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## **The Microbes**

**Section Editor: Terry McGenity**



# 1 Prokaryotic Hydrocarbon Degraders

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1	<i>Introduction</i>	1672
2	<i>Bacterial Taxonomy</i>	1673
3	<i>Currently Described Hydrocarbon-Degrading Bacteria</i>	1673
4	<i>Phylum Actinobacteria</i>	1681
5	<i>Phylum Bacteroidetes</i>	1681
6	<i>Phylum Cyanobacteria</i>	1681
7	<i>Phylum Deinococcus-Thermus</i>	1682
8	<i>Phylum Firmicutes</i>	1682
9	<i>Phylum Proteobacteria</i>	1682
10	<i>Archaeal Hydrocarbon Degradation</i>	1683
11	<i>Evolution in Real Time?</i>	1683
12	<i>Research Needs</i>	1684

**Abstract:** Hydrocarbons have been part of the biosphere for millions of years, and a diverse group of prokaryotes has evolved to use them as a source of carbon and energy. To date, all the formally defined genera are eubacterial, in 7 of the 24 major phyla currently recognized (Tree of Life, 2009); principally in the Actinobacteria, the Bacteroidetes, the Firmicutes, and the Proteobacteria. Some Cyanobacteria have been shown to degrade hydrocarbons on a limited scale, but whether this is of any ecological significance remains to be seen – it is likely that all aerobic organisms show some basal metabolism of hydrocarbons by nonspecific oxygenases, and similar “universal” metabolism may occur in anaerobes. More recently, some thermophilic, acidophilic methanotrophs from the phylum Verrucomicrobia have also been isolated (Chapter 26, Vol. 3, Part 1); we may expect more diversity as research proceeds.

There have been publications indicating that halophilic archaea are significant hydrocarbon-degraders in some environments, but these have not yet been rigorously, or formally, described.

## 1 Introduction

Hydrocarbons have always been part of earth's biosphere. They are found in interstellar space (Tielens, 2008), are produced by living organisms (Fuentes et al., 2007; Howard and Blomquist, 2005; Ladygina et al., 2006), and are produced by geological processes (Vandenbroucke and Largeau, 2007) and during incomplete combustion (Lima et al., 2005). Hydrocarbons are relatively stable molecules, but can provide a source of carbon and energy to any organism able to activate them. It is this activation that distinguishes hydrocarbon-degrading organisms from their brethren, for once activated by the aerobic insertion of oxygen or anaerobic addition of succinate (Chapter 14, Vol. 2, Part 4), for example, hydrocarbons enter the standard biochemistry of living organisms and are readily oxidized to carbon dioxide and water.

All aerobic organisms seem to have some ability to metabolize hydrocarbons (e.g., Coon, 2005), and it would not be surprising if similar basal metabolism occurred in anaerobes. But this article focuses on those organisms able to grow in pure culture using hydrocarbons as sole, or major source of carbon for growth. Only an isolated organism can be given a valid taxonomic name, and the limitation that an organism must be available in pure culture must substantially underestimate the diversity of organisms that productively metabolize hydrocarbons, because it is becoming clear that organisms often grow in mutually beneficial consortia (e.g., Allen and Banfield, 2005; Brenner et al., 2008). Co-metabolism may be essential for some compounds (see Kanaly and Harayama, 2000), and may require interspecies “cooperation.” The phenomenon of syntrophy, where organisms cooperate to metabolize substrates with benefits for all, is also beginning to be understood (e.g., McInerney et al., 2008). Indeed the need for interspecies interactions may well be a principal reason for the oft-quoted statement that only a tiny fraction of microbes can be “cultivated.” Nevertheless some species thrive in pure culture in the laboratory, and these have allowed a detailed understanding of their biochemistry.

The following chapters in Part 10 of this handbook highlight the diversity, taxonomy, biogeography, and physiology of oil-degrading organisms, ranging from overviews of phyla like the Actinobacteria to detailed synopses of genera like *Alcanivorax*. Chapters are ordered according to: eubacterial phylogeny, activity in extreme environments, methane oxidation, anaerobic degradation, and finally eukaryotic hydrocarbon degrading microbes. In some chapters the emphasis is solely on hydrocarbon-degraders, while others also consider those microbes that degrade derivatized hydrocarbons. Here, we provide context by listing all genera (known to us) with species that can degrade hydrocarbons, and outline their taxonomy.

## 2 Bacterial Taxonomy

Despite its origins before the Darwin-Wallace identification of Natural Selection as the driving force for speciation (Darwin and Wallace, 1858), Linnean taxonomy still plays the central role in describing organisms, giving each organism a binomial name consisting of a generic and a specific identifier (e.g., Gest, 1999). Genera are then grouped in families, families in orders, orders in phyla, and phyla into domains. In theory this classification ought to fit neatly into an evolutionary classification – the taxonomy should reflect phylogeny. Indeed it is fairly effective for multicellular sexual organisms, where species can be defined as organisms that can interbreed, genera can be distinguished on morphological grounds, and there has been little gene transfer between otherwise unrelated organisms.

Microbial taxonomy is rather more complicated, and widely discussed (Gest, 1999; Hugenholtz, 2002; Rappé and Giovannoni, 2003; Rosselló-Mora and Amann, 2001; Vandamme et al., 1996). As can be seen in [Table 1](#), some genera were defined in the early nineteenth century, but an explosion in their number has occurred since the advent of molecular taxonomy based on ribosomal RNA (Woese, 1987; Cole et al., 2009). As this has developed, it has become clear that microbial diversity is only poorly understood – Rappé and Giovannoni (2003) note that only about half the putative phyla within the bacterial domain contain cultivated representatives. The uncultivated and therefore metabolically unknown phyla are not necessarily minor components of the biosphere – for example, SAR11 was known to be the most abundant organism in the world's oceans before it was cultivated and formally described as *Pelagibacter ubique* (Rappé et al., 2002). We may thus confidently expect that many more organisms will be cultured and described when more emphasis is placed on classical microbial cultivation (Gest, 2008). It is noteworthy that some of what are currently believed to be the most important and widespread oil-consuming genera, such as *Alcanivorax* (Yakimov et al., 1998) and *Cycloclasticus* (Dyksterhouse et al., 1995) were discovered only rather recently.

