Effect of site-specific methylation on restriction endonucleases and DNA modification methyltransferases

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We present in **Table I** an updated list of the sensitivities of 298 restriction endonucleases and 20 DNA methyltransferases to site-specific modification at 4-methylcytosine (^{m4}C), 5-methylcytosine (^{m5}C), 5-hydroxymethylcytosine (^{hm5}C), and 6-methyladenine (^{m6}A) (McC14), four modifications that are common in the DNA of prokaryotes, eukaryotes, and their viruses (Mc2,Mc5,Mc8,Mc11,Ne3,Ne4). In addition, new information is included on restriction endonuclease cleavage at sites modified with 5-hydroxymethyluracil (^{hm5}U).

Knowledge of the sensitivity of restriction endonucleases to site-specific modification can be used to study cellular DNA methylation. Several restriction-modification enzymes share the same recognition sequence specificity, but have different sensitivities to site-specific methylation. **Table II** lists 32 known isoschizomer pairs and one isomethylator pair, along with the modified recognition sites at which they differ.

The data presented here and an additional three other tables are available in printed form or as a text file on a 3.5" Macintosh diskette. The extra tables include **Table III** which is a list of over 205 characterized DNA methyltransferases. A detailed list of cloned restriction-modification genes has been made by Wilson (Wi4). **Table IV** lists the sensitivities of over 20 Type II DNA methyltransferases to ^{m4}C, ^{m5}C, ^{hm5}C, and ^{m6}A modification. Most DNA methyltransferases are sensitive to non-canonical modifications within their recognition sequences (Bu9,Mc10, Ne3,Po4), and this sensitivity often differs from that of their restriction endonuclease partners. **Table V** gives a list of restriction systems in this review alphabetized by recognition sequence. The data can be supplied as a Microsoft Word, Macwrite or MS-DOS file. Please contact Michael McClelland at CIBR, phone 619 535 5486, FAX 619 535 5472.

Molecular basis for sensitivity restriction enzymes to methylation

^{m4}C, ^{m5}C, ^{hm5}C, and ^{m6}A are bulky alkyl substitutions in the major groove of DNA. Site-specific DNA methylation can interfere with many sequence-specific DNA binding proteins (e.g. St2,Wa8), including binding of restriction endonucleases and DNA methyltransferases. At the molecular level, the inability of restriction enzymes to cut modified DNA can be explained using *EcoRI* and *EcoRV* endonucleases as instructive models. DNA modification can interfere with substrate binding and/or conformational changes of the enzyme: substrate complex.

Based on the *EcoRI*: DNA co-crystal structure (Mc15,Ro8), methylation of either adenine (G^{m6}AATTC or GA^{m6}ATTC)

perturbs essential hydrogen bond contacts to Glu-144 and Arg-145. Therefore aminomethylation of either adenine inhibits DNA cleavage at the level of *EcoRI*: substrate binding (Br2). In contrast, cytosine ring methylation at GAATT^{m5}C would not be expected to interfere with critical DNA: protein contacts inferred from the X-ray crystal structure (Mc15). Therefore, the reduced rate of *EcoRI* cleavage at GAATT^{m5}C can be attributed to steric distortions of the enzyme:substrate complex during catalysis (He3).

Based upon the X-ray structure of *EcoRV* endonuclease (Wi5), hydrogen bonding of Asn-185 to the first adenine of GATATC is perturbed by 'canonical' methylation at the G^{m6}ATATC. The canonical site is the site of methylation by the corresponding methylase in the same restriction system, in this case M⁺.*EcoRV*. However, *EcoRV* cannot cleave canonically modified G^{m6}ATATC sites because non-productive enzyme: substrate complexes are formed (Ta4,Ne12). Therefore the mechanism by which canonical DNA methylation inhibits cleavage is very different in the cases of *EcoRI* and *EcoRV* endonucleases.

Although DNA modification often results in complete inhibition of restriction enzyme cleavage, a range of rate effects are observed when non-canonically modified DNA is used as a substrate, as listed in the footnotes to **Table I**. Rate effects at ^{m5}C-hemi-methylated restriction endonuclease target sites are listed in Ne10.

Rate of cleavage at methylated restriction sites

DNA methylation may cause long-range perturbations of DNA minor and major grooves, and a range of rate effects are observed when modified substrates are used in endonuclease cleavage reactions. Results can be summarized as follows.

(1) Canonical site-specific methylation *always* inhibits DNA cleavage by a restriction endonuclease. For example, M.*BamHI* methylase modifies GGAT^{m4}CC; and *BamHI* endonuclease cannot cut this methylated sequence.

(2) In about one half of the cases tested, methylation at non-canonical sites inhibits the rate of duplex DNA cleavage at least ten-fold (**Table I**). However, in other cases non-canonical methylation has no effect on restriction cleavage. For example, *BamHI* cuts DNA which has been modified at GGATC^{m4}C or GGATC^{m5}C, but cannot cut DNA methylated at GGAT^{m5}CC.

(3) There are a few examples in which non-canonical methylation slows the rate of cleavage or permits nicking of one strand of a hemi-methylated duplex. Examples of such rate effects are presented in footnotes to **Table I**.

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(4) Sometimes base modifications which lie *outside* a recognition sequence can influence the rate of DNA cleavage by a restriction enzyme. For example, *NarI* does not cut at overlapping M·*MvaI*-*NarI* GGCGCC^{m4}CCWGG sites (Ne1), *HaeIII* cannot cut certain GGCC^{mT} sites, where ^{mT} are modified thymine residues (Wi1), and *MspI*, *HpaII*, *SmaI*, and *HhaI* are unable to cut DNAs in which bases adjacent to their recognition sequences are modified with hydroxymethyluracil (Ho1). Such methylation-induced 'action at a distance' may be more common than has been previously appreciated. We have tested only a few enzymes for sensitivity to base modifications *outside* their canonical recognition sequences.

DNA modifications other than ^{m4}C, ^{m5}C, ^{hm5}C, ^{hm5}U, and ^{m6}A

The effects of several other site-specific DNA modifications on the rate of restriction endonuclease cleavage, such as 5-bromodeoxycytidine, 5-bromodeoxyuridine, 5-iododeoxycytidine, deoxyinosine, 2-aminopurine, 2,6-diaminopurine, 2-chloroadenosine, 7-deazaguanosine, and deoxynucleotide phosphorothioate deoxynucleotides, are listed elsewhere (Bo1, Be6, Mo4, Br2, Ta5, He4, Gr3, Se4, Vo2).

Effect of ^{m5}CG and ^{m5}CNG on restriction endonucleases

Enzymes that are *not* sensitive to site-specific methylation are particularly useful for achieving complete digestion of methylated DNA. For instance, endonucleases that are unaffected by ^{m5}CG and ^{m5}CNG are useful for the digestion of plant DNA, which is frequently methylated at these positions. Endonucleases that are unaffected by these two cytosine modifications include: *AccIII*, *AflIII*, *AhaIII*, *AseI*, *Asp700I*, *AsuII*, *BbuI*, *BclI*, *BspHI*, *BspNI*, *BstEII*, *BstNI*, *CviQI*, *DpnI*, *DraI*, *EcoRV*, *HinCII*, *HpaI*, *KpnI*, *MboII*, *MseI*, *NdeI*, *NdeII*, *PacI*, *RsaI*, *RspXI*, *SpeI*, *SphI*, *SspI*, *SwaI*, *TaqI*, *Tsp509I*, *TthHBI* and *XmnI*.

CpG sequences occur infrequently and are often methylated in mammalian genomes (Mc9). Almost all the enzymes that could generate large fragments of mammalian DNA are blocked by this ^{m5}CpG modification at overlapping sites, including *AatII*, *ApeI*, *AviII*, *BbeI*, *BmaDI*, *BssHII*, *BspMII*, *BstBI*, *ClaI*, *CspI*, *Csp45I*, *EagI*, *EclXI*, *Eco47III*, *FseI*, *FspI*, *Kpn2I*, *MluI*, *Mlu9273I*, *Mlu9273II*, *MroI*, *NaeI*, *NarI*, *NotI*, *NruI*, *PfuI*, *PmlI*, *PpuAI*, *PvuI*, *RsrII*, *SalI*, *SalDI*, *Sbo13I*, *SfiI*, *SmaI*, *SnaBI*, *SplI*, *Spol*, *SrfI*, *XhoI* and *XorII* (see Table I). Only five enzymes suitable for pulsed field mapping of eukaryotic chromosomes are known to cut ^{m5}CG-modified DNA: *AccIII*, *AsuII*, *Cfr9I*, *PmeI* and *XmaI*.

^{m4}C, ^{m5}C, and ^{hm5}C cytosine modifications

In some cases, a restriction enzyme may differ in sensitivity to ^{m4}C and ^{m5}C at a particular sequence. For example, *BstNI* and *MvaI* cut ^{m5}C, but not ^{m4}C modified CCWGG sequences. *RsaI* cuts GTA^{m5}C but not GTA^{m4}C. *KpnI* cuts GGTAC^{m5}C but not GGTAC^{m4}C. *BstYI* cuts RGAT^{m5}CY but not RGAT^{m4}CY. Similarly, *CviIII* cuts T^{m5}CGA but not T^{hm5}CGA.

