Uptake of Polycyclic Aromatic Hydrocarbons across Bacterial Membrane

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Abstract

Polycyclic aromatic hydrocarbons (PAHs) are important pollutants, whose biodegradation and bioremediation with microorganisms are the promising ways to clean environments and reduce their exposure to humans. Although the transportation of PAHs across bacterial membrane is the first step forwards their biodegradation, it receives less attention. In this mini-review, we explore which transport system for uptake of carbon sources can serve for uptake of PAHs in bacteria, and try to uncover some patterns in their transport mechanisms. Collectively, 1) the major carbohydrate transport system, PTS, is unlikely to take PAHs because PAHs lack a hydroxy group for phosphorylation but aromatic acids are good candidates; 2) PAHs could probably go through H^+ symporters, especially the low-molecular-weight PAHs, which are partially dissolvable in water; 3) it is unlikely that PAHs can produce chemiosmotic ion gradients to go through uniporters; and 4) antiporters could serve as transporters to transport PAHs across bacterial membrane only after the metabolism of PAHs generates extra H^+ inside cell. Accordingly, the basic mechanism for uptake of PAHs is whether they can donate H^+ in order to generate an electrochemical proton gradient to go through symporters.

Keywords

Bacteria, Polycyclic Aromatic Hydrocarbon, Transport Mechanisms

1. Introduction

Polycyclic aromatic hydrocarbons (PAHs) are important pollutants coming from crude oil, creosote, asphalt, coal tar, combustion of fossil fuels, burning of sugarcane, etc. [1]. Their existence is harmful not only to humans but also to environments [2]. Microbial degradation is a promising way for recovery of envi-

ronment from PAH contamination [3] [4]. It turns out that some bacteria use PAHs as their sole carbon source to survive (Table 1).

Utilization of PAHs is possible because the benzene ring is one of the most abundant chemical structures in the biosphere, its derivatives are accessible to microorganisms as their growth substrates [22] and PAHs are largely natural products [23]. However, an important difference between PAHs and non-PAHs carbon sources is that most PAHs are generally hydrophobic although 2-ring and several 3-ring PAHs are dissolvable in water to some degree [24]. Of various factors, the size and angularity of PAH contribute to its hydrophobicity and electrochemical stability [25]. Glucose is highly soluble in water, by contrast, PAHs reveal low aqueous solubility; however, they are easily absorbed to solid particles in soil [26]. Because bacteria usually take degraded solvable chemicals [24], an interesting question is how PAHs are transported across bacterial membrane. Indeed, bacteria can secrete surfactants [27] [28], for example, *P. aeruginosa* can secrete rhamnolipid to facilitate the uptake of hydrophobic substrates [29] [30]. Can a bacterium evolve a specific transporter to transport PAHs from environment into cells? It could be possible, because a bacterium may encounter a few types of PAHs during its lifetime. On the other hand, it is hard to imagine that a bacterium would evolve many specific transporters for each type of PAHs because at least 660 PAH structures have so far been defined [31]. Therefore, it is highly likely that bacteria would use their non-specific transport systems to move PAHs into cells rather than to evolve specific transporters for each PAH.

Although the catabolism of PAHs in bacteria has been intensively studied and reviewed, the transportation of PAHs across bacterial membrane has yet to receive great attention. In broader sense, PAHs are aromatic compounds including aromatic acids so that the uptake of aromatic compounds should draw more attention.

Table 1. Some PAH compounds as sole carbon source for survival of bacteria.

