad substrate range [163,164]. However, some bacterial species are defective in some components, which results in accumulation of intermediates. In comparison with desulfurization pathway, the enzymes for lateral dioxygenation and consecutive reactions are very different (Kodama pathway, Scheme 7). Many bacterial species have been reported to metabolize dibenzothiophene through Kodama pathway [120,150,165]. Although no detailed research has been done, the structural similarities of the metabolites suggest that common PAH dioxygenase and enzymes in successive steps may be involved in Kodama pathway.



Scheme 8: Proposed BT transformation pathways by Sphingomonas sp. XLDN2-5. The compounds in the box were tentatively identified. The compound in brackets was not detected. Dashed arrows indicate transformations that occur during the extraction of products.

Gai et al. [166] investigated the transformation of benzothiophenes (BT) by Sphingomonas sp. XLDN2-5, employing carbazole as an auxiliary substrate. Among the benzothiophenes tested, BT, 2-methylbenzothiophene (2-MBT) and 5-methylbenzothiophene (5-MBT) were co-metabolically converted. For 3-methylbenzothiophene, there was complete inhibition of growth on carbazole. The common transformation products for BT, 2-MBT and 5-MBT are the corresponding sulfoxides and sulfones. The authors then concluded that aerobic transformation of benzothiophenes to sulfoxides and sulfones can reduce their toxicity, and facilitate their biodegradation. The proposed metabolic pathways of benzothiophene suggested by the authors are summarized in Scheme 8.

Phylogeny of the oil-degrading microbes

Oil-degrading microorganisms are ubiquitous in the environment, particularly in the oil-polluted sites. Both fungi and bacteria have been found to be useful in biodegradation process, even though many researches have been on bacteria in the recent times. Although a wide phylogenetic diversity of microorganisms is capable of aerobic degradation of contaminants, *Pseudomonas* species and closely related organisms have been the most extensively studied owing to their ability to degrade many different contaminants [167]. The oil-degrading populations are widely distributed in the lands and water bodies.

Microbial biodiversity in terrestrial ecosystem

A conceptualization of the functioning of the ancient terrestrial biosphere necessarily requires a general understanding of modern, analog microbial communities to evaluate their living requirements, diversity, physiology, and environmental impact, and to characterize any potential biosignature that could be used to recognize them in the rocks [168,169]. Modern terrestrial microbial communities are found worldwide and in a great variety of local conditions, in surface (solid rock, regolith) and subsurface (caves, groundwater, deep ground) environments. However, it is unclear which one is more productive in terms of biomass [170] and what metabolisms have dominated those systems - and to what extent - over geologic time scales [171]. An understanding of the biology and distribution of modern microbes, which are ubiquitous in today's Earth's biosphere, seems essential for an understanding of their ancient counterparts and their impact on early terrestrial ecosystems. The genetic diversity and biomass distribution in drastically different environments [172-174] depict the ample range of strategies that terrestrial organisms, particularly primary producers, have developed for living on the land. Oxygenic photoautotrophy seems to be a particularly important capability of terrestrial organisms, simply because their energy source (light), reductant power (water), and carbon source (CO_2) are readily available in these environments. In comparison, other primary producers such as chemolithotrophs are restricted to aqueous environments because they require soluble sources of reductants (e.g., H_2, Fe^{2+}, H_2S, HS^-) and exergonic reactions to maintain their metabolism [175]. They are also less energy-efficient than oxygenic photoautotrophs [176-178], and less likely dominant in subaerial environments.

