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REVIEW PAPER

Aerobic bacteria degrading both *n*-alkanes and aromatic hydrocarbons: an undervalued strategy for metabolic diversity and flexibility

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Abstract Environmental pollution with petroleum toxic products has afflicted various ecosystems, causing devastating damage to natural habitats with serious economic implications. Some crude oil components may serve as growth substrates for microorganisms. A number of bacterial strains reveal metabolic capacities to biotransform various organic compounds. Some of the hydrocarbon degraders are highly biochemically specialized, while the others display a versatile metabolism and can utilize both saturated aliphatic and aromatic hydrocarbons. The extended catabolic profiles of the latter group have been subjected to systematic and complex studies relatively rarely thus far. Growing evidence shows that numerous bacteria produce broad biochemical activities towards different hydrocarbon types and such an enhanced metabolic potential can be found in many more species than the already well-known oil-degraders. These strains may play an important role in the removal of heterogeneous contamination. They are thus considered to be a promising solution in bioremediation applications. The main purpose of this article is to provide an overview of the current knowledge on aerobic bacteria involved in the mineralization or transformation of both *n*-alkanes and aromatic hydrocarbons. Variant scientific approaches enabling to evaluate these features on biochemical as well as genetic levels are presented. The distribution of multidegradative capabilities between bacterial taxa is systematically shown and the possibility of simultaneous transformation of complex hydrocarbon mixtures is discussed. Bioinformatic analysis of the currently available genetic data is employed to enable generation of phylogenetic relationships between environmental strain isolates belonging to the phyla Actinobacteria, Proteobacteria, and Firmicutes. The study proves that the co-occurrence of genes responsible for concomitant metabolic bioconversion reactions of structurally-diverse hydrocarbons is not unique among various systematic groups.

Keywords *n*-Alkanes · Aromatic hydrocarbons · Bacterial aerobic metabolism · Biotransformation · Bioremediation · Environmental strains

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Introduction

Petroleum is a heterogeneous and complex mixture, consisting mostly of hydrocarbons, such as aliphatic

compounds (linear, branched, saturated and unsaturated), cycloalkanes, mono- and polyaromatics, asphaltenes and resins. On average, saturated and aromatic hydrocarbons together make up 80% of crude oil (Widdel and Rabus 2001). Oil polluted sites are plagued by these compounds, although *n*-alkanes, the major constituents of petroleum, are also found in uncontaminated environments (van Beilen et al. 2003; Nie et al. 2014). The exploitation of petroleum, along with its storage and transport of its products, generally poses a risk of environmental contamination. Some aromatic substances such as BTEX (benzene, toluene, ethylbenzene, and xylene) and PAHs (polycyclic aromatic hydrocarbons) are particularly toxic and carcinogenic (An 2004; Delgado-Saborit et al. 2011). Therefore, their persistence in the environment is of great concern. Many microorganisms, especially bacteria, fungi and yeast, utilize hydrocarbons as sources of carbon and energy (Das and Chandran 2011). Moreover, microbial biotransformation is a main environmental process affecting the fate of PAHs in terrestrial and aquatic ecosystems. Bacteria are the first respondents to oil pollution, participating in the degradation of hazardous organic waste (Das and Chandran 2011). Numerous unique pathways for bacterial hydrocarbon metabolism have been well documented in several thorough reviews (Peng et al. 2008; Rojo 2009; Seo et al. 2009; Das and Chandran 2011; Wang and Shao 2013). For the case of alkane degraders the Rojo's classification (2009) has distinguished two microbial groups, namely, (1) highly specialized microbes, and (2) microorganisms using a broad spectrum of compounds as sources of carbon. The latter category also covers the organisms that are able to catabolize both saturated aliphatic and aromatic hydrocarbons. Considering these capabilities, this paper is focused on aerobic processes, although anaerobic strategies have also been observed (Widdel and Rabus 2001). Not neglecting the role of the latter processes, the remediation methods based on aerobic bacterial metabolism bring the most rapid and efficient decomposition of organic compounds. These methods are primarily considered for in situ treatments of sites polluted by non-halogenated organic compounds (Steliga et al. 2012). As regards aromatic compounds, taking into account their diversity, the article mainly concerns the BTEX- and PAH-degrading capabilities.

The aim of this review is to spread the current knowledge on aerobic bacteria that can metabolize both *n*-alkanes and aromatic hydrocarbons. The metabolic capacities of microorganisms are shown together with the relevant genomic evidence. Bacterial potential to simultaneously degrade both hydrocarbon groups is discussed. Further bioinformatic analysis of the currently available genomic data is carried out to reveal phylogenetic relationships between particular strains and to prove that genes enabling concomitant metabolism of *n*-alkanes, BTEX and PAHs can be frequently found in various bacterial taxa. We believe that this is the first attempt to report and compile the distribution of the enhanced biodegradation potential towards structurally diverse organic compounds in the microbial world.

Bacteria able to metabolize both *n*-alkanes and aromatic hydrocarbons

Microorganisms capable of transforming both saturated aliphatic and aromatic hydrocarbons should occur in the environment widely, which can be assumed based on (1) the heterogeneity of petroleum contamination, directly related to the presence of *n*-alkanes and aromatic hydrocarbons in many types of petroleum pollution, (2) the higher concentration of *n*-alkanes compared to other constituents in most petroleum contaminants, (3) the enhanced bioavailability of PAHs within pollution as these compounds are dissolved in other petroleum components, and finally (4) the natural occurrence of various non-polar compounds at unpolluted sites. Therefore, the multi-degradative properties may facilitate bacterial colonization of contaminated as well as pristine environments. The uniqueness of such diverse metabolic profiles seems to be an ecologically competitive advantage in comparison to specialization strategy (e.g. exclusively alkane degradation), as microbes displaying the combined activities are not dependent on the presence of just one type of carbon source. In consequence, bacteria that reveal metabolism of both structurally diverse hydrocarbon groups, that is *n*-alkanes and aromatic compounds, may have a beneficial adaptation potential by being able to easily change their growth substrates when there is a limited availability of a certain group of compounds. This feature implies lower competition pressure when compared to the specialized hydrocarbon-degraders. On the other hand, a question arises whether the

degradative genes of aliphatic and aromatic hydrocarbons can really coexist in a single bacterium, or is their occurrence mutually exclusive? It should be noted that the regulation and expression of several concurrent degradation pathways, the active maintenance of these pathways when not all the mentioned sources of carbon are accessible, and the transfer of genetic information about this machinery to other generations are energetically costly. Some of these aspects were earlier notified by Whyte et al. (1997). Hence, producing such complex activities may be an enormous energetic challenge or even an impediment for microbes. In general, individual degraders have been isolated and characterized on the basis of their metabolic capacities to biotransform individual petroleum compounds or classes of substances (e.g. low molecular weight (LMW) PAHs, *n*-alkanes). However, they have been classified much less often according to their metabolic potential towards a broad range of various hydrocarbons. Thus, the ecological and evolutionary status of the discussed microorganisms is not explicit. In this context, several scientific questions should be answered, namely: (1) Are these bacteria widespread or is their occurrence limited to specific sites? (2) Are the enhanced metabolic capacities unique or are they quite common among hydrocarbon-degraders? (3) If these preferences for diverse substrates are not unique, are they related to particular genera and species? Finally, (4) can both groups of compounds be removed concomitantly or separately?

The studies regarding the enhanced metabolic potential among bacteria started in the 1990s. Foght et al. (1990) first postulated that bacteria capable of degrading both *n*-alkanes and aromatic hydrocarbons may exist, although many of the 200 environmentally isolated strains were shown to mineralize just one source of carbon, not both. On the other hand, 36% of the hydrocarbon-utilizing strains isolated by Stosky et al. (1994) possessed genes involved in the metabolism of both *n*-alkanes (*alkB*) and aromatic hydrocarbons (*xylE*). However, phenotypic observations did not confirm these findings. Finally, Whyte et al. (1997) indicated the coexistence of multi-degradative capacities in one microorganism (*Pseudomonas* sp. strain BI7), showing both genetic evidence and phenotypic responses. The number of studies involving this bacterial group has increased since the publication of the cited articles, although there is still a lack of papers that systematize the information on such microbes. In order to describe the natural diversity of bacteria that are capable of degrading both *n*-alkanes and the selected aromatic hydrocarbons, this review highlights the importance of genera *Mycobacterium*, *Rhodococcus* and *Pseudomonas* and also notes other bacterial groups involved in these processes. To provide the reader with a more comprehensive overview of data presented in the following paragraphs ("*Mycobacterium*", "*Rhodococcus*", "Other Actinobacteria", "*Pseudomonas*", "Other Gammaproteobacteria", "Alpha- and Betaproteobacteria", "Firmicutes", "Deinococcus–Thermus" sections), for most of the strains phylogenetic trees were generated (Fig. 1a–c).

Mycobacterium (Actinobacteria, Fig. 1a)

There are many reports dealing with catabolic preferences exhibited by various representatives of Actinobacteria. However, *Mycobacterium* and *Rhodococcus* are genera addressed the most often in research papers referring to metabolism of miscellaneous petroleum compounds. It should be noted here, that for the case of *Mycobacterium*, Gupta et al. (2018), based on the great body of evidence, has recently proposed the division of the known mycobacterial species into five new taxa. According to this new classification, all the bacteria described in this chapter belong to the genus *Mycolicibacterium*. However, for clarity, we kept the original strain names as they appeared in the published work. Studies in regard to PAH biotransformation by *Mycobacterium* have significantly advanced since the first research work conducted on the isolate *Mycobacterium* sp. PYR-1 (later described as *M. vanbaalenii* PYR-1) in the late 1980s. This pyrene-degrading bacterium, isolated from oil-polluted sediments, was the subject of many extensive investigations devoted to different aspects of PAH metabolism (Heitkamp et al. 1988a, b; Heitkamp and Cerniglia 1988; Kim et al. 2008a; Kweon et al. 2011). The obtained results indicated that PYR-1 utilized a wide range of compounds. In addition to the four-ring pyrene, it was able to transform other compounds such as two-, three-, and four-ring PAHs as well as their alkyl derivatives (more details are given in Table 1). Moreover, the strain also biodegraded nC_{13}–nC_{23} (Kim et al. 2015). Further

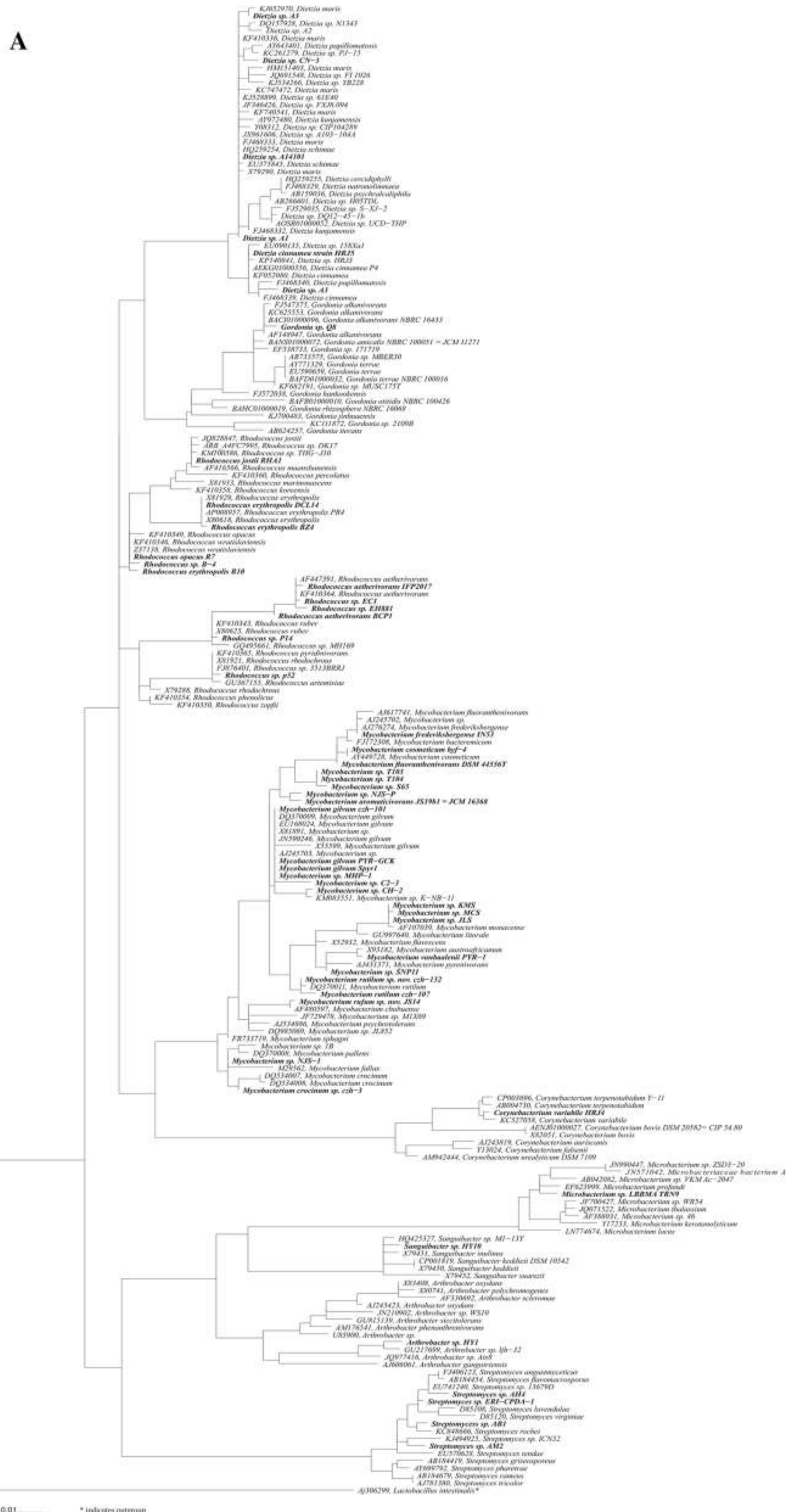
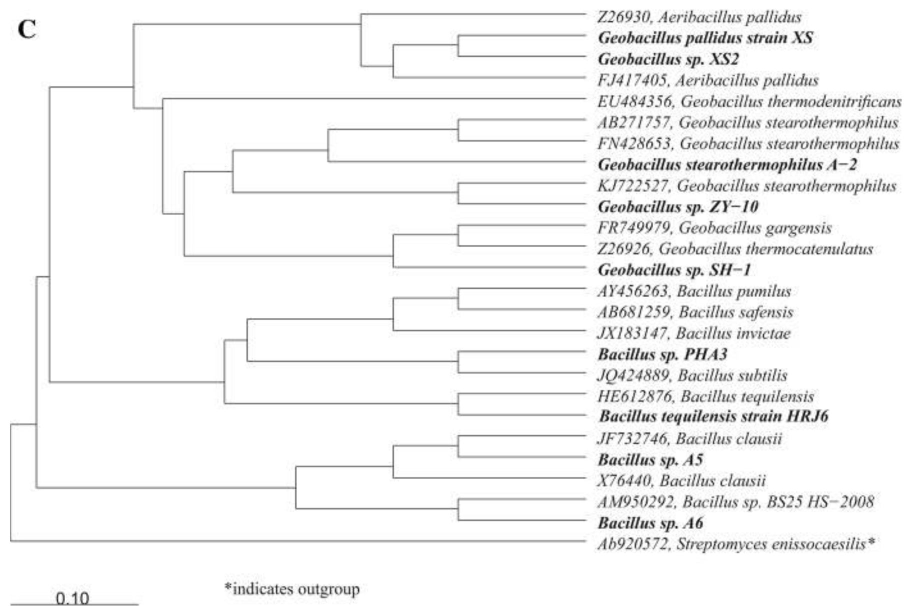


Fig. 1 Neighbor-joining phylogenetic trees, based on 16S rRNA gene sequences, showing the relationship between bacterial isolates belonging to the phyla: **a** Actinobacteria, **b** Proteobacteria, **c** Firmicutes. The bacteria were capable of degrading both *n*-alkanes and aromatic hydrocarbons. The tree topologies are based on the consensus of trees of N 1000 informative positions generated using the Neighbor Joining and Maximum Likelihood methods (ARB phylogenetic package). The scale bars represent 1, 10, and 10% of estimated differences in nucleotide sequence positions for **a–c**, respectively. The names of strains mentioned in the text were marked in bold

Fig. 1 continued

Fig. 1 continued



research aimed at the isolation and identification of PAH-oxidizing bacterial strains provided valuable information about other *Mycobacterium* representatives (Table 1). The broadly distributed PAH-degrading capacities among mycobacteria have probably resulted from extensive HGT (horizontal gene transfer) events in genomic regions that contain genes for HMW PAHs (high molecular weight PAHs) metabolism (Kweon et al. 2015). Principally, the utilization of aromatic compounds was demonstrated, while the capabilities of *n*-alkane degradation were not reported in many cases. On the other hand, the observed high frequency of the mycobacterial *alkB* gene encoding alkane monooxygenase, led to the presumption that *n*-alkane oxidation is a common property in this genus. Note that this activity can also be found in slow-growing pathogenic mycobacteria. Smits et al. (2002) claimed that *alkB* in *M. tuberculosis* may be a relict of a free-living ancestor, while Nie et al. (2014) suggested that *alkB* could be a core gene in the *Mycobacterium* genus. The latter authors further indicated *alkB* prevalence in most of the sequenced genomes belonging to this taxon. The role of AlkB in slow-growing, pathogenic organisms such as *M. tuberculosis* and *M. bovis* is still unknown, but some hypotheses were postulated (van Beilen et al. 2003; Rojo and Martínez 2010). The proven *n*-alkane-utilizing capabilities of some strains include not only linear *n*-alkanes but also branched pristane (Table 1). Interestingly, Kim et al. (2015) demonstrated preferential *n*-alkane utilization by *M. vanbaalenii* PYR-1 (the highest removal yields obtained for nC_{12} and nC_{13}) suggesting narrow substrate specificity of *n*-alkane metabolic routes. However, to reliably evaluate *n*-alkane utilization preferences (broad or narrow) within this taxon, more detailed studies are required.

