**Title Page**

# A novel mobile RND-type efflux pump gene cluster, *tmexC3D2-toprJ3*, confers tigecycline resistance in *Pseudomonas alcaligenes*

Shotaro Maehana[1,2,3], Ryotaro Eda[2], Nagi Niida[2], Aki Hirabayashi[4], Kouji Sakai[5], Takashi Furukawa[6], Kazunari Sei[6], Hidero Kitasato[1,2,3,*], and Masato Suzuki[4,*]

[1]Department of Microbiology, School of Allied Health Sciences, Kitasato University, Kanagawa, Japan

[2]Department of Environmental Microbiology, Graduate School of Medical Sciences, Kitasato University, Kanagawa, Japan

[3]Regenerative Medicine and Cell Design Research Facility, School of Allied Health Sciences, Kitasato University, Kanagawa, Japan

[4]Antimicrobial Resistance Research Center, National Institute of Infectious Diseases, Tokyo, Japan

[5]Department of Veterinary Science, National Institute of Infectious Diseases, Tokyo, Japan

[6]Department of Environmental Hygiene, School of Allied Health Sciences, Kitasato University, Kanagawa, Japan

*Corresponding authors.

E-mail address: hkita@kitasato-u.ac.jp (H. Kitasato); suzuki-m@nih.go.jp (M. Suzuki)

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**Abstract**

Tigecycline exhibits promising activity against multidrug-resistant gram-negative bacteria (MDR-GNB), whose infections are difficult to treat with antimicrobials. However, mobile tigecycline resistance genes, such as *tmexCD-toprJ*, have emerged in Enterobacterales isolated in China, Vietnam, and possibly other countries in the world. TMexCD-TOprJ complexes function as RND efflux pumps for multiple antimicrobials including tigecycline. To date, *tmexCD1-toprJ1*, *tmexCD2-toprJ2*, and *tmexCD3-toprJ3* have been reported as variants of *tmexCD-toprJ* genes. Here, we identified a novel hybrid type of *tmexCD-toprJ* gene cluster, named *tmexC3D2-toprJ3*, in tigecycline- and carbapenem-nonsusceptible isolates of *Pseudomonas alcaligenes*, a rare opportunistic human pathogen, obtained from medical sewage in Japan in 2020. Complete genomic analysis revealed that the *P. alcaligenes* isolate KAM426 co-harbors *tmexC3D2-toprJ3* consisting of *tmexC3*, *tmexD2*, and *toprJ3*, along with two copies of the carbapenemase gene $bla_{\text{IMP-1}}$ on the chromosome. *tmexC3D2-toprJ3* in KAM426 was flanked by the IS*5*/IS*1182* family transposase gene, suggesting that the gene cluster was acquired by horizontal gene transfer (HGT). Comparative genomic analysis using the public genome database showed that *tmexC3D2-toprJ3* has spread to other *Pseudomonas* species such as *Pseudomonas aeruginosa* via HGT mediated by mobile gene elements such as a plasmid. This study suggests that diverse *tmexCD-toprJ*-like tigecycline resistance genes have spread among MDR-GNB worldwide and further epidemiological genomic studies are needed.

52 **Materials and methods**

53 **Bacterial isolation and antimicrobial susceptibility testing**

54 Eight cephalosporin-resistant isolates of *P. alcaligenes* (KAM426, KAM428,
55 KAM429, KAM430, KAM432, KAM434, KAM435, and KAM436) were obtained
56 from sewage water from a medical institution in Japan in February, 2020.
57 Environmental water samples were collected and cultured using DHL agar
58 containing 2 mg/L of ceftriaxone. Bacterial species identification was performed
59 using MALDI Biotyper (Bruker). Antimicrobial susceptibility testing (AST) using
60 *Escherichia coli* ATCC 25922 as quality control was performed according to the
61 broth dilution method based on the CLSI 2020 guidelines or according to the Etest
62 (bioMérieux) based on the manufacturer instructions. For tigecycline, AST was
63 additionally performed in the presence or absence of 75 mg/L of the efflux pump
64 inhibitor 1-(1-naphthylmethyl)-piperazine (NMP) as used in the previous study (1).

