Chapter 8
Mobile Genetic Elements (MGEs) Carrying Catabolic Genes

Masaki Shintani and Hideaki Nojiri

Abstract Mobile genetic elements (MGEs) are important "vehicles" of diverse genes in the microbial genetic pool. Exchange of MGEs in the microbial community confers new traits to their hosts and promotes their rapid adaptation to various environments. For decades, a variety of bacteria capable of degrading "xenobiotic" compounds have been isolated for their potential importance in the removal of these compounds from contaminated environments. The genes responsible for the catabolic turnover of xenobiotics are sometimes located on MGEs such as plasmids, transposons, and integrative and conjugative elements (ICEs). This chapter summarizes our current knowledge of major MGEs that carry catabolic genes, and briefly describes their features. Recent works focused on the behavior of MGEs in natural environmental samples have also been described here.

Keywords Mobile genetic elements (MGEs) • Horizontal gene transfer (HGT) • Transposons • Catabolic plasmids • Xenobiotics

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M. Shintani (✉)
Present address: Department of Materials Science and Chemical Engineering,
Faculty of Engineering, Shizuoka University, 3-5-1 Johoku, Naka-ku, Hamamatsu,
432-8561, Shizuoka, Japan

Japan Collection of Microorganisms, RIKEN BioResource Center
3-1-1 Kouyadai, Tsukuba, Ibaraki 305-0074, Japan
e-mail: tmshint@ipc.shizuoka.ac.jp

H. Nojiri
Biotechnology Research Center, The University of Tokyo,
1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

Agricultural Bioinformatics Research Unit, The University of Tokyo,
1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

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1 Introduction

Horizontal gene transfer (HGT) is one of the important mechanisms for rapid bacterial evolution and adaptation. HGT proceeds mainly by conjugation (Frost et al. 2005; Heuer and Smalla 2007; Aminov 2011) and is mediated by mobile genetic elements (MGEs), which are DNA segments that can move between bacterial cells (intercellular mobility) (Frost et al. 2005). The elements carry various kinds of genes, such as antibiotic resistance genes, virulence genes, and catabolic genes, and thus, MGEs are important "vehicles" of pathogenically- and environmentally-relevant traits. Plasmids, integrative and conjugative elements (ICEs), and transposons are the important MGEs. Since the 1960s, various bacteria capable of degrading "xenobiotic" compounds have been isolated because of their potential importance in the removal of these compounds from contaminated environments. In this review, we use the term "xenobiotic" compounds in a broad sense to signify compounds that are not natural to the environment, but are rather "guest" chemicals, as defined by Leisinger (1983). The genes involved in catabolic turnover of xenobiotic compounds are sometimes identified on MGEs, especially on plasmids, ICEs, and transposons.

Plasmids are circular or linear extrachromosomal replicons, which are often transmissible by conjugation (Sota and Top 2008; Frost et al. 2005). ICEs are also self-transmissible conjugative elements, but they are generally integrated into the host chromosome (Burrus and Waldor 2004; Wozniak and Waldor 2010). Conjugation can spread genetic elements among bacteria effectively (Guglielmini et al. 2011), and therefore, it is one of the most important mechanisms for rapid evolution and adaptation of bacteria. On the other hand, transposons are genetic elements that are mobilized and transferred between replicons by the activity of a transposase (Mahillon and Chandler 1998). Once transposons integrate into plasmids or ICEs, they can also be transferred into other cells (Frost et al. 2005). Insertion sequences (IS) are a transposons that carry only the transposase gene, and homologous recombination between multiple copies of the same IS element can promote genomic rearrangements (Mahillon and Chandler 1998).

Although many reviews have been published on MGEs that carry catabolic genes for xenobiotic compounds (Tan 1999; Top et al. 2000, 2002; Top and Springael 2003; van der Meer and Sentchilo 2003; Nojiri et al. 2004; Dennis 2005), a large number of new catabolic MGEs have since been reported due to the recent revolution in nucleotide sequencing technology. This chapter summarizes recent studies of major and/or new MGEs that carry catabolic genes, and briefly describes their features.

2 Catabolic Plasmids

Plasmids have been classified into incompatibility (Inc) groups on the basis of their replication and partition systems. When two different plasmids cannot be maintained in the same bacterial cell line, these two plasmids are called "incompatible" and are considered to belong to the same "Inc" group. There are 27 Inc groups for the *Enterobacteriaceae* (Carattoli 2009), at least 14 groups for the *Pseudomonas* (Thomas and Haines 2004), and around 18 groups for the gram-positive bacteria (Frost et al. 2005;

Sota and Top 2008), although these groupings do not include all the identified plasmids such as plasmids in *Sphingomonas*. Recently, a new classification of plasmids was proposed, which is based on their transfer systems generally composed of two sets of proteins for mating pair formation (MPF) and mobilization (MOB) (Smillie et al. 2010; Garcillán-Barcia et al. 2009, 2011). Combination of four types of MPFs ($\mathrm{MPF_F}$, $\mathrm{MPF_I}$, $\mathrm{MPF_G}$, and $\mathrm{MPF_T}$) and six classes of MOBs ($\mathrm{MOB_F}$, $\mathrm{MOB_H}$, $\mathrm{MOB_Q}$, $\mathrm{MOB_C}$, $\mathrm{MOB_P}$, and $\mathrm{MOB_V}$) enables us to classify a larger number of plasmids whose sequences have been deposited in DNA databases.

Features of major catabolic plasmids, such as host, growth substrate of host, Inc groups, MOB classes and MPF types, and transferability, are listed in Tables 8.1, 8.2, 8.3 and 8.4. They have been identified in bacteria of the phylum *Proteobacteria*, such as *Pseudomonas* (*γ-proteobacteria*), *Achromobacter* (*β-proteobacteria*), and *Sphingomonas* (*α-proteobacteria*), and in gram-positive bacteria such as *Arthrobacter*, *Flavobacterium*, and *Rhodococcus*, since the 1970s. Because detailed features of IncP-1, IncP-7, and IncP-9 group plasmids have been already described in our previous review (Shintani et al. 2010), we focused especially on the catabolic plasmids in sphingomonads or gram-positive bacteria in this chapter.

2.1 Catabolic Plasmids from Genus Pseudomonas and Those Belonging to Pseudomonas Incompatibility Groups

Many catabolic plasmids are classified into the IncP-1, IncP-2, IncP-7, and IncP-9 groups, which carry genes involved in the degradation of various xenobiotic compounds, such as those for toluene/xylene (*xyl*), (chloro)benzoate (*cba*), (chloro)aniline (*dca*), 2,4-dichlorophenoxyacetic acid (2,4-D) (*tfd*), naphthalene (*nah*), and carbazole (*car*), amongst others (Table 8.1). The complete nucleotide sequences of several plasmids in these groups, except for the IncP-2 plasmids, have been determined, and an Inc group-specific plasmid backbone was proposed by comparative analyses (Fig. 8.1). Dennis (2005) compared the genetic organization of IncP-1 plasmids and showed that most catabolic genes (or other genes, such as antibiotic resistance genes) of IncP-1 plasmids were inserted between the *trfA* and *oriV* regions and the *parA* and *tra* operons (Fig. 8.1a; Dennis 2005). Sota et al. (2007) showed that the structural similarity of IncP-1 plasmids was a result of both the region-specific insertion of transposons and the selective pressure for maintaining transferability and stability of the plasmids. Based on the comparisons of the nucleotide sequences of plasmids, conserved regions of IncP-9 and IncP-7 plasmids (i.e., a plasmid backbone) were also proposed (Fig. 8.1b, c; Sota et al. 2006; Yano et al. 2010). One important difference between these plasmids is their host range. IncP-1 plasmids are known to be broad host range plasmids that can transfer among bacteria belonging to different classes, such as *α*-, *β*-, and *γ-proteobacteria*. Indeed, the host range of IncP-1 catabolic plasmids is broad, as listed in Table 8.1. As for the IncP-7 and IncP-9 plasmids, their host ranges are narrower than that of the IncP-1 plasmids, and most of their hosts belong to *γ-proteobacteria*, and in particular, to the genus *Pseudomonas* (Table 8.1).

Table 8.1 Catabolic plasmids from genus *Pseudomonas* and those belonging to *Pseudomonas* incompatibility groups[a]

Plasmid	Host	Substrate[b]	Size (kb)	Inc group	MOB class[c]	T4SS type[c]	Genes	Transferability	References
pA81[d]	*Achromobacter xylosocidans* A8	Chlorobenzoate	98	P1	MOB_P	MPF_T	*mocpRAB CDhybRABCD*	+	Jencova et al. (2008)
pAC25	*Pseudomonas putida* AC858	3-Chlorobenzoate	117	P1	NA	NA	NA	+	Chatterjee et al. (1981)
pADP-1[d]	*Pseudomonas* sp. ADP	Atrazine	109	P1	MOB_P	MPF_T	*atzABCDEF*	+	de Souza et al. (1998); Martinez et al. (2001)
pBRC60	*Alcaligenes* sp. BR60	3-Chlorobenzoate	75	P1	NA	NA	*cba*	+	Fulthorpe and Wyndham (1991)
pC1	*Delftia acidovorans* CA28	3-Chloroaniline	100	P1	NA	NA	*tdnQ*	+	Boon et al. (2001)
pCNB1[d]	*Comamonas* sp. CNB-1	4-chloronitro-benzene	91	P1	MOB_P	MPF_T	*cnb*, *cat*	NA	Wu et al. (2005, 2006); Ma et al. (2007)
pEMT3	Unknwon soil bacterium	2,4-D, 3-Chlorobenzoate	60	P1	NA	NA	*tfdABC*	+	Top et al. (1995); Gstalder et al. (2003)
pENH91	*Ralstonia eutropha* NH9	3-Chlorobenzoate	78	P1	NA	NA	*cbnABCD*	NA	Ogawa and Miyashita (1995)
pEST4011[d]	*Achromobacter xylosoxidans* subsp. *denitrificans* EST4002	2,4-D	70	P1	MOB_P	MPF_T	*tfdCEBKA*, *tfdF*, *mdc*	+	Mäe et al. (1993); Vedler et al. (2000, 2004)
pIJB1[d]	*Burkholderia cepacia* 2a	2,4-D, malonate	102	P1	NA		*tfd*, *mdc*, *bph*	NA	Xia et al. (1998); Poh et al. (2002)
pJP4[d]	*Ralstonia eutropha* JMP134	2,4-D, 3-Chlorobenzoate	80	P1	MOB_P	MPF_T	*tfdA*, *tfdB*, *tfdCDEF*	+	Don and Pemperton (1981); Don et al. (1985); Trefault et al. (2004)