PAH	Bacterium	References
anthracene	*Pseudomonas fluorescens* 5R	[5] [6]
naphthalene	*Comamonas testosteroni* GZ42	[7] [8]
naphthalene	*Rhodococcus* sp. NCIMB 12038, P200, P400	[9] [10] [11]
fluoranthene	*P. paucimobilis* EPA505 (now *Sphingomonas paucimobilis* EPA505)	[12] [13]
fluoranthene	*Mycobacterium vanbaalenii* PYR-1	[14]
phenanthrene	*Alcaligenes faecalis* AFK2	[15] [16]
phenanthrene	*Arthrobacter* sp. P1-1	[17]
phenanthrene	*Burkholderia* sp. C3	[18]
phenanthrene	*Comamonas testosteroni*	[7] [19]
phenanthrene	*P. fluorescens*	[5] [20]
pyrene	*M. vanbaalenii* PYR-1	[21]

As bacteria can use aromatic compounds as carbon sources, the system for uptake of carbon sources in bacteria should be considered in the first place. The first system for uptake of carbons is the phosphoenolpyruvate (PEP):carbohydrate phosphotransferase system (PTS), which is an active transporter consuming ATP. The second system is highly likely to be symporters, which are the secondary active transporters without consuming ATP.

In fact, many bacteria transfer aromatic acids into cells using major facilitator superfamily (MFS), of which the aromatic acid:H⁺ symporter is the most important one. The other MFS members, which are involved in transporting aromatic compounds, include: 1) BenK, which transfers benzaldehyde [32] [33] and benzoate (from which comes BenK), 2) GenK, which transfers 3-hydroxybenzoate and 2,5-dihydroxybenzoate (gentisate, from which comes GenK) [34], 3) MhbT, which transfers 3-hydroxybenzoate [35], and 4) PcaK, which transfers 4-hydroxybenzoate and 3,4-dihydroxybenzoate (protocatechuate, from which comes PcaK) [36] [37].

Besides MFS, aromatic compounds can be transported through several different transporters. For instance, phthalate is transported into *Burkholderia cepacia* through three pathways, 1) OphD [38], 2) OphFGH, which is an ATP-binding cassette (ABC) [39], and 3) OphP [39].

So far, it is not very clear whether there are other transporters involved in the uptake of carbon sources. In this mini-review, we explore through which transporters PAHs are transported across bacterial membrane.

2. Can PAHs Pass through PTS?

PTS is the major carbohydrate transport system in bacteria (upper part, **Figure 1**), which is usually composed of enzyme E I (EI), histidine protein (HPr,
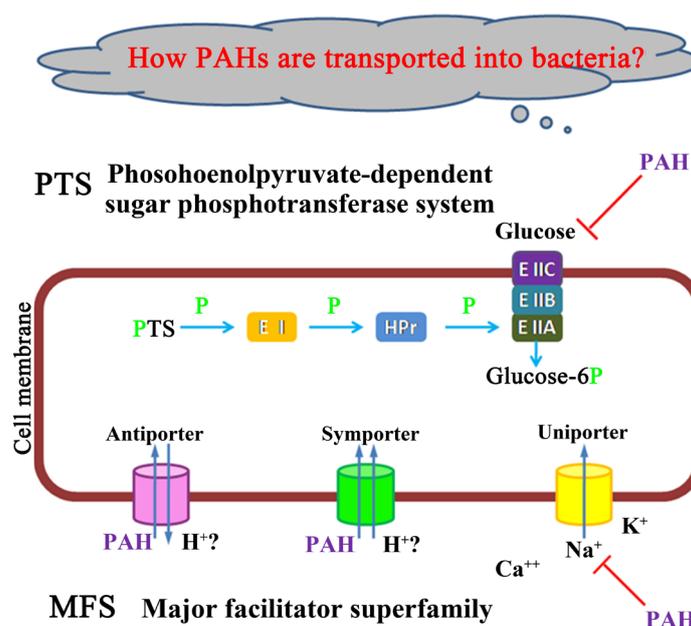
Figure 1. Possible transporters for uptake of PAHs in bacteria.

heat-stable protein) and enzyme E II (EII) [40] [41]. PTS only exists in bacteria, which was initially found in *Escherichia coli* [42] and then was found in other bacteria [41]. Although *E. coli* does not play an important role in PAH degradation, the knowledge on PTS of *E. coli* is useful for our understanding on whether PAHs can pass through PTS.