Effect of site-specific methylation on DNA methyltransferases

Twenty-three Type II methyltransferases have been tested for sensitivity to *non-canonical* DNA modifications, of which nine were blocked (Mc10 and Table IV). As with restriction endonucleases, rate effects are sometimes seen with DNA methyltransferases at non-canonically modified sequences. For

example, *E.coli* *Dam* methyltransferase is unaffected by GAT^{m4}C, but methylates GAT^{m5}C relatively slowly. Such data is summarized in Table IV and footnotes to Table I.

Methylase/endonuclease combinations can produce novel DNA cleavage specificities

Several strategies involving combinations of modification methyltransferases and restriction endonucleases have been used to generate rare or novel DNA cleavage sites (Ne13). For example, (i) certain adenine methyltransferases may be used in conjunction with the methylation-dependent restriction endonuclease *DpnI* to create cleavages at eight- to twelve-base-pair sequences (Mc6, Mc12, We1, Ha1). (ii) Protection of a subset of restriction endonuclease cleavage sites by methylation at overlapping methyltransferase/endonuclease targets has also been described (Hu1, Kl1, Ne6, Qi2). This two-step 'cross-protection' strategy has produced over 70 new cleavage specificities, and many more are possible (Ja2, Ka2, Kl1, Ne6). (iii) Methylases have been used to compete with endonucleases for recognition sites in a method called 'methylase-limited partial digestion'. This method is particularly useful for performing partial digests in agarose plugs for pulsed field gel electrophoresis (Ha2). (iv) Blocking a subset of DNA methyltransferase sites by overlapping methylation (sequential double-methylation) can expose a subset of restriction endonuclease sites for cleavage (Mc9, Ne3, Po3). For instance, M·*HpaII*, M·*BamHI*, and *BamHI* have been used in a sequential three-step reaction to achieve selective DNA cleavage at the ten base pair sequence, CCGGATCCGG (Mc10). (v) Polypyrimidine oligonucleotides in DNA triplexes have been used to selectively mask restriction-modification sites. For example, polypyrimidine triplexes which overlap M·*TaqI* sites have been used to enable selective restriction cleavage (Ma7, Ko9, Fe3). (vi) Finally, methods based on the sequential use of purified lac repressor protein, DNA methyltransferases, and restriction endonucleases have been used to achieve highly selective DNA cleavages (Ko2).

Methylation-dependent restriction systems in bacteria

E.coli K-12 contains at least three different methylation-dependent restriction systems which selectively restrict methylated target sequences: *mrr* (^{m6}A), *mcrA* (^{m5}CG), *mcrB* (R^{m5}C) (Br5, Di1, He2, Ra1, Ra2). *In vivo* or *in vitro* modified DNA is inefficiently cloned into *E.coli*. For example, human DNA which is extensively methylated at ^{m5}CpG is restricted by *mcrA* (Wo3) and other systems (Bu2). Appropriate non-restricting strains of *E.coli* (Go2, Kr2, Ra1, Ra2) should be chosen for efficient transformation and cloning of methylated DNA. Other species also have such restriction systems (e.g. Ma2).

Engineered altered methylase specificities

Many methylase genes have now been sequenced. Extensive homologies between closely related enzymes (Wi3) or common motifs (Po5, Sm3) allow new specificities to be developed (e.g. Ba4, Tr4).

Data in electronic form

This paper is available as a text file on a 3.5" Macintosh diskette. The data can be supplied as a Microsoft Word, Macwrite or MS-DOS file. Please contact Michael McClelland at CIBR, phone (619) 535 5486, FAX (619) 535 5472.

Table I. Methylation sensitivity of restriction endonucleases ^a

Restriction enzyme	Recognition sequence	Sites cut	Sites not cut	References
<i>AarI</i>	AGGCCT	?	AGG ^{m5} CCT AGGC ^{m5} CT AGGC ^{m4} CT	Ne1 So3 Ne1
<i>AarII</i>	GACGTC	?	GACGT ^{m5} C GA ^{m5} CGTC	Ne1 Fo1
<i>AccI</i>	GTMKAC	?	GTMK ^{m6} AC # GTMKA ^{m5} C ^b	Lu2,Mc3
<i>AccII</i>	CGCG	?	^{m5} CGCG	Ga2
<i>AccIII</i>	TCCGGA	T ^{m5} CCGGA ^b TC ^{m5} CGGA ^b	TCCGG ^{m6} A	Ke3,La2,Sc2
<i>Acc65I</i>	GGTACC	?	GGTAC ^{m5} C	Ne5
<i>AciI</i>	CCGC	?	C ^{m5} CGC	Fo1
<i>AfiI</i>	GGWCC	GGWC ^{m5} C	?	Mc11,Wh2
	GGWC ^{m4} C ^b			
<i>AfiIII</i>	CTTAAG	?	^{m5} CTTAAG	Ne1
	CTTA ^{m6} AG			
<i>AfiIII</i>	ACRYGT	?	A ^{m5} CRYGT	Ne1
<i>AgeI</i>	ACCGGT	?	A ^{m5} CCGGT	Ne1
		AC ^{m5} CGGT		
<i>AhaII</i>	GRCGYC ^b	?	GR ^{m5} CGYC	Ka2,Hu1
	GRCGY ^{m5} C			
<i>AluI</i>	AGCT	?	^{m6} AGCT AG ^{m4} CT AG ^{m5} CT # AG ^{hm5} CT GG ^{m6} ATC	Gr5,Mc11,Ne2 Hu1,Wo1,Zh1 Bu9 Ne4
<i>AlwI</i>	GGATC	?		
	GGAT ^{m4} C			
<i>AlwNI</i>	CAGN ₂ CCT	?	CAGN ₂ C ^{m5} CT	Ne5
<i>Alw44I</i>	GTGCAC	GTGC ^{m6} AC	GTG ^{m5} CAC	Ne1
<i>AlwNI</i>	CAGN ₂ CTG	?	CAGN ₂ C ^{m5} CTGG	Bo5
<i>AmaI</i>	TCGCGA	TCGCG ^{m6} A	?	Mc13
<i>AosII</i>	GRCGYC	?	GR ^{m5} CGYC	Eh2,Gr5,Va3
<i>ApaI</i>	GGGCCC	?	GGG ^{m5} CCC # GGGCC ^{m5} C A ^{m5} CGCGT	La9,Gu9 Ne1,Qi2
<i>ApeI</i>	ACGCGT	?	GTGCA ^{m5} C	Fo1,Ho2,Ho3
<i>ApaLI</i>	GTGCAC	GTGC ^{m6} AC GTG ^{m5} CAC		Ne1
<i>ApyI</i>	CCWGG	C ^{m5} CWGG ^b	^{m5} CCWGG	K11,Mc11,Ra3
<i>AquI</i>	CYCGRG	?	^{m5} CYCGRG #	Ka7,Ka8
<i>AscI</i>	GGCGCGCC	?	GG ^{m5} CGCGCC GGCG ^{m5} CGCC GGCGCG ^{m5} CC GGCGCGC ^{m5} C	Si2 Ne1
<i>AseI</i>	ATTAAT	ATT ^{m6} AAT	?	Ch4
<i>AspMDI</i>	GATC	G ^{m6} ATC	?	Ne1
<i>Asp700I</i>	GAAN ₄ TTC	GA ^{m6} AN ₄ TTC GAAN ₄ T ^{m5} C	G ^{m6} AAN ₄ TTC	
<i>Asp718I</i>	GGTACC	GGT ^{m6} A ^{m5} CC ^b	GGTAC ^{m5} C GGTA ^{m5} C ^{m5} C ^b	Mu2,Ne4
<i>AsuI</i>	GGNCC	GGNC ^{m5} C	?	Ra4
<i>AsuII</i>	TTCGAA	TT ^{m5} CGAA	?	Ne1
<i>AuCI</i>	TGATCA	?	TG ^{m6} ATCA	Ro3,Sc12
<i>AvaI</i>	CYCGRG	C ^{m5} CCGGG	^{m5} CYCGRG CY ^{m5} CGRG CTCG ^{m6} AG ^b	Eh2,Ne1 Ka4,Ka7,Mc11 Ne2
<i>AvaII</i>	GGWCC	GGWC ^{m4} C ^b	GGW ^{m5} CC GGWC ^{m5} C GGW ^{hm5} C ^{hm5} C	Ba3,Ko3 Mc10,Mc11 Hu1
<i>AviII</i>	TGCGCA	?	TG ^{m5} CGCA	Ne1
<i>BaeI</i>	ACN ₄ GTAYC	?	ACN ₄ GTYA ^{m5} C	Fo1
<i>Ball</i>	TGGCCA	?	TGG ^{m5} CCA #	Gi1,Gu9
	TGGC ^{m5} CA ^b			
<i>BamHI</i>	GGATCC	GGATC ^{m5} C GG ^{m6} ATCC GG ^{m6} ATC ^{m5} C GGATC ^{m4} C	GGAT ^{m4} CC # GGAT ^{m5} CC GGAT ^{hm5} C ^{hm5} C GGA ^{hm5} UCC	Br8,Dr1,Ha3,Hu1 La7 Ho1
<i>BamFI</i>	GGATCC	GG ^{m6} ATCC	GGAT ^{m4} CC	An1,Sh1
<i>BamKI</i>	GGATCC	GG ^{m6} ATCC	GGAT ^{m4} CC	An1,Sh1
<i>BanI</i>	GGYRCC ^b	GG ^{m5} CGCC GGYRC ^{m4} C	?	Co3,Ka2

Table 1. continued:

<i>BanII</i>	GRGCYC	GRGCY ^{m5} C	GRG ^{m5} CYC	Fo1,Ne2,Ne6
<i>BanIII</i>	ATCGAT	?	ATCG ^{m6} AT #	Su1
<i>BbeI</i>	GGCGCC	GGCG ^{m5} CC	GG ^{m5} CGCC	Co3,Ne2,Sh2
		GGCGC ^{m5} C		
<i>BbiII</i>	GRGCYC	?	GR ^{m5} CGYC	Co3
<i>BbrPI</i>	CACGTG	?	^{m5} CA ^{m5} CGTG	Wo1
<i>BbsI</i>	GAAGAC	GAAGA ^{m5} C	?	Fo1
<i>BbuI</i>	GCATGC	GCATG ^{m5} C	G ^{m6} ATGC	Ne1
<i>BbvI</i>	GCWGC	?	G ^{m5} CWGC #	Do1,Ha3,Va5
<i>Bca77I</i>	WCCGGW	WC ^{m5} CGGW	W ^{m5} CCGGW	Sc10
<i>BclI</i>	TGATCA ^b	TGAT ^{m5} CA	TG ^{m6} ATCA	Bi4,Br8,Eh3,Ro3
			TGAT ^{hm5} CA	Hu1
<i>BcnI</i>	CCSGG	^{m5} CCSGG	C ^{m4} CSGG #	Ja3,Ja6,Kl1
<i>BepI</i>	CGCG	?	^{m5} CGCG	Ku3
<i>BfiI</i>	CTTAAG	?	^{m5} CTTAAG	Wo1
<i>BglII</i>	GCCN ₅ GGC	GC ^{m5} CN ₅ GGC ^b	G ^{m5} CCN ₅ GGC	Kl1,Ko3,Mc11,Ne2
			GCCN ₅ GG ^{m5} C ^b	
			G ^{m4} CN ₅ GGC ^b	
<i>BglIII</i>	AGATCT ^b	AG ^{m6} ATCT	AGAT ^{m5} CT	Bi4,Br8,Dr1,Dy1,Eh3
		GAT ^{hm5} UC ^{hm5} U	AGAT ^{hm5} CT	Hu1,Pi6,Ho1
<i>BinI</i>	GGATC	?	GG ^{m6} ATC	Bo2
<i>BmaDI</i>	CGATCG	CG ^{m6} ATCG	CGAT ^{m6} CG	Qi2
<i>Bme216I</i>	GGWCC	?	GGW ^{m5} C	Ma9
<i>BnaI</i>	GGATCC	GG ^{m6} ATCC	GGAT ^{m4} CC	Ne1
			GGAT ^{m5} CC #	
<i>BsaI</i>	GGTCTC	GAGA ^{m5} C ^{m5} C	GGTCT ^{m5} C	Fo1,Ne5
<i>BsaAI</i>	YACGTR	?	YA ^{m5} CGTR	Fo1
<i>BsaBI</i>	GATN ₄ ATC	?	GATN ₄ AT ^{m5} C	Fo1
			G ^{m6} ATN ₄ ^{m6} AC	
<i>BsaHI</i>	GRGCYC	?	GR ^{m5} CGYC	Fo1
<i>BsaJI</i>	CCNNGG	C ^{m5} CNNGG	?	Fo1
<i>BsaWI</i>	WCCGGW	WC ^{m5} CGGW	?	Fo1
<i>BsgI</i>	CTGCAC	?	CTGC ^{m5} C	Fo1
<i>BsiEI</i>	CGRYCG	?	^{m5} CGRY ^{m5} CG	Fo1
<i>BsiWI</i>	CGTACG	?	^{m5} CGTA ^{m5} CG	Fo1
<i>BsII</i>	CCN ₇ GG	?	C ^{m5} CN ₇ GG	Fo1
<i>BsmI</i>	GAATGC	GAATG ^{m5} C	G ^{m6} AATGC	Fo1,Ne1
<i>BsmAI</i>	GTCTC	G ^{m6} AGAC	GTCT ^{m5} C	Fo1,Ne1
<i>BspDI</i>	ATCGAT	?	AT ^{m5} CGAT	Fo1
			^{m6} ATCG ^{m6} AT	
<i>BspEI</i>	TCCGGA	TC ^{m5} CGGA ^b	TCCGG ^{m6} A	Fo1
<i>BspHI</i>	TCATGA	?	TC ^{m6} ATGA	Pa2,Se3
			TCATG ^{m6} A	Mc1
<i>BspMI</i>	ACCTGC	ACCTG ^{m5} C	?	Fo1
<i>BspMII</i>	TCCGGA	TCCGG ^{m6} A	T ^{m5} CCGGA	La2,Sc2
			TC ^{m5} CGGA	
<i>BspOI</i>	CCWGG	C ^{m5} CWGG	?	Sc10
<i>BspXI</i>	ATCGAT	?	ATCG ^{m6} AT	Zi1
<i>BspXII</i>	TGATCA	?	TG ^{m6} ATCA	Zi1
<i>Bsp106I</i>	ATCGAT	?	ATCG ^{m5} AT #	Ne5
<i>Bsp1286I</i>	GDGCHC	GDGCH ^{m5} C	GDG ^{m5} CHC	Fo1,Ne2,Ne6
<i>BsrBI</i>	GAGCGG	GAG ^{m5} CGG ^b	?	Fo1
<i>BsrFI</i>	RCCGGY	?	RC ^{m5} CGGY	Fo1
<i>BssHII</i>	GCGCGC ^b	?	G ^{m5} CGCGC	Ne4,Qi3
<i>BstI</i>	GGATCC	GG ^{m6} ATCC	GGAT ^{m4} CC	Ne4
		GGATC ^{m5} C	GGAT ^{m5} CC	
			GGATC ^{m4} C	
<i>BstBI</i>	TTCGAA	?	TTCG ^{m6} AA	Ne1
		Wo1		Ne4
<i>BstEII</i>	TT ^{m5} CGAA	GGTNA ^{m5} C ^{m5} C ^b	GGTNA ^{hm5} C ^{hm5} C	Hu1,Mc11
	GGTNACC	GGTNAC ^{m4} C	Ne1	
<i>BstEIII</i>	GATC ^b	?	G ^{m6} ATC	My1,Ro3
<i>BstGI</i>	TGATCA	?	TG ^{m6} ATCA	Ro3
<i>BstNI</i>	CCWGG ^b	^{m5} CCWGG ^b	^{hm5} C ^{hm5} CWGG	Br8,Gr5,Hu1,Mc11
		C ^{m5} CWGG	C ^{m4} CWGG	Ne1,Ro3
		^{m5} C ^{m5} CWGG ^b		
<i>BstUI</i>	CGCG	?	^{m5} CGCG	Ne5
<i>BstXI</i>	CCAN ₆ TGG	?	^{m5} CCAN ₆ TGG	Ne2
<i>BstYI</i>	RGATCY	RG ^{m6} ATCY	RGAT ^{m4} CY	Ne4
		RGAT ^{m5} CY		Ne1
<i>Bst1107I</i>	GTATAC	?	GTATA ^{m5} C	Fo1
<i>BsuBI</i>	CTGCAG	?	CTGC ^{m6} AG #	Gal,Je1,Sh1,St5

Table I. continued:

<i>BsuEI</i>	CGCG	?	m^5 CGCG #	Ga1,Je1,Sh1,St5
<i>BsuFI</i>	CCGG	?	m^5 CCGG #	Je1
<i>BsuMI</i>	CTCGAG	?	CT^{m^5} CGAG #	Je1
<i>BsuRI</i>	GGCC	?	$GG^{m^5}CC$ # b	Gu8,Ki2,Ki3
<i>Bsu15I</i>	ATCGAT	?	$ATCG^{m^6}AT$ #	Ra4
<i>Bsu36I</i>	CCTNAGG	?	m^5 CCTNAGG	Ne5
<i>CbiI</i>	TTCGAA	$TTCG^{m^6}AA$	?	Mu1
<i>CcrI</i>	CTCGAG	?	$CTCG^{m^6}AG$	Ne1
<i>CfoI</i>	GCGC	?	$G^{m^5}CGC$	Eh1
			$G^{hm^5}CG^{hm^5}C$	Hu1
<i>CfrI</i>	YGGCCR	?	$YGG^{m^5}CCR$ #	Kl1
<i>Cfr6I</i>	CAGCTG	?	$CAG^{m^4}CTG$ #	Bu9
			$CAG^{m^5}CTG$	
<i>Cfr9I</i>	CCCGGG ^b	$CC^{m^5}CCGGG$ $CC^{m^5}CGGG$	m^4 CCCGGG m^5 CCCGGG $C^{m^4}CCGGG$ # $CC^{m^4}CGGG$	Bu10
			$R^{m^5}CCGGY$ #	Bi5,Kl1
<i>Cfr10I</i>	RCCGGY	?	$RC^{m^5}CCGGY$	Ne1
<i>Cfr13I</i>	GGNCC	?	$GGN^{m^5}CC$ #	Bi5,Kl1
<i>ClaI</i>	ATCGAT	?	m^6 ATCGAT $AT^{m^5}CGAT$ b $ATCG^{m^6}AT$ #	Ca4,Mc11,Mc12,Ne4 Wo1
			$TG^{m^6}ATCA$	Mc3
<i>CpeI</i>	TGATCA	?	$CGGW^{m^5}CCG$	Fi1,Ro3
<i>CspI</i>	CGGWCCG	$CGGW^{m^5}CG$	m^5 CGGWCCG	Mc11
			$TTCG^{m^6}AA$	Ne4,Sc11
<i>Csp45I</i>	TTCGAA	?	$G^{m^6}ATC$ #	Ri2
<i>CtyI</i>	GATC	?	$G^{m^6}ATC$	Ne1,Xi1,Xi6
<i>CviAI</i>	GATC	$GAT^{m^5}C$	$C^{m^6}ATG$ #	Ne1
<i>CviAII</i>	CATG	m^5 CATG	$G^{m^6}ANTC$ #	Xi3
<i>CviBI</i>	GANTC	?	$RG^{m^5}CY$ #	Sh3,Xi2
<i>CviJI</i>	RGCY	?	m^5 CC #	Xi4
<i>CviPI</i>	CC	$C^{m^5}C$	$GT^{m^6}AC$ #	Xi5
<i>CviQI</i>	GTAC	$GTA^{m^5}C$	$TGC^{m^6}A$ #	Ne1
<i>CviRI</i>	TGCA	?	$TG^{m^5}CA$	
			$TCG^{m^6}A$ #	Ne1
<i>CviSIII</i>	TCGA	Tm^5 CGA	Thm^5 CGA	
			m^5 CTNAG #	Ho4,Ne2
<i>DdeI</i>	CTNAG	?	CTNm6AG	Hu1
		hm^5 CTNAG	GATC	Ne1
			Ne4	La3,Mc11,Vo1
<i>DpnI</i>	$G^{m^6}ATC$ b $G^{m^6}AT^{m^5}C$ b	$G^{m^6}ATC$ $GAT^{m^4}C$ $G^{m^6}AT^{m^4}C$	$GAT^{m^5}C$ $G^{m^6}ATC$ #	Ne5
<i>DpnII</i>	GATC	?	?	De1,La3,La4,La5,Ma6,Vo1
<i>DraI</i>	TTTAAA	$TTTA^{m^6}AA$	?	Ne1
<i>DraII</i>	RGGNCCY	?	$RGGNC^{m^5}CY$	Sc8
<i>DrdI</i>	GACN ₆ GTC	?	$GA^{m^5}CN_6GT^{m^5}C$	Fo1
<i>EaeI</i>	YGGCCR	?	$YGG^{m^5}CCR$ #	Ja2,Wh1
			$YGGC^{m^5}CR$	
<i>EagI</i>	CGGCCG	?	$CGG^{m^5}CCG$ m^5 CGGC ^{m5} CG	Mc11
			?	Fo1
<i>Eam1105I</i>	GACN ₅ GTC	$GA^{m^5}CN_5GT^{m^5}C$	$G^{m^6}AAGAG$	Fo1,Ne4
<i>EarI</i>	GAAGAG	$CTCTT^{m^5}C$	$GAAG^{m^6}AG$ m^5 CT ^{m5} CTT ^{m5} C	
			$GGTN^{m^6}ACC$ #	Ne1
<i>EcaI</i>	GGTNACC	?	m^5 CGGC ^{m5} CG	Br2??
<i>EclXI</i>	CGGCCG	?	$CGG^{m^5}CCG$	Qi3
			$GAGCT^{m^5}C$	Fo1
<i>Ecl136I</i>	GAGCTC	?	$G^{m^6}AGN_7G^{m^6}TCA$ # b	Bi2,Co6,Fu2
<i>EcoAI</i>	GAGN ₇ GTCA ^b	?	$TG^{m^6}AN_8^{m^6}TGCT$ # b	Bi2,La10,La11
<i>EcoBI</i>	TGAN ₈ TGCT ^b	?	$TCAN_7^{m^6}AA^{m^6}TC$ # b	Pi1
<i>EcoDXXI</i>	TCAN ₇ AATC ^b	?	$G^{m^6}AGN_7ATGC$	Co6,Fu2
<i>EcoEI</i>	GAGN ₇ ATGC ^b	?	$A^{m^6}ACN_6G^{m^6}TGC$ # b	Bi2,Bi3,Ka1
<i>EcoKI</i>	AACN ₆ GTGC ^b	?	$RGGNC^{m^5}CY$	Sc8
<i>EcoO109I</i>	RGGNCCY	?	$AG^{m^6}ACC$ #	Ba1,Ba2,Ha4,Re4
<i>EcoPI</i>	AGACC ^b	$AGA^{hm^5}C^{hm^5}C$	$CAGC^{m^6}AG$ #	Hu2,Me2
<i>EcoP15I</i>	CAGCAG ^b	?	$G^{m^6}AATTC$ b	Mc11,Ne2,Ru1
<i>EcoRI</i>	GAATTC	$GAATT^{hm^5}C$ $GAA^{hm^5}U^{hm^5}UC$	$GA^{m^6}ATTC$ # $GAATT^{m^5}C$ b	Br1,Br8,Du1,Ho1 Hu1,Ka3,Ta1

Table I. continued:

<i>EcoRII</i>	CCWGG C ^{m4} CWGG	m ⁵ CCWGG ^b Bu8,Na5,Ro3	m ⁴ CCWGG C ^{m5} CWGG # CC ^{m6} AGG hm ⁵ C ^{hm5} CWGG G ^{m6} ATATC # GAT ^{m6} ATC GA ^{m6} AN ₆ RTCG GAAN ₆ R ^m TCG m ⁶ A ATG ^{m5} CAT ATG ^{m6} AT GGT ^{m5} CTC # Gm6AGACC # GGWC ^{m5} C GGNC ^{m5} C AG ^{m5} CGCT CTGA ^{m6} AG CTTC ^{m6} AG GG ^{m5} CGCC GG ^{hm5} CG ^{hm5} C ^{hm5} C G ^{m5} CTNAGC m ⁵ CGTCTC GGT ^{m5} CTC # GAG ^{m6} ACC # G ^{m5} CNGC GCNG ^{m5} C m ⁵ CGCG CG ^{m5} CG ? GG ^{m6} ATG C ^{m6} ATCC Ne1 GG ^{m5} CCGG ^{m5} CC GGC ^{m5} CGGCC GG ^{m5} CCGGCC TG ^{m5} CGCA GGWC ^{m5} C RG ^{m5} CGCY RCCG ^{m5} CY RG ^{hm5} CG ^{hm5} CY GG ^{m5} CC # ^b GG ^{hm5} C ^{hm5} C C ^{m5} CGG # GA ^{m5} CGC GACG ^{m5} C GWG ^{m5} CWC GGW ^{m5} C ^{m5} C GGYR ^{m5} CC # GGWC ^{m5} C GR ^{m5} CGY ^{m5} C GT ^{m5} CGAC # GGWC ^{m5} C GR ^{m5} CGY ^{m5} C GGYRC ^{m5} C G ^{m5} CGC # GCG ^{m5} C G ^{hm5} CG ^{hm5} C G ^{m6} ANTC # GTYR ^{m6} AC # GTYR ^{hm5} C GTYR ^{m6} AC # GTYR ^{hm5} C m ⁶ AAGCTT # AAC ^{m5} CTT ^b AAG ^{hm5} CTT G ^{m6} ANTC GANT ^{hm5} C G ^{m5} CGC GTTA ^{m6} AC # GTTA ^{hm5} C G ^{hm5} U ^{hm5} UAAC m ⁴ CCGG m ⁵ CCGG ^b	Ku1,Yo1 Bo7,Mc11 Bu7 Hu1,Ka3 Mc11,Ne2,Wo1 Fl1,Ho1 Pr2,Pr3 Bi1 Pr1,Pr2 Ne1 Bu8 Ja5 Po6 Ne1,Ne4 Ja8,Po6 Co2,Ne1 Ne4 Fo1 Ja3 Gu9,Ko3 Ga1,Ga2,Ne2,Ne6,St6 Lu1,Ne2 Po3,Po4,Sc2 Ne7 Ne4 Le1 Eh2,Gr5,Ka2,Ko3,Mc11,Pi5 Ne1 Hu1 Ba3,Ka2,Ko3,Ma5 Hu1 Eh2,Wa1 Ne1 Mc11 Fo1,Ne2,Wh3 Ra4 Er1 Er1 Ra4 Ra4 Er1 Sw1 Wh3 Eh2,Ko3,Sm1 Mc11, Hu1 Gr5,Ro7 Hu1 Ro7 Br8,Gr5,Ne1,Ro7 Ho1,Ne2 Hu1,Ka3 Ch1,Co1,Ne2,Pe1 Hu1 Mc11,Ne6 Br8,Gr5,Hu1,Yo3 Hu1 Ho1 Be3,Bu10,Eh2,Ma5 Ko3,Ou1,Wa5
<i>EcoRV</i>	GATATC	GATAT ^{m5} C ^b GATAT ^{hm5} C		
<i>EcoR124I</i>	GAAN ₆ RTCG ^b	?		
<i>EcoR124/3I</i>	GAAN ₇ RTCG ^b	?		
<i>EcoT22 I</i>	ATGCAT	?		
<i>Eco31I</i>	GGTCTC	?		
<i>Eco47I</i>	GGWCC	?		
<i>Eco47II</i>	GGNCC	?		
<i>Eco47III</i>	AGCGCT	m ⁶ AGCGCT		
<i>Eco57I</i>	CTGAAG	?		
<i>EheI</i>	GGCGCC GGCG ^{m5} CC	?		
<i>EspI</i>	GCTNAGC	GCTNAG ^{m5} C		
<i>Esp3I</i>	CGTCTC	?		
<i>Fnu4HI</i>	GCNGC	?		
<i>FnuDII</i>	CGCG	?		
<i>FnuEI</i>	GATC	G ^{m6} ATC ^b		
<i>FokI</i>	CATCC	CAT ^{m5} CC CATC ^{m5} C ^b CATC ^{m4} C		
<i>FseI</i>	GGCCGGCC	?		
<i>FspI</i>	TGCGCA	?		
<i>FsuI</i>	GGWCC	?		
<i>HaeII</i>	RGCGCY ^b	?		
<i>HaeIII</i>	GGCC	GGC ^{m5} C		
<i>HapII</i>	CCGG	?		
<i>HgaI</i>	GACGC	?		
<i>HgiAI</i>	GWGCWC	GWGCW ^{m5} C		
<i>HgiBI</i>	GGWCC	?		
<i>HgiCI</i>	GGYRCC	?		
<i>HgiCII</i>	GGWCC	?		
<i>HgiDI</i>	GRCGYC	?		
<i>HgiDII</i>	GTCGAC	?		
<i>HgiEI</i>	GGWCC	?		
<i>HgiGI</i>	GRCGYC	?		
<i>HgiJII</i>	GGYRCC	?		
<i>HhaI</i>	GCGC	?		
<i>HhaII</i>	GANTC	?		
<i>HincII</i>	GTYRAC	GTYRA ^{m5} C		
<i>HindII</i>	GTYRAC	?		
<i>HindIII</i>	AAGCTT	A ^{m6} AGCTT # AAGC ^{hm5} U ^{hm5} U		
<i>HinfI</i>	GANTC	GANT ^{m5} C ^b		
<i>HinPI</i>	GCGC	?		
<i>HpaI</i>	GTTAAC	GTTA ^{m5} C		
<i>HpaII</i>	CCGG	?		