pNB2	*Comamonas testosteroni* I2	3-Chloroaniline	60	P1	NA	NA	*tdnQ*	+	Boon et al. (2000, 2001); Bathe (2004)
pNB8c[d]	*Delftia acidovorans* B8c	3-Chloroaniline	60	P1	NA	NA	*dca*	+	Boon et al. (2001); Dejonghe et al. (2002); Król et al. (2012)
pPS12-1	*Burkholderia* sp. PS12	1,2,4,5-Tetrachlorobenzene	85	P1	NA	NA	*tecAB*	NA	Beil et al. (1999)
pSS50	*Alcaligenes* sp. A5	4-Chlorobenzoate	53	P1	NA	NA	*bph*	+	Shields et al. (1985); Hooper et al. (1989); Layton et al. (1992)
pSS60	*Achromobacter* sp. LBS1C1	4-chlorobenzoate	63	P1	NA	NA	*bph*	+	Burlage et al. (1990)
pTSA	*Comamonas testosteroni* T-2	*p*-Toluenesulfonic acid	85	P1	NA	NA	*tsaMBCDR*, *psbAC*	+	Junker and Cook (1997); Tralau et al. (2001)
pUO1[d]	*Delftia acidovorans* B	Haloacetates	65	P1	$\mathrm{MOB}_{\mathrm{P}}$	$\mathrm{MPF}_{\mathrm{T}}$	*dehA1*, *dehA2*	+	Kawasaki et al. (1981); Sota et al. (2003)
pWDL7[d]	*Comamonas testosteroni* WDL2	3-Chloroaniline		P1	NA	NA	*dcaRBA2A1TQ*	+	Król et al. (2012)
CAM	*Pseudomonas putida* PpG1	Camphor	500	P2	NA		*cam*	NA	Chakrabarty (1973); Rheinwald et al. (1973); Tan (1999)
OCT	*Pseudomonas olevorans* PpG6	Camphor	500	P2	NA		*alkBFGHJKL*, *alkST*	+	Chakrabarty (1973)
pVI150	*Pseudomonas* sp. CF600	Phenol	NA	P2	NA		*dmp*	+	Bartilson et al. (1990)
pAK5	*Pseudomonas putida* AK5	Naphthalene	115	P7	NA		NA	NA	Izmalkova et al. (2005)
pCAR1[d]	*Pseudomonas resinovorans* CA10	Carbazole	199	P7	$\mathrm{MOB}_{\mathrm{H}}$	$\mathrm{MPF}_{\mathrm{F}}$	*carABCDEF* *antABC*	+	Nojiri et al. (2001); Maeda et al. (2003); Takahashi et al. (2009)

(continued)

Table 8.1 (continued)

Plasmid	Host	Substrate[b]	Size (kb)	Inc group	MOB class[c]	T4SS type[c]	Genes	Transferability	References
pDK1[d]	*Pseudomonas putida* HS1	Xylene, toluene	180	P7	NA	NA	*xyl*	+	Kunz and Chapman (1981); Yano et al. (2010)
pFME	*Pseudomonas fluorescens* FME4	Naphthalene	77	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pME5	*Pseudomonas fluorescens* FME5	Naphthalene	80	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pND6-1[d]	*Pseudomonas* sp. ND6	Naphthalene	102	P7	–	–	*nah*	–	Li et al. (2004)
pNK33	*Pseudomonas fluorescens* NK33	Naphthalene	100	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pNK43	*Pseudomonas fluorescens* NK43	Naphthalene	123	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pOS18	*Pseudomonas fluorescens* OS18P	Naphthalene	135	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pOS19	*Pseudomonas fluorescens* OS19P	Naphthalene	122	P7	NA	NA	NA	NA	Izmalkova et al. (2005)
pWW53[d]	*Pseudomonas putida* MT53	Xylene, Toluene	107	P7	–	–	*xyl*	–	Keil et al. (1985, 1987); Tsuda and Genka (2001); Yano et al. (2007)

NAH7[d]	*Pseudomonas putida* G7	Naphthalene, Phenanthrene, Anthracene	83	P9	MOB_F	MPF_T	*nah*	+	Dunn and Gunsalus (1973); Connors and Barnsley (1980); Sota et al. (2006)
NPL-1	*Pseudomonas putida* BS 202	Naphthalene	100	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
p15C	*Pseudomonas* sp. 15C	Naphthalene	110	P9	NA	NA	NA		Sevastsyanovich et al. (2008)
p8C	*Pseudomonas* sp. 8C	Naphthalene	110	P9	NA	NA	NA		Sevastsyanovich et al. (2008)
pBS1141	*Pseudomonas putida* BS 3701	Naphthalene	120	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS1181	*Pseudomonas putida* BS 3750	Naphthalene	120	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS1191	*Pseudomonas putida* BS 3790	Naphthalene	100	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS240	*Pseudomonas putida* BS 639	Naphthalene	160	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS243	*Pseudomonas putida* BS 638	Naphthalene	160	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS265	*Pseudomonas putida* BS 394	ε-Caprolactam	130	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS267	*Pseudomonas putida* BS 394	ε-Caprolactam	130	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pBS268	*Pseudomonas putida* BS 394	ε-Caprolactam	85	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pDTG1[d]	*Pseudomonas putida* NCBI9816-4	Naphthalene	81	P9	MOB_F	MPF_T	*nah*	–	Simon et al. (1993); Stuart-Keil et al. (1998); Dennis and Zylstra (2004)
pFKY1[e]	Unidentified soil bacterium	Naphthalene	200	P9	NA	NA	*nah*	+	Ono et al. (2007)

(continued)

Table 8.1 (continued)

Plasmid	Host	Substrate[b]	Size (kb)	Inc group	MOB class[c]	T4SS type[c]	Genes	Transferability	References
pFKY4[e]	Unidentified soil bacterium	Naphthalene	80	P9	NA	NA	*nah*	+	Ono et al. (2007)
pNAH20[d]	*Pseudomonas fluorescens* PC20	Naphthalene	83	P9	MOB_F	MPF_T	*nag*	+	Heinaru et al. (2009)
pNL22	*Pseudomonas fluorescens* 41a	Naphthalene	100	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pNL25	*Pseudomonas putida* 21a	Naphthalene	75	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pNL29	*Pseudomonas* sp. 58	Naphthalene	NA	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pNL31	*Pseudomonas aeruginosa* 56	Naphthalene	NA	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pNL4	*Pseudomonas putida* 10a	Naphthalene	75	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pNL60	*Pseudomonas fluorescens* 18d	Naphthalene	120	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pOV17	*Pseudomonas aureofaciens*OV17	Naphthalene	85	P9	NA	NA	NA	NA	Sevastsyanovich et al. (2008)
pSAH	*Alcaligenes* sp. O-1	2-Aminobenzene-sulfonate	180	P9	NA	NA	*abs*, *scm*	+	Jahnke et al. (1990); Ruff et al. (2010)
pSN11	*Pseudomonas putida* SN11	Naphthalene	83	P9	NA	NA	NA		Sevastsyanovich et al. (2008)
pSVS15	*Pseudomonas putida* SVS15	Toluene, Xylene	90	P9	NA	NA	NA		Sevastsyanovich et al. (2008)
pWW0[d]	*Pseudomonas putida* mt-2	Xylene, Toluene	117	P9	MOB_F	MPF_T	*xyl*	+	Williams and Murray (1974); Greated et al. (2002)

SAL1	*Pseudomonas putida* R1	Salicylate	85	P9	NA	NA	*sal*	+	Chakrabarty (1972)
NIC	*Pseudomonas convexa* Pc1	Nicotine, Nicotinate	NA	NA	NA	NA	NA	NA	Thacker et al. (1978)
pAC27	*Pseudomonas putida* AC867	3-Chlorobenzoate	110	NA	NA	NA	*clcABD*, *tfdC*	+	Chatterjee and Chakrabarty (1982, 1984); Ghosal et al. (1985); Frantz and Chacrabarty (1987); Ghosal and You (1988)
pAM10.6	*Pseudomonas fluorescens* biotype F Cb36	Phenol	11	NA	NA	NA	*pheBA*	NA	Peters et al. (1997)
pCg1	*Pseudomonas putida* Cg1	Naphthalene	86	NA	NA	NA	*nah*	+	Park et al. (2003)
pCINNP	*Pseudomonas putida* CINNP	Cinnamate	75	NA	NA	NA	NA	+	Andreoni and Bestetti (1986)
pCIT1	*Pseudomonas* sp. CIT1	Aniline	100	NA	NA	NA	NA	NA	Anson and Mackinnon (1984)
pCS1	*Pseudomonas diminuta*	Parathion	66	NA	NA	NA	*opd*	NA	Serdar et al. (1982); Mulbry et al. (1986)
pCT14[d]	*Pseudomonas* sp. CT14	Toluene	55	NA	$\mathrm{MOB_F}$	–	*cbz*, *bphK*	NA	Bramucci et al. (2006)
pDBT2	*Pseudomonas alcaligenes* DBT2	Dibenzothiophene	80	NA	NA	NA	NA	NA	Foght and Westlake (1990); Top et al. (2000)
pEMT1[e]	Unidentified soil bacterium	2,4-D, 3-Chlorobenzoate	84	NA	NA	NA	*tfdARCGEFB*	+	Top et al. (1995)
pEMT8[e]	Unidentified soil bacterium	–[f]	75	NA	NA	NA	*tfdA*	+	Top et al. (1996)