65

66 **Whole-genome sequencing and subsequent bioinformatics analysis**

67 Whole-genome sequencing of all eight cephalosporin-resistant isolates of *P.*
68 *alcaligenes* was performed using HiSeq X (Illumina), and the isolate KAM426 was
69 further sequenced MinION [Oxford Nanopore Technologies (ONT)] with the
70 R9.4.1 flow cell. The library for Illumina sequencing (paired-end, insert size of
71 500-900 bp) was prepared using Nextera XT DNA Library Prep Kit and the library
72 for ONT sequencing was prepared using Rapid Barcoding Kit (SQK-RBK004).
73 Illumina reads were assembled de novo using Shovill v1.1.0
74 (https://github.com/tseemann/shovill) with default parameters, resulting in the
75 draft genome sequences. For KAM426, ONT reads were basecalled using Guppy

76 v4.2.2 with the high-accuracy mode, and then both Illumina and ONT reads were
77 assembled de novo using Unicycler v0.4.8.0 (https://github.com/rrwick/Unicycler)
78 with default parameters, resulting in the complete circular chromosome sequence
79 (accession no.: AP024354). CDS annotation and average nucleotide identity
80 (ANI) analysis were performed using the DFAST server (https://dfast.nig.ac.jp).
81 Antimicrobial resistance (AMR) genes were detected using ResFinder v4.1
82 (http://www.genomicepidemiology.org) with default parameters using the
83 customized AMR gene database including known *tmexCD-toprJ* genes. Linear
84 comparison of sequence alignment was performed using BLAST and visualized
85 by Easyfig v.2.2.2 (http://mjsull.github.io/Easyfig/).
86

87 **Introduction**

88 Tigecycline is considered a last-resort antimicrobial against infections caused
89 by multidrug-resistant gram-negative bacteria (MDR-GNB). Recently, mobile
90 tigecycline resistance genes, *tet*(X3), *tet*(X4), and other variants, *tet*(X5) to
91 *tet*(X15), encoding flavin-dependent monooxygenases that catalyze tigecycline
92 degradation have emerged in Enterobacterales and *Acinetobacter* species in
93 China and other countries (2-5). Furthermore, mobile tigecycline resistance gene
94 clusters, *tmexCD1-toprJ1*, *tmexCD2-toprJ2*, and *tmexCD3-toprJ3*, encoding the
95 resistance–nodulation–cell division (RND) efflux pumps that excrete multiple
96 antimicrobials, including tetracyclines such as tigecycline, cephalosporins,
97 fluoroquinolones, and aminoglycosides, have emerged predominantly in
98 Enterobacterales in China and Vietnam (1, 6-10). Mobile *tmexCD-toprJ* genes
99 are estimated to originate from chromosomal *mexCD-oprJ* genes in
100 *Pseudomonas* species (1). Interestingly, however, *tmexCD1-toprJ1* has also
101 been shown to spread to *Pseudomonas putida* by a megaplasmid (7).

102 Here, we report *Pseudomonas alcaligenes* isolates harboring a novel variant
103 of *tmexCD-toprJ* along with two copies of a metallo-β-lactamase (MBL) gene,
104 $bla_{\text{IMP-1}}$. *P. alcaligenes* is a gram-negative aerobic rod belonging to the bacterial
105 family Pseudomonadaceae, of which members are common inhabitants of soil
106 and water and are rare opportunistic human pathogens (11). *P. alcaligenes* has
107 also been suggested to be a causative agent of secondary bacterial infection
108 during COVID-19 pneumonia (12). However, little is known about the clinical
109 importance of *P. alcaligenes*, mainly because of the difficulties in identifying and
110 distinguishing this bacterium from closely related *Pseudomonas* species such as

111 *P. aeruginosa*, *P. mendocina,* and *P. pseudoalcaligenes*, in medical settings.