Cyanobacteria have been the only organisms that developed special pigments and enzymatic capabilities for using water as a source of electrons. This process has allowed them to live outside the water in any suitable environment, even where water might be a limiting factor, such as deserts [179]. Oxygenic photosynthesis also contributed to the oxidation of the atmosphere (both by sequestering CO_2 and by producing O_2), a global and ongoing process with profound geochemical, atmospheric, hydrological, and biological implications [166,180,181]. Cyanobacteria and other prokaryotes, can also fix gaseous nitrogen, which seems of great advantage for an independence from dissolved N species, such as NH_4 and NO_3 [183]. The appearance of cyanobacterial akinetes (for N_2 fixation) in the Paleoproterozoic [184] attests to this early adaptation. The limiting nutrients such as P, can be supplied for organisms on land by dust deposition [185,186], which may be an alternative process for replenishment of nutrient loss by runoff and leaching in such environments [168,187]; S can also be

acquired from minerals, aerosols, and as gaseous sources, likely present in the early atmosphere [188]. Thus, the nutritional requirements for oxygenic, photoautotrophic, primary producers seem not to have been a limiting factor for the colonization of the land.

On the basis of the rapid achievement of diversity and distribution of early microbial biota and from microbial successions in modern "barren" lands [189-191], it is expected that heterotrophic organisms were also part of land communities, as they seem to be an inevitable component in this type of consortia. Under this perspective, primitive microbial ecosystems cannot be understood as composed only of autotrophic primary producers, but also a myriad of other microbes finding their niche within such pre-existent microenvironments. For example, actinobacteria in modern cryptogamic covers (CGC) not only degrade large quantities of organic exudates from cyanobacteria, a process which influences the carbon (C) cycle, but they also seem to be structural components of these sedimentary biostructures [192]. The same applies to other bacteria such as Bacteroidetes and Proteobacteria that secrete large quantities of mucopolysaccharides, which aid in gluing soil particles together and may also have a critical role in the hydraulic conductivity of the surface substrate [193].

Microbial biodiversity in aquatic ecosystem

The emphasis on the organizational level of biodiversity responsible for ecosystem processes is shifting from a species-centered focus to include genotypic diversity. Communities with intermediate species richness show high genotypic diversity while species-poor communities do not [194]. Disturbance of these communities disrupts niche space, resulting in lower genotypic diversity despite the maintenance of species diversity.

Heterotrophic bacteria dwelling in aquatic environments are highly diverse. At coarse level the gram-positive bacteria, the Verrucomicrobiales and the Alpha- and Gamma-Proteobacteria are distributed throughout a range of aquatic habitats including marine and fresh water systems. Some phylogenetic groups appear to be adapted to more narrowly defined niches such as anoxic water and sediments (Delta-Proteobacteria) or aggregates (Bacteroidetes). Beta-proteobacteria have been detected throughout freshwater habitats, but these organisms are largely absent from open ocean environments. At narrower level of identification some phylotypes are probably globally distributed as they have been detected in geographically disparate environments. High diversity of heterotrophic bacteria in aquatic environment is explained by high variety of ecological niches occurring and wide spectrum of substrates these organisms utilize.

The abundance of viruses exceeds that of Bacteria and Archaea by approximately 15-fold in the world ocean. However, because of their extremely small size, viruses represent only approximately 5% of the prokaryotic biomass because their content of matter is low. Most abundant groups of viruses found in aquatic environments are bacterio- and cyanophages. The first metagenomic studies of viral communities have revealed that viral communities contain large amounts of sequences with very low homology to any described sequences available in the literature [195].

Microbial biodiversity in marine ecosystem

Microbial communities from coastal sediments vary more from one location to another than those from open waters, and have much greater community evenness [196]. Moreover, in sediments, cells are much more concentrated, resulting in a greater likelihood of interactions, which becomes even more prevalent in biofilms where cells are more densely packed. Highly productive photosynthetic microbial mats develop at the water-sediment interface. These multispecies biofilms consist of horizontally stratified layers with extremely steep gradients of light, redox potential, oxygen, sulfur species etc. The exceptionally high microbial diversity within a few microns covers a large range of metabolic groups (oxygenic and anoxygenic phototrophs, sulfate reducers, methanogens etc.) [197]. The communication mechanisms in environments (open water, sediment and biofilms), where small molecules, either diffusing from cell to cell [198], or transported by vesicles [199] or via nanotubes bridging cells [200], elicit intra- and inter-species effects that could be antagonistic or beneficial.