The data listed in Table 1, combined with the abovementioned facts, indicate that a great number of mycobacteria are able to metabolize both aromatic hydrocarbons and *n*-alkanes. Within this group, the range of utilized compounds seems to be strain-specific. However, some restrictions concerning PAH-metabolizing pattern were observed (Table 1). For example, *Mycobacterium fluoranthenivorans* DSM 44556^T (Hormisch et al. 2004) and *Mycobacterium* sp. strain KR20 (Rehmann et al. 2001) used just fluoranthene as a carbon source among the many tested compounds (naphthalene, anthracene, phenanthrene, acenaphthene, acenaphthylene, fluorene, chrysene, and pyrene). Other strains degraded phenanthrene, fluoranthene and pyrene (Table 1). Based on the range of metabolized PAHs, three mycobacterial groups can be distinguished. Namely, (1) mycobacteria capable of utilization of all the three compounds: pyrene, phenanthrene, and fluoranthene, (2) mycobacteria degrading both pyrene and

Table 1 Environmental *Mycobacterium* strains, capable of degrading or transforming both *n*-alkanes and polyaromatic hydrocarbons (PAHs)

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacteria with broad range of utilized hydrocarbons											
Mycobacterium vanbaalenii PYR-1	nC_{13}–nC_{23}	+	+	+	+	+	+	+	+	Degradation of: 7,12-dimethylbenz[a]anthracene, acenaphthene, acenaphtylene, identified the presence *nidA*, *nidA3B3*	Kelley et al. (1990, 1991), Kelley and Cerniglia (1995), Moody et al. (2001, 2003, 2004, 2005), Kweon et al. (2007) and Kim et al. 2015
Mycobacterium austroafricanum GTI-23 (yellow colonies)	nC_{12}, nC_{16}	n.d.[a]	+	n.d.[a]	+	T	+	+	n.d.[a]	n.d.[b]	Bogan et al. (2003)
Mycobacterium austroafricanum VM451	n.d.[a]	n.d.[a]	+	–	±*	–	+	n.d.[a]	n.d.[a]	*Partial utilization of pyrene probably due to an incomplete pyrene mineralization pathway	Johnsen et al. (2002) and Uyttebroek et al. (2006)
Mycobacterium pyrenivorans 17A3[T] (scotochromogenic, yellow colonies)	n.d.[a]	n.d.[a]	+	–	+	n.d.[a]	+	–	n.d.[a]	n.d.[b]	Derz et al. (2004)
Mycobacterium frederiksbergense strain FAn9[T] (scotochromogenic yellow colonies)	n.d.[a]	+*	+	+*	+	–	+	–	n.d.[a]	Identified the presence of *nidA*, *nidB*; *degraded in a mixture of naphthalene, anthracene and pyrene	Willumsen et al. (2001), Mahanty et al. (2010) and Brezna et al. (2003)
Mycobacterium frederiksbergense LB-501[T]	utilized diesel oil	–	+	+	+	–	+	n.d.[a]	n.d.[a]	No degradation of acenaphthene	Bastiaens et al. (2000), Wick et al. (2003) and Johnsen et al. (2002)
Mycobacterium frederiksbergense IN140 (yellow colonies)	nC_7, nC_{10}, nC_{18}	+	+	+	+	–	+	n.d.[a]	n.d.[a]	No degradation of toluene, xylene and chrysene	Brzeszcz (2017)
Mycobacterium crocinum sp. nov. czh-3	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	–	n.d.[a]	Identified the presence of *nidA*, *nidB*	Hennessee et al. (2009) and Hennessee and Li (2016)
Mycobacterium rutilum sp. nov. czh-107	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	+	n.d.[a]	n.d.[b]	Hennessee et al. (2009)

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium gilvum PYR-GCK (previously *M. flavescens*), (yellow colonies)	n.d.[a,*]	–	+	–	+	–	+	–	n.d.[a]	No degradation of chrysene, acenaphthene; detected *nidA*, *nidB;* *identified *alkB* in genome sequence (*locus tags*: MFLV_RS16095, MFLV_RS23700);	Dean-Ross and Cerniglia (1996) and Brezna et al. (2003)
Mycobacterium gilvum BB1 (scotochromogenic, yellow colonies)	n.d.[a]	–	+	–	+	-*	+	n.d.[a]	n.d.[a]	*Cometabolism of fluorene; detected *nidA*, *nidB*	Boldrin et al. (1993), Böttger et al. (1997) and Brezna et al. (2003)
Mycobacterium gilvum czh-101	n.d.[a]	n.d.[a]	+*	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	*Degraded, but not used as a sole carbon source for growth; detected *nidA*, *nidB*	Hennessee and Li (2016)
Mycobacterium gilvum Spyr1 (previously: *Mycobacterium* sp. Spyr1)	n.d.[a,*]	n.d.[a]	n.d.[a]	+	+	+	+	n.d.[a]	n.d.[a]	*2 copies of *alkB* identified in genome sequence (*locus tags*: MSpyr1_RS13285, MSpyr1_RS19985)	Karabika et al. (2008)
Mycobacterium gilvum LB307[T]	utilized diesel oil	–	+	–	*	–	+	n.d.[a]	n.d.[a]	*Difficulties in proper evaluation of growth	Bastiaens et al. (2000)
Mycobacterium gilvum LB208	utilized diesel oil	–	+	–	+	–	+	n.d.[a]	n.d.[a]	No degradation of acenaphthene	Bastiaens et al. (2000)
Mycobacterium aromaticivorans sp. nov. JS19b1[T] (yellow colonies)	n.d.[a,]*	n.d.[a]	+**	n.d.	+	+	+	–	n.d.[a]	*1 copy of *alkB* (*locus tag:* Y900_006430); **PHE degradation via C-1, 2, C-3,4 and C-9,10 dioxygenation routes	Seo et al. (2007, 2010, 2012)
Mycobacterium spp. HH1, HH2 (yellow colonies)	n.d.[a]	n.d.[a]	+	+	+	+	+	n.d.[a]	n.d.[a]	n.d.[b]	Zhou et al. (2008)
Mycobacterium sp. HH3 (pink colonies)	n.d.[a]	n.d.[a]	+*	+*	+*	+	+	n.d.[a]	n.d.[a]	*Low biodegradation rate	
Mycobacterium sp. C2-3 (yellow colonies)	nC_{16}, nC_{17}	–	+	n.d.[a]	+	+	+	n.d.[a]	n.d.[a]	n.d.[b]	Lee et al. (2001)

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium sp. strain AP1 (yellow colonies)	nC_{16}, nC_{12}-nC_{40}, pristane, phytane	T	+	T	+	T	+	n.d.[a]	T	Transformation of not-supporting growth compounds: acenaphthene, acenaphtylene, NAP, FLU; no degradation of chrysene	Vila and Grifoll. (2009) and López et al. (2005)
Mycobacterium sp. strain 1B	nC_{10}, nC_{16}	–	+	n.d.[a]	+	–	+	–	n.d.[a]	No degradation of:toluene and benzene	Dandie et al. (2004)
Mycobacterium sp. CP1 (orange colonies)	nC_{16}, pristane	T	+*	+	+	T	+	n.d.[a]	n.d.[a]	Transformation of NAP, FLU and acenaphthene; *three routes for FLUO degradation	López et al. (2005)
Mycobacterium sp. CP2 (orange colonies)	nC_{16}	T	+	+	+	T	+*	n.d.[a]	n.d.[a]	No degradation of acenaphtene; *three routes for FLUO degradation	
Mycobacterium sp. strain CH1 (yellow colonies)	nC_{12}, C_{16}, nC_{18}, C_{22}, nC_{28}, pristane	–	+	–	+	–	T	n.d.[a]	n.d.[a]	n.d.[b]	Churchill et al. (1999)
Mycobacterium sp. strain CH-2	*n*-alkanes	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	Churchill et al. (2008)
Mycobacterium sp. BS5 (creamy to yellow-orange colonies)	nC_6, nC_7, nC_{16}	–	+	+	+	–	+	–	+	Degradation of: dibenz[a,h]anthracene, benzene, toluene, xylene; no degradation of acenaphthylene, chrysene	Lease et al. (2011)
Mycobacterium sp. KA5 (creamy to yellow colonies)	nC_6, nC_7, nC_{16}	–	+	–	+	–	+	–	+	Degradation of: benzene, toluene, xylene, chrysene dibenz[a,h]anthracene; no degradation of: acenaphthylene	
Mycobacterium sp. KF4 (creamy to yellow colonies)	nC_6, nC_7, nC_{16}	–	+	+	+	–	+	–	+		
Mycobacterium sp. A1-PYR (gold colonies)	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	Zhong et al. (2006)

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium sp. S65 (creamy yellow colonies)	n.d.[a]	–	+	–	+	–	+	n.d.[a]	n.d.[a]	Identified two *loci* encoding *nidA/pdoA* or *nidA* homologues	Sho et al. (2004)
Mycobacterium spp. G1, G3, G4 (gold colonies)	*n*-C_{12}, *n*-C_{16},	n.d.[a]	+	n.d.[a]	+	+	+	n.d.[a]	n.d.[a]	n.d.[b]	Lloyd-Jones and Hunter (1997)
Mycobacterium sp. G2 (gold colonies)	*n*-C_{12}, *n*-C_{16},	n.d.[a]	–	n.d.[a]	+	+	+	n.d.[a]	n.d.[a]	n.d.[b]	
Mycobacterium sp. O3 (orange colonies)	*n*-C_{12}, *n*-C_{16},	n.d.[a]	+	n.d.[a]	–	+	+	n.d.[a]	n.d.[a]	n.d.[b]	
Mycobacterium sp. SNP11 (yellow colonies)	n.d.[a]	–	+	–	+	+	+	n.d.[a]	n.d.[a]	No degradation of BTEX; identified *nidA* and *pdoA2* (designated *phdA* in this study)	Pagnout et al. (2007)
Mycobacterium spp. PYR400,	*n*C_{16}	n.d.[a]	+	–	+	n.d.[a]	+	–	n.d.[a]	n.d.[b]	Kim et al. (2005)
PYR11, PYR100, PYR102, PYR103, PYR200, PYR211, PYR213, PYR 300											
Mycobacterium sp. S10	*n*C_{16}	n.d.[a]	+	+	+	n.d.[a]	+	–	n.d.[a]	n.d.[b]	
Mycobacterium sp. NJS-1 (yellow colonies)	n.d.[a]	n.d.[a]	+	+	+	n.d.[a]	+	+	n.d.[a]	n.d.[b]	Zeng et al. (2010)
Mycobacterium sp. NJS-P (pale-white colonies)	n.d.[a]	n.d.[a]	+	+	+	n.d.[a]	+	+	n.d.[a]	n.d.[b]	

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium austroafricanum Ri465a	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	Identified *pdo* gene similar to the one found in *Mycobacterium* sp. 6PY1	Johnsen et al. (2007)
Mycobacterium aurum Ri464	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	
Mycobacterium vaccae Ri471c, **Ri487, Ri486ba** Ri496	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	**Ri487** and **Ri486ba**: identified *pdo* gene similar to the one found in *Mycobacterium* sp. 6PY1	
Mycobacterium sp. MHP-1	n.d.[a]	n.d.[a]	+	+	+*	n.d.[a]	+	n.d.[a]	n.d.[a]	*PYR degradation occurred under alkaline conditions (pH 9); identified presence of *nidAB*	Habe et al. (2004)
Mycobacterium sp. RJGII135 (yellow colonies)	n.d.[a]	n.d.[a]	+	+	+	n.d.[a]	n.d.[a]	+	+	Identified presence of *nidA*	Schneider et al. (1996) and Brezna et al. (2003)
Mycobacterium sp. MR-1 (yellow colonies)	n.d.[a]	+	+*	–	+*	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	*Cross-induction of PYR and PHE	Molina et al. (1999)
Mycobacterium sp. BG1 (orange colonies)	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Guerin and Jones (1988)
Mycobacterium sp.	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	–	n.d.[a]	No degradation of chrysene	Jimenez and Bartha (1996)
Mycobacterium sp. KMS	n.d.[a,*]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	+	n.d.[a]	*1 copy of *alkB* (*locus tag*: MKMS_RS06710); identified *nidA/B*	Miller et al. (2004)
Mycobacterium sp. JLS	n.d.[a,*]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	–	n.d.[a]	*1 copy of *alkB* (*locus tag*: MMJLS_RS06825)	Miller et al. (2004)
Mycobacterium sp. MCS	n.d.[a,*]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	+	n.d.[a]	*1 copy of *alkB* (*locus tag*: MMCS_RS06685)	Miller et al. (2004)
Mycobacterium sp. 6PY-1	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	Identified *pdo1* and *pdo2*	Krivobok et al. (2003)
Mycobacterium gilvum VM552	*n*-C_{10}, *n*-C_{12}, *n*-C_{16}	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Wick et al. 2002 and Uyttebroek et al. (2006)

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium frederiksbergense VM531	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Uyttebroek et al. (2006)
Mycobacterium crocinum sp. nov. czh-42^T	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	Hennessee et al. (2009)
Mycobacterium pallens sp. nov. czh-8^T	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	Hennessee et al. (2009)
Mycobacterium rutilum sp. nov. czh-132	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	+	–	n.d.[a]	n.d.[b]	Hennessee et al. (2009)
Mycobacteria degrading pyrene and phenanthrene but not fluoranthene											
Mycobacterium sp. strain KR2 (yellow colonies)	n.d.[a]	–	+	–	+	n.d.[a]	–	–	–	No degradation of chrysene	Rehmann et al. (1998)
Mycobacterium austroafricanum Ri452b	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	–	n.d.[a]	n.d.[a]	Identified the presence of *pdo1*	Johnsen et al. 92007)
Mycobacterium gilvum Ri455, Ri457, Ri470a, Ri484b, **Ri481b**, Ri489	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	–	n.d.[a]	n.d.[a]	**Ri481b**: identified *pdo* gene similar to the one found in *Mycobacterium* sp. 6PY1	
Mycobacterium gilvum Ri455, Ri457, Ri470a, Ri484b, Ri481b, Ri489	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	–	n.d.[a]	n.d.[a]	n.d.[b]	
Mycobacterium aurum Ri469, **Ri483a**	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	–	n.d.[a]	n.d.[a]	**Ri483a**: identified *pdo* gene similar to the one found in *Mycobacterium* sp. 6PY1	

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium sp. strain KR2 (yellow colonies)	n.d.[a]	–	+	–	+	n.d.[a]	–	–	–	No degradation of chrysene	Rehmann et al. (1998)
Mycobacterium rutilum sp. nov. czh-117[T]	n.d.[a,*]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	–	–	n.d.[a]	1 copy of *alkB* (*locus tag:* WP_083409909); identified the presence of *nidA*, *nidB*	Hennessee et al. (2009) and Hennessee and Li (2016)
Mycobacterium frederiksbergense IN53 and IN139 (yellow colonies)	nC_7, nC_{10}, nC_{18}	+	+	+	+	–	–	n.d.[a]	n.d.[a]	No degradation of toluene, xylene and chrysene	Brzeszcz (2017)
Mycobacterium spp. PYR110, PYR210, PYR212	nC_{16}	n.d.[a]	+	–	+	n.d.[a]	–	–	n.d.[a]	n.d.[b]	Kim et al. (2005)
Mycobacteria utilizing only fluoranthene as a sole source of carbon											
Mycobacterium fluoranthenivorans DSM 44556[T] (nonchromogenic)	n.d.[a]	–	–	–	–	–	+	n.d.[a]	n.d.[a]	No degradation of chrysene, acenaphthene, acenaphthylene	Hormisch et al. (2004)
Mycobacterium rufum sp. nov. JS14[T] (previously: *Mycobacterium* sp. JS14; orange colonies)	n.d.[a,*]	n.d.[a]	–	n.d.[a]	–	–	+	–	n.d.[a]	*2 copies of *alkB* (*locus tags*: EU78_07635, EU78_14125)	Lee et al. (2007) and Hennessee et al. (2009)
Mycobacterium sp. strain KR20 (scotochromogenic yellow colonies)	n.d.[a]	–	–	–	–	–	+	n.d.[a]	n.d.[a]	No degradation of chrysene	Rehmann et al. (2001)
Mycobacterium sp. CFt2 (yellow colonies)	pristane*	–	–	–	–	–	+**	n.d.[a]	n.d.[a]	*No degradation of nC_{16}; **only C1,2 and C2,3-dioxygenation pathways of FLUO	López et al. (2005)
Mycobacterium sp. CFt6 (yellow colonies)	nC_{16}, pristane	–	–	+	–	–	+*	n.d.[a]	n.d.[a]	No degradation of acenaphtene; *only C1,2 and C2,3-dioxygenation pathways of FLUO	

Table 1 continued

Strain	Degradative capabilities									Additional information	References
	n-alkanes	PAHs									
		NAP	PHE	ANT	PYR	FLU	FLUO	B[A]P	B[a]A		
Mycobacterium spp. O1, O2, O4, O5 (orange colonies)	*n*-C_{12}, *n*-C_{16}	n.d.[a]	–	n.d.[a]	–	–	+	n.d.[a]	n.d.[a]	n.d.[b]	Lloyd-Jones and Hunter (1997)
Mycobacterium holderi sp. nov EMI2[T] (yellow colonies)	n.d.[a]	n.d.	-*	-*	-*	-*	+	n.d.[a]	n.d.[a]	*None of compounds was degraded in the absence of FLUO, but they were cooxidized in the presence of FLUO	Kleespies et al. (1996)
Mycobacterium crocinum sp. nov. czh-1A	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	–	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[b]	Hennessee et al. (2009)

The strains with the detected *pdo* gene were marked in bold

NAP naphthalene, *ANT* anthracene, *PHE* phenanthrene, *FLU* fluorene, *FLUO* fluoranthene, *PYR* pyrene, *B[a]P* benzo[a]pyrene, + capability of degrading selected compounds, – lack of degrading capability, *n.d.[a]* no data concerning hydrocarbon degrading capabilities, *n.d.[b]* no genetic and biochemical information referring *n*-alkane as well as aromatic hydrocarbon metabolism, *T* transformation, the compound did not served as a growth-supporting substrate, *pdo* gene cluster encoding PAH ring hydroxylating dioxygenase (PdoA2B2 diplays higher activity towards PHE than PYR); *nidA* and *nidA3B3*: genes encoding for pyrene dioxygenase, (NidA3B3 converts PYR more effectively than PdoA2B2)

phenanthrene, but not fluoranthene, and (3) mycobacteria catabolizing only fluoranthene (Table 1). Unfortunately, for the case of some strains the lack of complete information regarding the entire range of metabolized compounds has limited proper classification. The proposed division is convergent with the observations made by Rehmann et al. (2001), who noticed that fluoranthene-degrading mycobacteria formed two subgroups with respect to their metabolizing capabilities. Some of these microorganisms (strains CFt6, CFt2, KR20, EMI2[T]) had just two metabolic routes for fluoranthene degradation initated by dioxygenation at C1,2 and C2,3 positions (Kleespies et al. 1996; Rehmann et al. 2001; López et al. 2005). This may explain the relatively lower versatility in PAH utilization by these bacteria (Table 1) as compared to strains additionally revealing C7,8- and C8,C9-dioxygenation pathways (i.e. *Mycobacterium vanbaalenii* PYR-1). It should be noted, however, that the described study of Rehmann et al. (2001) did not consider bacteria that exhibited metabolic activities oxidizing both pyrene and phenanthrene but not fluoranthene. Most of the studied mycobacteria exhibited broad range of utilized compounds with preferences to phenanthrene, fluoranthene and pyrene (Table 1). The enzymes involved in initial dioxidation of the mentioned PAHs (i.e. NidAB, NidA3B3, and PdoA2B2) can convert all the three substances, but with different specificities. NidAB is more active against pyrene, whereas NidA3B3 transforms fluoranthene more effectively than pyrene (Kweon et al. 2010). In turn, PdoA2B2 preferentially converts the three-ring phenanthrene (Pagnout et al. 2007). Note that, the pyrene-utilizing bacteria were also able to grow on phenanthrene (Table 1). These organisms might possibly catabolize the LMW PAHs through the *o*-phthalate pathway which was recognized within representatives of the described genus (Moody et al. 2001; Krivobok et al. 2003). In such a case pyrene would be shuttled into the phenanthrene pathway through formation of 3,4-dihydroxyphenanthrene (Fig. 3). Fluoranthene is converted to *o*-phthalate via either 9-fluorenone-1-carboxylic acid or acenaphthenone routes (López et al. 2005, Fig. 3). Therefore, *Mycobacterium* strains with broadened metabolic profiles presumably employ both pyrene and fluoranthene pathways, whereas more specialized bacteria possess only one metabolic route. In order to fully elucidate mycobacterial degradation of aromatic

hydrocarbons, more studies determining the metabolic pathways and catabolic genes within PAH-utilizing strains should be performed, however. Another interesting aspect of some mycobacteria is their capability of converting less bioavailable HMW PAHs (Table 1). In addition to four-ring pyrene and chrysene, the five-ring benzo[a]pyrene (B[a]P) was also transformed by several *Mycobacterium* strains (Bogan et al. 2003; Moody et al. 2004; Hennessee et al. 2009). Principally, co-metabolism of B[a]P was demonstrated (Bogan et al. 2003; Moody et al. 2004); however, *M. rutilum* czh-7 used this substrate as a sole carbon and energy source (Hennessee et al. 2009). The recorded degradation yield was less than 10% of B[a]P at initial 50 ppm over 28 days. Among pyrene-utilizing mycobacteria, there are a few alkaliphilic strains in which transformation of this compound was documented at alkaline conditions (Habe et al. 2004; Wang et al. 2012).