(continued)

Table 8.1 (continued)

Plasmid	Host	Substrate[b]	Size (kb)	Inc group	MOB class[c]	T4SS type[c]	Genes	Transferability	References
pEST1026	*Pseudomonas putida* EST1020	Phenol	109	NA	NA	NA	*pheBA*	+	Kivisaar et al. (1990, 1991)
pHMT112	*Pseudomonas putida* ML2	Benzene	NA	NA	NA	NA	*bedC1C2BA*, *bedD*	NA	Tan and Mason (1990); Fong et al. (1996)
pKA4	*Pseudomonas pikettii 712*	2,4-D	41	NA	NA	NA	*tfdA*	+	Ka and Tiedje (1994)
pKJ1	*Pseudomonas* sp. TA8	Toluene	225	NA	NA	NA	NA	+	Yano and Nishi (1980)
pKW1	*Pseudomonas putida* GJ31	Chlorocatechol	180	NA	NA	NA	*cbz*	NA	Kunze et al. (2009)
pMH1	*Pseudomonas*sp. HF-1	Nicotine	21	NA	NA	NA	*hsp*	–	Wang et al. (2009)
pNB1	*Pseudomonas putida* HS12	Nitrobenzene	59	NA	NA	NA	*nbzA*, *nbzCDE*	NA	Park and Kim (2000)
pNB2	*Pseudomonas putida* HS12	Nitrobenzene	44	NA	NA	NA	*nbzB*	NA	Park and Kim (2000)
pP51	*Pseudomonas* sp. P51	Chlorinated Benzene	110	NA	NA	NA	*tcbCDEF*, *tcbAB*	+	van der Meer et al. (1991b)
pPGH1	*Pseudomonas putida* H	Pheonol	220	NA	NA	NA	*phlABCDEFGH*	NA	Herrmann et al. (1988)
pPOB	*Pseudomonas pseudoalcaligenes* POB310	Carboxyldiphenyl ethers	–	NA	NA	NA	*pabAB*	NA	Dehmel et al. (1995)
pRA500	*Pseudomonas putida* NCIB 9869	3,5-Xylenol	500	NA	NA	NA	*pchACXFHG*	+	Hopper and Kemp (1980); Top et al. (2000)
pRE4	*Pseudomonas putida* RE204	Isopropyl benzene	105	NA	NA	NA	*ipbABCEGFHD*	+	Eaton and Timmis (1986)

pTDN1	*Pseudomonas putida* UCC22	Aniline	NA	NA	NA	NA	*tdnQTA1A2BR*	NA	Saint et al. (1990)
pTKO	*Pseudomonas putida* PPK1	Toluene	150	NA	NA	NA	NA	NA	Keshavarz et al. (1985)
pUU204	*Pseudomonas* sp. E4	2-Chloropropionic acid	294	NA	NA	NA	Dehalogenase	–	Hardman et al. (1986)
pWW100	*Pseudomonas* sp. CB406	Biphenyl, Benzoate	200	NA	NA	NA	*bph*	–	Lloyd-Jones et al. (1994)
pZWL0	*Pseudomonas* sp. WBC-3	Methyl parathion, *p*-Nitrophenol	~70	NA	NA	NA	*mph*	+	Liu et al. (2005)

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[a] Several original plasmid hosts of IncP-1 and P-9 groups are not necessarily of the genus *Pseudomonas*

[b] 2,4-D represents 2,4-Dichlorophenoxyacetic acid

[c] Classification of MOB and MPF classes is based on the report of Smillie et al. (2010). NA means not available

[d] Whole nucleotide sequences are available

[e] This plasmid was captured by performing exogenous plasmid isolation from soil bacteria, and its original host was therefore unidentified

[f] This plasmid was able to complement the deficiency of 2,4-D metabolism of *tfdA*-disrupted-host

Table 8.2 Catabolic plasmids in sphingomonads

Plasmid	Host	Substrate[a]	Size (kb)	Rep type[b]	MOB class[c]	T4SS type[c]	Genes	Transferability	References
pCAR3[d]	*Novosphingobium* sp. KA1	Carbazole	240	pNL1	MOB_F	MPF_F	*car*	–	Habe et al. (2002); Shintani et al. (2007)
pCHQ1[d]	*Sphingobium japonicum* UT26	γ-HCH	191	pCHQ1	NA	NA	*linRED*	+	Nagata et al. (2006, 2010, 2011)
pISP1	*Sphingomonas* sp. MM-1	γ-HCH	200	NA	NA	NA	*lin*	NA	Tabata et al. (2011)
pISP3[d]	*Sphingomonas* sp. MM-1	γ-HCH	40	NA	NA	NA	*lin*	NA	Tabata et al. (2011)
pISP4	*Sphingomonas* sp. MM-1	γ-HCH	30	NA	NA	NA	*lin*	NA	Tabata et al. (2011)
pLA1[d]	*Novosphingobium pentaromativorans* US6-1	PAHs	188	pCHQ1	NA	NA	*bph*	NA	Luo et al. (2012)
pLA2[d,e]	*Novosphingobium pentaromativorans* US6-1	PAHs		pLB1	NA	NA	–	NA	Luo et al. (2012)
pLB1[d]	Unidentified soil bacterium	γ-HCH	66	pLB1	MOB_P	MPF_T	*linB*	+	Miyazaki et al. (2006)
pNL1[d]	*Novosphingobium aromaticivorans* DSM 12444	Biphenyl, Naphthalene	184	pNL1	MOB_F	MPF_F	*bph*, *xyl*	+	Stillwell et al. (1995); Romine et al. (1999)
pNL2[d,e]	*Novosphingobium aromaticivorans* DSM 12444	Biphenyl, Naphthalene	487	NA	–	–	–	NA	Fredrickson et al. (1991)

pSLGP^{d,e}	*Sphingobium* sp. SYK-6	Lignin		pCHQ1	NA	NA	–	NA	Masai et al. (2010)
pSPHCH01^{d,e}	*Sphingobium chlorophenolicum* L-1	Pentachlorophenol		pCHQ1	NA	NA	–	NA	Copley et al. (2012)
pSWIT01^{d,e}	*Sphingomonas wittichii* RW1	Dibenzo-*p*-dioxin	310	Unclassified	NA	NA	–	NA	Miller et al. (2010)
pSWIT02^{d}	*Sphingomonas wittichii* RW1	Dibenzo-*p*-dioxin	223	pNL1	$\mathrm{MOB_P}$	$\mathrm{MPF_T}$	*dxn*	NA	Miller et al. (2010)
pBN6	*Sphingomonas xenophaga* BN6	Naphthalenesulfonate	180	pNL1	NA	NA	*nsa*	+	Basta et al. (2004); Keck et al. (2006)
pCF01-05	*Sphingomonas* sp. CF06	Carbofuran	NA	NA	NA	NA	NA	+	Feng et al. (1997a, b)
pKS14	*Sphingomonas* sp. KS14	Phenanthrene, naphthalene	>500	NA	NA	NA	NA	NA	Cho and Kim (2001)
pZL	*Sphingomonas* sp. ZL5	PAHs	~60	NA	NA	NA	NA	+	Liu et al. (2004)
Megaplasmid	*Sphingopyxis* sp. 113P3	Polyvinyl alcohol	NA	NA	NA	NA	*pvaA*	NA	Hu et al. (2008)
Large plasmid	*Sphingopyxis terrae*	Polyethilene glycol	NA	NA	NA	NA	*pegB*	NA	Tani et al. (2007)
Plasmid	*Sphingomonas paucimobilis* TNE12	Fluoranthene	240	NA	NA	NA	NA	NA	Shuttleworth et al. (2000)
Plasmid a	*Sphingobium francense* SP+	γ-HCH	<32	NA	NA	NA	*linB*	NA	Cérmémonie et al. (2006)

(continued)

Table 8.2 (continued)

Plasmid	Host	Substrate[a]	Size (kb)	Rep type[b]	MOB class[c]	T4SS type[c]	Genes	Transferability	References
Plasmid b	*Sphingobium francense* SP+	γ-HCH	<32	NA	NA	NA	*linE*	NA	Cérmémonie et al. (2006)
Plasmid e	*Sphingobium francense* SP+	γ-HCH	~214	NA	NA	NA	*linA*, *linX*	NA	Cérmémonie et al. (2006)
Plasmid	*Sphingobium indicum* B40	γ-HCH	~214	NA	NA	NA	*linA*	NA	Cérmémonie et al. (2006)
Plasmid	*Sphingomonas* sp. HH69	Dibenzofuran	240	pNL1	NA	NA	*dxnA*	NA	Basta et al. (2004)

[a] γ-HCH indicates γ-hexachlorocyclohexane and PAHs indicate polycyclic aromatic hydrocarbons

[b] Rep type is classified on the basis of the amino acid sequence identity (>70%) of putative Rep genes of each sequenced plasmid. As for pBN6 and the plasmid of *Sphingomonas* sp. HH69, the classification is based on the Southern blot analysis of Basta et al. (2005)

[c] Classifications of MOB classes and MPF types are based on the report of Smillie et al. (2010). NA means not available