112

113 **Results and discussion**

114 Eight cephalosporin-resistant isolates of *P. alcaligenes* were obtained from
115 medical wastewater in Japan in 2020. Whole-genome sequence analysis of *P.*
116 *alcaligenes* isolates by Illumina HiSeq X and the core genome phylogeny based
117 on their draft genome sequences showed that these isolates were
118 phylogenetically very similar (Fig. S1). Moreover, all *P. alcaligenes* isolates
119 harbored the same set of antimicrobial resistance (AMR) genes, including
120 *tmexCD-toprJ*-like genes, $bla_{IMP-1}$ (MBL gene conferring carbapenem resistance),
121 *aac(6')-Ib-cr* (aminoglycoside resistance gene), *fosE* (fosfomycin resistance
122 gene), *qacG2* (multidrug resistance gene), and *sul1* (sulfonamide resistance
123 gene), suggesting that these isolates were clonally disseminated (Fig. S1).

124 One of the *P. alcaligenes* isolates, KAM426, was further sequenced using ONT
125 MinION, and hybrid sequence analysis using both Illumina and ONT reads
126 resulted in the circular complete chromosome sequence (4.68 Mb, accession no.
127 AP024354). Average nucleotide identity (ANI) analysis revealed that KAM426 is
128 96.5% identical to *P. alcaligenes* strain NCTC 10367$^{T}$ (type strain, accession no.
129 UGUP00000000), and the isolate harbored *tmexCD-toprJ*-like genes along with
130 two copies of $bla_{IMP-1}$ on its chromosome (Fig. S2). Antimicrobial susceptibility
131 testing showed that *P. alcaligenes* KAM426 was nonsusceptible to tigecycline
132 and broad-spectrum β-lactams, including carbapenems. According to the broth
133 dilution method, the minimum inhibitory concentration (MIC) of tigecycline against
134 KAM426 was 2 mg/L and was decreased to 1 mg/L in the presence of the efflux
135 pump inhibitor NMP. According to the Etest, the MICs of imipenem and
136 meropenem against KAM426 were 8 and >32 mg/L, respectively, and these were

137 decreased to <1 and 0.19 mg/L, respectively, in the presence of the MBL inhibitor
138 EDTA. These results suggested that *tmexCD-toprJ*-like genes and $bla_{IMP-1}$ are
139 responsible for tigecycline and carbapenem resistance in this isolate.

140 The coding sequences of *tmexCD-toprJ*-like genes in *P. alcaligenes* KAM426
141 (KAM426_19240, KAM426_19250, and KAM426_19260 in accession no.
142 AP024354) were highly identical to those of *tmexCD1-toprJ1* in *Klebsiella*
143 *pneumoniae* strain AH58I (accession no. MK347425) isolated from livestock in
144 China in 2017 (1), those of *tmexCD2-toprJ2* in *Raoultella ornithinolytica* strain
145 NC189 (accession no. MN175502) isolated from a human in China in 2018 (8),
146 and those of *tmexCD3-toprJ3* in *Proteus mirabilis* strain RGF134-1 (accession
147 no. CP066833) isolated from a pig in China in 2019 (9), respectively. The
148 identities of the *tmexC*-like gene in KAM426 (KAM426_10690) compared with
149 *tmexC1*, *tmexC2*, and *tmexC3* were 94.0% (1094/1164 nt), 94.6% (1101/1164 nt),
150 and 98.6% (1148/1164 nt, the gene product was 98.7% identical to TMexC3 with
151 five amino acid substitutions), respectively. For the *tmexD*-like gene in KAM426
152 (KAM426_10700), these identities were 96.5% (3025/3136 nt), 99.1%
153 (3108/3135 nt, the gene product was perfect match to TMexD2), and 97.1%
154 (3046/3136 nt), respectively. For the *toprJ*-like gene in KAM426
155 (KAM426_10710), the identities were 99.9% (1433/1434 nt), 99.9% (1417/1419
156 nt), and 100% (1434/1434 nt, the gene product was perfect match to TOprJ3),
157 respectively. Thus, we designated *tmexCD-toprJ*-like genes in KAM426 as
158 *tmexC3D2-toprJ3*.