Table I. continued:

		C ^{m4} CGG ^b	C ^{m5} CGG [#] hm ⁵ Chm ⁵ CGG	
<i>Hph</i> I	TCACC	TCAC ^{m5} C	T ^{m5} CACC [#] TCAm ⁵ CC GGTG ^{m6} A	Hu1 Fo1,Mc11,Ne2
<i>Kas</i> I	GGCGCC	?	GG ^{m5} CGCC	Fo1
<i>Kpn</i> I	GGTACC ^b	GGTA ^{m5} CC GGTAC ^{m5} C GGTA ^{m5} C ^{m5} C ^b GGT ^{m6} ACC	GGT ^{m6} ACC [#] GGTAC ^{m4} C	Eh3,Ki4,Mc11 Ne1
<i>Kpn</i> 2I	TCCGGA	TCCGG ^{m6} A	T ^{m5} CCGGA TC ^{m5} CGGA	Mc1,Ne1 Ne1
<i>Ksp</i> I	CCGCGG	?	m ⁵ CCGCGG C ^{m5} CGCGG	Ne1 Qi2
<i>Mae</i> II	ACGT	?	A ^{m5} CGT ^b	Mo2
<i>Mam</i> I	GATN ₄ ATC	?	G ^{m6} ATN ₄ ^{m6} ATC	St4
<i>Mbo</i> I	GATC ^b	GAT ^{m4} C GAT ^{m5} C ^b GA ^{hm5} UC	G ^{m6} ATC [#] GAT ^{hm5} C	Br5,Ge1,Mc8 Hu1,Ro3 Ho1
<i>Mbo</i> II	GAAGA	T ^{m5} CTT ^{m5} C ^b G ^{m6} AAGA	GAAG ^{m6} A [#] GA ^{m6} AGA	Ba3,Mc11,Mc12,Ne2
<i>Mfl</i> I	RGATCY ^b	?	RG ^{m6} ATCY RGAT ^{m4} CY RGAT ^{m5} CY	On1
<i>Mlu</i> I	ACGCGT	m ⁶ ACGCGT	A ^{m5} CGCGT	Mc11,Sh1,St5,Qi3
<i>Mlu</i> 9273I	TCGCGA	?	T ^{m5} CGCGA	Ne1
<i>Mlu</i> 9273II	GCCGGC		G ^{m5} CCGGC	Ne1
<i>Mme</i> II	GATC	?	G ^{m6} ATC	Bo6
<i>Mnl</i> I	CCTC	?	m ⁵ CCTC m ⁵ C ^{m5} CT ^{m5} C	Eh3,Mc11
<i>Mph</i> I	CCWGG ^b	?	C ^{m5} CWGG	Ro3
<i>Mro</i> I	TCCGGA TC ^{m5} CGGA	TCCGG ^{m6} A Ne1	T ^{m5} CCGGA	Mc1,Ne1
<i>Msc</i> I	TGGCCA	?	TGGC ^{m5} CA	Fo1
<i>Msp</i> I	CCGG ^b	m ⁴ CCGG C ^{m4} CGG	m ⁵ CCGG [#] hm ⁵ Chm ⁵ CGG	Eh2,Je2,Va3,Wa1,Wa5 Bu10,Hu1
C ^{m5} CGG				
<i>Mst</i> II	CCTNAGG	m ⁵ CCTNAGG	?	Ne5
<i>Mth</i> II	GGCC	?	GG ^{m5} CC [#]	No4
<i>Mva</i> I	CCWGG	C ^{m5} CWGG ^b m ⁵ CCWGG	C ^{m4} CWGG [#] CC ^{m6} AGG ^b m ⁴ CCWGG ^b m ⁵ C ^{m5} CWGG ^b	Bu8,Ku2 Gr4,Ku1 Ne1
<i>Mun</i> I	CAATTG	?	CA ^{m5} ATTG [#]	St8
<i>Mvn</i> I	CGCG	?	m ⁵ CGCG	Ne1
<i>Nae</i> I	GCCGGC	?	G ^{m5} CCGGC GC ^{m5} CGGC GCCGG ^{m5} C	Eh3,Kl1,Mc11,Ne5
<i>Nan</i> II	G ^{m6} ATC ^b	G ^{m6} ATC G ^{m6} AT ^{m5} C ^b	GATC GAT ^{m5} C	Pa1,Ne5
<i>Nar</i> I	GGCGCC	GGCGC ^{m5} C	GG ^{m5} CGCC GGCGC ^{m4} C GGCGC ^{m5} C GG ^{hm5} C ^{hm5} Ch ^{hm5} C	Ko3,Mc11,Ne5 Ne1
<i>Nci</i> I	CCSGG	m ⁵ CCSGG	C ^{m4} CSGG C ^{m5} CSGG ^b	Br8,Ko3,Mc11
<i>Nco</i> I	CCATGG	CC ^{m6} ATGG	m ⁴ CCATGG ^b m ⁵ CCATGG	Kl1,Ne2,Ne4
<i>Ncr</i> I	AGATCT	AG ^{m6} ATCT ^b	?	Qi1
<i>Ncu</i> I	GAAGA	?	GAAG ^{m6} A	Mc13
<i>Nde</i> I	CATATG	m ⁵ CATATG ^b	m ⁶ A	Be4,Mc11
<i>Nde</i> II	GATC	GAT ^{m5} C ^b	G ^{m6} ATC	Mc9
<i>Ngo</i> I ^b	RGCGCY	?	RG ^{m5} CGCY	Ko3,Ko5
<i>Ngo</i> II ^b	GGCC	?	GG ^{m5} CC [#] GGC ^{m5} C ^b	Ko3,Ko5 Su3,Su4
<i>Ngo</i> BI ^b	TCACC	?	T ^{m5} CACC	Pi3,Pi4
<i>Ngo</i> MI	GCCGGC	?	GC ^{m5} CGGC	Fo1
<i>Nhe</i> I	GCTAGC	?	GCTAG ^{m5} C	Kl1,Mc11,Ne2
<i>Nla</i> III	CATG	?	C ^{m6} ATG [#] m ⁵ CATG	La1,Mo3 Zh2
<i>Nla</i> IV	GGNNCC	?	GGNN ^{m4} CC	Ne1
<i>Nmu</i> DI	G ^{m6} ATC ^b	G ^{m6} ATC	GATC	Pa1
<i>Nmu</i> EI	G ^{m6} ATC ^b	G ^{m6} ATC	GATC	Pa1
<i>Not</i> I	GCGGCCGC	GCGGCCG ^{m5} C	GCGG ^{m5} CCGC	Mc11

Table I. continued:

<i>Nru</i> I	TCGCGA	TCG ^{m5} CGA	GCGGC ^{m5} CGC	St5, Qi2
<i>Nsi</i> I	ATGCAT	TG ^{m5} CATA	T ^{m5} CGCGA	Ne1, Qi3
<i>Nsp</i> I	RCATGY	?	TCGCG ^{m6} A	Ne2
<i>Nsp</i> BII	CMGCKG	C ^{m5} CGCKG	ATGC ^{m6} AT	Be5, Wo1
<i>Pfi</i> MI	CCAN ₃ TGG	?	RC ^{m6} ATGY	Ne1
<i>Pfa</i> I	GATC	G ^{m6} ATC	R ^{m5} CATGY	Ne1
<i>Pfu</i> I	CGTACG	?	?	Ne1
<i>Pae</i> R7I	CTCGAG	?	C ^{m4} CAN ₃ TGG	Ne1
<i>Pme</i> I	GTTTAAAC	GTTTAA ^{m5} C	C ^{m5} CAN ₃ TGG	St7
<i>Pml</i> I	CACGTG	?	?	Ro3
<i>Ppu</i> AI	CGTACG	?	CGTA ^{m5} CG	Ne1
<i>Ppu</i> MI	RGGWCCY	?	CTCG ^{m6} AG [#]	Gi3
<i>Pst</i> I	CTGCAG	?	CT ^{m5} CGAG ^b	Gh1
			?	Fo1
			CA ^{m5} CGTG	Fo1
			CGTA ^{m5} CG	Ne1
			RGGWC ^{m5} CT	Fo1
			m ⁵ CTGCAG ^b	Do1, Gr5, Mc11, Ne2
			CTGC ^{m6} AG [#]	
			C ^{hm5} UGCAG	Ho1
<i>Pvu</i> I	CGATCG ^b	CG ^{m6} ATCG	CGAT ^{m4} CG	Br8, Bu7, Eh3
<i>Pvu</i> II	CAGCTG	?	CGAT ^{m5} CG	
<i>Rfi</i> FI	GTCGAC	?	CAG ^{m4} CTG [#]	Br8, Bu9, Do1
<i>Rfi</i> FII	AGTACT	?	CAG ^{m5} CTG ^b	Eh3, Ja3, Ro1
<i>Rrh</i> 4273I	GTCGAC	?	GTCG ^{m6} AC	Mo5
<i>Rsa</i> I	GTAC ^b	GTA ^{m5} C ^b	AGT ^{m6} ACT	Mo5
			GTCG ^{m6} AC	Ba6
			GT ^{m6} AC	Eh3, Fo1, Ne1, Ne4, Ne5
<i>Rsh</i> I	CGATCG	CG ^{m6} ATCG	GTA ^{m4} C	Wo2
<i>Rsp</i> XI	TCATGA	?	?	Ly1
			TC ^{m6} ATGA	Pa2
<i>Rsr</i> I	GAATTC	?	TCATG ^{m6} A	Ne4
	GA ^{m6} ATTC ^{# b}	Ba5	G ^{m6} AATTC	Mc11
<i>Rsr</i> II	CGGWCCG	?	m ⁵ CGGWCCG	Mc11, Qi3
			CGGW ^{m5} CCG	
			CGGW ^{m5} CG	
<i>Sac</i> I	GAGCTC	G ^{m6} AGCTC	GAG ^{m5} CTC	Mc11
		GAGCT ^{m5} C	Fo1	
<i>Sac</i> II	CCGCGG	?	m ⁵ CCGCGG	K11, Ne2
<i>Sal</i> I	GTCGAC	GTCGA ^{m5} C	GT ^{m5} CGAC ^b	Br8, Eh2, Lu2, Qi1
			GTCC ^{m6} AC [#]	Mc3, Ro4, Ro5, Va4
			G ^{hm5} UGCAC	Ho1
<i>Sal</i> DI	TCGCGA	TCGCG ^{m6} A	T ^{m5} CGCGA	Mc13, Ne1, Qi3
<i>Sau</i> 3AI	GATC ^b	G ^{m6} ATC	GAT ^{m5} C ^{# b}	Dr1, Eh2, Ja3, Mc3, Ro3, Se1
		GA ^{hm5} UC	GAT ^{m4} C	Ho1, Ne5
			GAT ^{hm5} C	Hu1
<i>Sau</i> 96I	GGNCC	?	GGN ^{m5} CC [#]	Ko3, Ne2, Pe1
			GGN ^{m5} C	
			GGN ^{hm5} C ^{hm5} C	Hu1
<i>Sau</i> 3239I	CTCGAG	?	CTCG ^{m6} AG [#]	Ra4
<i>Sbo</i> 13I	TCGCGA	TCGCG ^{m6} A	T ^{m5} CGCGA	Mc11, Ne1
<i>Scal</i> I	AGTACT	AGTA ^{m5} CT	?	Wo1
<i>Scr</i> FI	CCNGG	m ⁵ CCNGG	C ^{m5} CNGG	Da4, Mc11, Ne2
			C ^{m4} CNGG	Ne1
<i>Sfa</i> NI	GATGC	GATG ^{m5} C	G ^{m6} ATGC	Mc11, Po4
<i>Sfi</i> I	GGCCN ₃ GGCC	GG ^{m5} CCN ₃ GG ^{m5} CC ^b	GGC ^{m5} CN ₃ GGCC	Mc11, Qi2
		GGCCN ₃ GGC ^{m5} C		
<i>Sfi</i> I	CTGCAG	?	CTGC ^{m6} AG	Br8
<i>Sgr</i> AI	CRCCGGYG	?	CRC ^{m5} CGGYG	Ta3
<i>Sin</i> I	GGWCC	?	GGW ^{m5} CC [#]	Ka5, Ka6
<i>Sma</i> I	CCCGGG	C ^{m5} CCGGG	m ⁴ CCCGGG	Br8, Bu10, Eh2, Ga4
			m ⁵ CCCGGG ^b	Ja3, Ka7, Mc3, Qu1
			C ^{m4} CCGGG ^b	
			CC ^{m4} CGGG	
			CC ^{m5} CGGG ^b	
<i>Sna</i> BI	TACGTA	?	TA ^{m5} CGTA	Fo1, Ya1
			T ^{m6} ACGT ^{m6} A	
<i>Sno</i> I	GTGCAC	?	GTG ^{m5} CA ^{m5} C	Ho3, Wo1
<i>Spe</i> I	ACTAGT	?	m ⁶ ACTAGT	Ho2
			A ^{m5} CTAGT	Wo1
<i>Sph</i> I	GCATGC	GCATG ^{m5} C	GC ^{m6} ATGC	Mc11, Mo3, Ne2
		G ^{hm5} CATG ^{hm5} C		

Table I. continued:

<i>SpII</i>	CGTACG	CGT ^{m6} ACG	CGTAm5CG	Ne1,Ne4,Qi3
<i>Spol</i>	TCGCGA	TCGCC ^{m6} A	T ^{m5} CGCGA	Ne1,Ne4
<i>SrfI</i>	GCCCCGGGC	?	TCCG ^{m5} CGA	Ma11
			G ^{m5} CCCCGGGC	
			GC ^{m5} CCGGGC	
			GCC ^{m5} CGGGC	
			GCCCCGGG ^{m5} C	
<i>SsoI</i>	GAATTC	?	G ^{m6} AAATTC [#]	Ni4
<i>SsoII</i>	CCNGG	?	C ^{m5} CNCGG	Vi1
			m ⁵ CCNCGG	Gr4
<i>SspRFI</i>	TTCGAA	?	TTCG ^{m6} AA	Li1
<i>SstI</i>	GAGCTC	?	GAG ^{m5} CTC	Br8,Ro1
			GAG ^{hm5} CT ^{hm5} C	Hu1
<i>SstII</i>	CCGCGG	?	m ⁵ CCGCGG	Ne5
			C ^{m5} CGCGG	Ne5
<i>SrsI</i>	GGATG	?	GG ^{m6} ATG [#]	Ki5
			C ^{m6} ATCC [#]	
<i>SnaI</i>	AGGCCT	?	AGG ^{m5} CCT	Ca4,Mc11
			AGGC ^{m5} CT	So3
			AGGC ^{m4} CT	Ne1
<i>SpySBI</i>	GAGN ₆ RTAYG ^b	?	G ^{m6} AGN ₆ R ^m TAYG ^{#b}	Na1,Na2
<i>SpySPI</i>	AACN ₆ GTRC ^b	?	A ^{m6} ACN ₆ G ^m TRC ^{#b}	Na1,Na2
<i>TaqI</i>	TCGA	T ^{m5} CGA ^b	TCG ^{m6} A [#]	Gr5,Hu1,Mc3,Va3
		T ^{hm5} CGA ^b	Hu1	
<i>TaqII</i>	GACCGA	?	G ^{m6} ACCGA	Ne4
CACCCA				
<i>TaqXI</i>	CCWGG	m ⁵ CCWGG	?	Gr1
C ^{m5} CWGG				
<i>TfiI</i>	GAWTC	GAWT ^{m5} C	?	Fo1
<i>TfiI</i>	TCGA	?	TCG ^{m6} A	Sa3,Va6
<i>ThaI</i>	CGCG	m ⁵ CGCG	m ⁵ CGCG	Ga1,Ne1
			hm ⁵ CG ^{hm5} CG	Hu1
<i>TthIII I</i>	GACN ₃ GTC	GA ^{m5} CN ₃ GTC	?	Fo1
		GACN ₃ GT ^{m5} C		
<i>TthHBI</i>	TCGA	T ^{m5} CGA	TCG ^{m6} A [#]	Sa3
<i>Tsp509I</i>	AAATT	?	m ⁶ AAATT	Fo1
<i>XbaI</i>	TCTAGA	?	TCTAG ^{m6} A [#]	Mc13,We1
			T ^{m5} CTAGA ^b	Gr5,Hu1,Ne2
			T ^{hm5} CTAGA	
<i>XcyI</i>	CCCGGG	?	C ^{m4} CCGGG [#]	Wi6
<i>XhoI</i>	CTCGAG ^b	?	CT ^{m5} CGAG	Br8,Eh2,Eh3,Ka7
			CTCG ^{m6} AG	Mc3,Va3
			m ⁵ CTCGAG	
<i>XhoII</i>	RGATCY	RG ^{m6} ATCY	RGAT ^{m5} CY ^b	Br8
<i>XmaI</i>	CCCGGG	CC ^{m5} CGGG ^b	m ⁴ CCCGGG	Bu10,Yo5,Yo6
			m ⁵ CCCGGG	
			C ^{m4} CCGGG	
			CC ^{m4} CGGG	
<i>XmaIII</i>	CGGCCG	?	CGG ^{m5} CCG	Gu9,Ne2
<i>XmnI</i>	GAAN ₄ TTC	GA ^{m6} AN ₄ TTC	G ^{m6} AAAN ₄ TTC	Mc11,Ne2
			GAAN ₄ TT ^{m5} C ^b	
<i>XorII</i>	CGATCG	?	CGAT ^{m5} CG	Br8,Eh2
			CG ^{m6} ATCG ^b	
			hm ⁵ CGAT ^{hm5} CG	Hu1,Sm4