Modern molecular taxonomy uses ribosomal RNA genes as the preeminent molecular signature for understanding the relatedness of different organisms (Cole et al., 2009). This is certainly reasonable in that it is hard to imagine an organism replacing such an essential part of its metabolism. But lateral gene transfer is now very well established (Jain et al., 2002; Koonin and Wolf, 2008; Ochman et al., 2000; Thomas and Nielsen, 2005), using the “mobilome” – plasmids, bacteriophages, and transposons (Frost et al., 2005). Phenotypic traits such as hydrocarbon degradation are frequently carried on plasmids (e.g., Oct, Nah7, dox, TOL, etc., see Van Hamme et al., 2003), and might be expected to pass readily between even quite unrelated organisms, at least on an evolutionary timescale. Such transfer means that different traits will exhibit different phylogenies from that of the ribosomal RNA molecules, and may well be dispersed over a broad taxonomic space. The fact that hydrocarbon degradation is not yet found in all bacterial phyla may indicate some barriers to such transmission, or merely that such organisms have not yet been found.

## 3 Currently Described Hydrocarbon-Degrading Bacteria

Bacterial taxonomy is curated at several sites; The German Collection of Microorganisms and Cell Cultures (DSMZ, 2009), The National Center for Biological Information (NCBI, 2009), Bergey (2009), RDP (2009), and Euzéby (2009) for examples. [Table 1](#) lists the more than 175

■ **Table 1**

**Currently published genera of organisms able to grow using hydrocarbons as sole or major carbon source**

Genus	Typical substrate	References <sup>a</sup>
<b>Phylum Actinobacteria</b>		
<b>Order Actinomycetales</b>		
<i>Actinomyces</i> Harz (1877)	Crude oil	ZoBell (1946)
<i>Aeromicrobium</i> Miller et al. (1991)	Crude oil	Chaillan et al. (2004)
<i>Arthrobacter</i> Conn & Dimmick (1947)	Gas oil	Le Petit et al. (1975)
<i>Brevibacterium</i> Breed (1953)	Alkanes	Pirnik et al. (1974)
<i>Cellulomonas</i> Bergey et al. (1923)	Biphenyl	Plotnikova et al. (2006)
<i>Cellulosimicrobium</i> Schumann et al. (2001)	Crude oil	Dashti et al. (2009)
<i>Citricoccus</i> Altenburger et al. (2002)	Crude oil	Al-Awadhi et al. (2007)
<i>Clavibacter</i> Davis et al. (1984)	Naphthalene	Dore et al. (2003)
<i>Corynebacterium</i> Lehmann and Neumann (1896)	Fuel oil	Chaîneau et al. (1999)
<i>Dietzia</i> Rainey et al. (1995)	Alkanes	Yumoto et al. (2002)
<i>Georgenia</i> Altenburger et al. (2002)	Crude oil	Al-Awadhi et al. (2007)
<i>Gordonia</i> Stackebrandt et al. (1989)	Alkanes	Kummer et al. (1999)
<i>Isophtericola</i> Stackebrandt et al. (2004)	Crude oil	Al-Awadhi et al. (2007)
<i>Janibacter</i> Martin et al. (1997)	Phenanthrene	Yamazoe et al. (2004)
<i>Kocuria</i> Stackebrandt et al. (1995)	Crude oil	Dashti et al. (2009)
<i>Kytococcus</i> Stackebrandt et al. (1995)	Crude oil	Al-Saleh et al. (2009)
<i>Leifsonia</i> Evtushenko et al. (2000)	Crude oil	Dashti et al. (2009)
<i>Microbacterium</i> Orla-Jensen (1919)	Pyrene	Gauthier et al. (2003)
<i>Micrococcus</i> Cohn (1872)	Hexadecane	Ilori et al. (2000)
<i>Mycobacterium</i> Lehmann and Neumann (1896)	Phenanthrene	Willumsen et al. (2001)
<i>Nocardia</i> Trevisan (1889)	Alkanes	Mikolasch et al. (2003)
<i>Nocardioides</i> Prauser (1976)	Alkanes	Hamamura and Arp (2000)
<i>Nocardiosis</i> Brocq-Rousseau (1904)	Crude oil	Dixit and Pant (2000)
<i>Pseudonocardia</i> Henssen (1957)	Toluene	Juteau et al. (1999)
<i>Rhodococcus</i> Zopf (1891)	Phenanthrene	Meyer et al. (1999)
<i>Smaragdicoscus</i> Adachi et al. (2007)	Crude oil	Adachi et al. (2007)
<i>Streptomyces</i> Waksman and Henrici (1943)	Alkanes	Barabas et al. (2001)
<i>Terrabacter</i> Collins et al. (1989)	Fluorene	Iida et al. (2003)
<i>Williamsia</i> Kampfer et al. (1999)	Crude oil	Obuekwe et al. (2009)
<b>Order Rubrobacterales</b>		
<i>Thermoleophilum</i> Zarilla and Perry (1984)	Alkanes	Zarilla and Perry (1984)
<b>Phylum Bacteroidetes</b>		
<b>Order Flavobacteriales</b>		
<i>Chryseobacterium</i> Vandamme et al. (1994)	Kerosene	Szoboszlay et al. (2008)
<i>Flavobacterium</i> Bergey et al. (1923)	Diesel oil	Stucki and Alexander (1987)