159 The *nfxB*-like gene, which has been suggested to be involved in the expression
160 of the *tmexCD-toprJ*-like gene (1), was found upstream *tmexC3D2-toprJ3* in *P.*

161 *alcaligenes* KAM426 (KAM426_19230 in accession no. AP024354), and
162 *tmexC3D2-toprJ3* was flanked by the IS*5*/IS*1182* family transposase gene (Fig.
163 1A upper). Furthermore, the genomic region containing *nfxB* and *tmexC3D2-*
164 *toprJ3* in KAM426 was surrounded by many putative mobile gene elements
165 (MGEs), and this genomic region was not present in *P. alcaligenes* strain NEB
166 585 (accession no. CP014784) (Fig. 1A). NEB 585 was isolated from a water
167 environment in the United States in 1989 and is the only other *P. alcaligenes*
168 strain for which the complete chromosome sequence has been reported (13)
169 other than KAM426. The genomic recombination regions in KAM426 and NEB
170 585 encoded a set of common genes (KAM426_19430 to KAM426_19470 in
171 accession no. AP024354, and A0T30_13575 to A0T30_13555 in accession no.
172 CP014784) (Fig. 1A), although their functions are unknown. The results suggest
173 that KAM426 acquired *tmexCD-toprJ*-like genes, which confer resistance to
174 multiple antimicrobials including tigecycline, via horizontal gene transfer (HGT)
175 mediated by MGEs.

176 BLASTn analysis using megablast revealed that two *Pseudomonas* species
177 strains in the NCBI database of Nucleotide collection (nr/nt) have the exact same
178 sequence containing the *tmexC3D2-toprJ3* gene cluster along with *nfxB*. A $bla_{DIM-}$
179 $_{2}$-harboring *Pseudomonas* species strain, BJP69, isolated from a human in China
180 in 2015 (14) carries *tmexC3D2-toprJ3* on its chromosome (accession no.
181 CP041933) and a $bla_{KPC-2}$-harboring *P. aeruginosa* strain, NDTH9845, isolated
182 from a human in China in 2018 carries *tmexC3D2-toprJ3* on plasmid pNDTH9845
183 (accession no. CP073081) (Fig. 1B). ANI analysis confirmed that BJP69 is 98.0%
184 identical to *Pseudomonas juntendi* strain BML3$^{T}$ (type strain, accession no.

185 BLJG01000000) and that NDTH9845 is 99.2% identical to *P. aeruginosa* DSM
186 50071$^{T}$ (type strain, accession no. FUXR01000000). *tmexC3D2-toprJ3* was
187 determined to be flanked by the IS*5*/IS*1182* family transposase gene in *P.*
188 *aeruginosa* pNDTH9845, whereas no MGE was found upstream or downstream
189 of *tmexC3D2-toprJ3* in *P. juntendi* BJP69 (Fig. 1B). Together with *P. alcaligenes*
190 KAM426 in this study, these three *Pseudomonas* species strains harbor acquired
191 carbapenemase genes, in addition to *tmexC3D2-toprJ3*, showing that they have
192 accumulated clinically relevant AMR genes.

193 The integron-integrase IntI1 catalyzes site-specific recombination between the
194 *attI1* and *attC* sites (15). The class 1 integron gene cassette consisting of *intI1*
195 with the *attI1* site, *qacEΔ1* (disrupted form of *qacE*), and *sul1* in *P. alcaligenes*
196 KAM426 (accession no. AP024354) contain several AMR genes, including *fosE*,
197 two copies of *aac(6')-Ib-cr*, $bla_{IMP-1}$, and *qacG2* with their *attC* sites (Fig. 2A). The
198 $bla_{IMP-1}$-containing integron gene cassette in KAM426 was found to be
199 surrounded by many putative transposase genes, and this MGE-containing
200 genomic region was not present in *P. alcaligenes* NEB 585 (accession no.
201 CP014784) (Fig. 2A). The genomic region around ATP-dependent helicase
202 genes (KAM426_37950 and KAM426_36180 in accession no. AP024354, and
203 A0T30_05350 in accession no. CP014784) could be a hot spot for HGT (Fig. 2A),
204 but there have been no reports to suggest this possibility to date.