So far, PTS has been classified into four superfamilies according to their EII's phylogeny [43]: 1) the glucose-fructose-lactose superfamily including glucose, fructose-mannitol and lactose families, 2) the ascorbate-galactitol superfamily including ascorbate [44] [45] and galactitol families [46] [47], 3) the mannose family [48], and 4) the dihydroxyacetone family [49]. Taking glucose as an example, the main mechanism for such transportation across the cell membrane is to phosphorylate glucose into glucose-6-phosphate using enzyme II B (EIIB) with consumption of ATP when glucose crosses plasma membrane through the trans-membrane enzyme II C (EIIC). Thus, the transport of glucose is an active process.

The PTS substrates include monosaccharides (glucose, fructose and mannose), disaccharides (cellobiose), amino sugars (glucosamine, N-acetylglucosamine and N-acetylmannosamine), as well as polyols [41] [42]. Clearly, this list does not include any PAHs, so a question is whether PAHs can be transported into bacteria through PTS.

The size of PTS substrates varies largely. For monosaccharides, glucose has long and short axes of 8.6 Å and 8.4 Å [50], and fructose has long and short axes of 9.8 Å and 8.5 Å [50]. For polyols, mannitol has a size of 11.92 Å × 8.11 Å × 7.38 Å [51].

For PAHs, they are usually grouped as low-molecular-weight PAHs with 2 to 4 benzene rings (naphthalene, phenanthrene, anthracene and fluorene) and high-molecular-weight PAHs with more than 4 benzene rings (fluoranthene, benzo[*a*]pyrene, benz[*a*]anthracene and 7,12-dimethylbenz[*a*]anthracene) [52]. The size of five typical PAHs is listed in Table 2. As can be seen, the sizes of 2-ring naphthalene and 3-ring anthracene and phenanthrene are compatible with the size of mannitol, so PTS could at least accommodate a portion of low-molecular-weight PAHs in terms of their size.

In addition to PAH size, another necessary prerequisite for PTS transportation is whether PAHs can be phosphorylated because phosphorylation is the first

Table 2. Size of 5 PAH compounds [31].

PAH	Long axis	Short axis
2-ring naphthalene	9.195 Å	7.428 Å
3-ring anthracene	11.650 Å	7.439 Å
3-ring phenanthrene	11.750 Å	8.031 Å
4-ring fluoranthene	11.160 Å	9.240 Å
4-ring pyrene	11.660 Å	9.279 Å

step to transport glucose across membrane. To achieve this, PAHs need to have a hydroxy group on any of its carbons for phosphorylation. This prerequisite, however, needs to add oxygen to PAHs as a necessary step before phosphorylation because PAHs have no oxygen. Take naphthalene as an example for this possibility (Figure 2), naphthalene needs an oxygen to form a hydroxy group, and then it can go through phosphorylation with consumption of ATP, and then finally it can go through PTS into bacteria. However, the addition of oxygen requires oxygenase, which could break the aromatic ring as the ring-cleaving dioxygenases do [53], so PAHs are unlikely to be transported by PTS. On the other hand, the inhibition of surfactant, Triton X-100, on the metabolism of fluoranthene and glucose in *Sphingomonas paucimobilis* strain EPA505 [54] might suggest the possibility that the transporters for fluoranthene and glucose share some similarity.

Aromatic acids, such as benzoate and phenylacetic acid, appear to be possible candidates for PTS because they have a hydroxy group (Figure 3), which can be

Figure 2. Possible mechanism for PAHs to be transported by PTS with naphthalene as an example.