Table 1 (Continued)

Genus	Typical substrate	References <sup>a</sup>
<i>Myroides</i> Vancanneyt et al. (1996)	Crude oil	Maneerat et al. (2006)
<i>Weeksella</i> Holmes et al. (1987)	Crude oil	Yuste et al. (2000)
<i>Yeosuana</i> Kwon et al. (2006)	Benzo[a]pyrene	Kwon et al. (2006)
<b>Order Sphingobacteriales</b>		
<i>Cytophaga</i> Winogradsky (1929)	Crude oil	Bossert and Bartha (1984)
<i>Pedobacter</i> Steyn et al. (1998)	Diesel	Margesin et al. (2003)
<b>Phylum Chlamydiae</b>		
<b>Order Verrucomicrobia</b>		
'Methylococcoides'	Methane	Hou et al. (2008)
<b>Phylum Cyanobacteria</b>		
<b>Order Chroococcales</b>		
<i>Agmenellum</i> De Brebisson (1839)	Phenanthrene	Narro et al. (1992)
<i>Aphanocapsa</i> Nägeli (1849)	Crude oil	Raghukumar et al. (2001)
<i>Aphanothece</i> Nägeli (1849)	Alkanes	Abed et al. (2005)
<i>Coccochloris</i> Sprengel (1807)	Naphthalene	Cerniglia (1979)
<b>Order Nostocales</b>		
<i>Anabaena</i> St. Vincent (1886)	Alkanes	Gamila et al. (2003)
<i>Nostoc</i> Vaucher (1888)	Naphthalene	Cerniglia et al. (1992)
<b>Order Oscillatoriales</b>		
<i>Dactylococcopsis</i> Hansgirg (1893)	Alkanes	Abed et al. (2005)
<i>Halothece</i> Margheri et al. (2008)	Alkanes	Abed et al. (2005)
<i>Microcoleus</i> Desmazières (1892)	Alkanes	Al-Hasan et al. (1998)
<i>Oscillatoria</i> Vaucher (1892)	Alkanes	Gamila et al. (2003)
<i>Phormidium</i> Kutzing (1892)	Alkanes	Al-Hasan et al. (1998)
<i>Plectonema</i> Thuret (1892)	Crude oil	Raghukumar et al. (2001)
<b>Phylum Deinococcus-Thermus</b>		
<b>Order Thermales</b>		
<i>Thermus</i> Brock and Freeze (1969)	Pyrene	Feitkenhauer et al. (2003)
<b>Phylum Firmicutes</b>		
<b>Order Bacillales</b>		
<i>Bacillus</i> Cohn (1872)	Toluene	Li et al. (2008)
<i>Brevibacillus</i> Shida et al. (1996)	Crude oil	Dashti et al. (2009)
<i>Exiguobacterium</i> Collins et al. (1984)	Diesel oil	Mohanty and Mukherji (2008)
<i>Geobacillus</i> Nazina et al. (2001)	Crude oil	Nazina et al. (2001)
<i>Oceanobacillus</i> Lu et al. (2002)	Crude oil	Al-Awadhi et al. (2007)
<i>Paenibacillus</i> Ash et al. (1994)	Phenanthrene	Meyer et al. (1999)
<i>Planococcus</i> Migula (1894)	Benzene	Li et al. (2006)
<i>Planomicrobium</i> Yoon et al. (2001)	Alkanes	Engelhardt et al. (2001)
<i>Staphylococcus</i> Rosenbach (1884)	Diesel	Saadoun et al. (1999)



■ **Table 1 (Continued)**

Genus	Typical substrate	References <sup>a</sup>
<b>Order Lactobacillales</b>		
<i>Lactobacillus</i> Beijerinck (1901)	Crude oil	Floodgate (1984)
<b>Order Clostridiales</b>		
<i>Desulfotomaculum</i> Campbell and Postgate (1965)	<i>o</i> -Xylene	Morasch et al. (2004)
<i>Desulfosporosinus</i> Stackebrandt et al. (1997)	Gasoline	Robertson et al. (2001)
<i>Peptococcus</i> Kluyver and van Niel (1936)	Crude oil	Floodgate (1984)
<i>Sarcina</i> Goodsir (1842)	Crude oil	Bossert and Bartha (1984)
<b>Phylum Proteobacteria</b>		
<b>Class Alpha Proteobacteria</b>		
<b>Order Caulobacteriales</b>		
<i>Brevundimonas</i> Segers et al. (1994)	Fuel oil	Chaineau et al. (1999)
<b>Order Kordiimonadales</b>		
<i>Kordiimonas</i> Kwon et al. (2006)	Benzo[a]pyrene	Kwon et al. (2005)
<b>Order Rhizobiales</b>		
<i>Afipia</i> Brenner et al. (1992)	Phenanthrene	Bodour et al. (2003)
<i>Agrobacterium</i> Conn (1942)	Gasoline	Prantera et al. (2002)
<i>Beijerinckia</i> Derx (1950)	Phenanthrene	Surovtseva et al. (1999)
<i>Blastochloris</i> Hiraishi (1997)	Toluene	Zengler et al. (1999)
<i>Hyphomicrobium</i> Stutzer and Hartleb (1898)	Crude oil	Ozaki et al. (2006)
<i>Methylobacterium</i> Patt et al. (1976)	Phenanthrene	Bodour et al. (2003)
<i>Methylocapsa</i> Dedysh et al. (2002)	Methane	Dedysh et al. (2002)
<i>Methylocella</i> Dedysh et al. (2000)	Methane	Dedysh et al. (2000)
<i>Methylocystis</i> Bowman et al. (1993)	Methane	Bowman et al. (1993)
<i>Methylosinus</i> Bowman et al. (1993)	Methane	Bowman et al. (1993)
<i>Ochrobactrum</i> Holmes et al. (1988)	Crude oil	Peressutti et al. (2003)
<i>Parvibaculum</i> Schleheck et al. (2004)	Linear alkanes	Schleheck et al. (2004)
<i>Rhizobium</i> Frank (1889)	Phenanthrene	Bodour et al. (2003)
<i>Sinorhizobium</i> Chen et al. (1988)	Phenanthrene	Bodour et al. (2003)
<i>Xanthobacter</i> Wiegel et al. (1978)	Dibenzothiophene	Padden et al. (1997)
<b>Order Rhodobacterales</b>		
<i>Stappia</i> Uchino et al. (1999)	Crude oil	Al-Awadhi et al. (2007)
<i>Tranquillimonas</i> Harwati et al. (2008)	Alkanes	Harwati et al. (2008)
<i>Tropicibacter</i> Harwati et al. (2009b)	Naphthalene	Harwati et al. (2009b)
<i>Tropicimonas</i> Harwati et al. (2009a)	Alkanes	Harwati et al. (2009a)
<b>Order Rhodospirillales</b>		
<i>Acidocella</i> Kishimoto et al. (1995)	Naphthalene	Dore et al. (2003)
<i>Azospirillum</i> Tarrand et al. (1979)	Alkane	Roy et al. (1988)
<i>Magnetospirillum</i> Schleifer et al. (1992)	Toluene	Shinoda et al. (2005)