Microbes exhibit all of the types of social behaviour (mutual benefit, selfishness, altruism and spite) seen in multicellular organisms [201]. However, it is often difficult to categorise such behaviour in complex multi-species natural environments. Therefore, a better understanding of crude-oil biodegradation, and thus the capability to more rationally remediate contaminated environments, requires considering the mechanisms of the associations between different hydrocarbon-degrading microbes and with non-degrading organisms [15]. Although fungi are considered to be largely terrestrial, they have been found in marine mats [202] and it is known that many can function in saline conditions [203], but in general salt-adapted fungi have received little attention despite a potentially major role in coastal PAH degradation. The ubiquitous co-existence of bacteria and fungi in soil and sediments [204] and their known catabolic cooperation suggests that physical interactions between them may be of importance for PAH degradation.

Marine phototrophs (primarily eukaryotic microalgae and cyanobacteria) contribute half the Earth's primary production and half of the oxygen liberated to the atmosphere [205]. However, they do not exist in isolation, and their phycosphere (loosely defined as the zone around algal cells in which bacteria feed on algal products) constitutes an important habitat that is colonised by an abundant and diverse community of heterotrophic bacteria [206,207].

Bacteria are also found living inside microalgal cells - many with unknown function [145]. The composition of free-living marine microbial communities is frequently very different from those attached to microalgae [208], with certain groups often preferring the attached lifestyle and showing higher levels of activity [194]. Moreover, different species of microalgae host distinct bacterial communities that change with time and environmental conditions [209,210]. However, there is likely to be a large spectrum of bacterial heterotroph-phototroph specificity [211], and certainly many attached bacteria can also live in the absence of a microalgal or cyanobacterial host [212]. While antagonistic interactions occur between marine phototrophs and their attached microbiota [213,214], mutualistic interactions are common. The host supplies carbon and energy sources [215], while the bacteria have been shown to provide iron [216], haem [217], vitamin B_{12} [218] to consume oxygen [219] and provide protection from reactive oxygen species [220]. Symbiotic cyanobacteria supply fixed nitrogen to diatoms [221] and other algae and protests [222], and heterotrophic N_2-fixing bacteria may also be important in interactions with microalgae, as evidenced by the abundance of alpha-proteobacterial diazotrophs in seawater size fractions of >10 μm [223].

Marine microbes offer great opportunities for biodiscovery [224,225], yet that potential is yet to be realised. Despite a huge microbial diversity, there is a lack of laboratory cultures of the microbes that are most abundant in the environment that severely limits development of biodiscovery research. Bacteria probably grow as consortia in the sea and reliance on other bacteria for essential nutrients and substrates is

not possible with standard microbiological approaches. Joint et al. [226] highlighted the advantages of novel technologies, such as encapsulation into gel micro-droplets and development of consortia over standard microbiological approaches for biodiscovery programmes. These technologies, according to the authors resulted in the isolation and culturing of many previously uncultured microbes.

Conclusions

This review provides the detailed knowledge on the ability of microorganisms capable of degrading hydrocarbons which has accumulated significantly in the past two decades. Studies show that much richer microbial diversity exists in the environment that can efficiently degrade petroleum compounds. Microbial degradation processes aid the elimination of spilled oil from the environment after critical removal of large amounts of the oil by various physical and chemical methods. This is possible because microorganisms have enzymic systems that degrade and utilize different crude oil compounds as source of carbon and energy.

Microbial degradation of oil has been shown to occur by attack on aliphatic or light aromatic fractions of the oil, with high-molecular-weight aromatics, resins, and asphaltenes considered to be recalcitrant or exhibiting only very low rates of biodegradation, although some studies have reported their removal at high rates under optimal conditions. The biodegradation of petroleum compounds depends on the specific microbial population present. Further studies should be carried out to identify new bacterial strains that can metabolize a broad range of compounds contained in crude oil, especially the highly persistent components. Also, a better knowledge of the

diversity of catabolic pathways would certainly bring valuable information for the development of robust bioremediation processes.

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