Figure 3. Possible mechanism for benzoate and phenylacetic acid with their hydroxy group to be transported by PTS.

used for phosphorylation. This can explain why benzoate and phenylacetic acid can be utilized in *Pseudomonas* prior to glucose as organic acids [55]. In reality, benzoate and phenylacetic acid are transported through aromatic acid:H⁺ symporter [56], but if they could be phosphorylated, they would block the uptake of glucose through PTS, then the preference order of utilization of carbon sources would be different in *Pseudomonas.*

3. Can PAHs Pass through MFS?

MFS (lower part, **Figure 1**) is the largest family of secondary active membrane transporters [57], and transports the non-PTS substrates because these substrates are not subject to phosphorylation. About 25% of all known membrane transport proteins belong to MFS in prokaryotes [58].

MFS has three types of transporters: 1) uniporter, which transports the substrates whose concentration gradient push power transportation; 2) symporter, which simultaneously transports two or more substrates in the same direction because of the electrochemical gradient of one of its substrates; and 3) antiporter, which transports two or more substrates in opposite directions. MFS can transport ions, simple sugars [59] [60], sugar phosphates, oligosaccharides, inositols, drugs [61], neurotransmitters, nucleosides, amino acids and peptides, organophosphate esters, Krebs cycle metabolites, lipids, and a large variety of organic and inorganic anions and cations [57] [62].

Uniporter

Can PAHs go through uniporter (right-lower corner of **Figure 1**) along the concentration gradient across the membrane? In plain words, can PAHs diffuse through plasma membrane? It seems unlikely because uniporters appear to be merely involved in transport of calcium, sodium and potassium [60] [63], although PAHs should generate a PAH concentration gradient across the bacterial membrane. The key point is that PAHs are not able to produce chemiosmotic ion gradients.

Symporter

Can PAHs go through symporters (middle lower part of **Figure 1**)? Aromatic acids could produce electrochemical gradients, and thus go readily through symporters. Aromatic acid:H⁺ symporter (AAHS) family (TC# 2.A.1.15) is the best studied symporter in terms of transportation of aromatic acids. AAHS family includes at least BenK, GenK, MhbT, MucK [64], PcaK and VanK for transportation of aromatic acids. After passing through BenK, MucK, PcaK and VanK, aromatic acids undergo mineralization via β-ketoadipate pathway [65] [66].

As aromatic acids can pass through symporters, can PAHs pass through aromatic AAHS family? Essentially, the substrates for AAHS family are 1-ring aromatic acids, *i.e.*, 3-hydroxybenzoate, 4-hydroxybenzoate, 2,4-dihydroxybenzoate, 2,5-dihydroxybenzoate (gentisate), 3,4-dihydroxybenzoate (protocatechuate), 4-hydroxy-3-methoxybenzoate (vanillate), benzaldehyde, benzoic acid, and sa-

licylate. Evidently, the size of 1-ring aromatic acids is smaller than any typical PAHs.

In eukaryotic organisms, the pathogenic yeast *Candida parapsilosis* has permeases Hbt1 and Hbt2, which are similar to bacterial aromatic acid:H$^+$ symporters (AAHS) such as GenK, MhbT and PcaK. Permeases Hbt1 and Hbt2 transport 3-hydroxybenzoate, 4-hydroxybenzoate and protocatechuate into *C. parapsilosis* [67], and then are metabolized through different pathways. For example, 3-hydroxybenzoate and 2,5-dihydroxybenzoate are metabolized via the gentisate pathway, while hydroquinone, resorcinol, 4-hydroxybenzoate, 2,4-dihydroxybenzoate (*β*-resorcylate) and 3,4-dihydroxybenzoate (protocatechuate) are metabolized via 3-oxoadipate pathway [68] [69] [70].

In general, the mechanism for transportation of aromatic acids is simplified as [56]: benzoate (out) + H$^+$ (out) → benzoate (in) + H$^+$ (in).