■ **Table 1 (Continued)**

Genus	Typical substrate	References <sup>a</sup>
'Oleomonas' Kanamori et al. (2002)	Toluene, alkanes	Kanamori et al. (2002)
<i>Thalassospira</i> Lopez-Lopez et al. (2002)	Pyrene	Kodama et al. (2008)
<b>Order Sphingomonadales</b>		
' <i>Lutibacterium</i> ' Chung and King (2001)	Phenanthrene	Chung and King (2001)
<i>Novosphingobium</i> Takeuchi et al. (2001)	Phenanthrene	Shi et al. (2001)
<i>Porphyrobacter</i> Fuerst et al. (1993)	Phenanthrene	Gauthier et al. (2003)
<i>Sphingobium</i> Takeuchi et al. (2001)	Phenanthrene	Prakash and Lal (2006)
<i>Sphingomonas</i> Yabuuchi et al. (1990)	Dibenzofuran	Halden et al. (1999)
<b>Class Beta Proteobacteria</b>		
<b>Order Burkholderiales</b>		
<i>Achromobacter</i> Yabuuchi and Yano (1981)	Gas oil	Le Petit et al. (1975)
<i>Acidovorax</i> Willems et al. (1990)	Phenanthrene	Meyer et al. (1999)
<i>Alcaligenes</i> Castellani and Chalmers (1919)	Gas oil	Le Petit et al. (1975)
<i>Alicyciphilus</i> Mechichi et al. (2003)	Benzene	Weelink et al. (2008)
<i>Brachymonas</i> Hiraishi et al. (1995)	Cyclohexane	Brzostowicz et al. (2005)
<i>Burkholderia</i> Yabuuchi et al. (1993)	Toluene	Parales et al. (2000)
<i>Castellaniella</i> Kämpfer et al. (2006)	$\alpha$ -Pinene	Kämpfer et al. (2006)
<i>Comamonas</i> De Vos et al. (1985)	Phenanthrene	Meyer et al. (1999)
<i>Cupriavidus</i> Makkar and Casida (1987)	Biphenyl	Wittich and Wolff (2007)
<i>Hydrogenophaga</i> Willems et al. (1989)	Benzene	Fahy et al. (2008)
<i>Janthinobacterium</i> De Ley et al. (1978)	Phenanthrene	Bodour et al. (2003)
<i>Leptothrix</i> Kutzing (1843)	Phenanthrene	Bodour et al. (2003)
<i>Massilia</i> La Scola et al. (2000)	Phenanthrene	Bodour et al. (2003)
<i>Methylibium</i> Nakatsu et al. (2006)	Toluene	Nakatsu et al. (2006)
<i>Pandoraea</i> Coenye et al. (2000)	Crude oil	Ozaki et al. (2006)
<i>Polaromonas</i> Irgens et al. (1996)	Naphthalene	Jeon et al. (2004)
<i>Ralstonia</i> Yabuuchi et al. (1996)	Toluene	Parales et al. (2000)
<i>Rhodoferax</i> Hiraishi et al. (1992)	Propylbenzene	Eriksson et al. (2005)
<i>Sphaerotilus</i> Kutzing (1833)	Crude oil	Austin et al. (1977)
<b>Order Hydrogenophilales</b>		
<i>Thiobacillus</i> Beijerinck (1904)	Phenanthrene	Bodour et al. (2003)
<b>Order Nitrosomonadales</b>		
<i>Spirillum</i> Ehrenberg (1832)	Crude oil	Bossert and Bartha (1984)
<b>Order Rhodocyclales</b>		
' <i>Aromatoleum</i> '	Ethylbenzene	Trautwein et al. (2008)
<i>Azoarcus</i> Reinhold-Hurek et al. (1993)	Toluene	Hess et al. (1997)
<i>Dechloromonas</i> Achenbach et al. (2001)	Benzene	Coates et al. (2001b)
<i>Georgfuchsia</i> Weelink (2008)	Toluene	Weelink (2008)
<i>Thauera</i> Macy et al. (1993)	Toluene	Shinoda et al. (2004)