a. # denotes canonical modification MTase specificity. M= A or C, K= G or T, N= A,C,G, or T, R= A or G, Y= C or T, W= A or T, S= G or C, D= A,G or T, H= A,C or T. Sequences are in 5'-3' order. ^{m4}C= N4-methylcytosine; ^{m5}C= C5-methylcytosine; ^{hm5}C=hydroxymethylcytosine; ^{hm5}U=hydroxymethyluracil; ^mC= methylcytosine, N4 or C5-methylcytosine unspecified; ^{m6}A= N6-methyladenine. Nomenclature is according to (Sm2) and (Co4).

b. *AccI* nicks slowly in the unmethylated strand of the hemi-methylated sequence GTMKA^{m5}C. *AccI* cuts slowly at hemimethylated GTMKA^{m5}C (Ne10).
AccIII cuts slowly at T^{m5}CCGGA and T^{m5}CCGGA (Sc10).
AflI cuts slowly at GGWC^{m4}C.
AhaII (GRCGYC) will cut GRCGCC faster if these sites are methylated at GRCG^{m5}CC (Ne5), but will not cut GRCGY^{m5}C sites (Ne2,Ne5).
Asp718I cuts M·CviQI-modified (GT^{m6}AC) *Chlorella* virus NY2A DNA. *Asp718I* does not cut GGTAC^{m5}CWGG overlapping *dcm* sites (Mu2) or ^{m5}C-substituted phage XP12 DNA, whereas *KpnI* cuts XP12 readily (Ne4).
AvaI nicking occurs slowly in the unmethylated strand of the hemi-methylated sequence CTCG^{m6}AG/CTCGAG (Ne5).
AvaII cuts slowly at GGWC^{m4}C.
Bacillus species have been surveyed for G^{m6}ATC and C^{m5}CWGG specific methylases. Many species have G^{m6}ATC specific methylases but none had C^{m5}CWGG specific methylases (Di2).
BalI sites overlapping *dcm* sites (TGGC^{m5}CAGG) are 50-fold slower than unmethylated sites (Gi1).
BanI gives various rate effects when its recognition sequence is ^{m4}C- or ^{m5}C-methylated at different positions.
BglI cleavage rate at certain GC^{m5}CN₃GGC, GC^{m4}CN₃GGC, and GCCN₃GG^{m5}C hemi-methylated sites is extremely slow. However, ^{m5}C bi-methylated M·HaeIII–*BglI* sites are completely refractory to *BglI* (Ko3,Ne2).
BspEI cleavage slowed by TC^{m5}CGGA (Fo1).

BsrBI cleavage slowed by GAG^{m5}CGG (Fo1).

BssHIII does not cut M·*HhaI*-modified DNA, in which two different cytosine positions are hemi-methylated, G^{m5}CGCGC/GCG^{m5}CGC (Ne4).

M·*BstI* modifies the internal cytosine GGAT^{m5}CC, but it is not known whether this modification is ^{m5}C or ^{m4}C (Le3).

BstEII cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5).

BstNI cuts C^{m5}CWGG, ^{m5}CCWGG and ^{m5}C^{m5}CWGG (Ne5). *BstNI* isoschizomers that are insensitive to C^{m5}CWGG include *AorI*, *ApyI*, *BspNI*, *MvaI* and *TaqXI* (Mc4).

BsuRI nicking occurs in the unmethylated strand of the hemi-methylated sequence GG^{m5}CC/GGCC.

CfrI, see reference Bu10 for rate effects.

ClaI cuts slowly at hemimethylated AT^{m5}CGAT (Ne10).

M·*CreI* is from the unicellular eukaryote *Chlamydomonas reinhardtii* (Sa2).

DpnI requires adenine methylation on both DNA strands. Isoschizomers of *DpnI* include *CfuI*, *NanII*, *NmuEI*, *NmuDI* and *NsuDI* (Ca1). *DpnI* cuts *dam* modified XP12 DNA (Ne6).

M·*Eco dam* modifies GAT^{m5}C at a reduced rate (Ne5). Many other bacteria that modify their DNA at G^{m6}ATC are listed in references Ba1 and Lo1.

EcoAI, *EcoBI*, *EcoDI*, *EcoEI*, *EcoDXXI*, *EcoKI* are Type I restriction endonucleases. ^{m5}T represents a 6-methyladenine in the complementary strand.

EcoPI is a Type III restriction endonuclease (Ba1, Ba2, Ha4).

EcoP15I is a Type III restriction endonuclease (Hu2).

EcoRI cannot cut hemi-methylated G^{m6}AATTC/GAATTC sites. Bimethylated GA^{m6}ATTC/GA^{m6}ATTC sites are not cut by *EcoRI* or *RsrI* (Ne5). *EcoRI* shows a reduced rate of cleavage at hemi-methylated GAATT^{m5}C (Tr1) and does not cut an oligonucleotide that contains GAATT^{m5}C in both strands (Br1).

EcoRII does not cleave some DNA molecules that carry only a single site. However, oligonucleotides containing the *EcoRII* site can be used to transactivate sites that are resistant to cleavage (Re5). *EcoRII* isoschizomers that are sensitive to C^{m5}CWGG include *AruBI*, *AruII*, *BsrGII*, *BinSI*, *EclII*, *EcaII*, *Eco27I*, *Eco38I* and *MphI* (Ro3). *EcoRII* shows reduced rate of cleavage at hemi-methylated ^{m5}CCWGG/CCWGG sites (Yo1).

EcoRV cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5).

EcoR124I and *EcoR124/3I* are Type I restriction endonucleases. ^{m5}T represents a 6-methyladenine in the complementary strand.

FokI cuts about two-fold to four-fold more slowly at CATC^{m5}C than at unmodified sites (Ne5).

M·*FokI* in ref Po3 corresponds to M·*FokIA* in ref Po4.

HaeII shows a reduced rate of cleavage when its recognition sequence is modified at RGCG^{m5}CY.

HaeIII nicking occurs in the unmethylated strand of the hemi-methylated sequence GG^{m5}CC/GGCC.

HinfI cuts GANT^{m5}C, however, detectable rate differences are observed between unmethylated, hemi-methylated (GANT^{m5}C/GANTC) and bi-methylated (GANT^{m5}C/GANT^{m5}C) target sequences (Co1, Gr5, Ne5, Ne10). However, the rate difference between unmethylated and fully methylated *HinfI* sites is only about ten-fold (Hu1, Ne5, Pe1).

HindIII cuts slowly at hemimethylated AAG^{m5}CTT (Ne10).

HpaII nicking in the unmethylated strand of the hemi-methylated sequence ^{m5}CCGG/CCGG is in dispute (Be3, Bu10, Ko3). *HpaII* cuts hemimethylated mCCGG fifty times slower and fully methylated mCCGG 3000 times slower than unmethylated DNA (Ko3). See reference (Bu10) for *HpaII* rate effects.

KpnI sensitivity to hemi-methylated GGTA^{m5}CC and GGTA^{m5}C sites has been reported. *KpnI* cuts ^{m5}C-substituted phage XP12 DNA (Ne4) but cuts slowly at hemimethylated GGTA^{m5}C^{m5}C (Ne10).

MaeII nicks slowly in the unmethylated strand of hemi-methylated A^{m5}CGT/ACGT (Mo2).

MboI isoschizomers that are sensitive to G^{m6}ATC include *BssGII*, *BsaPI*, *Bsp74I*, *Bsp76I*, *Bsp105I*, *BstXII*, *BstEIII*, *BssGII*, *CpaI*, *CryI*, *CviAI*, *CviBII*, *CviHI*, *DpnII*, *FnuAII*, *FnuCI*, *HaeI*, *MeuI*, *MkrAI*, *MmeII*, *MnoIII*, *MosI*, *Msp67II*, *MthI*, *MthAI*, *NdeII*, *NflAII*, *NflBI*, *NflI*, *NlaDI*, *NlaII*, *NmeCI*, *NphI*, *NsiAI*, *NspAI*, *NsuI*, *Pfal*, *RluI*, *SalAI*, *SalHI*, *Sau6782I*, *SinMI*, *TruII* (Ro3).

MboII cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5), although certain hemi-methylated ^{m5}C-containing substrates are reported not to be cut (Gr5).

MflI cuts slowly at ^{m6}AGATCY sites (On1).

Mammalian methylase is the ^{m5}CG methyltransferase from *Mus musculus*. (mouse) (Be7).