Both *n*-alkanes and PAHs seem to be susceptible to mycobacterial attack. On the other hand, there are also several reports describing strains which could catabolize *n*-alkanes and some monoaromatic hydrocarbons, namely, *m*-, *p*-xylene, toluene, and benzene (see

Table 2 Environmental *Mycobacterium* strains, capable of degrading or transforming both *n*-alkanes and monoaromatic hydrocarbons

Strain	Degradative capabilities							Additional information	References
	n-alkanes	Monoaromatic hydrocarbons							
		B	EB	TOL	*o*-xyl	*m*-xyl	*p*-xyl		
Mycobacterium vaccae JOB5	nC_8, nC_{10}, nC_{16} and mono-, di- and trimethyl alkane derivatives	+	n.d.[a]	+	n.d.[a]			n.d.[b]	Ooyama and Foster (1965) and Burback and Perry (1993)
Mycobacterium cosmeticum byf-4	n.d.[a]	+	+	+*	+	n.d.[a]	n.d.[a]	*Detected *tod* genes	Zhang et al. (2012c)
Mycobacterium sp. IFP2173	nC_4, nC_5, nC_7, nC_8, nC_{10}, nC_{16}, mono-, di- and trimethyl derivatives of alkanes, pristane, isooctane	–	–	+	–*	+	+	*Not degraded *o*-xylene as supplied individually but degraded in the mixture; not degraded phenanthrene (information found in Bogan et al. 2003)	Solano-Serena et al. (2000)
Mycobacterium chubuense NBB4	nC_2–nC_{16}*	n.d.[a]	n.d.[a]	+	n.d.[a]			*2 copies of *alkB* (*locus tags*: Mycch_RS06595, Mycch_RS13610); not degraded naphthalene	Coleman et al. (2011)
Mycobacterium spp. A11, D7	nC_{16}	n.d.[a]	n.d.[a]	+	n.d.[a]			n.d.[b]	Kołwzan (2005)
Mycobacterium sp. T103 (yellow colonies)	n.d.[a]	–	n.d.[a]	+	–	–	–	n.d.[b]	Tay et al. (1998)
Mycobacterium sp. T104 (yellow colonies)	n.d.[a]	–	n.d.[a]	+	+	+	+	n.d.[b]	Tay et al. (1998)

B benzene, *EB* ethylbenzene, *TOL* toluene, *X* xylene, + capability of degrading selected compounds, – lack of degrading capability, *n.d.*[a] no data concerning hydrocarbon degrading capabilities, *n.d.*[b] no genetic and biochemical information referring *n*-alkane as well as aromatic hydrocarbon metabolism, *tod* gene encoding for toluene 1,2-dioxygenase

Table 2). Most of these bacteria utilized only selected monoaromatic compounds, whereas *Mycobacterium* spp. BS5, KA5, and KF4 were able to grow on benzene, toluene, and xylene as well as on some PAHs (Lease et al. 2011). Interestingly, none of these isolates could use LMW PAHs (naphthalene, acenaphthylene or fluorene) as sole carbon and energy sources, while phenanthrene and pyrene were transformed efficiently. Within the mentioned microbial group, only the *M. chubuense* strain NBB4 (Coleman et al. 2011) and *Mycobacterium* sp. IFP2173 (as mentioned in the work of Bogan et al. 2003) were shown not to grow on naphthalene and phenanthrene, respectively. Therefore, it is not clear if other BTEX-oxidizing microorganisms displayed narrower (limited to monoaromatic compounds) or broader (extended to PAHs) metabolic profiles. On the other hand, restrictions regarding the BTEX utilization by bacteria were observed (Parales et al. 2008). To sum up, the metabolism of three- and four-ring PAHs is a common attribute among mycobacteria that can degrade aromatic hydrocarbons (Table 1). However, other interesting metabolic preferences were also reported. For example, a combined alkene/alkane-assimilating bacterium *Mycobacterium* sp. NBB4 could efficiently degrade chlorinated aliphatic compounds (1,2-dichloroethane, vinyl chloride and *cis*-dichloroethane; Le and Coleman 2011). In turn, *Mycobacterium vaccae* JOB5 oxidized several cyclic ethers (Lan et al. 2013). Vila and Grifoll (2009) documented removal of alkyl-PAHs from the *Prestige* tanker fuel by *Mycobacterium* sp. AP1. The observed metabolic versatility in acting on wide range of recalcitrant compounds point to the important role of mycobacteria in clean-up of environments polluted by various organic products. Multidegradative, environmental *Mycobacterium* strains are fast-growing and free-living microorganisms with unique morphological traits, as most of the reported strains produce scotochromogenic creamy to yellow-orange colonies (Table 1). They were isolated from petroleum-polluted soils (Lee et al. 2001; Vila et al. 2001; Kim et al. 2005), PAH-contaminated ecosystems (e.g. soils from former coal gasification sites; Bogan et al. 2003; Leys et al. 2005; Kim et al. 2005; Lease et al. 2011), creosote-contaminated soils (López et al. 2005), and gasoline-polluted groundwater (Solano-Serena et al. 2000; Leys et al. 2005). In many cases, the isolation of PAH-utilizing strains was performed on enrichment cultures, mostly containing pyrene (Grosser et al. 1991) or fluoranthene (Rehmann et al. 2001). However, direct isolation on phenanthrene plates was also reported (Sho et al. 2004). Some studies demonstrated the natural selection of fast-growing mycobacteria in PAH-polluted soil enriched with HMW PAHs (Leys et al. 2005). Thanks to these observations, PAH-degrading mycobacteria are currently considered to be essential members of bacterial communities occurring in PAH-contaminated soils. At the same time, unpolluted soils may also be alternative habitats for these bacteria (Kim et al. 2005; Lease et al. 2011). The report of Leys et al. (2005) supported these findings as the authors suggested no correlation between PAH contamination and *Mycobacterium* biodiversity. In addition, Kim et al. (2005) showed the presence of a constitutive enzyme in *Mycobacterium vanbaalenii* PYR-1 that was responsible for PAH transformation.

Rhodococcus (Actinobacteria, Fig. 1a)

The role of rhodococci in the conversion of many recalcitrant and toxic organic substances such as aliphatic and aromatic compounds is well documented (Martínková et al. 2009; Larkin et al. 2010a; Lee et al. 2010; Song et al. 2011; Margesin et al. 2013). Therefore, these microbes are regarded as the most promising candidates in the clean-up of polluted sites and are often applied in bioremediation treatments (Steliga et al. 2012). The mastery of their metabolic versatility is also reflected by their catabolic potential towards both saturated aliphatic and aromatic hydrocarbons. These capacities are widespread among the *Rhodococcus* members, but the strain 1B was the first characterized representative (Andreoni et al. 2000). It biodegraded diverse hydrocarbons, namely, *n*-alkanes (nC_6 and nC_{16}–nC_{28}), toluene, benzene and naphthalene, both at 4 °C and 30 °C. In addition, it concomitantly removed an *n*-alkane (nC_{16}) and a PAH (naphthalene) from a two-component mixture. In the case of a mixture consisting of naphthalene and monoaromatic compounds the stepwise removal was observed where naphthalene was metabolized first, and then toluene and benzene. Such complex activities were confirmed by the documented coexistence of the *alk* and *nar* genes involved in degradation of *n*-alkanes and naphthalene, respectively. These observations supported the earlier mentioned hypothesis of Foght et al. (1990). They also expanded our knowledge

Table 3 *Rhodococcus* strains capable of degrading or transforming both *n*-alkanes and aromatic hydrocarbons

Strain	Degradative capabilities														Additional information	References
	n-alkanes	BTEX						PAHs								
		B	EB	TOL	*o*-xyl	*m*-xyl	*p*-xyl	NAP	ANT	PHE	FLU	FLUO	PYR	B[a]P		
Rhodococcus jostii RHA1 (formerly *Rhodococcus* sp. strain RHA1)	n.d.[a,*]	+**	+***	+ ***	+	n.d.[a]	n.d.[a]	–	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	*1 copy of *alkB* (*locus tag:* RHA1_RS12390), 1 copy of gene encoding for biphenyl 2,3-dioxygenase (*locus tag:* RHA1_RS02620); 1 copy of **naphthalene 1,2-dioxygenase** (*locus tag*: RHA1_RS01890), 1 copy of gene encoding for methane/ phenol/toluene hydroxylase (*locus tag*: RHA1_RS02175); **dihydroxylated by biphenyl or ethylbenzene dioxygenase; ***dioxidation by biphenyl 2,3-dioxygenase	Amouric et al. (2009) and Patrauchan et al. (2008)
Rhodococcus sp. EH831	nC_6	+	+	+	+	+	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[b]	Lee et al. (2010)
Rhodococcus sp. EC1	nC_6	+	+	+	+	+	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[b]	Lee and Cho (2008)
Rhodococcus sp. strain p52	nC_{14}, nC_{24}, nC_{32},* pristane	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+ **	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	2 copies of *alkB* (*locus tags*: IM25_RS02605, IM25_RS21935); *onoterminal, diterminal, and subterminal oxidation; ** monooxygenation; *** mono- and dioxygenation	Yang et al. (2014)
Rhodococcus sp. P14	nC_{17}–nC_{21}	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+ *	n.d.[a]	n.d.[a]	+	+	*dioxygenation (ring-hydroxylating dioxygenase gene cluster was similar to the phenanthrene degradation gene cluster (*phd*) in *Nocardioides* sp. strain KP7); 2 copies of *alkB* (*locus tags:* OEY_RS0107500, OEY_RS0108790); 1 copy of gene encoding for **benzene 1,2-dioxygenase** (*locus tag*: OEY_RS0102150),	Song et al. (2011) and Zhang et al. (2012a)
Rhodococcus sp. H45	nC_{16}, pristane	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Kołwzan (2005)
Moderately halotolerant *Rhodococcus* sp. DB11	nC_8	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	–	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Plotnikova et al. (2001)

Table 3 continued

Strain	Degradative capabilities														Additional information	References
	n-alkanes	BTEX						PAHs								
		B	EB	TOL	*o*-xyl	*m*-xyl	*p*-xyl	NAP	ANT	PHE	FLU	FLUO	PYR	B[a]P		
Rhodococcus sp. DK17	n.d.[a]	+	+	+	+	–	–	–	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	1 copy of *alkB* (*locus tag:* W9Y_RS0120600); 1 copy of gene encoding methane/phenol/toluene hydroxylase (*locus tag*: W9Y_RS0110635)	Kim et al. (2002, 2007)
Rhodococcus sp. 1BN	*n*C_6, *n*C_{16}–*n*C_{28}	+	+	+	+	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	detected *alkB* and *nar* genes	Andreoni et al. (2000)
Rhodococcus erythropolis B10	*n*-olefins, *n*-paraffins	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	+	+	+	+	+	n.d.[a]	n.d.[b]	Pasternak et al. (2011)
Psychrotolerant *Rhodococcus erythropolis* BZ4	*n*C_{12}–*n*C_{22},	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[b]	Margesin et al. (2013)
Rhodococcus erythropolis DCL14	*n*C_5–*n*C_{16}, isooctane	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	de Carvalho and da Fonseca (2005)
Rhodococcus erythropolis NTU-1	*n*C_6, *n*C_8, *n*C_{12}, *n*C_{14}, *n*C_{16}, *n*C_{18}, pristane	+	n.d.[a]	+	+, however not specified which isomer			–	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Liu et al. (2009)
Rhodococcus rhodochrous TRN7	*n*C_8, *n*C_{16}, *n*C_{20}, *n*C_{24}, *n*C_{30}, *n*C_{50}, *alkB*	n.d.[a]	n.d.[a]	+	+, however not specified which isomer			+	+	+	n.d.[a]	n.d.[a]	+	n.d.[a]	1 copy of *alkB* (*locus tag:* BN3482_RS00970); 1 copy of gene encoding methane/phenol/toluene hydroxylase (*locus tag:*BN3482_RS05040)	Rodrigues et al. (2015)
Rhodococcus wratislaviensis IFP2016	*n*C_8, *n*C_{16}, isooctane	+	+	+	+	+	+	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	1 copy of *alkB* (*locus tag:* RWRATISLAV_RS18235), *nidA, 2 copies of* ***benzene 1,2-dioxygenase*** *(locus tags:* RWRATISLAV_RS04295, RWRATISLAV_RS04300), toluene monooxygenase *(locus tag:* RWRATISLAV_RS25420)	Auffret et al. (2009, 2015)

Table 3 continued

Strain	Degradative capabilities														Additional information	References
	n-alkanes	BTEX						PAHs								
		B	EB	TOL	*o*-xyl	*m*-xyl	*p*-xyl	NAP	ANT	PHE	FLU	FLUO	PYR	B[a]P		
Rhodococcus aetherivorans IFP2017	nC_8, nC_{16}, isooctane	+	–*	–*	–*	–*	–	n.d.[a,*]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	*Not degraded as a single compound, but degraded as supplied in a mixture	Auffret et al. (2009, 2015)
Rhodococcus opacus R7	nC_{10}, nC_{12}, nC_{16}, nC_{20}, nC_{24}, nC_{36},	n.d.[a]	+	+	+	–	–	+	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	*alkB* for medium-chain length *n*-alkanes, longer than C_{20} other alkane hydroxylases, *nar;* 4 copies of *alkB (locus tags:* EP51_27580, EP51_30050, EP51_30260, EP51_43435) 3 copies of **benzene 1,2-dioxygenase** *(locus tag:*EP51_30920, EP51_30925, EP51_30930), **naphthalene 1,2-dioxygenase** (*locus tag:*EP51_44085)	Di Gennaro et al. (2001, 2010) and Zampolli et al. (2014)
Rhodococcus opacus B-4	nC_6, nC_8, nC_{10}	+*	+	+	+	+	+	+	–	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	*benzene dioxygenase pathway, *bnzA1A2* genes are involved in benzene catabolism, 2 copies of *alkB* (*locus tags*: ROP_RS11230, ROP_RS37955), 2 copies of **benzene dioxygenase** (bnzA1 *locus tag*: ROP_pROB02-01580, bnzA2 *locus tag*: ROP_pROB02-01590)	Na et al. (2005)
Rhodococcus opacus M213	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	+	–	–	–	n.d.[a]	n.d.[a]	n.d.[a]	approximately 22% of the protein-coding genes were connected to KEGG pathways, with 401 genes involved in the metabolism of polycyclic aromatic hydrocarbons (PAHs) (NAP, PHE, ANT, and benzo[a]pyrene), genome, 1 copy of *alkB* (*locus tag*: WSS_RS19655), 2 copies of **benzene 1,2-dioxygenase** (*locus tags:* WSS_RS07135, WSS_RS07140), methane/phenol/toluene hydroxylase (*locus tag*: WSS_RS38805)	Uz et al. (2000)

Table 3 continued

Strain	Degradative capabilities														Additional information	References
	n-alkanes	BTEX						PAHs								
		B	EB	TOL	*o*-xyl	*m*-xyl	*p*-xyl	NAP	ANT	PHE	FLU	FLUO	PYR	B[a]P		
Rhodococcus aetherivorans BCP1(also known as *Rhodococcus* sp. BCP1)	nC_6–nC_{36}, pristane, phytane,	+	+	+	+	+	+	+	–	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	5 copies of *alkB* (*locus tags:* N505_RS18440, N505_RS20230, N505_0118345, N505_0118460,N505_0120250), 3 copies of **benzene 1,2-dioxygenase** (*locus tags*: N505_0122305, N505_0122310, N505_0122315), 2 copies of biphenyl 2,3-dioxygenase (*locus tag:*N505_0127505, N505_0101765)	Orro et al. (2015)
Rhodococcus sp. IN129	nC_7, nC_{10}, nC_{16}, pristane	n.d.[a]	n.d.[a]	+	+, not determined which isomer			+	+	–	–	+	+	+	n.d.[b]	Brzeszcz (2017)
Rhodococcus sp. WN1	nC_6, nC_8, nC_{10}	n.d.[a]	n.d.[a]	+	+, not determined which isomer			+	–	–	n.d.[a]	–	–	n.d.[a]	n.d.[b]	Kästner et al. (1994)
Rhodococcus wratislaviensis CUP11	nC_{16}, pristane, squalene,	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[b]	Supel et al. (2016)
Rhodococcus sp. MK1	*n*-C_9, *n*-C_{16}	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	+	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	n.d.[a]	5 copies of *alkB*	Kis et al. (2017)

The presence of genes encoding for benzene 1,2-dioxygenase and naphthalene 1,2-dioxygenase were marked in bold

B benzene, *EB* ethylobenzene, *TOL* toluene, *o-xyl o*-xylene, *m-xyl m*-xylene, *p-xyl p*-xylene, *NAP* naphthalene, *ANT* anthracene, *PHE* phenanthrene, *FLU* fluorene, *FLUO* fluoranthene, *PYR* pyrene, *B[a]P* benzo[a]pyrene, + capability of degrading selected compounds, – lack of degrading capability, *n.d.*[a] no data concerning hydrocarbon degrading capabilities, *n.d.*[b] no genetic and biochemical information referring *n*-alkane as well as aromatic hydrocarbon metabolism, *alkB* gene encoding for alkane 1-monooxygenase, *nar* gene cluster encoding for naphthalene 1,2-dioxygenase, *nid* gene cluster encoding for naphthalene-inducible dioxygenase

regarding the occurrence of the enhanced metabolic potential not only in *Pseudomonas* as postulated by Whyte et al. (1997) but also in actinobacterial strains.