■ **Table 1** (Continued)

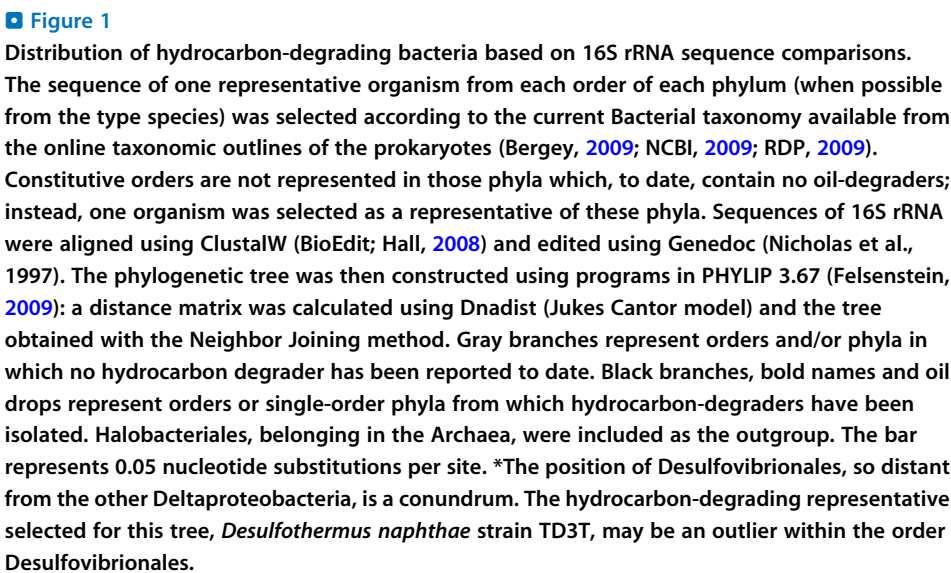
Genus	Typical substrate	References <sup>a</sup>
<b>Class Gamma Proteobacteria</b>		
<b>Order Aeromonadales</b>		
<i>Aeromonas</i> Stanier (1943)	Diesel	Odokumal and Dickson (2003)
<b>Order Alteromonadales</b>		
<i>Alteromonas</i> Baumann et al. (1972)	Crude oil	Iwabuchi et al. (2002)
<i>Marinobacter</i> Gauthier et al. (1992)	Crude oil	Gauthier et al. (1992)
<i>Microbulbifer</i> Gonzalez et al. (1997)	Crude oil	Brito et al. (2006)
<i>Shewanella</i> MacDonell and Colwell (1986)	Crude oil	Gentile et al. (2003)
<b>Order Enterobacteriales</b>		
<i>Enterobacter</i> Hormaeche and Edwards (1960)	Alkanes	Saadoun et al. (1999)
<i>Erwinia</i> Winslow et al. (1920)	Alkanes	Saadoun et al. (1999)
<i>Klebsiella</i> Trevisan (1885)	Crude oil	Odokumal and Dickson (2003)
<i>Leclercia</i> Tamura et al. (1987)	Pyrene	Sarma et al. (2004)
<i>Pantoea</i> Gavini et al. (1989)	Crude oil	Obuekwe et al. (2009)
<i>Proteus</i> Hauser (1885)	Crude oil	Odokumal and Dickson (2003)
<i>Rahnella</i> Izard et al. (1981)	Naphthalene	Ma et al. (2006)
<i>Serratia</i> Bizio (1823)	Crude oil	Odokumal and Dickson (2003)
<b>Order Methylococcales</b>		
<i>Clonothrix</i> Roze (1896)	Methane	Vigliotta et al. (2007)
<i>Crenothrix</i> Cohn (1870)	Methane	Stoecker et al. (2006)
<i>Methylobacter</i> Bowman et al. (1993)	Methane	Bowman et al. (1993)
<i>Methylocaldum</i> Bodrossy et al. (1998)	Methane	Bodrossy et al. (1998)
<i>Methylococcus</i> Foster and Davis (1966)	Methane	Bowman et al. (1993)
<i>Methylohalobius</i> Heyer et al. (2005)	Methane	Heyer et al. (2005)
<i>Methylomonas</i> Leadbetter (1974)	Methane	Bowman et al. (1993)
<i>Methylothermus</i> Tsubota et al. (2005)	Methane	Tsubota et al. (2005)
<i>Methylomicrobium</i> Bowman et al. (1995)	Methane	Kalyuzhnaya et al. (2008)
<i>Methylosarcina</i> Wise et al. (2001)	Methane	Wise et al. (2001)
<i>Methylosoma</i> Rahalkar et al. (2007)	Methane	Rahalkar et al. (2007)
<i>Methylosphaera</i> Bowman et al. (1997)	Methane	Bowman et al. (1997)
<b>Order Oceanospirillales</b>		
<i>Alcanivorax</i> Yakimov et al. (1998)	Alkanes	Yakimov et al. (1998)
<i>Halomonas</i> Vreeland et al. (1980)	Crude oil	Wang et al. (2007)
<i>Neptunomonas</i> Hedlund et al. (1999)	Naphthalenes	Hedlund et al. (1999)
<i>Oleiphilus</i> Golyshin et al. (2002)	Alkanes	Golyshin et al. (2002)
<i>Oleispira</i> Yakimov et al. (2003)	Alkanes	Yakimov et al. (2003)
<i>Salinicola</i> Anan'ina et al. (2007)	Naphthalene	Anan'ina et al. (2007)
<i>Thalassolituus</i> Yakimov et al. (2004)	Alkanes	Yakimov et al. (2004)
<b>Order Pasteurellales</b>		
<i>Pasteurella</i> Trevisan (1887)	Fluoranthene	Sepic et al. (1997)