[d] Whole nucleotide sequences are available

[e] No catabolic genes have been reported in the plasmid so far

Table 8.3 Catabolic plasmids in other gram-negative bacteria

Plasmid	Host	Substrate	Size (kb)	MOB class[a]	T4SS type[a]	Genes	Transferability	References
pWW174	*Acinetobacter calcoaceticus* RJE174	Benzene	200	NA	NA	*cat*	+	Winstanley et al. (1987)
pYA1	*Acinetobacter* sp. YAA	Aniline	NA	NA	NA	*atdA*	NA	Fujii et al. (1997)
pCPE3	*Alcaligenes* sp. CPE3	Chlorobenzoates	16	NA	NA	*cbaABC*	+	Di Gioia et al. (1998)
pKA2	*Alcaligens paradoxus* 2811P	2,4-D[b]	43	NA	NA	*tfdA*	+	Ka and Tiedje (1994)
pCMS1	*Brevundimonas diminuta* MG	Organophospate	66	NA	NA	*opd*	+	Mulbry et al. (1987); Pandeeti et al. (2011)
pTOM	*Burkholderia cepacia* G4	Toluene	108	NA	NA	*tom*	+	Shields et al. (1995)
pNF1	*Burkholderia* sp. NF100	Methylhydroquinone	105	NA	NA	*mhq*	+	Hayatsu et al. (2000); Tago et al. (2005)
pOPH1	*Comamonas acidovorans* UCC61	Phtalate	70	NA	NA	*pht*	NA	Dutton et al. (1995)
pBS1010	*Comamonas testosteroni* BS1310	*p*-Toluenesulfonate	130	NA	NA	NA	NA	Top et al. (2000)

(continued)

Table 8.3 (continued)

Plasmid	Host	Substrate	Size (kb)	MOB class[a]	T4SS type[a]	Genes	Transferability	References
pMC1	*Delftia acidovorans* MC1	Dichlorprop[c]	NA	NA	NA	*rdpA* *sdpA*	NA	Schleinitz et al. (2004)
pBRX1	*Klebsiella ozaenae*	Bromoxynil	82	NA	NA	*bxn*	NA	Stalker and McBride (1987)
pPNAP01[d]	*Polaromonas naphthalenivorans* CJ2	Naphthalene	353	MOB_H, MOB_P	MPF_T	*bph*, *pht*[e]	NA	Jeon et al. (2003, 2006); Yagi et al. (2009)
pPNAP04[d]	*Polaromonas naphthalenivorans* CJ2	Naphthalene	144	–	–	*pht*[e]	NA	Jeon et al. (2003, 2006); Yagi et al. (2009)
pAC200	*Rhizobium* sp. AC100	Carbaryl[f]	25	BA	NA	*cehA*	NA	Hashimoto et al. (2002)

[a] Classifications of MOB classes and MPF types are based on the report of Smillie et al. (2010). NA means not available

[b] 2,4-D represents 2,4-Dichlorophenoxyacetic acid

[c] Dichlorprop represents 2(2,4-dichlorophenoxy)propionate

[d] Whole nucleotide sequences are available

[e] Putative biphenyl- and phthalate-degradative genes were located on pPNAP01 and pPNAP04, although naphthalene degradative genes were not detected

[f] Carbaryl represents 1-naphtyl-N-methylcarbamate

Table 8.4 Catabolic plasmids in gram-positive bacteria

Plasmid	Host	Substrate[a]	Size (kb)	Linear/circular	MOB class[b]	T4SS type[b]	Genes	Transferablity	References
pRE1	*Arthrobacter keyseri* 12B	Phthalate	130	NA	NA	NA	*pht*, *pcm*	NA	Eaton (2001)
pAO1[c]	*Arthrobacter nicotinovorans*	Nicotine	165	Circular	NA	NA	*ndh*	+	Baitsch et al. (2001); Igloi and Brandsh (2003)
Plasmid	*Arthrobacter nicotinovorans* HIM	Atrazine	96	NA	NA	NA	*atzABC*	NA	Aislabie et al. (2005)
pAL1[c]	*Arthrobacter nitroguajacolicus* Rü61a	2-Methylquinoline	113	linear	NA	NA	*qox*, *moq*,*hod*, *amq*	+	Overhage et al. (2005); Parschat et al. (2007)
Plasmid	*Arthrobacter* sp. DNS10	Atragine	NA	NA	NA	NA	NA	NA	Zhang et al. (2011b)
pRC1	*Arthrobacter* sp. RC100	Carbaryl, 1-naphthol	130	NA	NA	NA	NA	+	Hayatsu et al. (1999)
pRC2	*Arthrobacter* sp. RC100	Carbaryl, 1-naphthol	120	NA	NA	NA	NA	+	Hayatsu et al. (1999)
Plasmid	*Bacillus licheniformis*	Dimethoate	54	NA	NA	NA	NA	+	Mandel et al. (2005)
pPDL2	*Flavobacterium* sp. ATCC27551	Organophosphate	39	NA	NA	NA	*opd*	NA	Mulbry et al. (1987); Siddavattam et al. (2003)
pOAD2[c]	*Flavobacterium* sp. KI723T1	Nylon	46	Circular	NA	NA	*nylABC*	NA	Negoro et al. (1980); Negoro and Okada (1982); Kato et al. (1995)

(continued)

Table 8.4 (continued)

Plasmid	Host	Substrate[a]	Size (kb)	Linear/circular	MOB class[b]	T4SS type[b]	Genes	Transferablity	References
pLW1071[c]	*Geobacillus thermodentrificans* NG80-2	Long-chain alkane	58	Circular	MOB_Q	–	*ladA*	NA	Feng et al. (2007)
p174	*Gordonia polyiso prenivorans* VH2	Rubber	174	Circular	NA	NA	*lcp2*	NA	Hiessl et al. (2012)
pGKT2[c]	*Gordonia* sp. KTR9	Hexahydro-1,3,5-trinitro-1,3,5-trazine	182	Circular	NA	NA	*xplABglnA-xplB*, *xplA*, *xplR*	NA	Indest et al. (2010)
pKB1[c]	*Gordonia westfalica* Kb1	Poly (*cis*-1,4-isoprene)	101	Circular	MOB_F	–	*cad*	+	Bröker et al. (2004, 2008)
Small plasmid	*Gordonia* sp. CC-NAPH129-6	Naphthalene	97	NA	NA	NA	*nar*	NA	Lin et al. (2012)
Plasmid	*Nocardioides* sp. DF412	Dibenzofuran	NA	NA	NA	NA	*dfdA*	NA	Miyauchi et al. (2008)
pNC30	*Rhodococcus carallinus* B-276	Propene	185	Linear	NA	NA	*amoABC*	NA	Saeki et al. (1999)
pBD2[c]	*Rhodococcus erythropolis* BD2	Isopropylbenzene	210	Linear	NA	NA	*ipb*	+	Darbrock et al. (1994); Kesseler et al. (1996); Stecker et al. (2003)
pREL1[c]	*Rhodococcus erythropolis* PR4	Alkane	272	Linear	NA	NA	*alk*	NA	Sekine et al. (2006)
pREC1[c]	*Rhodococcus erythropolis* PR4	Alkane	104	Circular	MOB_F	–	β-oxydation enzymes	NA	Sekine et al. (2006)
pTSA421	*Rhodococcus erythropolis* TA421	Biphenyl/PCBs	560	Linear	NA	NA	*bph*	NA	Kosono et al. (1997)

pLP6	*Rhodococcus globerulus* P6	Biphenyl/PCBs	650	Linear	NA	NA	*bphC2*	NA	Kosono et al. (1997)
pRHL1[c]	*Rhodococcus jostii* RHA1	Biphenyl/PCBs, ethylbenzene, limonene, carveol	1100	Linear	NA	NA	*bph*, *etb*	NA	Masai et al. (1997); Shimizu et al. (2001)
pRHL2[c]	*Rhodococcus jostii* RHA1	Biphenyl/PCBs, ethylbenzene, limonene, carveol	450	Linear	NA	NA	*bph*, *etb*	+	Masai et al. (1997); Shimizu et al. (2001)
pRHL3[c]	*Rhodococcus jostii* RHA1	Biphenyl/PCBs, ethylbenzene, limonene, carveol	330	Linear	NA	NA	Limonene monooxygenase	NA	Warren et al. (2004)
p1CP	*Rhodococcus opacus* 1CP	Chloroaromatic compounds	740	Linear	NA	NA	*macA*, *clc*	NA	König et al. (2004)
pNUO1	*Rhodococcus opacus* M213	–	ca 750	Linear	NA	NA	*edoD*	NA	Uz et al. (2000)
Plasmid	*Rhodococcus rhodochrous* K37	PCBs	200	Linear	NA	NA	*bphC*	NA	Taguchi et al. (2004)
pRTL1	*Rhodococcus rhodochrous* NCIMB 13064	1-Chloroalkane	100	NA	NA	NA	*dhaA*, *adhA*, *aldA*	+	Kulakova et al. (1995, 1997)

(continued)

Table 8.4 (continued)

Plasmid	Host	Substrate[a]	Size (kb)	Linear/circular	MOB class[b]	T4SS type[b]	Genes	Transferabllity	References
Plasmid	*Rhodococcus* sp. I24	Naphthalene, toluene	50	NA	NA	NA	*nid*	+	Priefert et al. (2004)
Plasmid	*Rhodococcus* sp. I24	Naphthalene, toluene	340	NA	NA	NA	Toluene inducible dioxygenase	–	Priefert et al. (2004)
pDBF1	*Terrabacter* sp. DBF63	Dibenzofuran, fluorene	160	Linear	NA	NA	*dbf*-*fln*, *pht*, *pca*	NA	Nojiri et al. (2002); Habe et al. (2005)
pDBF2	*Terrabacter* sp. DBF63	Dibenzofuran, fluorene	190	Linear	NA	NA	*dbf*-*fln*, *pht*, *pca*	NA	Nojiri et al. (2002); Habe et al. (2005)
pYK3	*Terrabacter* sp. YK3	Dibenzofuran	NA	NA	NA	NA	*dfdA*	NA	Iida et al. (2002)