Subsequent studies revealed the biochemical diversity and plasticity of hydrocarbon-degrading rhodococci (Table 3). In contrast to the relatively more specialized PAH-oxidizing mycobacteria, many *Rhodococcus* strains biodegraded a broader range of *n*-alkanes and aromatic compounds (BTEX as well as LMW PAHs). Nevertheless, some strain-specific preferences were found. For example, *R. erythropolis* NTU-1 could not grow in the presence of naphthalene (Liu et al. 2009), while *R. opacus* M213 utilized this compound (Uz et al. 2000). In spite of the fact that some aromatic compounds were not tested, the predominance of BTEX-degrading capabilities was clearly observed among rhodococci (Table 3). Besides naphthalene, some bacteria also utilized higher homologues; however, these activities were not as common as they were in mycobacteria. Only a few reports indicated B[a]P biotransformation (Song et al. 2011; Qu et al. 2015), which seems to be a unique feature for the *Rhodococcus* genus.

The prevalence of the enhanced metabolic activities in rhodococci is reflected by a great amount of evidence (Table 3). These bacteria can successfully degrade aromatic hydrocarbons due to a wide range of produced RHDs (ring hydroxylating dioxygenases; Larkin et al. 2010a; Zhang et al. 2012a; Orro et al. 2015), broad substrate specificity and genome plasticity (Larkin et al. 2010b). In turn, the alkane-oxidizing capabilities of rhodococci are considered permanent and typical traits since in most of the strains the *alkB* gene is predominant (Nie et al. 2014) and it occurs in multiple copies (Zhang et al. 2012a; Orro et al. 2015; Table 3). On the other hand, only one copy of chromosomally encoded *alkB* was identified in the *R. opacus* R7 genome sequence (Orro et al. 2015). However, a great number of genes coding for putative P450 monooxygenases were shown in this strain, and these enzymes may also be involved in alkane metabolism (Orro et al. 2015). Based on the recently available information regarding genome sequences of *Rhodococcus opacus* (9 sequences have been deposited in the NCBI GenBank until April 2018) it is apparent that particular strains of this species may possess different numbers of the *alkB* gene copies. For example, in contrast to R7, there are two gene copies in *R. opacus* 04-OD7 and B4 whereas the strain NRRL B-24011 harbors four *alkB* genes). Taking into account the above facts, the prevalence of catabolic capacities towards both *n*-alkanes and aromatic hydrocarbons in the *Rhodococcus* strains is not surprising. Thanks to specific physiological and genetic attributes, rhodococci represent an abundant constituent of microbial communities in hydrocarbon-polluted localizations and are easily isolated from such ecosystems (Song et al. 2011). *Rhodococcus* strains with the hybrid metabolism preferentially colonize hydrocarbon-impacted environments (Plotnikova et al. 2001; Di Gennaro et al. 2001; Pasternak et al. 2011; Song et al. 2011; Margesin et al. 2013; Brzeszcz 2017) as well as sites that are rich in organic compounds (Supel et al. 2016). However, pristine soils may also serve as their habitats (Brzeszcz 2017).

Under aerobic conditions, low temperatures severely limit hydrocarbon degradation. *Rhodococcus* strains can often be found in cold, petroleum-polluted ecosystems. Moreover, psychrotolerant strains capable of concomitant degradation of aliphatic and aromatic compounds were also reported to occur in oil-contaminated alpine soils (Margesin et al. 2013). In addition to psychrotolerant *Rhodococcus erythropolis* BZ4 (Margesin et al. 2013), other psychrotolerant bacterial strains with broader set of metabolic activities were isolated from both contaminated and pristine alpine terrestrial ecosystems (Brzeszcz 2017). In addition, some sediments were also inhabited by these microbes (de Carvalho and da Fonseca 2005). Another study (Pasternak et al. 2011) strongly supported rhodococcal capabilities of enzymatic attack on structurally diverse compounds at low temperatures. The authors demonstrated the concomitant biotransformation of aliphatic and aromatic hydrocarbons in a coal tar at 15 °C. Biodegradation of *n*-alkanes at saline conditions is an additional, interesting aspect of *Rhodococcus* biology. Such an activity was revealed by several strains (de Carvalho and da Fonseca 2005; Liu et al. 2009). *Rhodococcus* sp. DCL14 could grow on the tested compounds under salt levels of up to 2.5% (de Carvalho and da Fonseca 2005), while *R. erythropolis* NTU-1 efficiently utilized nC_{16} at an initial NaCl concentration of up to 3.6% (Liu et al. 2009). Thus, *Rhodococcus* strains may also be considered as potential favorable agents in bioremediation of oil-polluted, moderately saline environments. The application of these bacteria could prevent

costly salt removal actions before biological treatments or dilutions necessary to lower the salinity.

Other Actinobacteria (Fig. 1a)

The reports of the enhanced biodegradation potential in other Actinobacteria are less frequent compared to mycobacteria and rhodococci. The ability to transform both *n*-alkanes and aromatic compounds was found in some representatives of the well-known hydrocarbon-degrading genera, such as *Dietzia, Nocardia, Arthrobacter* and *Microbacterium.* The members of *Streptomyces* and *Corynebacterium* also revealed the mentioned metabolic diversity. These findings are even more interesting in the context of the fact that the two genera are rarely or not at all recognized as being involved in hydrocarbon catabolism (Balachandran et al. 2012; Ferradji et al. 2014; Gurav et al. 2017). The described tailored metabolic potential was exhibited not only by non-halophilic and mesophilic Actinobacteria but also by extremely halophilic and psychrotolerant strains (Al-Mueini et al. 2007; Lo Giudice et al. 2010). The bacterial strains were isolated from a wide range of sources such as oil-contaminated soils (von der Weid et al. 2007), sediments (Gao et al. 2015; Chen et al. 2017), seawaters (Chanthamalee and Luepromchai 2012) or production water of a deep subterranean oil-reservoir (Wang et al. 2011).

Some of the *Dietzia* strains are known as potential human pathogens, while the other ones have proved to transform petroleum compounds (Gharibzahedi et al. 2014). Among the latter organisms, there are environmental strains that exhibit the broad set of catabolic activities. However, monoaromatic hydrocarbons are rarely used as growth substrates. *Dietzia* sp. DQ12-45-1b utilized saturated aliphatic (nC_6–nC_{40}) and aromatic hydrocarbons (fluorene, chrysene, naphthalene, and phenanthrene; Wang et al. 2011), whereas *Dietzia* sp. A14101 could remove *n*-alkanes (nC_5–nC_{18}) and monoaromatic compounds (*o*-xylene, toluene) from crude oil (Bødtker et al. 2009). *Dietzia cinnamae* P4, obtained from Brazilian tropical rainforest soil, oxidized medium- and long-chain *n*-alkanes (nC_{11}-nC_{36}), phytane, pristane and toluene as well as LMW PAHs (von der Weid et al. 2007). The genome sequencing of P4 showed a repertoire of metabolic genes that are involved in hydrocarbon decomposition. These observations demonstrate the coexistence of multidegradative pathways of *n*-alkanes (single *alk* gene cluster), aromatic and phenolic compounds (Procópio et al. 2012, 2013). Another strain, the salt-tolerant *Dietzia cinnamae* HRJ5, also displayed metabolic diversity and flexibility (Gurav et al. 2017). Lower chain *n*-alkanes (nC_8–nC_{19}) were readily biodegraded among the tested aliphatic hydrocarbons, while naphthalene and a mixture of pentacyclic aromatic compounds were utilized preferentially over other substances. The documented presence of both the *alkB* and *nah* genes in HRJ5 confirmed these activities. Moreover, among the other studied strains, HRJ5 exhibited the highest number of copies of the *nah* gene enabling maximum yield of naphthalene degradation. This result was possibly achieved due to a target-specific catabolic function of naphthalene dioxygenase, a product of the *nah* gene coding for the key step in aerobic oxidation of the mentioned bicyclic PAH. Al-Awadhi et al. (2007) isolated alkaliphilic *Dietzia* sp. A3 that utilized a wide range of *n*-alkanes and phenanthrene. Recent studies reveal diverse metabolic preferences of *Dietzia* sp. CN-3 obtained from oil-contaminated sediments in China’s Bohai Bay (Chen et al. 2017). The strain could grow on nC_{14}–nC_{31}, pristane, pyrene, phenanthrene, and crude oil. In addition, the authors reported the role of *cyp153* in *n*-alkane degradation, especially in long-chain nC_{26} transformation. *Dietzia* spp. A1, A2, A3 also exhibited broadened metabolic potential; these microorganisms utilized *n*-alkanes, naphthalene, phenanthrene, fluorene and chrysene (Gao et al., 2015). A similar catabolic profile of *Micrococcus* sp. A2 was demonstrated by Al-Awadhi et al. (2007). The *Arthrobacter* genus, commonly occurring in soil, especially in polluted cold terrestrial ecosystems (Lo Giudice et al. 2010; Margesin et al. 2013), represents particularly interesting properties. Many bacteria belonging to the mentioned taxon (according to the previous classification, see Busse 2016) convert various xenobiotics (Margesin et al. 2013), mainly aromatic hydrocarbons. Hence, some representatives are known as PAH-degraders (Kallimanis et al. 2007; Ren et al. 2015). The catabolic capabilities towards both groups of substances among *Arthrobacter* were not subjected to extensive studies, in spite of the fact that Efroymson and Alexander (1991) first reported such features at the beginning of the 1990s. In their study, the strain *Arthrobacter* sp. R1 mineralized *n*-hexadecane as well as naphthalene, which were supplied in nondissolved and dissolved forms in 2,2,4,4,6,8,8-heptamethylnonane. The resultant

biotransformation yield grew along with the increasing solvent volume. Later studies aimed at the isolation of PAH-degraders from salt-contaminated soils demonstrated the utilization of nC_8 and two-ring PAH by a moderately halotolerant *Arthrobacter* sp. SN17 (Plotnikova et al. 2001). In addition, Lo Giudice et al. (2010) found psychrotolerant *Arthrobacter* sp. H15 which consumed nC_{11}-nC_{16} and tricyclic phenanthrene while growing poorly in the presence of benzene, fluoranthene and fluorene. The authors also reported other strains capable of utilizing both groups of compounds (*Arthrobacter* spp. HY1 and HY1a); however their growth in the presence of these substances was regarded as only moderate. Other psychrotolerant strains able to transform some *n*-alkanes and BTEX were isolated from alpine soils (Brzeszcz 2017). Note, that these microorganisms could colonize both oil-polluted and unpolluted soil (Brzeszcz 2017).

n-alkanes and aromatic compounds were catabolized by the thermophilic *Nocardia otitidiscaviarum* TSH1 (Zeinali et al. 2007a, b). The strain grew on nC_{12}, nC_{16}, phenanthrene, anthracene, naphthalene and pyrene at 50 °C. Similar metabolic potential was displayed by *Nocardia* sp. H17-1 which degraded long-chain aliphatic hydrocarbons (nC_{12}–nC_{26}) and utilized, although poorly, some PAHs (naphthalene, phenanthrene, and pyrene; anthracene was not tested as a growth substrate for this strain; Baek et al. 2006). Moreover, the detection of some genes involved in the metabolism of *n*-alkanes (*alkB*) and alkylated aromatic hydrocarbons (*catA,* the gene coding for catechol 1,2-dioxygenase) further supported the observations implying hybrid metabolism. At the same time, other genes involved in degradation of aromatic compounds (*xylE* encoding catechol 2,3-dioxygenase and *nar* encoding naphthalene dioxygenase) were not present. Rodrigues et al. (2015) reported *Nocardia farcinica* TRH1 which displayed a versatile metabolism towards various substances including *n*-alkanes, mono- and polyaromatic hydrocarbons. In contrast to the bacterial strains mentioned earlier, *Nocardia* sp. H4 showed a more restricted catabolic profile. The strain converted only hexadecane as well as toluene (Kołwzan 2005). Linear, branched *n*-alkanes and alkyl-benzene were transformed by *Nocardia cyriacigeorgica* (Nhi-Cong et al. 2010). The degradation of other aromatic hydrocarbons was not reported. *Gordonia*-like environmental strain BP9 could use the tested *n*-alkanes, pyrene, naphthalene, phenanthrene and fluoranthene as sole carbon and energy sources, whereas anthracene was not degraded (Kästner et al. 1994). A seawater-borne *Gordonia* sp. JC11 displayed the highest oil removal efficiency among the other studied strains, and it grew well on both nC_{14} and phenanthrene (Chanthamalee and Luepromchai 2012). Moreover, it removed linear as well as saturated and aromatic components in the tested waste lubricants and in crude oil. Qi et al. (2017) has recently documented the metabolic activities of *Gordonia* sp. Q8 able to biotransform *n*-alkanes and a wide range of PAHs present in crude oil. *Microbacterium* sp. Sphe1 was demonstrated by Zhang et al. (2004) to degrade *n*-alkanes and phenanthrene. It seems to be the first paper describing these features among the mentioned genus. Recently, Rodrigues et al. (2015) noted the similar metabolic activities in two novel *Microbacterium* strains. The strain TRN9 grew on nC_{16}, nC_{24} and naphthalene, whereas TRN10 used nC_{24} and two- and three-ring PAHs. Both nC_{14} and phenanthrene served as growth substrates for *Microbacterium* sp. JC9, isolated from oil-contaminated sea sand (Chanthamalee and Luepromchai 2012). Unique preferences were found in *Microbacterium esteraromaticum* strain SBS-1 (Wongbunmak et al. 2017). This bacterium was able to grow on all six BTEX substrates, hexane and naphthalene.

Streptomyces, typical soil bacteria, are not regarded as efficient hydrocarbon degraders. There are a few reports indicating that *Streptomyces* could be important players in these processes by removing both *n*-alkanes and aromatic compounds. Some strains such as AH4, AB1 and AM2 exhibited broad-ranging substrate specificities as they grew on *n*-alkanes (nC_{11}–nC_{30}) and bicyclic PAHs (Ferradji et al. 2014). Furthermore, the cited authors suggested that production of extracellular humic acid peroxidases HaP1, HaP2 and HaP3 might serve as an essential mechanism in naphthalene transformation by these organisms. *Streptomyces* sp. ERI-CPDA-1 utilized similar compounds as the abovementioned strains, but its naphthalene degradation pathways differed (Balachandran et al. 2012).

The versatile catabolism of *Actinopolyspora* sp. DPD1 was the subject of investigations conducted by Al-Mueini et al. (2007). An extremely halophilic, fluorene-degrading DPD1, isolated from the Omani oil field soils, efficiently removed aliphatic hydrocarbons

(up to nC_{15}). *Sanguibacter* is yet another representative of Actinobacteria that exhibited the mutlidegradative preferences. In addition to several medium-chain *n*-alkanes, *Sanguibacter* sp. HY10 grew well on benzene, toluene, naphthalene, fluoranthene, phenanthrene and fluorene (Lo Giudice et al. 2010). In turn, *Corynebacterium variabile* HRJ4 inhabiting polluted soil, preferentially utilized long-chain *n*-alkanes (nC_{20}–nC_{30}) as well as a wide range of aromatic hydrocarbons (from bicyclic to hexacyclic ones). However, its *n*-alkane removal efficiency was higher than that of aromatic compounds. The coexistence of genes involved in the metabolism of both groups of organics (*alkB* and *nah* genes) supported the observed capacities of HRJ4 (Gurav et al. 2017).

Pseudomonas (Gammaproteobacteria, Fig. 1b)

Even though the *Pseudomonas* taxon is known for numerous strains able to degrade various organic compounds including both aliphatic and aromatic hydrocarbons, these features have also been recognized in other genera of Gammaproteobacteria. Nevertheless, the metabolic activities of *Pseudomonas* have been studied much more extensively than for the case of other microbial groups. A wealth of papers addressing hydrocarbon transformation confirms the key role of this genus among other oil-degraders. As mentioned above, Whyte et al. (1997) first reported hydrocarbon-degrading, psychrotrophic *Pseudomonas* strains that metabolized nC_5–nC_{12}, toluene and naphthalene at both 5 °C and 25 °C. In addition, the authors were the first to show that two different catabolic plasmids, *alkB*$^{+}$ and NAH, could coexist in a naturally occurring bacterium. A wider range of utilized compounds was displayed by the halophilic organism *Pseudomonas* sp. BZ-3. It transformed nC_6, xylene, benzene, naphthalene, phenanthrene, anthracene and pyrene (Lin et al. 2014). The authors reported that 75% of the phenanthrene (initial concentration of 50 mg L^{-1}) was degraded in the presence of NaCl (20 g L^{-1}). *Pseudomonas aeruginosa* DQ8, isolated from petroleum-contaminated soil in a Chinese Daqing oilfield, utilized *n*-alkanes as well as some PAHs (e.g. fluorene, phenanthrene, pyrene, fluoranthene). None of the BTEX group was metabolized, however (Zhang et al. 2011). Moreover, the genome sequencing of DQ8 showed the presence of an *alk* cluster, confirming the phenotypic observations (Gai et al. 2012). Interestingly, the strain exhibited two diversified, well recognized for various bacteria, enzymatic strategies towards fluorene. It could oxidize the compound via both C9-monooxidation and C3,C4-dioxidation (Gai et al. 2012). *P. aeruginosa* strain W10 also preferentially utilized *n*-C_{16} as well as naphthalene, phenanthrene, fluoranthene, and pyrene (Chebbi et al. 2017). However, its growth was not supported by any of the BTEX compounds, nor by *n*-C_8. In turn, *Pseudomonas* spp. strains DN34 and D36 metabolized *n*-alkanes as well as LMW PAHs (naphthalene, fluorene, and phenanthrene; Fuentes et al. 2016). Then, further investigations also revealed similar metabolic capacities in other *Pseudomonas aeruginosa* strains RM1 and SK1 that inhabited tropical polluted soil. These organisms removed both aliphatic and aromatic hydrocarbons from waste engine oil (Salam 2016). Significant concentration decrease of nC_{13}–nC_{16}, nC_{23}–nC_{26}, pristane, anthracene and pyrene in the tested medium was recorded. Chaerun et al. (2004) studied the microbial activities of the Atake seashores impacted by the *Nakhodka* oil spill in the Sea of Japan, and they isolated *P. aeruginosa* spp. A5 and A6, which also displayed hydrocarbon multidegradative capabilities. Besides saturated aliphatic compounds, A5 utilized several PAHs, whereas A6 also grew on toluene. The study aimed at the catabolic potential of *Pseudomonas* sp. WJ6 (Xia et al. 2014) showed that the strain was able to transform several *n*-alkanes (nC_{12}, nC_{22}, nC_{32}, nC_{40}) and diverse PAHs (naphthalene, fluorene, phenanthrene, and pyrene). It grew noticeably and rapidly on medium- and long-chain *n*-alkanes up to nC_{32}, while slightly more slowly when utilizing nC_{40} and PAHs. Fluorene degradation proceeded more efficiently than that of naphthalene and phenanthrene, as well. The authors emphasized that WJ6 used a broader range of crude oil components as carbon sources than other *Pseudomonas* strains. *Pseudomonas* sp. LGM2, isolated from oil-polluted soil, metabolized phenanthrene, pyrene, B[a]P and aliphatic compounds: nC_{18} and pristane (Guermouche M'rassi et al. 2015). The bacterial strains PS-I, PS-II and PS-III, also identified as *Pseudomonas,* removed not only the aliphatic but also aromatic fractions of crude oil (Mittal and Singh 2009). The metabolic spectrum of *Pseudomonas* spp. G2, H10, B3 covered, among others, nC_{16} and toluene (Kołwzan 2005). The research conducted by Aislabie et al. (2000) revealed

the presence of *Pseudomonas* strains in Antarctic oil-contaminated soils. These bacteria, the strains Ant30 and 8/48, could transform nC_7, nC_{11}, monoaromatic (toluene, *m*-, *p*-xylene) and diaromatic hydrocarbons. In turn, Auffret et al. (2015) isolated *Pseudomonas* sp. from a bacterial consortium Mix3. This bacterium utilized *n*-alkanes (nC_8, nC_{16}), all the members of BTEX group as well as naphthalene. Another study demonstrated the presence of a broad metabolic profile in psychrotolerant *Pseudomonas* spp. 7/167 and 8/46 (Farrell et al. 2003). Both organisms were capable of growing on a wide range of compounds, including medium-chain *n*-alkanes and some aromatic hydrocarbons. Even though the isolates utilized similar substances, some preferences were observed. For example, the isolate 8/46 could degrade benzene and 7/167 could not, whereas the isolate 7/167, unlike 8/46, was able to grow on 2-methylnaphthalene. Among the isolates obtained from the surface seawater collected from Antarctic coastal areas, the psychrotolerant *Pseudomonas* sp. HY7a grew on selected *n*-alkanes, benzene and toluene (Lo Giudice et al. 2010). A narrower range of oxidized hydrocarbons was displayed by *Pseudomonas mendocina* KR-1, as it converted only nC_5–nC_8 and toluene (Smith et al. 2003).