Table 1 (Continued)

Genus	Typical substrate	References <sup>a</sup>
<b>Order Pseudomonadales</b>		
<i>Acinetobacter</i> Brisou & Prévot (1954)	Gas oil	Le Petit et al. (1975)
<i>Alkanindiges</i> Bogan et al. (2003)	Alkanes	Bogan et al. (2003)
<i>Azotobacter</i> Beijerinck (1901)	Paraffins	Gradova et al. (2003)
<i>Moraxella</i> Lwoff (1939)	Biphenyl	Stucki and Alexander (1987)
<i>Pseudomonas</i> Migula (1894)	Gas oil	Le Petit et al. (1975)
<b>Order Thiotrichales</b>		
<i>Cycloclasticus</i> Dyksterhouse et al. (1995)	Biphenyl	Dyksterhouse et al. (1995)
<i>Leucothrix</i> Oersted (1844)	Crude oil	Floodgate 1984)
<b>Order Vibrionales</b>		
<i>Vibrio</i> Pacini (1854)	Phenanthrene	Hedlund and Staley (2001)
<b>Order Xanthomonadales</b>		
<i>Alkanibacter</i> Friedrich and Lipski (2008)	Hexane	Friedrich and Lipski (2008)
<i>Hydrocarboniphaga</i> Palleroni et al. (2004)	Alkanes	Palleroni et al. (2004)
<i>Nevskia</i> Famintzin (1892)	Toluene	Juteau et al. (1999)
<i>Pseudoxanthomonas</i> Finkmann et al. (2000)	Toluene	Kim et al. (2008)
<i>Singularimonas</i> Friedrich and Lipski (2008)	Hexane	Friedrich and Lipski (2008)
<i>Stenotrophomonas</i> Palleroni and Bradbury (1993)	Pyrene	Juhasz et al. (2000)
<i>Xanthomonas</i> Dowson (1939)	Phenanthrene	Hamann et al. (1999)
<i>Xylella</i> Wells et al. (1987)	Alkanes	Yuste et al. (2000)
<b>Class Delta Proteobacteria</b>		
<b>Order Desulfobacterales</b>		
<i>Desulfatibacillum</i> Cravo-Laureau et al. (2004)	Alkanes	Cravo-Laureau et al. (2004)
<i>Desulfatiferula</i> Cravo-Laureau et al. (2007)	Alkenes	Cravo-Laureau et al. (2007)
<i>Desulfobacterium</i> Bak and Widdel (1988)	Xylene	Harms et al. (1999)
<i>Desulfobacula</i> Rabus et al. (2000)	Toluene	Rabus et al. (1993)
<i>Desulfosarcina</i> Widdel (1981)	Xylene	Harms et al. (1999)
<i>Desulfotignum</i> Kuever et al. (2001)	Toluene	Ommedal and Torsvik (2007)
<b>Order Desulfovibrionales</b>		
<i>Desulfothermus</i> Kuever et al. (2005)	alkanes	Kuever et al. (2005)
<b>Order Desulfuromonadales</b>		
<i>Geobacter</i> Lovley et al. (1995)	Toluene	Coates et al. (2001a)
<i>Pelobacter</i> Schink and Pfennig (1983)	Acetylene	Schink (1985)
<b>Order Syntrophobacterales</b>		
<i>Desulfoglaeba</i> Davidova et al. (2006)	Alkanes	Davidova et al. (2006)

<sup>a</sup>references are to a 'typical' reference, not necessarily the first, last or best

Notes: Early work ascribed several hydrocarbon degraders to *Sphingomonas*, but this genus has undergone taxonomic scrutiny, and most have been moved to *Sphingobium* or *Novosphingobium*. *Lutibacterium* is closely allied [Leys et al. (2004); Pal et al. (2006); Kim et al. (2007); Kertesz and Kawasaki (2009)]. 'Aromatoleum', 'Lutibacterium', 'Oleomonas' and 'Methylacidiphilum' do not seem to have been validly published. *Crenothrix* was originally thought to be an alga [Cohn (1873)]



Distribution of hydrocarbon-degrading bacteria based on 16S rRNA sequence comparisons. The sequence of one representative organism from each order of each phylum (when possible from the type species) was selected according to the current Bacterial taxonomy available from the online taxonomic outlines of the prokaryotes (Bergey, 2009; NCBI, 2009; RDP, 2009). Constitutive orders are not represented in those phyla which, to date, contain no oil-degraders; instead, one organism was selected as a representative of these phyla. Sequences of 16S rRNA were aligned using ClustalW (BioEdit; Hall, 2008) and edited using Genedoc (Nicholas et al., 1997). The phylogenetic tree was then constructed using programs in PHYLIP 3.67 (Felsenstein, 2009): a distance matrix was calculated using Dnadist (Jukes Cantor model) and the tree obtained with the Neighbor Joining method. Gray branches represent orders and/or phyla in which no hydrocarbon degrader has been reported to date. Black branches, bold names and oil drops represent orders or single-order phyla from which hydrocarbon-degraders have been isolated. Halobacteriales, belonging in the Archaea, were included as the outgroup. The bar represents 0.05 nucleotide substitutions per site. \*The position of Desulfovibrionales, so distant from the other Deltaproteobacteria, is a conundrum. The hydrocarbon-degrading representative selected for this tree, *Desulfothermus naphthae* strain TD3T, may be an outlier within the order Desulfovibrionales.

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currently published genera of organisms able to grow using hydrocarbons as sole or major carbon source, and [Fig. 1](#) illustrates the phylogenetic distribution of known hydrocarbon-degraders.