[a] Carbaryl represents 1-naphthyl-*N*-methylcarbamate. PCBs represents polychlorinated biphenyls

[b] Classifications of MOB classes and MPF types were based on the report of Smillie et al. (2010). NA means not available

[c] Whole nucleotide sequences are available

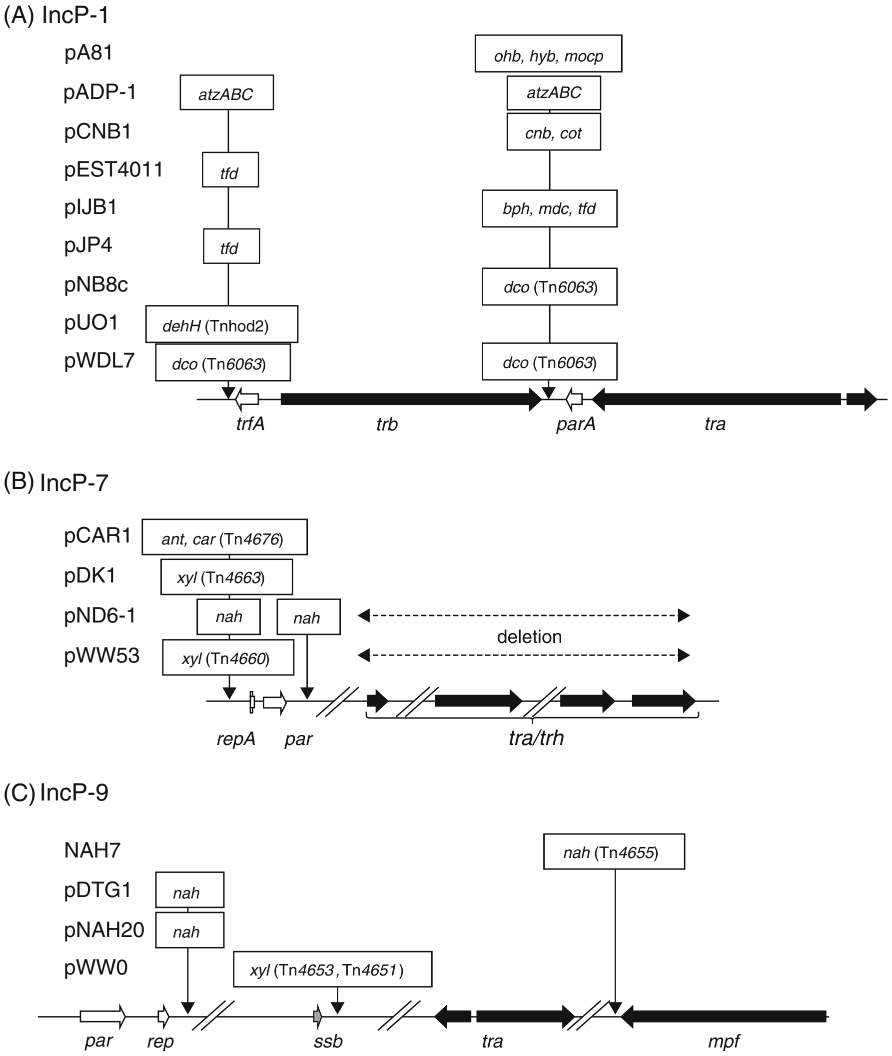

Fig. 8.1 Proposed IncP-1 (**a**), IncP-7 (**b**), and IncP-9 (**c**) backbones in conjunction with the insertion sites (*vertical arrows*) of catabolic genes on each plasmid (see Table 8.1). *Horizontal white arrows* indicate genes for replication and stability of the plasmid, and those in *black* indicate genes for conjugative transfer. The *ssb* gene of the IncP-9 backbone is shown in *gray*. The *tra*/*trh* genes of the IncP-7 backbone were deleted in pND6-1 and pWW53

On the other hand, many other catabolic plasmids have been isolated from *Pseudomonas*. However, the nucleotide sequences of replication or transfer regions for these plasmids are not available, and therefore, it is difficult to classify these plasmids. One exception is pCT14, which carries several genes for a *meta* cleavage pathway for aromatic rings, including *cbzTEXG*, *bphK*, and *tdnG* (Bramucci et al. 2006). Although the gene encoding its replication protein and the *oriV* region were proposed, there are no genes of similar sequence in the GenBank/EMBL/DDBJ database; this plasmid is predicted to be of the $\mathrm{MOB_F}$ class (Table 8.1).

2.2 Catabolic Plasmids of Sphingomonads

Over the past decade, many catabolic plasmids from xenobiotic-degrading sphingomonads (genera *Sphingomonas*, *Sphingobium*, *Novosphingobium*, and *Sphingopyxis*) belonging to the class *α-proteobacteria*, have been identified (Table 8.2). pNL1 was isolated from *Novosphingobium aromaticivorans* DSM 12444 (its previous name was *N. aromaticivorans* F199), and it is the first catabolic plasmid in sphingomonads whose 184-kb nucleotide sequence has been reported (Romine et al. 1999). Some xenobiotic-degrading sphingomonads carry multiple plasmids in one cell (Basta et al. 2004; Cérémonie et al. 2006; Tabata et al. 2011).The strain DSM 12444 also carries another plasmid of 487 kb, pNL2 (Fredrickson et al. 1991). Basta et al. (2005) compared plasmids from 16 sphingomonad strains that degrade various polycyclic aromatic hydrocarbons (PAHs). Based on Southern blot analyses, a plasmid of the naphthalenesulfonate-degrader *Sphingomonas xenophaga* BN6 and a plasmid of the dibenzofuran-degrader *Sphingomonas* sp. HH69 were shown to possess a pNL1-type Rep (replication initiation protein) gene (Basta et al. 2005). Nucleotide sequence comparisons revealed that similar Rep genes were also found in pCAR3, which also carries *car* genes, in the carbazole-degrader *Novosphingobium* sp. KA1 (its previous name was *Sphingomonas* sp. KA1, Shintani et al. 2007), and in pSWIT02, which also carries *dxn* genes, in the dibenzo-*p*-dioxin degrader *Sphingomonas wittichii* RW1 (Miller et al. 2010). The Rep type is classified based on the amino acid sequence identity (>70%) of putative Rep gene products of each sequenced plasmid.

Notably, many plasmids were identified in γ-hexachlorocyclohexane (γ-HCH)-degrading sphingomonads (Table 8.2, Nagata et al. 2007). *Sphingobium japonicum* UT26 is an archetypal γ-HCH-degrading bacterium, and its whole genome sequence has been determined (Nagata et al. 2010, 2011). This strain has three plasmids, and one of them is the 191-kb pCHQ1, which carries *linRDEB* (Nagata et al. 2007, 2010, 2011). No Inc groups have been suggested for plasmids from sphingomonads; however, several types of Rep genes are known to be conserved among these bacteria. Indeed, there are other plasmids in sphingomonads that contain genes which show high identities with the Rep gene of pCHQ1 (Table 8.2): pLA1, which was identified in a PAHs-degrader, *Novosphingobium pentaromativorans* US6-1, and carries *bph* and *xyl* genes involved in biphenyl and toluene/xylene degradation (Luo et al. 2012); pSLGP in a lignin-degrader, *Sphingobium* sp. SK-6 (Masai et al. 2012); and pSPHCH01, in a pentachlorophenol-degrader, *Sphingobium chlorophenolicum*

L-1 (Copley et al. 2012). The last two plasmids, however, do not carry catabolic genes. pLB1 also carries the *linB* gene, which was identified by performing an exogenous plasmid isolation technique from γ-HCH-contaminated soil using a *linB*-disrupted UT26 mutant. The original host of pLB1 was unidentifiable, but the plasmid can transfer to *Sphingobium japonicum* UT26 (Miyazaki et al. 2006). The Rep type of pLB1 is different from that of pCHQ1 because it shows compatibility to pCHQ1 (Miyazaki et al. 2006). Similarly, in addition to pLA1 (pCHQ1-type), *N. pentaromativorans* US6-1 harbors another plasmid, pLA2, which carries the pLB1-type Rep gene but has no catabolic genes. The conservation of the Rep genes suggests that many plasmids in sphingomonads may be self-transmissible, although this property has been experimentally proved to exist in only a few (Table 8.2).

Plasmids belonging to the same *Pseudomonas* incompatibility groups always have the same types of genes for conjugative transfer (Table 8.1). In contrast, plasmids in sphingomonads have different types of genes for conjugative transfer, whereas they have the same Rep genes, suggesting that they have "mosaic" genetic structures. While the Rep gene of pSWIT02 is pNL1-like, the genes for plasmid transfer show higher similarity to those of pCHQ1 than to those of pNL1. On the other hand, putative plasmid transfer genes of pLA1 are more similar to those of pNL1 than to those of pCHQ1, while its Rep gene is more similar to that of pCHQ1 (Luo et al. 2012). In addition, several catabolic genes, such as *bph* on pNL1, *car* on pCAR1, or *lin* on pCHQ1 are not organized in a single operon but dispersed on the plasmid or host chromosome in sphingomonads (Romine et al. 1999; Shintani et al. 2007; Nagata et al. 2011). The varied distribution of similar genes and dispersed organization of genes indicate that catabolic plasmids in sphingomonads might have been transferred among the genus, and might have undergone DNA rearrangements with other plasmids and host chromosomes, resulting in the "mosaic" structure.