Other Gammaproteobacteria (Fig. 1b)

Besides *Pseudomonas*, another member of the Pseudomonadales order, that is *Acinetobacter calcoaceticus* S30, displayed a broadened catabolic profile. The strain grew well on *n*-alkanes up to nC_{33}, pristane and naphthalene (Lal and Khanna 1996). In turn, *Acinetobacter* sp. AA64 utilized *n*-alkanes as well as anthracene (Fuentes et al. 2016). However, this catabolic potential seems to be unique within the *Acinetobacter* genus since there are no other data references available. Metabolic diversity and flexibility were also identified in the Xanthomonadaceae family within the Gammaproteobacteria class (Kim et al. 2008b; Klankeo et al. 2009; Patel et al. 2012; Nopcharoenkul et al. 2013). Nevertheless, the observed hybrid metabolism is not as prevalent as among *Pseudomonas*, and it is restricted to a few microorganisms (Klankeo et al. 2009; Jiménez et al. 2011; Nopcharoenkul et al. 2013). These bacteria are known to colonize hydrocarbon-rich environments. The range of utilized compounds is strain-specific. Members of the *Pseudoxanthomonas* genus (Xanthomonadaceae) are generally not recognized as typical hydrocarbon degraders, although biotransformation of various petroleum substances by numerous bacterial strains was reported. The strain DMPV2 could decompose phenanthrene, pyrene, fluoranthene and nC_6 but not mono- and two-ring aromatic hydrocarbons (Patel et al. 2012). Moreover, the presence of the latter mentioned compounds inhibited phenanthrene degradation (Patel et al. 2012). On the other hand, Kim et al. (2008b) showed rare metabolic activities towards all the BTEXs in *Pseudoxanthomonas spadix* BD-a59. In addition, the authors also identified two *alkB* copies in the genome sequence of BD-a59, indicating alkane degradation potential of this strain. It is worth noting that the mentioned observations regarding monoaromatic compounds metabolism of *Pseudoxanthomonas* are the first and, so far, the only ones. Another strain, *Pseudoxanthomonas* sp. RN402, utilized saturated, linear aliphatic compounds (nC_{14}, nC_{16}; Nopcharoenkul et al. 2013) and some HMW PAHs (pyrene, fluoranthene, phenanthrene; Klankeo et al. 2009). The latter authors also demonstrated that the *nidA* genes, which are localized on a megaplasmid, are involved in PAH removal. Furthermore, they recorded a 99%-degradation of pyrene (100 mg L^{-1}) by RN402 during a 16-day incubation. Multiple degradative capacities were found in *Franconibacter pulveris* DJ34 inhabiting crude oil-rich environment. The bacterium was shown to utilize various compounds, namely *n*-C_{15}, *n*-C_{16}, benzene, ethylbenzene, and xylene (Pal et al. 2017). The authors supported the phenotypic observations with genome analysis. It revealed the genetic repertoire for alkane (genes encoding alkane monooxygenase and the enzymes subsequent in the oxidation pathway) and aromatic compounds (i.e. catechol 2,3-dioxygenase, ring-opening dioxygenase, protocatechuate 3,4-dioxygenase) degradation. Juhasz et al. (1997) isolated a strain VUN 10,003, currently known as *Stenotrophomonas maltophilia* (previously *Burkholderia cepacia*) that was able to convert *n*-alkanes (nC_6, nC_8), toluene, benzene and its complex derivatives: pyrene, phenanthrene, fluoranthene, B[a]P, dibenz[*a,h*]anthracene and coronene (Juhasz et al. 1997, 2000). The HMW PAHs biotransformation was observed for individually supplemented compounds as well as for a multicomponent mixture. In addition, a catabolic repression mechanism of B[a]P

and dibenz[*a,h*]pyrene caused by accumulation of intermediate(s) and/or by-product(s) was noted (Juhasz et al. 2002); however, the inhibitory compounds have not been identified so far.

Interestingly, marine hydrocarbon-degrading bacteria belonging to Gammaproteobacteria also revealed the broadened preferences towards structurally divergent groups of hydrocarbons. Among the true marine *Marinobacter* genus (Alteromonadaceae family) associated with *n*-alkane transformation, there are several strains metabolizing both saturated aliphatic and aromatic compounds. *Marinobacter hydrocarbonoclasticus* SP.17 was able to grow in media supplemented with nC_{14}, nC_{16}, nC_{20}, nC_{21}, pristane, phenyldecane and phenanthrene. This strain was isolated from sediments that had been chronically polluted by hydrocarbons in the Golf of Fos (Gauthier et al. 1992). While studying the hydrocarbon-utilizing bacterial communities inhabiting mangrove sediments, another *Marinobacter* strain GPM 2541 was found (Brito et al. 2006). It removed nC_8, pyrene and phenanthrene during a 21-day incubation. Noteworthy, the results indicated a much more efficient degradation of PAHs than that of the *n*-alkane (degradation rates: 50% for phenanthrene, 27% for pyrene and only 10% for nC_8). Later, the studies conducted by Al-Awadhi et al. (2007) provided further evidence that other *Marinobacter* strains could catabolize a broad set of petroleum hydrocarbons. Namely, the alkaliphilic *Marinobacter* sp. A1 as well as two halophilic strains, H2 and H5, oxidized both nC_{18} and phenanthrene. The reported conditions of hydrocarbon degradation were pH 11.0 and NaCl concentration of 3.5% for the alkaliphile and halophiles, respectively. Recently, Al-Mailem et al. (2013) have isolated two halophilic bacteria, *M. sedimentalis* and *M. falvimaris*, on the basis of their ability to transform a wide range of *n*-alkanes (nC_9–nC_{40}), benzene and some PAHs (naphthalene, phenanthrene, anthracene). Aside from *Marinobacter*, other marine bacteria also displayed new metabolic properties, and this observation should be regarded as important in a bioremediation context. Enhanced hydrocarbon metabolic activities exhibited another representative of Alteromonadaceae family, *Glaciecola* sp. NS168 (Chronopoulou et al. 2015). It utilized linear and branched alkanes as well as three-ring PAHs. Interestingly, the bacterium did not metabolize any of PAH components of crude oil, even though it grew on phenanthrene supplied solely. The members of the *Alcanivorax* genus participate in *n*-alkane oxidations in marine environments. Thus, these bacteria are recognized as important and highly specialized marine hydrocarbon degraders. Interestingly, a wide-ranged catabolic potential was exhibited by *Alcanivorax* sp. GPM 2509 (Alcanivoraceae family) as it utilized pyrene, phenanthrene and nC_8 (Brito et al. 2006). The authors reported that GPM 2509 transformed the mentioned PAHs more efficiently than the tested *n*-alkane. This result contrasted with the one observed for the abovementioned *Marinobacter* sp. GPM 2541. In another study, two marine *Alcanivorax* spp. isolates were also shown to oxidize *n*-alkanes and PAHs (Jiménez et al. 2011). Chronopoulou et al. (2015), who studied hydrocarbon-degrading bacterial communities in the oil-polluted water column of the North Sea, found many cosmopolitan marine generalists belonging to the genus *Pseudoalteromonas* (Pseudoalteromonadaceae family). Most of the isolates (NS17, NS43, NS50, NS77, NS97) grew on branched- and straight-chain *n*-alkanes as well as some PAHs (fluorene, phenanthrene and anthracene), while none of the bacteria utilized benzene, toluene, pyrene or cyclohexane. Moreover, the cited authors isolated also *Halomonas* sp. NS 165 (Halomonadaceae family), which grew on a wide range of substrates, including branched and straight-chain alkanes and PAHs.

Alpha- and Betaproteobacteria (Fig. 1b)

Hydrocarbon-degrading strains can be found among Alpha- and Betaproteobacteria, as well. For example, the role of *Sphingomonas*, *Ochrobactrum*, and *Burkholderia* in the transformation of PAHs and other aromatic hydrocarbons is well documented (Rentz et al. 2008; Baboshin et al. 2008; Ghosal et al. 2010; Andreolli et al. 2013). Some representatives of the mentioned classes display catabolic activities towards both aliphatic and aromatic hydrocarbons; however, a limited number of published papers suggest that these features are not as common as they are in Gammaproteobacteria. Juhasz et al. (1997) demonstrated that gram-negative *Burkholderia cepacia* spp. VUN 10,001 and VUN 10,002 (Betaproteobacteria) utilized *n*-alkanes (nC_6, nC_8), benzene and phenolic compounds. The authors found that the strain VUN 10,001 additionally transformed toluene. Other aromatic compounds also served as growth substrates for these

microbes, namely, pyrene, phenanthrene and fluoranthene. Moreover, both bacteria co-metabolized benzo[*a*]anthracene and dibenzo[*a,h*]anthracene in the presence of fluoranthene. A much more restricted degradation profile was shown in *Burkholderia* sp. AA1. The strain catabolized only medium- and long-chain *n*-alkanes (nC_{10}–nC_{25}) as well as toluene (Ma and Herson 2000). At the same time *m*-xylene, naphthalene, phenanthrene and some aliphats (nC_5, nC_6, nC_8, nC_{30}) were not utilized. For the case of *B. cepacia* 2A-12, Kim et al. (2003) provided direct experimental proof only for PAHs (naphthalene, phenanthrene) degradation. However, the authors also claimed that the strain could catabolize a broad range of *n*-alkanes (nC_{12}–nC_{30}). Contrary to the strain VUN 10,001, pyrene was not consumed by *B. cepacia* 2A-12. A complex hydrocarbon catabolism was documented in other strains that were classified within the Burkholderiales (Betaproteobacteria) order. Lal and Khanna (1996) reported *Alcaligenes odorans* P20, which grew well on *n*-alkanes up to nC_{33} and on pristane, but not on cycloalkanes. Moreover, the strain degraded several aromatic compounds, namely, anthracene, phenanthrene, fluorene, fluoranthene, pyrene and chrysene. Deng et al. (2014) investigated the conversion of *n*-alkanes (nC_{12}–nC_{27}) as well as some of three- and four-ring PAHs by *Achromobacter* sp. HZ01. The reported yield of PAH degradation reached 29.0–50.6% during a 30-day period. Considerable genetic potential towards various compounds was observed in *Polaromonas* sp. JS666, since many gene clusters encoding the enzymatic systems involved in aliphatic and aromatic hydrocarbons catabolism were found (Mattes et al. 2008).

As mentioned above, bacteria belonging to Sphingomonadaceae (Alphaproteobacteria) are known as PAH degraders. However, their alkane-metabolizing capabilities are not that widespread. Both of the discussed features were identified in *Sphingomonas* Ant17. It converted the mono- and di-alkyl derivatives of monoaromatic hydrocarbons, PAHs (Baraniecki et al. 2002) and some *n*-alkanes (nC_7, nC_{11}; Aislabie et al. 2000). Hesham et al. (2014) studied the catabolic potential of *Sphingomonas koreensis* ASU-06, which utilized several PAHs (naphthalene, anthracene, phenanthrene and pyrene). Furthermore, this strain was found to contain the genes involved in degradation of aromatic compounds (*nahAc, C12O, C23O*), as well. Enhanced pyrene removal rates occurred in a PAH mixture consisting of all the compounds mentioned above. Although the cited authors did not directly indicate any potential for alkane degradation, the genetic evidence (presence of *alkB* and *alkB1*) suggested that ASU-06 produced such activities. In another study (Abed 2010), *Sphingomonas* sp. GM42 was shown to catabolize both nC_5 and phenanthrene, while the other tested *n*-alkanes, BTEX and PAHs were degraded poorly or not biotransformed, at all. There are single reports describing the mentioned preferences in strains belonging to other alphaproteobacterial genera, such as *Paracoccus* and *Celeribacter*. *Paracoccus* strains are rarely reported in the biodegradation literature and are thus not considered to be typical degraders of organic xenobiotics; however, their metabolic capabilities seem to be promising for PAH biotransformation (Zhang et al. 2004; Guo et al. 2005). *Paracoccus* sp. Ophe1 is the first member of this genus with metabolism directed towards both *n*-alkanes and aromatic hydrocarbons. This strain was shown to use short- and long-chain *n*-alkanes (nC_6, nC_{12}, nC_{16}, nC_{18}, nC_{28}), anthracene, phenanthrene, fluorene, chrysene, and pyrene as its sole carbon and energy sources (Zhang et al. 2004). Neither xylene, nor toluene was degraded, but the bioconversion of *o*-, *m*-, *p*-cresol was observed. Similar metabolic preferences were found in another *Paracoccus* strain, isolated from a marine oil spill sample (Jiménez et al. 2011). The genetic potential for alkane degradation by *Paracoccus* was also evidenced by the broad distribution of *alkB* in the genomes deposited in NCBI (Nie et al. 2014). In addition to the mentioned representatives of the Rhodobacteraceae family, multidegradative capabilities were revealed in the *Celeribacter* genus. The first characterized fluoranthene-degrading strain, *C. indicus* P73^T, also transformed other lower PAHs such as naphthalene and phenanthrene (Cao et al. 2015). Its alkane conversion abilities were not studied; however, a closer look at the bioinformatic data deposited in NCBI GenBank enabled us to identify the *alkB* genes in the genome sequence of P73^T. This finding suggests that the strain may utilize saturated aliphatic hydrocarbons besides aromatic compounds. The metabolism of an *n*-alkane and phenanthrene was reported for the strain representing the genus *Stappia* (Rhodobacteraceae family; Al-Awadhi et al. 2007). This bacterium utilized both compounds at halophilic conditions (3.5% NaCl). Rodrigues et al. (2015), in turn, found the enhanced

degradative potential among *Tristella* genus (Rhodospirillaceae family). The strains were able to utilize *n*-alkanes (*n*-C_{16} and/or *n*-C_8) as well as selected PAHs (naphthalene, phenanthrene or pyrene).

Several strains of hydrocarbon-oxidizing bacteria can be found within the *Ochrobactrum* genus, but only a few ones were shown to exhibit diversified biochemical capabilities. Bhattacharya et al. (2015) isolated *Ochrobactrum* sp. C1 which could grow in the presence of a wide range of compounds (nC_{12}–nC_{28}, phenanthrene and anthracene) and waste lubricants. Furthermore, this microorganism efficiently removed many of the benzene-based chemicals from waste lubricating oils. Another strain, *O. intermedium* CN3, degraded both aliphatic and aromatic hydrocarbons found in petroleum sludge (Bezza et al. 2015). Short-chain *n*-alkanes ($nC < 12$) were easily removed, while the longer-chain ones as well as PAHs proved more resistant to biodegradation. Wang et al. (2015), based on genome sequencing, indicated that halotolerant, PAH-degrading *O. anthropi* W13P3 could transform *n*-alkanes, as well. The cited authors managed to identify in this strain several genes involved in decomposition of both substrate types, namely, two protocatechuate 3,4-dioxygenase and three *alkB* genes.

Firmicutes (Fig. 1c)

A broad metabolic activity regarding both groups of hydrocarbons seems to be a rare feature among Firmicutes. So far, it has been found predominately in some obligate thermophilic *Geobacillus* and *Bacillus* strains. However, Rodrigues et al. (2015) found enhanced degradative capabilities of both *n*-C_{16} and aromatic compounds in *Exiguobacterium* genus. The strain TRH3 also utilized xylene, whereas TRN3 additionally converted naphthalene. Hydrocarbon-rich environments, such as crude oil-contaminated soils from oil fields (Zheng et al. 2011), petroleum reservoirs and wells (Zhang et al. 2012b; Zhou et al. 2018) or even crude oil samples (Zhang et al. 2012b; Sun et al. 2015), were the habitats for *Geobacillus* strains utilizing either *n*-alkanes or aromatic substances. Aliphatic compounds (nC_{12}–nC_{33}) and naphthalene were metabolized by *Geobacillus* sp. SH-1 (Zhang et al. 2012b), whereas *Geobacillus* sp. ZY-10 also biodegraded higher PAHs (Sun et al. 2015). Zheng et al. (2011) studied similar metabolic preferences in *G. pallidus* spp. strains XS2 and XS3 (currently they belong to *Aeribacillus pallidus* genus; Miňana-Galbis et al. 2010). Both phenanthrene and fluorene were utilized by these strains. The range of consumed *n*-alkanes was dependent on strain specificities. XS3, in comparison to XS2, transformed more short-chain compounds than the long-chain ones. Thermophilic, hydrocarbon-degrading *G. stearothermophilus* strain A-2 efficiently oxidized both *n*-alkanes and aromatic hydrocarbons (Zhou et al. 2018), and preferred long-chain *n*-alkanes ($> nC_{21}$), naphthalene and methylated phenanthrene. Most of the mentioned strains were able to produce bioemulsifiers.