## 4 Phylum Actinobacteria

These gram-positive bacteria are colloquially known as Actinomycetes because some grow as branching filaments that resemble fungal mycelia. They are common in soil environments, and play a central role in the decomposition of organic matter and recycling of soil nutrients. Some produce potent antibiotics.

Two orders within the Actinobacteria have known hydrocarbon-degrading genera, the Actinomycetales and the Rubrobacterales – most characterized Actinobacterial oil-degraders are in the former ([Table 1](#)), and are typically mesophiles. The one characterized genus in the latter, *Thermoleophilum* (Zarillla and Perry, 1984) is obligately thermophilic, with an optimum growth temperature of 60°C. All are aerobes.

*Rhodococcus ruber* C208 seems able to grow on polyethylene and polyethylene as sole carbon sources (Mor and Sivan, 2008; Orr et al., 2004) – even on polystyrene 96 well plates in carbon free mineral medium! And strains of *Gordonia*, *Mycobacterium*, and *Rhodococcus* are able to remove sulfur from dibenzothiophene to yield hydroxybiphenyl (see Mohebbi and Ball, 2008).

## 5 Phylum Bacteroidetes

The phylum Bacteroidetes has three large groups; the Bacteroides, the Flavobacteriales, and the Sphingobacteriales (previously known as the Cytophagales). Only the latter two currently contain hydrocarbon-degraders ([Table 1](#)). All the known Bacteroidetes hydrocarbon-degraders are aerobes.

## 6 Phylum Cyanobacteria

The Cyanobacteria are typically considered obligate photoautotrophs, but in fact some can grow heterotrophically (Mannan and Pakrasi, 1993; Rippka, 1972), and many take advantage of reduced carbon compounds in their environment. Their ability to degrade hydrocarbons has been debated for some time, and while there are credible reports using labeled substrates ([Table 1](#)), there is some discussion as to how significant this is, and indeed whether the metabolism is actually carried out by the phototrophs, or by commensal bacteria (Abed and Köster, 2005; Radwan et al., 2005). *Microcoleus chthonoplastes*, for example, forms a consortium with heterotrophic bacteria within the cyanobacterial sheath (Sánchez et al., 2005). Axenic cultures of Cyanobacteria may well be a laboratory artifact – Morris et al. (2008) demonstrate that *Prochlorococcus* (not reported to degrade hydrocarbons) grows poorly in the absence of “helper” heterotrophs, at least in dilute cultures.

*Agmenellum quadruplicatum* (Narro et al., 1992) is still listed as a valid designation in the Integrated Taxonomic Information System (ITIS, 2009), but not, for example, in Cyanobase (Komárek and Hauer, 2009) or NCBI (2009). Many now assign it to *Synechococcus* (e.g., NCBI, 2009). Cyanobacterial taxonomy remains in flux, and current convention is to eschew specific names for new isolates, and to use numbers.

In summary, there is currently no evidence that any *Cyanobacterium* can grow with a hydrocarbon as sole carbon source, but it does seem clear that *Cyanobacteria* may provide at least some of the oxygen and nitrogen required by heterotrophic oil-degraders in oiled sediments (e.g., Musat et al., 2006). Microbial mats containing *Cyanobacteria* may be important sinks for hydrocarbon in the environment (e.g., Abed and Köster, 2005; Bordenave et al., 2008; Cohen, 2002; Hernandez-Raquet et al., 2006; Radwan et al., 2005).

## 7 Phylum *Deinococcus-Thermus*

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This phylum currently contains only a single species known to grow on hydrocarbons as sole source of carbon; *Thermus brockii* (Feitkenhauer et al., 2003). This aerobic organism degrades hexadecane and a broad spectrum of polycyclic aromatic hydrocarbons at an optimum temperature of 70°C, and retains some activity at 80°C.

## 8 Phylum *Firmicutes*

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Most *Firmicutes* (“strong-skinned”) are spore-forming gram-positive organisms, although the phylum includes the *Mollicutes*, otherwise known as the *Mycoplasmas*, which are renowned for their lack of a true cell wall. None of the *Mollicutes* are known to degrade hydrocarbons, but three other orders, the *Bacillales*, the *Lactobacillales* and the *Clostridiales*, all contain hydrocarbon-degrading genera (➤ Table 1). Strains of *Bacillus subtilis* and *Paenibacillus polymyxa* are able to remove sulfur from dibenzothiophene to yield hydroxybiphenyl (see Mohebbi and Ball, 2008). *Brevibacillus borstelensis*, a thermophilic aerobe, can even degrade polyethylene (Hadad et al., 2005).

The organism isolated by Engelhardt et al. (2001) as a *Planococcus* has been reassigned to *Planomicrobium* by Dai et al. (2005).

Two genera of the *Clostridiales*, *Desulfotomaculum* and *Desulfosporosinus*, are sulfate-reducers, and degrade hydrocarbons under anaerobic conditions.

The identification of *Sarcina* is curious – these organisms have a very characteristic morphology, occurring in packets of eight or more cells, but all the formally described species are fermentative anaerobes or microaerophiles. So are the formally described species of *Peptococcus* and *Lactobacillus*, and there have been few subsequent reports of such organisms as hydrocarbon-degraders. They were identified in aerobic incubations in the references cited in ➤ Table 1.