For more complicated mechanism, it would be functionally asymmetric in PcaK [71], where an electrochemical proton gradient ($\Delta\mu^-$H$^+$) or a membrane potential ($\Delta\Psi$), but not ΔpH alone, energizes asymmetric transportation [37]. This is why the number of substrates for AAHS is relatively small [37]. The implication is that PAHs should donate H$^+$ in order to generate an electrochemical proton gradient across the aromatic acid:H$^+$ symporters (AAHS), which is possible for low-molecular-weight PAHs because they are dissolvable in water to some extend [24]. So it is likely that naphthalene, for example, can go through AAHS in such a way (Figure 4).

Anion:cation symporter (ACS) family (TC# 2.A.1.14) includes OphD and OphP in *B. cepacia* [39], and Pht1 in *Pseudomonas putida* [72] for transporting phthalate. Actually, the size of phthalate can be very large and comparable with even high-molecular-weight PAHs, because phthalate can be as simple as phthalic acid but complicated with different functional groups (Figure 5). Therefore, there is a possibility that PAHs generate anion and cation to go through anion:cation symporter.

Similarly, the rest H$^+$ symporters follow the same reasoning for uptake of PAHs. Metabolite:H$^+$ symporter (MHS) family (TC# 2.A.1.6) includes MopB in *B. cepacia* for transporting 4-methyl-o-phthalate [73], PcaT in *P putida* for transporting beta-ketoadipate [74] and ferulic acid [75], and ShiA in *E. coli* for transporting shikimate [76].

Oligosaccharide:H$^+$ symporter (OHS) family 2 (TC# 2.A.1.5) includes lactose:H$^+$ permease (LacY) [57] from *Citrobacter freundii*, *Klebsiella pneumoniae*
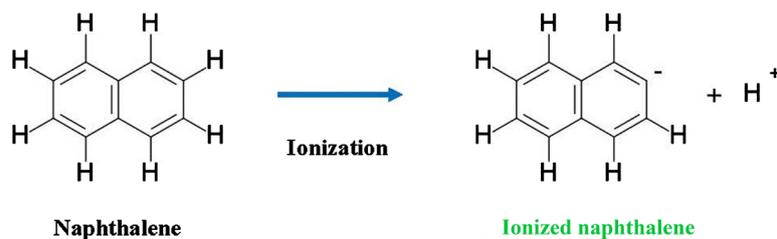
Figure 4. Possible mechanism for naphthalene to go through aromatic acid:H$^+$ symporters.
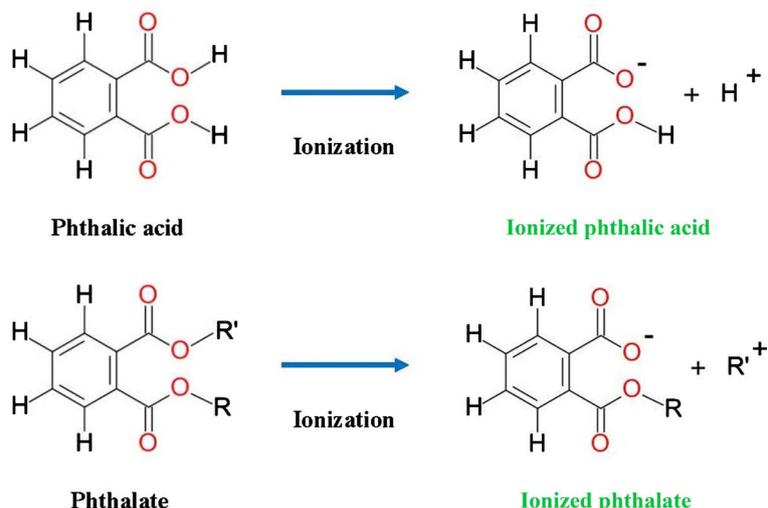
Figure 5. Possible mechanism for phthalic acid and phthalate to go through aromatic acid:H^+ symporters.

and *E. coli* [77] [78] [79] [80] [81]; sucrose permease (CscB) from *E. coli* [82] [83] [84]; melibiose permease (MelY) from *Enterobacter cloacae* [85] and melibiose permease MelB from *E. coli* [86] [87] [88] and *Salmonella typhimurium* [89]. This family transports galactosides such as lactose and melibiose [90] [91] [92] with electrochemical proton gradient. OHS family seems to be a very good candidate for transporting PAHs, because the LacY is a 6 nm × 3 nm oval shaped transporter on membrane surface [93].