As indicated above, some of the environmental spore-forming *Bacillus* strains inhabiting hydrocarbon-impacted environments displayed the enhanced metabolic activities. Among them, *B. stearothermophilus* transformed *n*-alkanes as well as aromatic compounds (Sorkhoh et al. 1993), whereas *Bacillus* sp. DHT grew on *n*-alkanes, naphthalene, pyrene and phenanthrene in the presence of 0–10% salinity and at 30–45 °C (Kumar et al. 2007). Al-Sharidah et al. (2000) isolated two strains belonging to *Bacillus subtilis* species from soil of the Burgan oil field. These bacteria, AHI and AHII, converted *n*-decane, diesel fuel and two-ring PAHs. Metabolic capability towards both *n*-alkane (nC_{18}) and phenanthrene was also observed in two alkaliphilic bacilli strains, namely, A5 and A6 (Al-Awadhi et al. 2007). Plotnikova et al. (2001) demonstrated *Bacillus* sp. DB11 growth on both nC_8 and naphthalene, while reporting no growth on phenanthrene. Salt-tolerant *Bacillus tequilensis* HRJ6 utilized nC_9–nC_{40} and the wide range of PAHs. Among the latter compounds, a mixture of hexacyclic PAHs ones was readily degraded (Gurav et al. 2017). HRJ6 harbored high number of *nah* gene copies involved in LMW PAH degradation; however, no presence of the *alkB* gene was documented. Hentati et al. (2016) reported for the first time fluoranthene-degrading capabilities among *Bacillus* genus. They found that *B. stratosphericus* strain FLU-5 grew in the presence of toluene, ethylbenzene, isomers of xylene, naphthalene, pyrene and octane. In turn, *Bacillus* sp. PHA3 revealed degradation of HMW-PAHs (pyrene, benzo[e]pyrene, benzo[a]- and benzo[k]fluoranthene), LMW-PAHs (naphthalene, fluorene, phenanthrene, anthracene) and less efficient *n*-alkane utilization (nC_{18}, nC_{24}; Hanano et al. 2017). In addition, the differential utilization of HMW-PAHs was reported

(pyrene, benzo[e]pyrene > benzo[a]fluoranthene, benzo[k]fluoranthene).

Deinococcus–Thermus

Considering enhanced microbial metabolism enabling biological transformation of two groups of petroleum compounds (*n*-alkanes and aromatics), another phylum, namely Deinococcus–Thermus, is worth noting here. This taxon consists of extremophilic bacteria. Although there is no strong evidence indicating the role of these microorganisms in hydrocarbon bioconversion, a single bacterial strain was reported to exhibit the described degradative preferences, that is a thermophilic *Thermus brockii* Hamburg. The authors showed that efficient PAH biotransformation required a second, degradable liquid phase. The mentioned bacterium metabolized both constituents of a hexadecane/pyrene mixture at 70 °C. The kinetic study indicated that the strain catabolized up to 40 mg L^{-1} h^{-1} pyrene and 1000 mg L^{-1} h^{-1} hexadecane (Feitkenhauer et al. 2003).

Metabolic aspects of *n*-alkane and aromatic hydrocarbon degradation

Having reviewed bacterial taxonomic groups, in this section some aspects of microbial hydrocarbon metabolic pathways are discussed. The structural diversity of hydrocarbons (saturated, unsaturated or aromatic) is reflected by their varied physico-chemical characteristics. This variety led to evolution of several different biochemical pathways in bacteria. Petroleum substances are in general hydrophobic, which affects their availability to microbial metabolism. For the case of aromatic compounds, BTEX substances are relatively well soluble in water in contrast to PAHs, which has an effect in lower bioavailability of the latter group of xenobiotics. These characteristics, as well as different chemical resistance of particular compounds, result in diversified susceptibility of hydrocarbons to microbial enzymatic attack. It tends to decrease in the following order: *n*-alkanes > branched alkanes > LMW aromatics > cyclic alkanes > PAHs (van Hamme et al. 2003). Aerobic biodegradation requires molecular oxygen as a final electron acceptor as well as a co-substrate to activate the carbon chain of *n*-alkanes or the aromatic ring of arenes (Rojo 2009; Seo et al. 2009). The catabolic routes of these compounds were schematically summarized in a simplified view in Fig. 2. Various aspects of *n*-alkane metabolism, such as its enzymology, physiology and genetics, are thoroughly discussed in the competent review articles (Rojo 2009; Wang and Shao 2013). Bacterial metabolism of aromatic hydrocarbons has also been the subject of many excellent reviews. The main catabolic pathways have been shown and explained in much detail (Peng et al. 2008; Seo et al. 2009; Parales et al. 2008).

Usually, alkane monooxygenase initiates degradation of *n*-alkanes by incorporation of an oxygen atom at the terminal or subterminal carbon. The intermediates are then transformed into their corresponding acids before entering the β-oxidation pathway (Rojo 2009). An alternative route, i.e. dioxidation of *n*-alkanes, was also reported (Fig. 2, Maeng et al. 1996). The differences in alkane bioavailabilities, regarding either their amount or molecular structures, are mirrored in the numerous evolved biochemical systems for *n*-alkane hydroxylation (Rojo 2009). Among them, the integral-membrane alkane monooxygenase AlkB has been extensively studied. In addition, for the case of the short- and medium-chain compounds degradation, the role of CYP153 has been emphasized (Wang and Shao 2013). Nonetheless, the biodiversity of alkane hydroxylases is much more complex and remains largely uncharacterized (Nie et al. 2014). Bacteria developed several environmental adaptations to effectively cope with a wide range of *n*-alkanes. Among them two strategies predominate, that is (1) the presence of multiple AlkB in one host, which possibly contributes to the degradation of variable chain-length compounds (Amouric et al. 2009), (2) the coexistence of AlkB and CYP153, which has been detected in both gram-negative and gram-positive cells (Liu et al. 2011; Nie et al. 2014). However, some robust alkane-degrading strains produce just one hydroxylating system (van Beilen et al. 2006). In the case of aromatic compounds, the dioxygenase-catalyzed oxidation step of BTEX and PAHs provides vicinal *cis*-dihydrodiols (the upper catabolic pathway, "initial oxidative reactions" stage of Fig. 2). These byproducts may then be cleaved by intradiol or extradiol ring-cleaving dioxygenases through either an *ortho*- or a *meta*-cleavage pathway resulting in intermediates such as protocatechuates and catechols (the lower catabolic pathway, "further metabolic

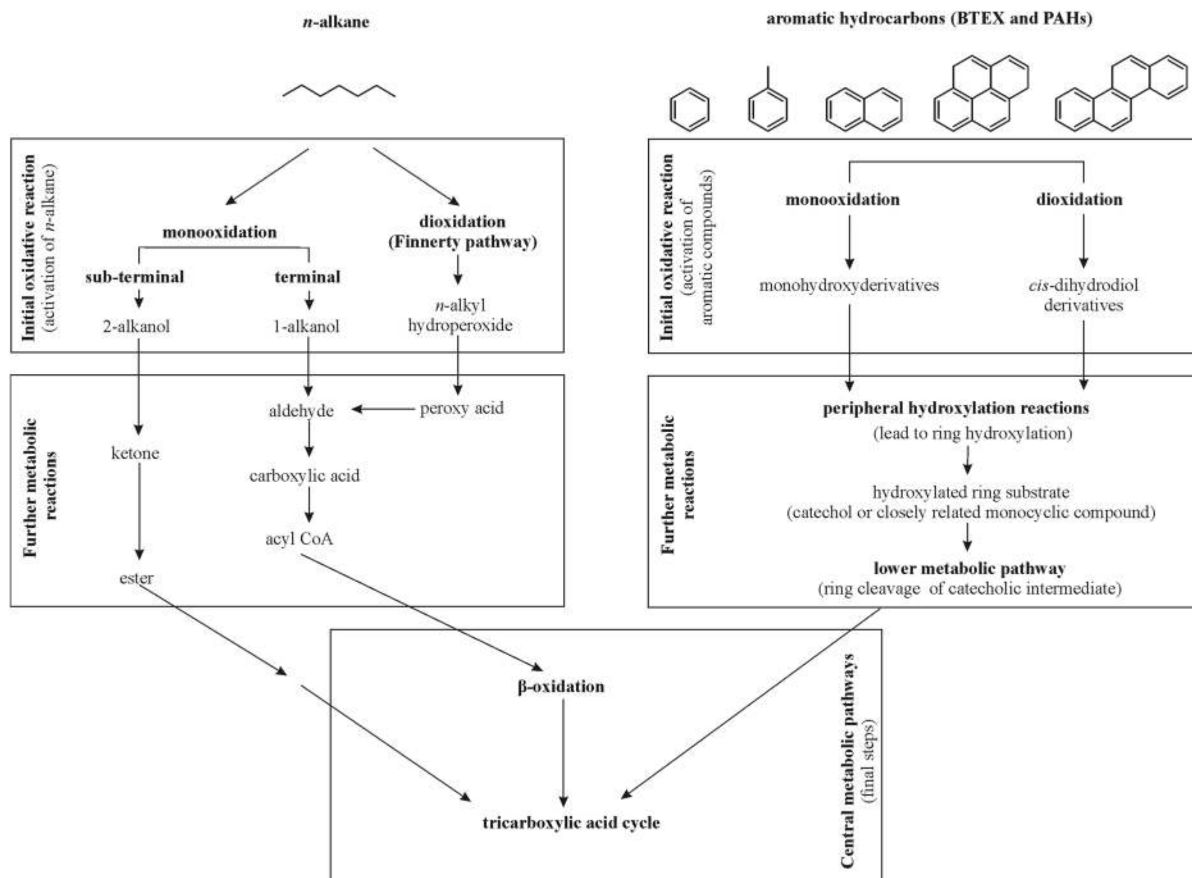


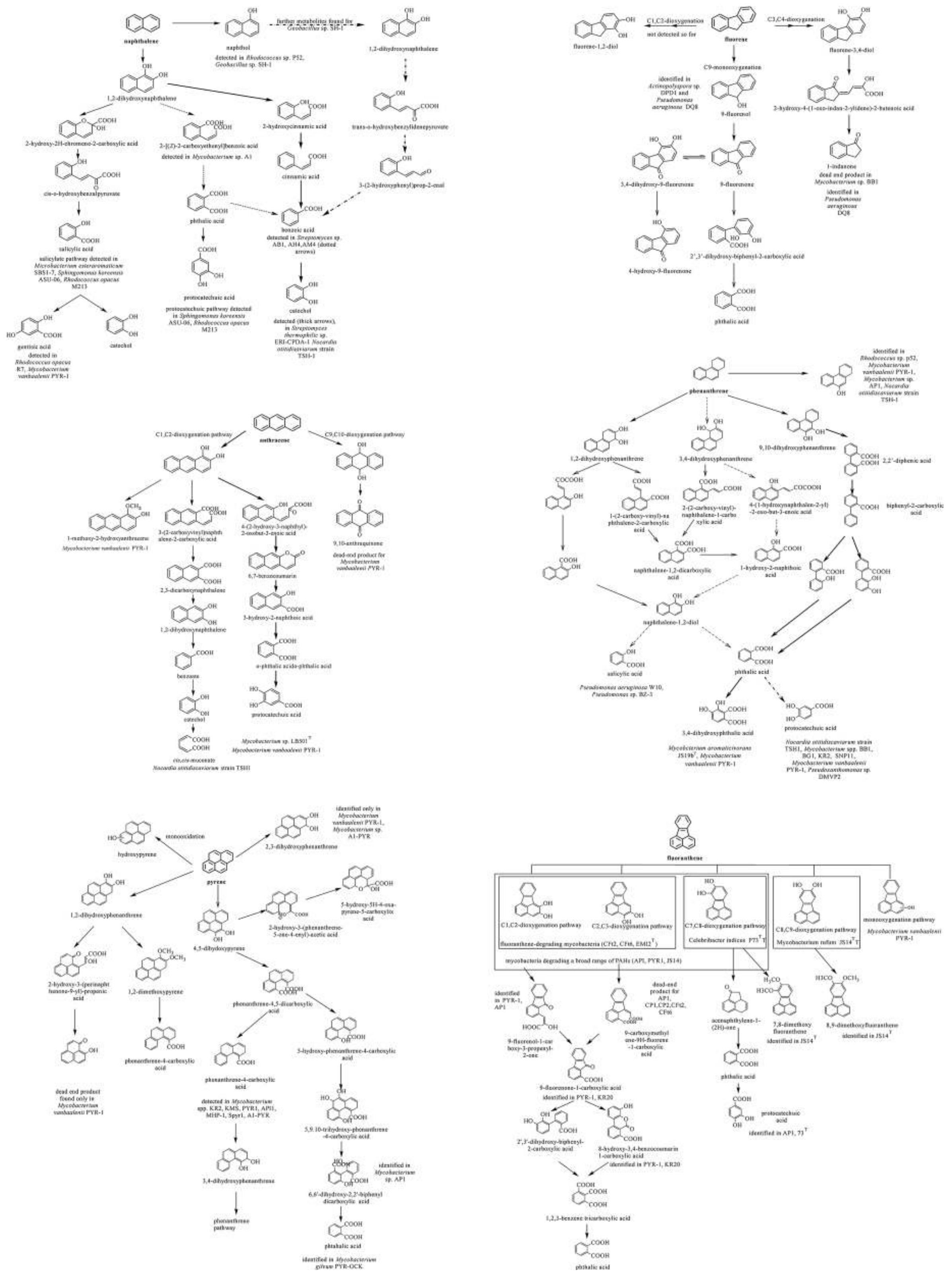
Fig. 2 Schematic view of aerobic pathways of aliphatic and aromatic hydrocarbons degradation by bacteria; based on Sierra-Garcia and de Oliveira (2013)

reactions" stage of Fig. 2). They are further converted to tricarboxylic acid cycle (TCA) intermediates ("central metabolic pathways" stage of Fig. 2; Peng et al. 2008; Seo et al. 2009). Note that, in addition to the dioxygenase-catalyzed oxidation, degradation of some aromatic hydrocarbons may proceed by an alternative route initiated by a monooxygenase (Parales et al. 2008).

As indicated above, the aerobic metabolism of *n*-alkanes differs totally from that of aromatic hydrocarbons. The variety of the recognized and characterized *n*-alkane catabolic pathways (terminal or subterminal; Rojo 2009) is limited compared to the numerous routes described for aromatic compounds (Peng et al. 2008; Seo et al. 2009). However, the overall metabolic strategy towards aromatic compounds remains the same, and it is particularly evident in the degradation trails of a variety of structurally diverse aromatic molecules. Namely, the channeling of a large number of compounds into a limited number of central pathways occurs due to the activity of plural RHDs which attack a wide range of substrates. Moreover, some of these enzymes can produce several types of oxidation reactions such as *cis*-dioxidation or monooxidation. The oxidation routes of individual compounds may vary among bacterial species or strains, and this variability is reflected by significant genetic and biochemical differences found for microorganisms (Kanaly and Harayama 2010). Generally, bacteria that grow on phenanthrene (but not on naphthalene) metabolize the substrate via the protocatechuate pathway (Saito et al. 2000), whereas the *Pseudomonas* strains that utilize both compounds metabolize them via the salicylate pathway (Peng et al. 2008). For another example, *Streptomyces* sp. ERI-CPDA-1 can transform naphthalene through benzoic acid (Balachandran et al. 2012), whereas *Bacillus thermoleovorans* converts it by a completely different

pathway, i.e. through 2,3-dihydroxynaphthalene (Annweiler et al. 2000). Moreover, the latter degradation route varies from the one known for mesophilic bacteria (through 1,2-dihydroxynaphthalene; Balachandran et al. 2012). Broad dissimilarities in catabolic pathways can also be found within pyrene-degrading mycobacterial strains (Liang et al. 2006, Fig. 3). Increasing evidence supports the occurence of multibranched catabolic pathways of aromatic hydrocarbons (Seo et al. 2012). Moreover, some bacteria are able to biotransform a given aromatic compound in several manners; however, metabolic preferences can at times be observed. For example, C2,C3-dioxygenation route of fluoranthene is a preferential choice of *Myobacterium vanbaalenii* PYR-1 (Kweon et al. 2007). In turn, C9,C10-dioxygenation dominates over C1,C2- and C3,C4-dioxygenation pathways during phenanthrene transformation by *Mycobacterium aromaticivorans* sp. JS19^{T} (Seo et al. 2012). Many naturally occurring strains display a versatile metabolism of various structurally similar compounds. To illustrate, *Rhodococcus jostii* RHA1 grows on benzene, ethylbenzene, biphenyl and styrene (Patrauchan et al. 2008). This strategy is determined by the simultaneous presence of multiple homologues of the RHDs. These enzymes exhibit broad, overlapping substrate preferences (Patrauchan et al. 2008), high structural homologies and relaxed substrate specificities towards differently sized compounds. Their limited regiospecificities often result in occurrence of a complicated mixture of dihydrodiols. For example, *Mycobacterium rufum* JS14^{T} oxidized fluoranthene at positions C1,2; C2,3; C7,8 and C8,9, as observed by Lee et al. (2007). Deeper insight into the metabolism of aromatic hydrocarbons indicates the existence of a complex network of catabolic reactions in a single bacterial cell. Note however, that PAH metabolic networks are rarely studied. Kweon et al. (2011) established an almost complete PAH metabolic network in *Myobacterium vanbaalenii* PYR-1. The authors integrated various data (proteomic, genetic, genomic and metabolic) related to metabolism of seven substrates (phthalate, fluorene, acenaphthylene, anthracene, phenanthrene, pyrene and benzo[a]pyrene) and proposed the hierarchical structure of network containing 183 metabolic compounds and 224 chemical reactions. To conclude, the factual data cited above indicate that the observed diversified biochemical machinery enables bacteria to convert many of the petroleum-derived compounds by adapting versatile catabolic pathways that already exist in particular strains (Fig. 3).