## 9 Phylum *Proteobacteria*

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The majority of the formally described genera of hydrocarbon-degrading bacteria are in this very large phylum of gram-negative organisms. The phylum is divided into five large classes, and all but the smallest (epsilon) contain hydrocarbon-degrading genera. Most methanotrophic bacteria are in this phylum (Bowman, 2006), which also contains the recently discovered obligate hydrocarbon-degraders (Yakimov et al., 2007), including some strains of *Alkanivorax*, *Cycloclasticus*, *Oleiphilus*, *Oleispira*, and *Thalassolituus*, and many organisms able to degrade hydrocarbons under anaerobic conditions. For example, *Alicyclophilus denitrificans*



degrades benzene under chlorate-reducing conditions (Weelink et al., 2008), and *Georgfuchsia toluolica* can grow on toluene and ethylbenzene at the expense of reducing nitrate,  $\text{MnO}_2$ , or ferric ions. *Blastochloris sulfoviridis* is a heterotrophic anaerobic phototroph that can degrade toluene (Zengler et al., 1999), although closely related strains cannot. *Rhodospirillum rubrum* oxidizes propylbenzene under iron-reducing conditions (Eriksson et al., 2005); other members of this genus are phototrophs. *Thauera* is able to degrade toluene under both aerobic and nitrate-reducing anaerobic conditions (Shinoda et al., 2004). A recent psychrophilic isolate of *Shewanella* is predicted to have a minimal growth temperature of  $-13^\circ\text{C}$  (Gentile et al., 2003).

Strains of *Novosphingobium* and *Acidovorax* are able to remove sulfur from dibenzothio-phenene to yield hydroxybiphenyl (see Mohebbi and Ball, 2008, although in that review they were identified as *Sphingomonas* and *Pseudomonas*).

*Methylobium petroleiphilum*, a member of the beta-proteobacteria, is able to degrade the gasoline oxygenate methyl-*t*-butylether (MTBE) as well as aromatic hydrocarbons such as toluene (Nakatsu et al., 2006).

Most known delta-proteobacterial hydrocarbon-degraders are sulfate-reducers and obligate anaerobes. One exception is *Geobacter*, which has catholic tastes and can use oxygen while “waiting” for its preferred anaerobic iron-reducing mode of growth (Lin et al., 2004). Another is *Pelobacter acetylenicus*, which ferments acetylene by disproportionation to acetate and ethanol (Schink, 1985).

## 10 Archaeal Hydrocarbon Degradation

There are currently no formally described archaeal hydrocarbon-degraders, although some have suggested that Halobacteria can play an important role in the biodegradation of hydrocarbons in extremely saline environments. Bertrand et al. (1990) isolated an archaean strain, EH4, which was able to biodegrade saturated and aromatic hydrocarbons in 3.5 M NaCl brine. No growth on hydrocarbons was observed at concentrations lower than 1.8 M NaCl. Alas no further publications on this strain have been forthcoming. Kulichevskaya et al. (1992) reported hydrocarbon-co-oxidation by *Halobacterium salinarium*, *H. volcanii*, and *H. distributum*, but again there have been no further publications on the topic. More recently, Kim and Crowley (2007) have found a wealth of archaeal halophiles inhabiting the La Brea tar pits in California, but whether they degrade hydrocarbons remains to be seen. There is no evidence that archaea play a significant role in oil biodegradation in marine systems, and indeed Røling et al. (2004) found that archaeal species disappeared when oil was applied to mesocosms, even though substantial biodegradation occurred.

## 11 Evolution in Real Time?

As mentioned in the introduction, hydrocarbons have always been part of the biosphere, but some molecular structures have only been present in recent years. We have already mentioned the biodegradation of polyethylene (Hadad et al., 2005) and polystyrene (Mor and Sivan, 2008), which have been present in the biosphere for less than 100 years. *Iso*-octane, 2,2,4-trimethylpentane, is another example; it is not found in crude oils, but only in gasolines containing alkylates (Ritter, 2005). These were first available in the 1930s. Nevertheless, *iso*-octane is readily aerobically degraded by microbes in apparently pristine waters (Prince



et al., 2007), and Solano-Serena et al. (2000) have isolated a *Mycobacterium* able to grow on it as sole carbon and energy source. The organism seems to use a modified alkane monooxygenase to attack the *iso*-octane at the *iso*-propyl end (Solano-Serena et al., 2004).

Methyl-*t*-butyl ether (MTBE) is another recent addition to the biosphere – it has only been in commerce since the 1980s. For some time it was thought to be very recalcitrant to biodegradation, but it is now recognized that the ability to degrade MTBE is quite widespread (Bradley et al., 2001; Prince, 2000), and bioreactors for its destruction have been developed (Maciel et al., 2008). Hristova et al. (2007) have found that important enzymes in the MTBE degradation pathway of *Methylibrium petroleiphilum* are plasmid borne, and suggest that the MTBE monooxygenase is related to alkane monooxygenases, albeit with a broader substrate acceptance. One can imagine that such plasmids would have a significant selective advantage, and be passed to other organisms.

Are these recently acquired activities? No anaerobic degradation has yet been reported, but now that these compounds are in the biosphere there would probably be an advantage to any organism able to use them under anaerobic conditions.

## 12 Research Needs

It remains a challenge to identify the most active hydrocarbon-degrading microbes in various environments. Approaches such as stable-isotope probing (SIP) provide a link between phylogeny and function and have demonstrated that there are novel hydrocarbon degraders to be found. For example, Gammaproteobacteria with less than 90% 16S rRNA sequence similarity to cultivated strains were identified as the main pyrene degraders in soil by SIP (Jones et al., 2008). Singleton et al. (2006) identified novel pyrene degraders that were barely detectable in clone libraries, and as such would not have been recognized as playing an important role in pyrene degradation without using SIP. Once identified, it is important to apply methods to quantify, locate, and further study such microbes in situ and also to try to grow them in the laboratory. Microbial taxonomy proceeds very rapidly, and many strains will be described in the near future. Understanding their taxonomic position will suggest new approaches to discovering novel pathways, and indicate areas of the taxonomic landscape that warrant closer attention.

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