2.3 Catabolic Plasmids of Other Gram-Negative Bacteria

Catabolic plasmids have also been observed in other gram-negative bacteria belonging to classes *α*-, *β*-, and *γ-proteobacteria*, as listed in Table 8.3, although they have not been investigated in detail. The whole genome sequence of the naphthalene-degrading *Polaromonas naphthalenivorans* CJ2 has been determined (Jeon et al. 2003, 2006; Yagi et al. 2009). This strain possesses eight plasmids, and at least two of them, pPNAP01 and pPNAP04, carry putative aromatic hydrocarbon-degradative genes (Yagi et al. 2009). The partial sequence of pCMS1, the organophosphate degradative plasmid of *Brevundimonas diminuta* MG, revealed that its putative transfer genes showed 67–74% identity with those of the IncP-1 plasmid pEST4011 (Pandeeti et al. 2011). This fact implied an evolutionary relationship between pCMS1 and IncP-1 plasmids. Analysis of the nucleotide sequences and identification of open reading frames on these plasmids will be important for elucidating the steps in the evolution of these plasmids in gram-negative bacteria.

2.4 Catabolic Plasmids of Gram-Positive Bacteria

Several plasmids have been identified in xenobiotic-degrading gram-positive bacteria belonging to classes *Actinobacteria*, *Bacilli*, and *Flavobacteriia* (Table 8.4). Some of these bacteria carry circular plasmids and others harbor linear plasmids (Table 8.4). The linear plasmids belong to a class of genetic elements called invertrons, which carry terminal inverted repeats (TIRs) that are covalently bound to terminal proteins at both 5′ termini (Sakaguchi 1990). Linear plasmids have been proposed to have evolved from bacteriophages (Hinnebusch and Tilly 1993). The details of the mechanisms of plasmid transfer between gram-positive bacteria are still unclear (Grohmann et al. 2003).

Rhodococcus is one of the most important genera among gram-positive degraders of alkanes, PCBs, and naphthalene, and many plasmids have been identified in the *Rhodococcus* species (Table 8.4). pBD2 is a conjugative linear plasmid that carries *ipb* genes for the catabolism of isopropylbenzene, and it was detected in *R. erythropolis* BD2 (Dabrock et al. 1994; Stecker et al. 2003). pREL1 and pREC1 were identified in *R. erythropolis* PR4, an alkane-degrader (Sekine et al. 2006). Several DNA regions in pREL1 and pBD2 are conserved, including genes that encode for terminal protein, lipoproteins, and heavy metal resistance. However, the degradative genes for alkane (pREL1) and for isopropylbenzene (pBD2) are not conserved (Sekine et al. 2006).

R. jostii RHA1 can degrade polychlorinated biphenyls (PCBs) (Seto et al. 1995), and its complete genome sequence has been determined (McLeod et al. 2006). This strain harbors three linear plasmids, pRHL1, pRHL2, and pRHL3 (Shimizu et al. 2001; Masai et al. 1997), and most of the genes involved in the biphenyl degradative pathway are located on the two larger plasmids, pRHL1 and pRHL2 (Shimizu et al. 2001). Notably, many catabolic isozyme genes are distributed throughout the RHA1 genome (Kitagawa et al. 2001; Sakai et al. 2002; McLeod et al. 2006). The four replicons of RHA1, including the three plasmids and its linear chromosome, were suggested to be similar types of linear elements, because their TIRs are highly similar (McLeod et al. 2006).

Arthrobacter utilizes a wide and varied range of xenobiotic compounds and several catabolic plasmids have been identified in this genus (Table 8.4). pAL1 is a linear catabolic plasmid that was detected in the 2-methylquinoline-degrading *Arthrobacter nitorguajacolicus* Rü61a strain (Parschat et al. 2007; Overhage et al. 2005). The replication region of pAL1 was analyzed in detail, and it revealed that this plasmid carries a novel Rep gene (Kolkenbrock et al. 2010; Wagenknecht and Meinhardt 2011). Parschat et al. (2007) showed that several regions of pAL1 are conserved in pAL1 and the pBD2, pREL1, and pRHL2 plasmids mentioned above, and also in the dibenzofuran-degradative plasmid pDBF1 from *Terrabacter* sp. DBF63 (Nojiri et al. 2002; Habe et al. 2005). One of the regions includes putative genes for a secretion system possibly involved in conjugation (Parschat et al. 2007). Similarly, 2,3-dihydroxybiphenyl dioxygenase BphC genes are conserved on pLP6 and pTSA421 found in *R. globerulus* P6 and *R. erythropolis* TA421 (Kosono et al. 1997).

Other types of catabolic plasmids have also been reported (Table 8.4). pLW1071 is a circular plasmid from *Geobacillus thermodentrificans* NG80-2 that carries degradative genes for long-chain alkanes (Feng et al. 2007). This plasmid is unique in comparison to other sequenced plasmids, except for a plasmid from *Geobacillus* sp., G11MC16 (accession no. NZ_ABVH01000017). The putative Rep gene of the plasmid of G11MC16 was similar to that of NG80-2. pGKT2 is a 182-kb circular plasmid carrying *xplAB* genes found in the hexahydro-1,3,5-trinitro-1,3,5-triazine degrader *Gordonia* sp. KTR9 (Indest et al. 2010). *Gordonia* spp. are a metabolically diverse group, with regards to their ability to degrade xenobiotic compounds, and recently, two other catabolic plasmids have been reported in this genus (Table 8.4). Catabolic genes in gram-positive bacteria may also be spread by self-transmissible plasmids (listed in Table 8.4), similar to that observed in the case of gram-negative plasmids, and have an important role in their HGT, although their host range remains unclear.

3 Catabolic Transposons

In some cases, catabolic genes are flanked by two copies of the same or highly-identical insertion sequences (ISs). These elements are known as composite transposons. Tn*5280* (van der Meer et al. 1991a), Tn*HadI* (Kawasaki et al. 1985); Sota et al. 2002), and *DEH* (Weightman et al. 2002) are composite transposons whose transposition ability has been experimentally validated (Table 8.5). As for Tn-*DhaI*, it encodes *pcrABCT* which is involved in reductive dechlorination of tetrachloroethene in *Desulfitobacterium hafniense* TCE1, and detection of the circular form of the transposon strongly indicated that it could transpose (Maillard et al. 2005). As genome sequences of an increasing number of xenobiotic-degrading bacteria are determined, many composite transposon-like genetic structures are being discovered (Table 8.5). Homologous recombination events among several copies of the identical ISs located on regions surrounding catabolic genes possibly increase the plasticity of the genome. There are two kinds of ISs, IS*6100* and IS*1071*, which were frequently associated with various catabolic genes. IS*6100* was originally isolated as part of the composite transposon Tn*6100* from *Mycobacterium fortuitum* (Martin et al. 1990), and was found in a wide range of host bacteria, such as *Sphingomonas* (Dogra et al. 2004), *Arthrobacter* (Kato et al. 1994), *Pseudomonas* (Hall et al. 1994), *Xanthomonas* (Sundin and Bender 1995), *Salmonella* (Boyd et al. 2000), and *Corynebacterium* (Tauch et al. 2002). The IS elements were also found in many kinds of xenobiotic-degrading bacteria, and some of them form composite transposon-like structures (Table 8.5). IS*6100* was found in many γ-HCH-degrading sphingomonads in the region flanking the *lin* genes involved in γ-HCH-degradation, suggesting that this IS may have played a key role in the recruitment of the *lin* genes in these bacteria (Nagata et al. 2011).

IS*1071* was originally identified in a chlorobenzoate-catabolic transposon, Tn*5271*, from *Comamonas testosteroni* BR60 (Nakatsu et al. 1991). IS*1071* belongs

Table 8.5 Catabolic transposons

Elements (plasmid)	Substrates^{a}	Host	Size (kb)	Transpos-ability^{b}	IS	Gene	References
Class I composite transposons							
Tn*5542*^{c} (pHMT112)	Benzene	*Pseudomonas putida* ML2	12	NA	IS*1489*	*bed*	Fong et al. (2000)
Tn*5280* (pP51)	Chlorobenzene	*Pseudomonas* sp. P51	9	+	IS*1066*, IS*1067*	*tcbAaAbAcAdB*	van der Meer et al. (1991a)
Tn*5707* (pENH91)	3-Chlorobenzoate	*Alcaligenes eutrophus* NH9	15	NA	IS*1600*	*cbnRABCD*	Ogawa and Miyashita (1999)
Tn*Ppu-alk1*	Pentane	*Pseudomonas putida* P1	22	NA	IS*Ppu4*	*alkST*, *alkBFGHJKLN*	van Beilen et al. (2001)
Tn*5271* (pBRC60)	Chlorobenzoates	*Comamonas testosteroni* BR60	17	NA	IS*1071*	*cbaABC*	Nakatsu et al. (1991)
Tn*5271*-like	Chlorobenzoates	*Alcaligenes* sp. CPE3	16	NA	IS*1071*	*cbaABC*	Di Gioia et al. (1998)
Tn*Had1* (pUO1)	Haloacetate	*Delftia acidovorans* B	9	+	IS*1071*	*dehH1*	Sota et al. (2002)
DEH^{c}	α-Halocarboxylic acids	*Pseudomonas putida* PP3	10	+	IS*Ppu12*	*dehI*, *dehR*	Weightman et al. (2002)
–^{c} (pWW0)	Xylene, Toluene	*Pseudomonas putida* mt-2	40	NA	IS*1246*	*xyl*	Tsuda and Iino (1987); Greated et al. (2002)
- (pTDN1)	Aniline	*Pseudomonas putida* UCC22	26	NA	IS*1071*	*tdnQA1A2B*	Saint et al. (1990); Fukumori and Saint (1997, 2001)
- (pTSA)	*p*-Toluenesulphonate	*Comamonas testosteroni* T2	21	NA	IS*1071*	*tsaMBCD*	Junker and Cook (1997); Tralau et al. (2001)
–^{c} (pADP-1)	Atrazine	*Pseudomonas* sp. ADP	13	NA	IS*1071*	*atzA*	Martinez et al. (2001)