Among wealth of reports related to bacteria with enhanced hydrocarbon preferences, their degradative pathways were investigated less often. In particular, the synchronous functioning of *n*-alkane and PAHs/BTEX metabolic pathways was studied rarely (Kim et al. 2015). In most cases the researchers mainly focused on catabolism of selected aromatic compounds, while additionally indicating a concomitant *n*-alkane removal, growth in the presence of an aliphatic substrate or the presence of *alkB* gene. In Fig. 3, several selected PAH-metabolic pathways restricted to some structurally-diverse compounds (i.e. naphthalene, anthracene, phenanthrene, fluorene, pyrene and fluoranthene) found for bacteria with the enhanced biodegradation capacities are presented. This information allowed for evaluation of the possible relations between *n*-alkane degradation and the existence of PAHs/BTEX catabolic routes. It is worth mentioning here that (1) pathways of aromatic compounds transformation within *Mycobacterium* genus were studied extensively, which is in contrast to the limited data found for other taxa; (2) the variety of metabolic pathways regarding aromatic compounds in the bacterial world is amazingly great. Furthermore, a single bacterium may possess diversified biochemical systems to convert one hydrocarbon (see, for an example *Mycobacterium vanbaalenii* PYR-1 and anthracene degradation), whereas in other cases one strain may contain just a sole pathway to utilize this substance (e.g. *Celebribacter indicus* 73^{T} and fluoranthene). The data regarding metabolic pathways of aromatic hydrocarbons combined with the information of *n*-alkane utilization indicate the possibility of coexistence of known assimilatory routes in a single strain. Figure 3 gives clear examples that the potential to degrade aliphatic compounds does not exclude capacities to biotransform PAHs. These observations are also reflected on the genetic level, which is a topic discussed below. In the case of studies dealing with the BTEX- and PAH-metabolic pathways, most of the empirical proofs were related to the genera *Rhodococcus*, *Mycobacterium* and *Pseudomonas* (see Fig. 3), and only a few reports concerned the other taxa. It should be emphasized that the information about concurrent metabolic routes of both aliphatic and aromatic compounds bioconversion in bacteria is not


naphthalene
naphthol
detected in Rhodococcus sp. P52, Geobacillus sp. SH-1
further metabolites found for Geobacillus sp. SH-1
1,2-dihydroxynaphthalene
1,2-dihydroxynaphthalene
2-hydroxy-2H-chromene-2-carboxylic acid
2-[(Z)-2-carboxyethenyl]benzoic acid
detected in Mycobacterium sp. A1
2-hydroxycinnamic acid
trans-o-hydroxybenzylidenepyruvate
cis-o-hydroxybenzalpyruvate
cinnamic acid
3-(2-hydroxyphenyl)prop-2-enal
phthalic acid
benzoic acid
detected in Streptomyces sp. AB1, AH4, AM4 (dotted arrows)
salicylic acid
salicylate pathway detected in Microbacterium esteraromaticum SBS1-7, Sphingomonas koreensis ASU-06, Rhodococcus opacus M213
protocatechuic acid
protocatechuic pathway detected in Sphingomonas koreensis ASU-06, Rhodococcus opacus M213
catechol
detected (thick arrows), in Streptomyces thermophilic sp. ERI-CPDA-1 Nocardia otitidiscaviarum strain TSH-1
gentisic acid
detected in Rhodococcus opacus R7, Mycobacterium vanbaalenii PYR-1
catechol
fluorene-1,2-diol
C1,C2-dioxygenation
not detected so far
fluorene
C3,C4-dioxygenation
fluorene-3,4-diol
C9-monooxygenation
identified in Actinopolyspora sp. DPD1 and Pseudomonas aeruginosa DQ8
9-fluorenol
2-hydroxy-4-(1-oxo-indan-2-ylidene)-2-butenoic acid
3,4-dihydroxy-9-fluorenone
9-fluorenone
1-indanone
dead end product in Mycobacterium sp. BB1
identified in Pseudomonas aeruginosa DQ8
4-hydroxy-9-fluorenone
2',3'-dihydroxy-biphenyl-2-carboxylic acid
phthalic acid
anthracene
C1,C2-dioxygenation pathway
C9,C10-dioxygenation pathway
1-methoxy-2-hydroxyanthracene
Mycobacterium vanbaalenii PYR-1
3-(2-carboxyvinyl)naphthalene-2-carboxylic acid
4-(2-hydroxy-3-naphthyl)-2-oxobut-3-enoic acid
9,10-anthraquinone
dead-end product for Mycobacterium vanbaalenii PYR-1
2,3-dicarboxynaphthalene
6,7-benzocoumarin
1,2-dihydroxynaphthalene
3-hydroxy-2-naphthoic acid
benzoate
o-phthalic acidα-phthalic acid
catechol
protocatechuic acid
cis,cis-muconate
Nocardia otitidiscaviarum strain TSHI
Mycobacterium sp. LB501 T
Mycobacterium vanbaalenii PYR-1
phenanthrene
identified in Rhodococcus sp. p52, Mycobacterium vanbaalenii PYR-1, Mycobacterium sp. AP1, Nocardia otitidiscaviarum strain TSH-1
1,2-dihydroxyphenanthrene
3,4-dihydroxyphenanthrene
9,10-dihydroxyphenanthrene
2,2'-diphenic acid
1-(2-carboxy-vinyl)-naphthalene-2-carboxylic acid
2-(2-carboxy-vinyl)-naphthalene-1-carboxylic acid
4-(1-hydroxynaphthalen-2-yl)-2-oxo-but-3-enoic acid
biphenyl-2-carboxylic acid
naphthalene-1,2-dicarboxylic acid
1-hydroxy-2-naphthoic acid
naphthalene-1,2-diol
salicylic acid
phthalic acid
Pseudomonas aeruginosa W10, Pseudomonas sp. BZ-3
3,4-dihydroxyphthalic acid
Mycobacterium aromaticivorans JS19b T, Mycobacterium vanbaalenii PYR-1
protocatechuic acid
Nocardia otitidiscaviarum strain TSH1, Mycobacterium spp. BB1, BG1, KR2, SNP11, Mycobacterium vanbaalenii PYR-1, Pseudoxanthomonas sp. DMVP2
hydroxypyrene
monooxidation
pyrene
2,3-dihydroxyphenanthrene
identified only in Mycobacterium vanbaalenii PYR-1, Mycobacterium sp. A1-PYR
1,2-dihydroxyphenanthrene
4,5-dihydroxypyrene
2-hydroxy-3-(phenanthrene-5-one-4-enyl)-acetic acid
5-hydroxy-5H-4-oxa-pyrene-5-carboxylic acid
2-hydroxy-3-(perinaphthanone-9-yl)-propenic acid
1,2-dimethoxypyrene
phenanthrene-4,5-dicarboxylic acid
phenanthrene-4-carboxylic acid
5-hydroxy-phenanthrene-4-carboxylic acid
dead end product found only in Mycobacterium vanbaalenii PYR-1
phenanthrene-4-carboxylic acid
detected in Mycobacterium spp. KR2, KMS, PYR1, AP1I, MHP-1, Spyr1, A1-PYR
5,9,10-trihydroxy-phenanthrene-4-carboxylic acid
3,4-dihydroxyphenanthrene
6,6'-dihydroxy-2,2'-biphenyl dicarboxylic acid
identified in Mycobacterium sp. AP1
phenanthrene pathway
phthalic acid
identified in Mycobacterium gilvum PYR-OCK
fluoranthene
C1,C2-dioxygenation pathway
C2,C3-dioxygenation pathway
fluoranthene-degrading mycobacteria (CFt2, CFt6, EMI2 T)
C7,C8-dioxygenation pathway
Celeribacter indicus P73 T T
C8,C9-dioxygenation pathway
Mycobacterium rufum JS14 T T
monooxygenation pathway
Mycobacterium vanbaalenii PYR-1
mycobacteria degrading a broad range of PAHs (API, PYR1, JS14)
identified in PYR-1, AP1
dead-end product for AP1, CP1, CP2, CFt2, CFt6
9-fluorenol-1-carboxy-3-propenyl-2-one
9-carboxymethylene-9H-fluorene-1-carboxylic acid
acenaphthylene-1-(2H)-one
7,8-dimethoxy fluoranthene
identified in JS14 T
8,9-dimethoxyfluoranthene
identified in JS14 T
9-fluorenone-1-carboxylic acid
identified in PYR-1, KR20
phthalic acid
protocatechuic acid
identified in AP1, 73 T
2',3'-dihydroxy-biphenyl-2-carboxylic acid
8-hydroxy-3,4-benzocoumarin-1-carboxylic acid
identified in PYR-1, KR20
1,2,3-benzene tricarboxylic acid
phthalic acid

◀**Fig. 3** Metabolic pathways of selected PAHs (naphthalene, anthracene, phenanthrene, fluorene, fluoranthene, pyrene) identified among bacterial strains capable of degrading both *n*-alkanes and aromatic hydrocarbons. The scheme was elaborated based on the literature data cited throughout this article

complete. The abovementioned findings need further support by data regarding wider, taxonomically-differentiated bacterial groups. Thus, more detailed studies are necessary, especially involving genera that belong to Proteobacteria, Actinobacteria, and Firmicutes. Since these biochemical processes are expected to occur also in other bacterial degraders with broad metabolic capacities, they await a more thorough research, as well. In particular, the peculiar metabolic pathways of mycobacteria require further investigation to deepen our understanding of PAH metabolism. Note that, besides a few, well-studied strains (i.e. *Mycobacterium vanbaalenii* PYR-1, *Mycobacterium* sp. AP1), the information gathered for most bacteria is based on selected metabolic intermediates only. It should be also stressed that the observed coexistence of metabolic degradation pathways of *n*-alkane and aromatic hydrocarbons does not directly imply a capacity to induce the two biochemical systems simultaneously. There is only a limited evidence regarding concomitant functioning of both catabolic routes (Vila and Grifoll 2009; Kim et al. 2015). While demonstrating removal of *n*-alkanes during biodegradation of the *Prestige* fuel oil with *Mycobacterium* sp. strain AP1, Vila and Grifoll (2009) detected the already known metabolic intermediates of phenanthrene, pyrene and fluoranthene. These findings suggested that the known PAH assimilatory pathways were induced together with the *n*-alkane utilization routes. The observations of Kim et al. (2015) for *Mycobacterium vanbaalenii* PYR-1 were convergent with the studies cited above.

PAH RHDs play a key role in metabolism of aromatic hydrocarbons. Wide distribution of these proteins across microbial taxa is well evidenced. Comparisons of similarities in amino acid sequences have revealed distinct PAH-RHDα families (Habe and Omori 2003). PAH-RHDα of gram-negative (Proteobacteria) and gram-positive bacteria (Actinobacteria) belong to two groups, which are separated into subclasses associated with bacterial classes. The type, range of converted compounds and regioselectivity of oxidizing process are linked with the structure of enzyme's active site, which is differentiated within bacterial taxa. RHDs belonging to Proteobacteria are much more active towards LMW than HMW PAHs, whereas actinobacterial proteins (NidAB/NidA3B3) effectively attack HMW PAHs (Kweon et al. 2010). With respect to information presented in the previous section, larger aromatic molecules were the preffered substrates for *Mycobacterium* and *Rhodococcus* strains (Tables 1, 3), whereas Proteobacteria generally utilized LMW compounds (*Pseudomonas* spp. Ant8/48, DN34, DN36). This phenomenon can be partially explained by the size of an active site. Namely, larger molecules are oxidized by actinobacterial enzymes exhibiting a larger substrate-binding pocket (Kweon et al. 2010).

As mentioned earlier, Whyte et al. (1997) revealed coexistence of *alkB* and *nah* genes in *Pseudomonas* sp. BI7. The cited authors indicated, however, that the occurrence of environmental strains containing both types of catabolic genes was rare. They supposed that the heavy metabolic load (two large clusters: *alk* and *nah*) of such bacteria outweighed their competitive environmental advantage in natural ecosystems contaminated with both *n*-alkanes and PAHs. Notwithstanding the above case, a large amount of data accumulated within the last decades proves the concomitance of *alkB* with genetic signatures involved in aromatic hydrocarbon degradation in various bacteria (see data in Tables 1, 2, 3). For example, Hesham et al. (2014) demonstrated the existence of both catabolic attributes (*alkB* and *nahAc*) in *Sphingomonas koreensis* ASU-06 which utilized several PAHs (naphthalene, anthracene, phenanthrene and pyrene). In turn, *alkB* together with the *nar* fragment encoding naphthalene 1,2-dioxygenase were identified in naphthalene- and anthracene-degrading *Rhodococcus opacus* R7 (Di Gennaro et al. 2010; Zampolli et al. 2014) as well as in naphthalene-converting *Rhocococcus* sp. 1BN (Andreoni et al. 2000). In turn, *R. wratislaviensis* strain IFP2016 contained both *alkB* and *nidA,* the latter coding for a naphthalene-induced dioxygenase (Auffret et al. 2009). The authors supposed that *nid* genes were involved in transformation of xylenes and naphthalene by IFP2016.

Due to rapid advances in genome sequencing, genomic data for some of the described strains are now publicly accessible and easily available. The authors of this review collected additional information

regarding degradative genes for some strains (see data in Tables 1, 2, 3). Our attention was focused on *alkB* as well as on the genes encoding: naphthalene 1,2-dioxygenase, benzene 1,2-dioxygenase, toluene monooxygenase and methane/phenol/toluene hydroxylase. The study enabled to indicate the co-occurrence of *alkB* and benzene 1,2-dioxygenase genes among *Rhodococcus* species. For the case of *Mycobacterium* genus (see the data listed in Table 1) it can be shown that the coexistence of *alkB* and *nidA*, *nidA3B3, pdoA2B2* (ring-hydroxylating dioxygenases involved in catabolism of HMW PAHs) is widely distributed. Although the *nidA* gene is believed to be linked predominately with gram-positive pyrene-degrading bacteria (Table 1, Habe and Omori 2003), it was also found in a gram-negative *Pseudoxanthomonas* sp. RN402 (Klankeo et al. 2009). This bacterium was also able to utilize a wider range of compounds (phenanthrene and fluoranthene in addition to pyrene), which was the feature similar to that observed for several mycobacterial strains (Table 1, Klankeo et al. 2009). To sum up, the genetic repertoire responsible for complex metabolism of structurally-diverse hydrocarbons (*n*-alkanes and BTEX/PAHs) appears as not unique and seems to be widely distributed within bacterial world.

Evaluation of metabolic preferences towards both *n*-alkanes and aromatic hydrocarbons

Culturable hydrocarbon-degrading bacteria, such as alkane-degraders, are typically isolated on the basis of their ability to utilize model *n*-alkanes (e.g. nC_{16}) as their sole carbon and energy sources. Next, the studied microorganisms are in most cases tested for their metabolic activity towards a specific range of *n*-alkanes. They are less often examined in terms of their capacity to transform a broad range of diverse compounds such as *n*-alkanes, BTEX or PAHs. In order to evaluate physiological and biochemical metabolic potential towards both *n*-alkanes and aromatic hydrocarbons, phenotypic observations should combine the appropriate bacterial growth tests and biodegradation or biotransformation experiments. Such an approach has been employed by some authors (Plotnikova et al. 2001; Lee and Cho 2008; Lee et al. 2010; Zhang et al. 2012b; Zhou et al. 2018), although the abovementioned metabolic features have only occasionally been studied in detail (Lee et al. 2010). As regards aromatic compounds, most of the current knowledge on microbial metabolism was obtained based on the studies of bacterial activities produced against single hydrocarbon types.

Considering methodological aspects of analyses of various hydrocarbons, the assessment of bacterial degradation potential the most often encompassed substrate removal determination performed by GC-FID (gas chromatography with the flame ionization detector; Vila and Grifoll 2009; Wongbunmak et al. 2017) or GC–MS (GC coupled with mass spectrometry; de Carvalho and da Fonseca 2005; Vila and Grifoll 2009; Kim et al. 2015), mineralization of ^{14}C-labelled compounds, production of CO_2 during growth (Whyte et al. 1997; Bogan et al. 2003), monitoring of cell population dynamics (Wang et al. 2011; Xia et al. 2014) or protein concentration changes (Vila et al. 2001; Feitkenhauer et al. 2003). To further support the observed activities, several authors also carried out additional studies involving detection of genetic elements of catabolic pathways (i.e. *alkB*, *nar*, *nid*, *tmo*; Whyte et al. 1997; Andreoni et al. 2000; Sho et al. 2004) as well as identification of particular metabolites (Vila and Grifoll 2009; Wongbunmak et al. 2017). Accordingly, the coexistence of genes relevant to the metabolism of divergent hydrocarbons was confirmed by phenotypic traits in several cases (Whyte et al. 1997; Andreoni et al. 2000; Auffret et al. 2009).

Another approach that has been applied is based on biodegradation of multicomponent mixtures containing both aliphatic and aromatic compounds, such as coal tar (Pasternak et al. 2011), fuel oil (Vila and Grifoll 2009), crude oil (Mittal and Singh 2009), lubricant wastes (Bhattacharya et al. 2015) or petroleum sludge (Bezza et al. 2015). In these cases, the GC–MS technique was found to be especially applicable by facilitating determination of individual compounds in the analyzed complex mixtures (Whyte et al. 1997; Pasternak et al. 2011) or accumulated metabolites (Vila et al. 2001; Vila and Grifoll 2009). For example, Vila and Grifoll (2009) used a combined approach to assess degradation potential of *Mycobacterium* sp. AP1 towards the *Prestige* fuel oil. They reported efficient degradation of total petroleum hydrocarbons (TPH) together with removal analyses of several selected components (*n*-alkanes, PAHs) and identification of particular metabolites. In turn,

Pasternak et al. (2011) employed GC–MS to document an almost complete degradation of bicyclic and some tricyclic PAHs present in coal tar by *Rhodococcus* sp. B10.

Detailed analyses of the total range of consumed petroleum hydrocarbons are subjects of random studies; however, during the last two decades, metabolic versatility has been investigated more often. Nevertheless, the lack of key metabolic information has a strong influence on the generalized view obtained exclusively upon physiological observations. On the other hand, the progressive development of genome sequencing techniques and affordable access to this technology has brought valuable information, available worldwide, on the genetic potential of the bacterial strains of interest. Thus, an extensively applied genome sequencing approach tends to complement the gained knowledge on catabolic potential of the studied microbes. This can be achieved by providing appropriate genomic evidence for the already reported and not-yet-studied metabolic traits. The genomic data have to date been applied mostly to characterize only selected bacterial features (e.g. the potential of *n*-alkane degradation; Wang et al. 2013). They have been relatively rarely used to assess the genetic potential for both *n*-alkane and aromatic hydrocarbon degradation as analyzed by Wang et al. (2015). To give examples, Orro et al. (2015) documented genes for the metabolism of a large set of aromatic and polyaromatic hydrocarbons by *Rhodococcus* sp. BCP1 and *R. opacus* R7, while Zhang et al. (2012a) identified at least 43 dioxygenase genes related to PAH metabolism by fully genome sequencing of the strain *Rhodococcus* sp. P14. None of the cited authors referred to the information on genetic attributes involved in *n*-alkane metabolism, even though the studied strains utilized these substances. Through genome sequencing, scientists could possibly account for the observable physiological responses and identify degradative genes involved in the relevant processes. In addition, genomic data can supply deeper insights into the metabolic potential of bacteria subjected to studies. Such new information sometimes helps to reveal details of the metabolic processes which are much more complex than they appear based upon mere phenotypic observations. For instance, Uz et al. (2000) suggested that for *Rhodococcus* sp. M213 a different naphthalene pathway was encoded compared to the well-known salicylate route, as salicylate was not metabolized by this organism. Later, Pathak et al. (2013) showed the generation of *o*-phthalate as an intermediate of naphthalene degradation. However, recent studies indicated dual naphthalene degradation pathways in the strain M213 based on its identified repertoire of metabolic genes (Pathak et al. 2013).