It was found that the amino acid-polyamine-organocation (APC) transporter such as BenE [94] and the outer membrane pore-forming protein (OMPP) such as BenP [33] transport aromatic substrates.

In other kingdoms, studies on basidiomycete *Trichosporon cutaneum* found an energy-dependent system for the uptake of phenol, where phenolate anions are co-transported with protons in stoichiometry 1:1 [95] [96]. In another basidiomycete *Fomitopsis palustris,* symporter with H^+ ion was shown for the uptake of vanillate [97]. In humans, sodium-coupled monocarboxylate transporters, *i.e.* SMCT1 and SLC5A8, are involved in the uptake of nicotinate and various aromatic monocarboxylates such as benzoate and salicylate [98].

For the non-PTS sugars, the uptake of raffinose [99] across the cytoplasmic membrane of *E. coli* is a secondary active transporter termed as the raffinose permease (RafB) [99] [100] [101] [102]. Interestingly, galactose belongs to monosaccharide but it does not pass PTS system. The uptake system for galactose [103], galactose permease or GalP, belongs to MFS [104] [105] [106] [107]. No information is found that these two transporters could transport PHAs across bacterial membrane.

In this context, symporters could potentially serve as a biosensor system [108] to detect the PAH influx as mitochondria as biosensors of calcium microdomains [109] or special antibody could be used for this purpose [110]. Clearly, more experimental evidence is in need to explore this aspect of symporters with PAH up-

take.

Antiporter

Can PAHs go through antiporters (left-lower corner of **Figure 1**)? This looks unlikely because there is usually no H$^+$ inside bacteria. However, the common catabolic pathway to salicylate from naphthalene [111], fluorine [112] and phenanthrene [18] can generate extra H$^+$. Still, the common catabolic pathway to phthalate from fluorine [113], anthracene [114], phenanthrene [18], and pyrene [21] can generate extra H$^+$. Thus the produced H$^+$ could be used for antiporter to transport PAHs; however this process could begin only after the beginning of metabolism of PAHs, so the uptake of PAHs through antiporter can occur at a later stage.

4. Conclusions

In this mini-review, every effort was made to find how PAHs are transported into bacterial cells in literature. Because of lack of recent research in this field, our review focuses on the theoretical derivation in order to stimulate the research interests. In a broader sense, this is the question of how hydrophobic substances are transported into bacteria and which transporter is used to transport less soluble substances. Although the substrate-dependent gene modulation can inhibit the glucose transport and metabolism [115], which would create the conditions for transporting PAHs and their utilization. Collectively, 1) the major carbohydrate transport system, PTS, is unlikely to take PAHs because PAHs lack a hydroxy group for phosphorylation but aromatic acids are good candidates; 2) PAHs could probably go through H$^+$ symporters, especially the low-molecular-weight PAHs which are partially dissolvable in water; 3) it is unlikely that PAHs can produce chemiosmotic ion gradients to go through uniporters; and 4) antiporters could serve as transporters to transport PAHs across bacterial membrane only after the metabolism of PAHs generates extra H$^+$ inside cell. Accordingly, the basic mechanism for uptake of PAHs is whether they can donate H$^+$ in order to generate an electrochemical proton gradient to go through symporters. However, it is still not clear how the high-molecular-weight PAHs are transported into cells. Thus, more studies are needed in order to understand how PAHs are transported into bacteria. The current literature has yet to provide sufficient knowledge on uptake dynamics if we consider the driving force in transportation as uptake kinetics. Therefore, the uptake dynamics should be a direction for pursuit.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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