–^{c} (pADP-1)	Atrazine	*Pseudomonas* sp. ADP	15	NA	IS*1071*	*atzB*	Martinez et al. (2001)
- (pPOB)	4-Carboxydiphenyl ether	*Pseudomonas pseudoalcaligenes* POB310	NA	NA	IS*1071*	*pobAB*	Dehmel et al. (1995)
Tn-*Dha1*^{c}	Tetrachloroehene	*Desulfitobacterium hafniense* TCE1	10	+^{d}	IS*Dha1*	*pcrABCT*	Maillard et al. (2005)
Tn*6063*^{c} (pWDL2)	3-Chloroaniline	*Comamonas testosteroni* WDL2	22	NA	IS*1071*	*dcaQTA1A2BR*	Król et al. (2012)
Tn*6063*^{c} (pNB8c)	3-Chloroaniline	*Delftia acidovorans* B8c	22	NA	IS*1071*	*dcaQTA1A2BR*	Król et al. (2012)
Tn*CNB1*	4-Chloronitrobenzene	*Comamonas* sp. CNB-1	45	NA	IS*1071*	*cnb*	Ma et al. (2007)
–^{c}	Aniline	*Delftia tsuruhatensis* AD9	~25	NA	IS*1071*	*tad*	Liang et al. (2005)
–^{c} (pJP4)	2,4-D	*Ralstonia eutropha* JMP134	~44	NA	IS*1071*	*tfd-I*, *tfd-II*	Trefault et al. (2004)
–^{c} (pJP4)	2,4-D	*Ralstonia eutropha* JMP134	~10	NA	IS*JP4*	*tfd-II*	Trefault et al. (2004)
–^{c} (pEST4011)	2,4-D	*Achromobacter xylosoxidans* subsp. *denitrificans* EST4002	48	NA	IS*1071*:: IS*1471*	*tfd*	Vedler et al. (2004)
Tn*AxI* (pA81)	Chlorobenzoate	*Achromobacter xylosocidans* A8	39	NA	IS*Ax1a*, IS*Ax1b*	*mocpRABCD*, *hybRABCD*	Jencova et al. (2008)
–^{c} (pSAH)	2-Aminobenzenesulfonate	*Alcaligenes* sp. O-1	12	NA	IS*1240*-like	*abs*	Ruff et al. (2010)
–^{c}	Carbazole	*Sphingobium yanoikuyae* XLDN2-5	8	NA	IS*6100*	*carRAaBaBbCAc*	Gai et al. (2010)

(continued)

Table 8.5 (continued)

Elements (plasmid)	Substrates[a]	Host	Size (kb)	Transpos-ability[b]	IS	Gene	References
–[c]	Carbazole	*Sphingobium yanoikuyae* XLDN2-5	4	NA	IS*6100*	*antRACAdAbAa*	Gai et al. (2010)
–[c]	Carbazole	*Sphingobium yanoikuyae* XLDN2-5	7	NA	IS*6100*	*fdr*	Gai et al. (2010)
–[c]	2-Chloronitrobenzene	*Pseudomonas stutzeri* ZWLR2-1	9	NA	IS*6100*	*cnbCEFAbAaD*	Liu et al. (2011)
–[c]	2-Chloronitrobenzene	*Pseudomonas stutzeri* ZWLR2-1	5	NA	IS*6100*	*cnbAcAd*	Liu et al. (2011)
–[c]	2-Chloronitrobenzene	*Pseudomonas stutzeri* ZWLR2-1	12	NA	IS*6100*	*cnbCEFAbAaD*, *cnbAcAd*	Liu et al. (2011)
Tn*mph*[c] (pZWL0)	Methyl parathion	*Pseudomonas* sp. WBC-3	4	+	IS*6100*	*mph*	Wei et al. (2009)
Tn*opdA*	Organophosphate	*Agrobacterium radiobacter* P230	6	+	IS*6100*	*opdA*	Horne et al. (2003)
–[c] (pLB1)	γ-HCH	Unidentified soil bacterium	4	NA	IS*6100*	*linB*	Miyazaki et al. (2006)
–[c] (pOAD2)	Nylon oligomers	*Flavobacterium* sp. K172	15	NA	IS*6100*	*nylABC*	Kato et al. (1994, 1995)
–[c] (pCAR1)	Carbazole	*Pseudomonas resinovorans* CA10	6	NA	IS*Pre1* IS*Pre2*	*antABC*	Nojiri et al. (2001); Maeda et al. (2003); Takahashi et al. (2009)
–[c] (pCAR1)	Carbazole	*Pseudomonas resinovorans* CA10	16	NA	IS*Pre1*	*carABCD*	Nojiri et al. (2001); Maeda et al. (2003); Takahashi et al. (2009)
–	Carbazole	*Pseudomonas stutzeri* OM1	55	NA	IS*Pst3*	*carABCDEF*, *antABC*	Shintani et al. (2003)

–[c] (pCAR3)	Carbazole	*Novosphingobium* sp. KA1	82	NA	ISSsp1	*car*, *and*, *cat*	Shintani et al. (2007)
–	Monobromoacetate	*X. autotrophicus* GJ10	NA	+	IS*1247*	*dhlB*	van der Ploneg et al. (1995)
Class II transposon							
Tn*4651*[c] (pWW0)	Xylene, tolene	*Pseudomonas putida* mt-2	56	+	–	*xyl*	Tsuda and Iino (1987); Tsuda et al. (1989)
Tn*4653*[c] (pWW0)	Xylene, toluene	*Pseudomonas putida* mt-2	70	+	–	*xyl*	Tsuda and Iino (1988); Tsuda et al. (1989)
Tn*4656*[c] (pWW53)	Xylene, toluene	*Pseudomonas putida* MT53	37	+	–	*xyl*	Tsuda and Genka (2001)
Tn*4657*[c] (pWW53)	Xylene, toluene	*Pseudomonas putida* MT53	86	+	–	*xyl*	Yano et al. (2007)
Tn*4660*[c] (pWW53)	Xylene, toluene	*Pseudomonas putida* MT53	62	–	–	*xyl*	Yano et al. (2007)
Tn*4663*[c] (pDK1)	Xylene, toluene	*Pseudomonas putida* HS1	41	+	–	*xyl*	Yano et al. (2010)
Tn*4655*[c] (NAH7)	Naphthalene	*Pseudomonas putida* G7	37	–[e]	–	*xyl*	Tsuda and Iino (1990); Sota et al. (2006)
Tn*Had2*[c] (pUO1)	Haloacetate	*Delftia acidovorans* B	16	+	–	*dehH1*, *dehH2*	Sota et al. (2002)
Tn*4676*[c] (pCAR1)	Carbazole	*Pseudomonas resinovorans* CA10	73	+	–	*carABCDEF*,	Maeda et al. (2003); Shintani et al. (2005, 2011)
–[c] (pKW1)	Chlorobenzene	*Pseudomonas putida* GJ31	15	NA	–	*cbz*	Kunze et al. (2009)

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[a] 2,4-D represents 2,4-Dichlorophenoxyacetic acid

[b] NA means not available

[c] Whole nucleotide sequences are available

[d] Strong indications for the transposition activity of IS*Dha1* were observed by PCR amplification and sequencing of the intervening sequence located between both IRs of IS*Dha1* (Maillard et al. 2005)

[e] Tn*4655* did not carry the *tnpA* gene but was able to form a cointegrate when the *tnpA* gene from Tn*4653* was supplied in *trans* (Tsuda and Iino 1990; Sota et al. 2006)

to the class II transposons, which generally carry the genes for their transposition (*tnpA*, *tnpR*, and *res*) and one or more phenotypic traits between their terminal inverted repeats (Grindley 2002). This type of transposon generates a cointegrate of donor and target molecules, and the cointegrate is then resolved at the resolution (*res*) sites by TnpR (resolvase). This resolution function, however, is lacking in IS*1071*. The copy number of class II transposons doubles after their transposition by means of a mechanism known as "copy and paste" transposition (Grindley 2002). Many IS*1071* sequences have been identified in close proximity to various xenobiotic-degradative genes on self-transmissible plasmids from environmental bacteria (Table 8.5). These data indicate that IS*1071* might have been involved in the recruitment of catabolic genes to these plasmids and in the dissemination of these genes among various host strains.

It should be noted that some class II transposons (Grindley 2002) that carry catabolic genes are found in various xenobiotic-degrading bacteria (Table 8.5). In addition to the extensively characterized Tn*4651*/Tn*4653* in the toluene/xylene-degradative plasmid pWW0 (IncP-9) (Tsuda and Iino 1987, 1988; Tsuda et al. 1989), these types of transposons are found in two other toluene/xylene-degradative plasmids, namely pWW53 (IncP-7) and pDK1 (IncP-7), the carbazole degradative plasmid pCAR1 (IncP-7), and the naphthalene degradative plasmid NAH7 (IncP-9). Notably, the transposition function of most of these transposons has been experimentally verified (Table 8.5, Yano et al. 2007, 2010; Shintani et al. 2005, 2011). Although Tn*4655* in NAH7 lacks the *tnpA* gene (Sota et al. 2006), it is able to form a cointegrate when the *tnpA* gene of Tn*4653* is supplied *in trans* (Tsuda and Iino 1990; Sota et al. 2006). These class II transposons might have been efficiently spread among bacterial replicons via their "copy and paste" transposition, and they can carry longer DNA regions than class I composite transposons can.

4 Catabolic ICEs

ICEs are self-transmissible MGEs that are integrated in the chromosome. These elements carry genes for conjugative transfer and also excision systems to excise from the chromosome (Burrus and Waldor 2004; Wozniak and Waldor 2010). They are replicated as a part of the chromosome, they excise from the chromosome, circularize and then transfer to new hosts, sometimes leading to the integration into these new host chromosomes (Burrus and Waldor 2004; Wozniak and Waldor 2010). ICEs are difficult to identify experimentally, because they are usually physically linked to the host chromosome (Wozniak and Waldor 2010). ICE$_{clc}$ (Ravatn et al. 1998a), *bph-sal* element (Nishi et al. 2000), and ICE$_{\mathrm{KKS}}$*4677* (Ohtsubo et al. 2003, 2006, 2012) are the ICEs that have been verified experimentally (Table 8.6). Among these, the most in-depth analyses, such as on the mechanisms for excision, transfer, and impact on the host cell, have been performed for ICE$_{clc}$ (Ravatn et al. 1998a, b; Gaillard et al. 2006, 2008, 2010; Sentchilo et al. 2009; Miyazaki and van der Meer 2011a, b).