MspI cuts the hemi-methylated sequence C^{m5}CGG/CCGG (Wa5) and C^{m4}CGG/CCGG duplexes (Bu10). *MspI* cuts very slowly at GGC^{m5}CGG (Bu6). An M *MspI* clone methylates ^{m5}CCGG (Wa5, Wa2). However, there is a report that *Moraxella* sp. chromosomal DNA is methylated at ^{m5}C^{m5}CGG (Je2).

MvaI nicking occurs in the unmethylated strand of the hemi-methylated sequence ^{m4}CCWGG/CCWGG and CC^{m6}AGG/CCTGG (Ku1). *MvaI* cuts XP12 DNA very slowly at ^{m5}C^{m5}CWGG.

NanII requires adenine methylation on both DNA strands (Ca1). *NanII* cuts M·*Eco dam* modified XP12 DNA (Ne5).

NciI may cut ^{m5}C^{m5}CGG methylated DNA (Br8, Je2). Possibly the second methylation negates the effect of C^{m5}CGG.

NcoI is blocked by M·*SecI* (CCNNGG) (Ne5).

NcrI is a *BglIII* isoschizomer from *Nocardia carnii* Beijing (Qi1).

NdeI cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5).

NdeII cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5).

Ngo. There is some confusion about naming restriction enzymes from these strains (Gu4). *NgoPII*, *NgoII* and *NgoSI* may be the same. *NgoPIII* may be *NgoIII*.

NgoII does not cut overlapping dcm sites (Su4).

NmuDI requires adenine methylation on both DNA strands (Ca1).

NmuEI requires adenine methylation on both DNA strands (Ca1).

PaeRI cuts hemimethylated CT^{m5}CGAG/CTCGAG sites 100-fold slower and cuts fully methylated CT^{m5}CGAG/CT^{m5}CGAG 2900 fold slower than unmethylated sites (Gh1). Hemi- or full methylation at ^{m6}A completely protects against *PaeRI* cleavage (Gh1).

PstI cuts slowly at hemimethylated ^{m5}CTG^{m5}CAG (Ne10).

PvuII cuts slowly at hemimethylated ^{m5}CAG^{m5}CTG (Ne10).

RsaI cuts the fully ^{m5}C-substituted phage XP12 DNA (Ne5), [contradicted by (Fo1)] but does not cut *Chlorella* virus NY2A DNA, which is modified at GT^{m6}AC (Ne4, Xi1). DNA from *Rhodobacter sphaeroides* species Kaplan is cut by *Asp718I*, but not by *RsaI* or *KpnI* (Ne4). It is likely that M·*RsaI* specifies GTA^{m4}C; and high levels of ^{m4}C are present in *R. sphaeroides* DNA (Eh3).

RsrI cannot cut hemi-methylated G^{m6}AATTC/GAATTC sites.

SalI cuts slowly at hemimethylated GT^{m5}CGAC (Ne10).

Sau3AI nicking occurs in the unmethylated strand of the hemi-methylated sequence GAT^{m5}C/GATC (St3). *Sau3AI* cuts at a reduced rate at ^{m6}AGATC (On1).

Sau3AI isoschizomers that are insensitive to G^{m6}ATC include *Bce243I*, *Bsp49I*, *Bsp51I*, *Bsp52I*, *Bsp54I*, *Bsp57I*, *Bsp58I*, *Bsp59I*, *Bsp60I*, *Bsp61I*, *Bsp64I*, *Bsp65I*, *Bsp66I*, *Bsp67I*, *Bsp72I*, *BspAI*, *Bsp91I*, *BspRI*, *CpfI*, *Csp5I*, *CpeI*, *FnuEI*, *MspBI*, *SauCI*, *SauDI*, *SauEI*, *SauFI*, *SauGI* and *SauMI* (Ro3).

SfiI cannot cut M·*BglII*-modified DNA (Ne1).

SmaI nicking occurs in the unmethylated strand of the hemi-methylated sequence CC^{m5}CGGG/CCCGGG (Bu10, Wa5). *SmaI* may cut C^{m5}C^{m5}CGGG methylated DNA (Br8, Je2). Possibly the second methylation negates the effect of CC^{m5}CGGG. There are conflicting results regarding *SmaI*: ^{m5}CCCGGG is not cut when modified by M·*AquI* methyltransferase (Ka7) or at overlapping M·*HaeIII*-*SmaI* sites (GG^{m5}CCCGGG, Ne5). Other investigators have reported that *SmaI* cuts at a reduced rate at hemi-methylated ^{m5}CCCGGG sites (Bu10).

SpeI cuts slowly at hemimethylated A^{m5}CTAGT (Ne10).

SplI cuts GT^{m6}AC-modified *Chlorella* virus NY2A DNA, but does not cut *KpnI*-digested XP12 DNA (Ne4).

SlySBI and *SlySPI* are Type I restriction endonucleases. ^{m5}T represents a 6-methyladenine in the complementary strand.

TaqI cuts very slowly at T^{hm5}CGA (Hu1). *TaqI* cuts the fully ^{m5}C substituted phage XP12 DNA (Hu1,Ne5).

M·*TaqI* methylates T^{m5}CGA at least 20 fold slower than unmodified TCGA (Mc7).

XbaI will cut T^{m5}CTAGA/TCAGA hemi-methylated DNA at high enzyme levels (> 100U *XbaI*/ug), but will not cut this sequence in twenty to forty-fold overdigestions (Ne5,Ne10).

XhoII nicking occurs slowly in the unmethylated strand of the hemi-methylated sequence RGAT^{m5}CY/RGATCY.

XmaI is claimed not cut CC^{m5}CGGG in one report (Br8). See reference Bu10 for rate effects.

XmnI cuts the fully ^{m5}C substituted phage XP12 DNA (Ne5). *XmnI* cuts slowly at some sites in DNA methylated on both strands at GAAN₄TT^{m5}C (Ne5).

XorII, according to the BRL-Gibco catalog, may cut CG^{m6}ATCG.

Table II. Isoschizomer pairs that differ in their sensitivity to sequence-specific methylation.

Methylated sequence ^c	Restriction isoschizomer pairs ^{a,b}		References
	Cut by	Not cut by	
m ⁵ CATG	CviAII	NlaIII	Zh2
m ⁴ CCGG	MspI	HpaII	Bu10
C ^{m5} CGG	MspI	HpaII,HapII	Eh2,Mc11
C ^{m4} CGG	MspI	HpaII	Bu10
CC ^{m5} CGGG	Cfr9I,XmaI	SmaI	Bu10
m ⁵ CCTNAGG	MstII	Bsu36I	Ne5
C ^{m5} CWGG	BstNI,MvaI	EcoRII ^d	Bu8
m ⁵ CCWGG	ApyI,EcoRII,MvaI	ApyI	Ke1,Ku1,Ne3,Yo1
CG ^{m6} ATCG	PvuI	XorII	Bi3,Br8,Sm4
GAAN ₄ TT ^{m5} C	Asp700I	XmnI	Ne1,Ne2
GA ^{m5} CN ₆ GT ^{m5} C	TthIII	DrdI	Fo1
GAGCT ^{m5} C	SacI	Ecl136II	Qi3,Fo1
G ^{m6} ATC	FnuEI,Sau3AI	MboI,NdeII	Ge1,Lu1,Mc9,Ro3
GAT ^{m5} C	MboI	Sau3AI	Ne4
GAT ^{m4} C	MboI	Sau3AI	Ne4
GGC ^{m5} C	HaeIII	NgoII	Su4
GGNC ^{m5} C	AsuI	Sau96I	Ko3
GTG ^{m5} CAC	ApaLI	Alw44	Ne1
GGTAC ^{m5} C	KpnI	Asp718I	Mu2
GGTA ^{m5} C ^{m5} C	KpnI	Asp718I	Ne4
GGWC ^{m5} C	AflI	AvaII,Eco47I	Ba3,Ja5,Wh2
RG ^{m6} ATCY	BstYI,XhoII	MflI	Mc9,Ne4,On1
RGAT ^{m5} CY	BstYI	XhoII	Ne4,On1
T ^{m5} CCGGA	AccIII	BspMII,Kpn2I,MroI	La2,Sc2
TC ^{m5} CGGA	AccIII	BspMII,Kpn2I,MroI	Sc2
TCCGG ^{m6} A	BspMII,Kpn2I,MroI	AccIII	Ke3,Ne4
T ^{hm5} CGA	TaqI	CviSIII	Mc14
TCGCG ^{m6} A	AmaI,SaDI,Sbo13I,SpoI	NruI	Mc11,Mc13,Ne4
TCG ^{m5} CGA	NruI	SpoI	Ne1,Qi1
TT ^{m5} CGAA	AsuII	BstBI,Csp45I	Wo1
TTCC ^{m6} AA	CblI	BstBI,Csp45I,SspRFI	Li1,Mu1,Sc11,Wo1
CGGWC ^{m5} CG	CspI	RsrII	Qi3

a. In each row the first column lists a methylated sequence, the second column lists an isoschizomer that cuts this sequence, and the third column lists an isoschizomer that does not cut this sequence.

b. An enzyme is classified as insensitive to methylation if it cuts the methylated sequence at a rate that is at least one tenth the rate at which it cuts the unmethylated sequence. An enzyme is classified as sensitive to methylation if it is inhibited at least twenty-fold by methylation relative to the unmethylated sequence.

c. See footnote 'a' of Table I.

d. See footnote 'b' of Table I.

ACKNOWLEDGEMENTS

This work is supported by grants AI34829 and HG00456 to MM from the U.S. National Institutes of Health.

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