Genomic data are a rich source of available information regarding the described microbes, as they complement the results obtained by conventional approaches. Moreover, they have influenced our recent views on the distribution of broadened preferences among bacterial genera. Taking the above into consideration, the distributional pattern of the mentioned preferences should be considered in a wider context. The hybrid metabolic capacities seem to be much more common than it could be deduced based on phenotypic data. This potential is not restricted to the well-known hydrocarbon degraders such as *Rhodococcus* or *Pseudomonas*, which was emphasized in the previous paragraphs. It is worth highlighting that the optimized methodological strategy targeted at understanding the hydrocarbon metabolism should merge the physiological observations with the compiled results of genomic, transcriptional and proteomic analyses. Thanks to such an approach, the catabolic potential of a given strain would be revealed and fully described at genetic, transcriptional and protein levels; however, this combined strategy is still rarely applied. Nevertheless, Kim et al. (2015) developed and applied a joint approach involving the chemical (determination of hydrocarbon concentration decrease) and molecular (proteomic and genetic analyses) methods to investigate the response of *Mycobacterium vanbaalenii* PYR-1 to crude oil from the *BP Deepwater Horizon* spill. Bacterial cultures were incubated with crude oil, and proteomes as well as degradation of *n*-alkanes and PAHs were analyzed over time. Such an integrated methodology led to observations of the crude oil impact on the regulation of bacterial enzymes responsible for PAH degradation.

This review presents the currently available data regarding degradation capabilities of both *n*-alkanes and aromatic hydrocarbons. However, the reader should be aware of the fact that the quality of the collected information varies strongly depending on the source and date of publication as well as experimental setup applied. The methodological reliability should be particularly concerned since there are many

different techniques used to evaluate the microbial catabolism of hydrocarbons (see above). For some well-characterized and thoroughly studied hydrocarbon degraders (such as *Mycobacterium vanbaalenii* PYR-1), there is considerable and widespread empirical evidence (genetic, genomic, proteomic) indicating catabolic preferences and elucidating metabolic pathways. On the other hand, biodegradation potential of some other strains were just preliminary estimated based on one selected method (e.g. decrease of hydrocarbon content) which is obviously insufficient to properly and fully explain complex degradative properties. Therefore, these bacteria should be further examined with other convincing, alternative techniques. The more divergent and complete are the experimental data, the better will be the reliability of the general information gained. For the reasons given above, the most suitable and promising strategy is suggested to involve a diversified approach based on direct hydrocarbon depletion determinations, identification of metabolic intermediates, enzymatic assays together with genetic analyses supported by bioinformatic tools. The expected outcome should bring a complete picture of biochemical and genetic aspects of bacterial metabolism.

Is simultaneous degradation of both *n*-alkanes and aromatic hydrocarbons possible?

It can be hypothesized that the active strains possessing metabolic routes which enable them to metabolize various compounds are capable of concomitantly biodegrading both groups of hydrocarbons (*n*-alkanes and aromatic compounds) in a complex mixture. This phenomenon would require simultaneous induction and expression of different, independent metabolic pathways in one bacterial cell. The problem has never been studied in enough detail, however. Therefore, to understand the complexity of the issue, an experimental verification is crucial, in which the following aspects should be taken into consideration: (1) involvement of possible catabolic repression mechanism(s), (2) overlapping or interference of the metabolic pathways, (3) preferential transformation of easily assimilated aliphatic compounds, (4) differential bioavailability of individual groups of hydrocarbons, and (5) different concentrations of particular hydrocarbons in petroleum contaminations. In addition, (6) the stimulating influence of a mixture of different substances on the process of concomitant degradation by co-metabolism should not be excluded.

Among the papers cited in this review, which refer to the multidegradative capabilities of microorganisms, only a few studies indicate or suggest the simultaneous transformation of aliphatic and aromatic compounds. It is worth mentioning here that Andreoni et al. (2000), employing a simple experimental model, were the first to demonstrate that *Rhodococcus* sp. 1B degraded nC_{16} and naphthalene concomitantly. The authors applied a two-component mixture (an *n*-alkane together with PAH) and this is, so far, the only reported attempt to study directly the simultaneous removal of both groups of hydrocarbons at 30 °C. Earlier, Whyte et al. (1997) suggested sequential growth of *Pseudomonas* spp. BI7 and BI8 on a mixture of *n*-octane, toluene and naphthalene. In their study a preferential degradation of naphthalene was observed (for BI8 at 5 °C and 25 °C, for BI7 at 25 °C), followed by octane and toluene depletion. In turn, Feitkenhauer et al. (2003) reported the concurrent utilization of both substrate groups in an nC_{16}/pyrene mixture by *Thermus* sp. at 70 °C.

Apart from the temperature conditions and chemical content of the treated hydrocarbon mixture, salinity and pH should be considered as key environmental factors influencing biodegradation process performance. High concentrations of salt generally result in the reduced hydrocarbon degradation rates. Elevated salinity leads to the increased PAH sorption (a "salting out" effect; Oh et al. 2013) and to lowering of bacterial biodiversity and hampering metabolic activity (Mille et al. 1991). The relation between NaCl concentration and simultaneous removal of *n*-alkanes and aromatic compounds is environmentally important, particularly in estuarine ecosystems. As described previously, halotolerant microorganisms were capable of utilizing both groups of organics. Plotnikova et al. (2001) demonstrated removal of several PAHs, whereas de Carvahlo and da Fonseca (2005) observed *n*-alkane consumption. Al-Awadhi et al. (2007) indicated utilization of both nC_{18} and phenanthrene in the presence of NaCl (3.5%) by individual halophilic strains. Recently, Gurav et al. (2017) showed that several salt-tolerant microorganisms (*Dietzia cinnamae* HRJ5, *Corynebacterium variabile* HRJ4 and *Bacillus tequilensis* HRJ6) were able to degrade a mixture of *n*-alkanes and aromatic

hydrocarbons in the presence of high NaCl concentration (20 g L^{-1}). These findings are promising in the context of future bioremediation treatments of hydrocarbon-polluted, saline environments. For other microorganisms, the impact of salinity on biodegradation of both *n*-alkanes and aromatic hydrocarbons has not been studied to date. As regards acidity, it is well known that hydrocarbon mineralization proceeds well at near neutral pH values (Kästner et al. 1998). However, alkaliphilic organisms were also shown to attenuate crude oil, metabolize selected *n*-alkanes as well as PAHs (Al-Awadhi et al. 2007). It should be emphasized here, however, that there is no literature data available regarding the effect of the two parameters (salinity and pH) on efficacy of degradation of multicomponent hydrocarbon mixtures containing both aliphatic and aromatic compounds.

The other available studies addressed microbial decomposition of more complex, multicomponent mixtures such as crude oil and petroleum products (de Carvalho and da Fonseca 2005; Bødtker et al. 2009; Mittal and Singh 2009; Zhou et al. 2018), gasoline (Solano-Serena et al. 2000) or coal tar (Pasternak et al. 2011). In most cases these processes were not analyzed in enough detail, however. Biodegradation kinetics of particular hydrocarbons was not monitored directly and qualitative analyses were incomplete or not thorough enough. For the above reasons it is difficult to precisely explain the metabolic background of the observed activities. Here, a more systematic and exhaustive work of Vila and Grifoll (2009) should be noted, which shows detailed metabolic and chromatographic records during action of *Mycobaterium* sp. AP1 on different components of the *Prestige* fuel oil. The authors revealed the degradation of both linear and branched *n*-alkanes as well as some growth-supporting (pyrene, fluoranthene, phenanthrene) and non-growth-supporting PAHs (anthracene, fluorene, benzo[a]anthracene).

Much more unambiguous evidence (e.g. metabolomic, transcriptomic and proteomic studies) is required to directly prove the course as well as mode (co-metabolism/competition) of simultaneous metabolism of *n*-alkanes and aromatic hydrocarbons. Solano-Serena et al. (2000) indicated that the presence of some aromatic compounds had no inhibitory effect on the *n*-alkane degradation process and vice versa. *n*-alkanes and some of the BTEX were utilized when they were supplied individually. The compounds were also degraded when they were supplemented within a commercial gasoline mixture, as well. Interesting observations were made by Auffret et al. (2009) who noticed that *Rhodococcus aetherivorans* IFP 2017 proved to be BTEX degrader only when these substances were supplemented in a mixture with other hydrocarbons (e.g. hexadecane), which clearly indicated a co-metabolism mechanism. The strain was shown not to mineralize any of the monoaromatic compounds added solely. Another study (de Carvalho and da Fonseca 2005) revealed successive removal of individual fractions of fuel oil by *Rhodococcus* sp. DCL14. The first compounds to be completely degraded were *n*-, iso- and cyclo-alkanes. They were followed by aromatics, biodegraded after a 9-month incubation. However, the authors did not specify which compounds present in the aromatic fractions underwent biotransformation. Zhou et al. (2018) studied degradation capacities of *Geobacillus stearothermophilus* A-2 and demonstrated the preferential removal of long-chain *n*-alkanes and several PAHs (naphthalene, methylated phenanthrene, C2-fluorenes and benzo[a]fluorenes) when they were supplied individually as well as in a mixture. Kim et al. (2015) have recently published a thorough research study which brings a detailed and comprehensive characterization of bacterial response to a hydrocarbon mixture. They evidenced simultaneous utilization of *n*-alkanes and selected PAHs from BP crude oil by *Mycobacterium vanbaalenii* PYR-1. Among the tested aliphatic compounds, nC_{12} and nC_{13} were degraded the most efficiently. The removal rates of pyrene and phenanthrene (but not fluoranthene) from crude oil were similar to the ones recorded in experiments where each of the PAHs was supplemented individually. It may be thus inferred that the exposure to complex mixture of hydrocarbons (as in crude oil) affected the regulation of enzymes involved in PAH degradation. The global functional metabolic network reconstructed by the authors indicated that both components of BP crude oil (*n*-alkanes and PAHs) were catabolized to H_2O and CO_2 via the TCA cycle and the respiratory chain. The *n*-alkane and aromatic hydrocarbon metabolism in PYR-1 involved a sequence of coordinated reactions. The authors explained the relation between enhanced input substrate diversity (*n*-alkanes together with PAHs) and the controlled production of limited intermediates of the

peripheral pathways by the funnel effects of channel management. Interestingly, this management seems to have an impact on the further degradation steps by concentrating the flux of metabolic products entering the central metabolic routes. Taken together, the data point to the genomic-wide coordinated reaction of *Mycobacterium vanbaalenii* PYR-1 upon exposure to crude oil. These results contribute much to our knowledge on the mechanisms of hydrocarbon biodegradation.

The issue of bacterial potential to utilize aliphatic and aromatic hydrocarbons simultaneously seems to be undervalued when contrasted with scientific efforts made to elucidate biotransformations of highly specialized microorganisms. Within recent years, however, growing evidence has supported the view that there exists an evolutionary strategy enabling to develop and maintain diversified metabolic and genetic traits. Still, much deeper understanding is required regarding biochemical and physiological processes occurring on the cellular level. Therefore, in addition to studies of cell physiological responses, the expression and succession of key catabolic enzymes should be a subject of future research. These suggestions are convergent with the claims of Kim et al. (2015) who addressed the problem of knowledge gap between physiology and biochemistry of hydrocarbons biodegradation as studied in vitro and in vivo.

Taking into consideration all the observations and analyses cited above, it is clear that the research on the concomitant degradation of *n*-alkanes and aromatic hydrocarbons should be based on testing complex hydrocarbon systems rather than simple, binary mixtures. The latter ones (a single *n*-alkane and a single aromatic compound) occur in the environment relatively rarely. On the other hand, multiple hydrocarbon mixtures such as petroleum products, crude oils, creosote, or other anthropogenic organic pollutants are widespread and thus serve as a real selective pressure for numerous microbial species. This, in turn, brings considerable practical potential in terms of biotechnological applications employing bacteria that exhibit hybrid hydrocarbon metabolism.

Bacteria exhibiting enhanced hydrocarbon degrading potential and bioremediation application

Petroleum hydrocarbons are the most widespread contaminants and their removal from the environment is of great concern. Bioremediation based on naturally-occurring bacterial degradation capabilities, is an effective and attractive tool for clean-up of polluted environments. Aromatic hydrocarbons usually form complex mixtures, often dissolved in aliphatic matrices. Therefore, the discussed tailored-metabolism should facilitate the growth of single bacterial populations on multicomponent mixtures. These microorganisms will then tend to predominate over other, more specialized hydrocarbon-degraders. In oil-contaminated environments, such spontaneously-developing, non-specialized microbial populations are believed to actively participate in the removal of both aliphatic and aromatic constituents of complex organic pollution. This activity should in turn be considered in the context of biotechnological applications. With respect to the data presented in the previous section, *Mycobacterium*, *Rhodococcus* and *Pseudomonas* genera seem to exhibit promising potential as sources of robust strains for biodegradation purposes. The mentioned taxa were shown to produce enhanced hydrocarbon catabolic activities which are widely distributed among numerous strains. These bacteria are capable of biotransforming broad ranges of compounds under various environmental conditions (pH, salinity, temperature), which makes them advantageous candidates for clean-up of sites contaminated by crude oil, fuel oil, creosote or petroleum derivatives. To develop a successful bioremediation strategy, a detailed knowledge is required regarding the microbiome of a given habitat together with a deep understanding of bacterial ecological status. Several studies revealed the presence of the mentioned genera or occurrence of catabolic genes related to these taxa in hydrocarbon-polluted environments (Margesin et al. 2003; Leys et al. 2005; de Menezes et al. 2012; Yergeau et al. 2013; Mukherjee et al. 2017). Margesin et al. (2003) found that microorganisms containing hydrocarbon-degradative genotypes related to *Pseudomonas* proliferated following oil contamination. Yergeau et al. (2013) reported an extensive expression of the *alkB* and naphthalene dioxygenase genes in both *Pseudomonas*

and *Rhodococcus* during bioremediation treatments. In turn, de Menezes et al. (2012) demonstrated an increased number of dioxygenase-associated transcripts belonging to *Mycobacterium* while investigating soil bacterial community responses to pollution with phenanthrene. Mukherjee et al. (2017) showed the presence of both *n*-alkane and aromatic hydrocarbon utilization genes of *Mycobacterium* in the soil samples collected from Chinese refineries. They suggested that bacteria of this genus were among the most important hydrocarbon degraders in the tested soils. Presumably the indigenous microbial representatives of the mentioned three taxa play an important role in in situ degradation processes of both *n*-alkanes and aromatic compounds. The strains of interest might also prove useful in bioaugmentation actions when bioremediation cases require inoculation with active xenobiotic degraders.

From among bacteria characterized by enhanced metabolic preferences (see "Bacteria able to metabolize both *n*-alkanes and aromatic hydrocarbons"), mycobacteria exhibit relatively broader capabilities of biotransforming HMW PAHs (see data in "*Mycobacterium*", "*Rhodococcus*", "Other Actinobacteria" sections, Tables 1, 2, 3; Kim et al. 2010). Numerous strains belonging to this microbial group can survive, proliferate, compete and degrade PAHs under diverse environmental conditions. This is achieved by the typical and widespread ability to produce many different enzymatic pathways (Fig. 1a). Moreover, these bacteria are often characterized by the presence of *nid*- and *pdo*-like genes (see data listed in Table 1) and high activities of NidA3 and NidA3B3 towards four-ring compounds (pyrene, fluoranthene, the activities are much higher than for LMW PAHs; Kweon et al. 2010). They can adapt to oligotrophic conditions (K-strategists; Brzeszcz et al. 2016) and their hydrophobic cell walls facilitate the uptake of aromatic compounds (Kim et al. 2010). For these ecological, genetic, enzymatic and physiological traits, mycobacteria bear particularly great potential in terms of biotechnological practice. Also, some members of *Rhodococcus* should be taken into account in the mentioned context. They are able to survive under harsh conditions (various temperatures and pH, "*Rhodococcus*" section) while effectively degrading hydrocarbons, which is often promoted by biosurfactant production. In addition, rhodococci are biochemically diverse (see Table 3, Larkin et al. 2010a) with a strong genetic background (a wide range of catabolic genes, Larkin et al. 2010b). Among other strains, some metabolically versatile pseudomonads ("*Pseudomonas*" section) might be considered favorable. The latter group, however, typically does not tolerate extreme environments (high salinity or extreme acidity) and these limitations should be taken into consideration (Palleroni et al. 2010).

To this day, the practical use of bacteria with enhanced hydrocarbon catabolic preferences has been at initial stages of biotechnological implementations. Evaluation of microbial bioremediation capacities has been limited to the representatives of *Mycobacterium* genus (Vila and Grifoll 2009; Kim et al. 2015). To show any potential applicational advantages of bacteria exhibiting the complex metabolic abilities, further studies and field tests are suggested involving two methodological approaches: (1) use of bacterial monocultures to degrade complex pollutant mixtures, and (2) construct microbial consortia consisting of bacteria with enhanced hydrocarbon preferences.

Concluding remarks

As summarized in this review, the data regarding bacterial degradation of both *n*-alkanes and aromatic hydrocarbons have significantly accumulated in the last decades. Such diversified metabolic possibilities have been most frequently linked to several actinobacterial genera (especially *Rhodococcus*) as well as to the genus *Pseudomonas*. However, a plethora of the more recent studies show wide distribution of these hybrid degradative features among other microbial taxa and demonstrate that such metabolic profiles are not limited to the well-known degraders. In this respect, extensively applied genome sequencing has greatly impacted the current understanding of this complex issue. The coexistence of multidegradative capacities has been proven for non-typical hydrocarbon-degraders (e.g. *Paracoccus*), for taxa that are known to be highly specialized in biotransformations of specific organic compounds (e.g. PAH-degrading *Sphingobacterium* or *Marinobacter*), or for genera that are typically not related to hydrocarbon metabolism (*Streptomyces*). However, more detailed research is necessary as a prerequisite to precisely determine the natural abundance of these particular properties among the culturable degraders. It is emphasized that

microbes exhibiting the mentioned capabilities have the potential to occupy various ecological niches, and tend to colonize the environments impacted by petroleum-derived substances. The phenotypes of both *n*-alkane and BTEX/PAH degradation are quite widespread in microbial world across various taxa. Presumably, such capacities are even more frequent. With respect to biotechnological potential of bacteria harboring enhanced metabolic preferences, culturomics is suggested as an attractive approach enabling to obtain new strains. The newly-obtained isolates should be tested against broad ranges of hydrocarbons. Then, the combined methodological approach, involving growth tests in the presence of a given compound, analyses of biodegradation kinetics, identification of metabolites and key genes, should bring important and reliable information on the strains' capacities on many different levels. Thorough systematic studies employing metagenomic, metatranscriptomic and proteomic approaches are expected to generate valuable data helpful in understanding of the activities and roles of these microbes in the natural metabolic processes that occur in oil-contaminated environments. Since the first isolated hydrocarbon-utilizing strain, an increasing interest in organic pollution degraders has been observed for their possible applications in environmental practice. Furthermore, the environmental-friendliness and cost-efficiency of bioremediation make such a biological technology a tempting alternative for conventional remediation actions of polluted sites. Hence, the construction of well-defined microbial consortia consisting of autochthonous microorganisms with the enhanced degradative potential seems to be a promising solution. It should give satisfactory results in terms of successful bioaugmentation of sites that have been contaminated by hazardous organic substances, and finally, prove more efficient than the currently employed methods.

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