Table 8.6 Catabolic ICEs

ICE	Host	ICE family[a]	Substrate	Size (kb)	Transferability[b]	Gene	References
ICE$_{\mathrm{KKS102}}$*4677*[c]	*Acirovorax* sp. KKS102	ICE$_{\mathrm{Tn}\mathit{4371}}$	Biphenyl	62	+	*bph*	Ohtsubo et al. (2003, 2006, 2012)
ICE-GI1[c]	*Bordetella petrii* DSM 12804	ICE$_{\mathit{clc}}$	–	255	NA	Putative monooxygenase	Lechner et al. (2009)
ICE-GI2[c]	*Bordetella petrii* DSMZ 12804	ICE$_{\mathit{clc}}$	–	143	NA	*ben*, *cat*	Lechner et al. (2009)
ICE-GI3[c]	*Bordetella petrii* DSM 12804	ICE$_{\mathit{clc}}$	–	102	+	*cat*	Lechner et al. (2009)
ICE*Bxe*LB400-1[c]	*Burkholderia xenovorans* LB400	ICE$_{\mathit{clc}}$	Biphenyl	123	NA	*clc*	Cain et al. (2006); Gaillard et al. (2006)
phn-island[c]	*Delftia* sp. Cs1-4	Unclassified	Phenanthrene	232	NA	*phn*, *oph*	Hickey et al. (2012)
bph-sal element	*P. putida* KF715	Unclassified	Biphenyl/salicylate	90	+	*bph*, *nah*	Nishi et al. (2000)
ICE$_{\mathrm{Tn}\mathit{4371}}$*6065*[c]	*Palaromonas naphthalenivorans* CJ2 (pPNAP01)	ICE$_{\mathrm{Tn}\mathit{4371}}$	Naphthalene	70	NA	*bph*, *nah*	Ryan et al. (2009)
ICE$_{\mathit{clc}}$(B13)[c]	*Pseudomonas knackmussii* B13	ICE$_{\mathit{clc}}$	Chlorocatechol	105	+	*clc*	Ravatn et al. (1998a)
ICE$_{\mathit{clc}}$(JS705)	*Ralstonia eutropha* JS705	ICE$_{\mathit{clc}}$	Chlorocatechol	115	NA	*clc*, *mcb*	Müller et al. (2003)
ICE$_{\mathrm{Tn}\mathit{4371}}$[c]	*Ralstonia oxalatica* A5	ICE$_{\mathrm{Tn}\mathit{4371}}$	Biphenyl	55	NA	*bph*	Springael et al. (1993); Merlin et al. (1999); Toussaint et al. (2003)

[a] Classification based on ICEberg (http://db-mml.sjtu.edu.cn/ICEberg/) and Bi et al. (2012)

[b] NA means not available

[c] Whole nucleotide sequences are available

Recently, *in silico* analyses of complete bacterial genomes have identified putative ICEs in several β- and γ-*proteobacteria*. Indeed, such analyses of many complete bacterial genomes showed that ICEs are spread among various bacterial subdivisions, and more than 400 putative ICEs are listed in ICEberg (http://db-mml.sjtu.edu.cn/ICEberg/) (Bi et al. 2012). Ryan et al. (2009) reported that an ICE$_{\mathrm{Tn}\mathit{4731}}$-related ICE was found in several bacterial genome sequences, and one of them, ICE$_{\mathrm{Tn}\mathit{4371}}$*6065*, carrying the *bph* gene, was found in a naphthalene degrader, *Polaromonas naphthalenivorans* CJ2. Interestingly, *Bordetella petrii* DSM 12804 possesses at least seven large ICEs mostly encoding metabolic functions involved in the degradation of aromatic compounds and detoxification of heavy metals (Lechner et al. 2009). Four of them, ICE-GI1, ICE-GI2, ICE-GI3, and ICE-GI6, are closely related to ICE$_{\mathit{clc}}$, and the first three carry putative catabolic genes (Table 8.6). It should be noted that their circular intermediates have been detected, and that transmissibility of ICE-GI3 has been confirmed (Lechner et al. 2009). Hichey et al. found a new ICE in the genome of the PAHs-degrader, *Delftia* sp. Ds1-4, which carries all of the required phenanthrene catabolic genes (Hickey et al. 2012). Because ICEs are not necessarily replicated as circular forms after their integration into the host chromosome, host ranges of ICEs are not dictated by whether the ICEs can be replicated in the host cells. Therefore, their host ranges are likely to be wider than that of other MGEs.

5 Behaviors of Catabolic MGEs

Bioaugmentation by inoculation of highly efficient xenobiotic degraders into polluted sites has been studied as an attractive approach to remove pollutants. However, it is difficult to maintain the high levels of degradative ability of these inoculants, because they are not necessarily able to compete or survive in natural environments (Top et al. 2002). The catabolic MGEs, especially conjugative elements, can be used in alternative bioaugmentation by utilizing the transferability of MGEs into the indigenous bacteria in the polluted sites. In bioaugmentation via inoculation with degraders harboring MGEs, known as "gene bioaugmentation" or "plasmid-mediated bioaugmentation," the survival of the inoculated degraders is not needed (Bathe 2004; Bathe et al. 2005; Dejonghe et al. 2000; Pepper et al. 2002). There are still, however, large gaps between laboratory conditions and natural systems, and the basic features of MGEs in laboratory conditions do not necessarily reflect their actual behavior in natural systems. Many trials have been conducted to bridge the differences between these conditions by using artificial model environments, which model natural habitats such as soil, plants, and water. While the behaviors of the IncP-1, P-7, and P-9 group plasmids have been summarized recently (Shintani et al. 2010), those of other plasmids, which belong to unknown Inc groups, have been also reported. Detailed analyses have been performed to analyze the effect of conjugative transfer of two kinds of 2,4-D degradative plasmids in soil by using pEMT1 and IncP-1 plasmid pEMT3 in different donors (Top et al. 1995; Dejonghe et al. 2000; Goris et al. 2002). Top et al. (2002) concluded that these catabolic plasmids were most often transferred to, and their genes expressed in, strains that belong to the genera *Burkholderia*, *Ralstonia*, and *Pseudomonas*. Transfer of the plasmid pTOM carrying constitutively transcribed toluene-degradative genes (*tom*) was shown from *Burkholderia cepacia* to different endogenous endophytic bacteria in yellow lupine (Barac et al. 2004) or poplar cuttings (Taghavi et al. 2005). Springael et al. reported that ICE$_{clc}$ (B13) of *P. putida* BN210 was transferred to different bacteria belonging to the class of *β-proteobacteria* in biofilm reactors under non-sterile conditions (Springael et al. 2002).

These studies, together with those of IncP-1, P-7 and P-9 plasmids, strongly indicate that HGT by means of catabolic MGEs generally occurs in natural environments. Nevertheless, it is still difficult to predict how the catabolic plasmids or their hosts behave in these environments. A more in-depth understanding of HGT of MGEs will be required for practical application of plasmid-mediated bioaugmentation. Behaviors of the MGEs should be analyzed in microbial communities that include uncultivated and non-cultivable bacteria in natural environments. Several cultivation-independent methods to monitor the behavior of environmental bacteria have been reported. Metagenomic analysis combined with reverse-transcriptase real-time PCR analysis revealed the changes in the bacterial community and in abundant functional genes in contaminated environments (Yergeau et al. 2012). Ishii et al. (2011) identified the active N_2O reducers in rice paddy soil using stable isotope probing and functional single-cell isolation by micromanipulation. In another study, fluorescence-activated cell sorting (FACS) and micromanipulation enabled the identification and cultivation of independent plasmid transconjugants (Musovic et al. 2006, 2010). The combinations of these cultivation-independent and cultivation-dependent methods will shed light on HGT in microbial communities in various natural environments.

6 Conclusion and Perspectives

As an increasing number of whole genome sequences of bacteria capable of degrading various kinds of xenobiotic compounds are analyzed, a large number of catabolic MGEs have been discovered and studied recently. *In silico* analyses of the genome sequences of these bacteria enable us to detect new ISs and ICEs; however, experimental confirmation of their ability to mobilize is still required to further our understanding of how they are transmitted among bacteria or replicons. On the other hand, nucleotide sequence information on other Inc group plasmids from *Pseudomonas*, such as IncP-2 or other plasmids not affiliated to any Inc group (Table 8.1), is also required for further classification of the newly-identified plasmids.

Jones and Marchesi (2007) developed a method for transposon-aided capture of plasmids to discover novel plasmids in various bacterial habitats. This method allowed them to identify plasmids that did not rely on the plasmids' own replication and transfer systems. Indeed, many novel MGEs have been identified in various sites by the method mentioned above and by metagenomic analyses, such as in activated sludge (Zhang et al. 2011a), river or sea sediments (Elsaied et al. 2011; Kristiansson et al. 2011), wastewater treatment plants (Szczepanowski et al. 2008), human dental plaque (Warburton et al. 2011), and human gut (Jones et al. 2010). These reports suggest that a huge number of unidentified MGEs exist in the environment. Detection and analyses of new catabolic MGEs will help us to understand the mechanism by which MGEs spread and also determine which MGEs are capable of spreading in natural bacterial communities, including those that contain uncultivated and non-cultivable bacteria. These MGEs can possibly be used as new tools for genetic analysis of unidentified bacteria.

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