205 The other copy of $bla_{IMP-1}$ was contained within a partial structure of the integron
206 gene cassette consisting of two copies of *aac(6')-Ib-cr* followed by $bla_{IMP-1}$, as
207 described previously herein (Fig. 2A), in a different location in the chromosome
208 of *P. alcaligenes* KAM426 (Fig. 2B). Interestingly, a comparison between the

209 *bla*$_{IMP-1}$-containing genomic region of *P. alcaligenes* KAM426 and the
210 corresponding genomic region in *P. alcaligenes* NEB 585 revealed the presence
211 of multiple copies of short repeated sequences (approximately 80 bp), which
212 were identical to PARs (*Pseudomonas alcaligenes* repetitive DNAs) within the
213 super-integron In*55044* in *P. alcaligenes* strain ATCC 55044 (accession no.
214 AY038186) (16) (Fig. 2B).

215 The super-integron, which was first identified in *Vibrio cholerae*, is
216 distinguished from conventional integrons in several respects, such as size and
217 the nature of the genes contained within cassettes and contributes to the
218 acquisition of AMR genes (17-19). The PARs were reported as recombination
219 sites for the integrase gene (*intI*$_{Pac}$ in accession no. AY038186) in the super-
220 integron in *P. alcaligenes* (16). The PARs in *P. alcaligenes* KAM426 and *P.*
221 *alcaligenes* NEB 585 contained conserved sequences of inverted repeats (1L, 2L,
222 2R, and 1R) with a PAR signature and variable regions between inverted repeats
223 2L and 2R, as shown in *P. alcaligenes* ATCC 55044 (16) (Fig. S3). Although
224 KAM426 and NEB 585 lacked the integrase gene flanking the PAR and most of
225 the contained genes had no known function, these plastic genomic regions in
226 both strains retained their evolutionary histories of gene acquisitions mediated by
227 the super-integron. There was no PAR around *bla*$_{IMP-1}$ in KAM426, suggesting
228 that the super-integron is not directly involved in the acquisition of *bla*$_{IMP-1}$, and
229 this genomic region is likely one of the hot spots for HGT. KAM426 is thought to
230 have incorporated *bla*$_{IMP-1}$ into the class 1 integron gene cassette first (Fig. 2A)
231 and then incorporated the partial structure containing *bla*$_{IMP-1}$ into the other
232 genomic region flanked by the super-integron (Fig. 2B), leading to a high level of

233 resistance by increasing the copy number of AMR genes.

234 Our study provides a glimpse into environmental bacteria that have been
235 rapidly and silently becoming resistant to clinically relevant antimicrobials,
236 including tigecycline and carbapenem, and highlights the importance of AMR
237 monitoring using wastewater to detect a future clinical crisis before it happens.
238 Furthermore, *P. alcaligenes* would be considered an important environmental
239 reservoir that supplies AMR genes to other related *Pseudomonas* species that
240 are more virulent and likely to cause nosocomial infections, such as *P. aeruginosa*.
241

242 **Nucleotide Sequences**

243 The complete genome sequence of *P. alcaligenes* KAM426 has been
244 deposited at GenBank/EMBL/DDBJ under the accession number AP024354.
245 Draft genome sequences of *P. alcaligenes* KAM428, KAM429, KAM430, KAM432,
246 KAM434, KAM435, and KAM436 have been deposited at GenBank/EMBL/DDBJ
247 under the accession numbers BPMN00000000, BPMO00000000,
248 BPMP00000000, BPMQ00000000, BPMR00000000, BPMS00000000, and
249 BPMT00000000, respectively.

250

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257 Technology (MEXT), Japan.

258

259 **Transparency declarations**

260 None to declare.

261

262 **Legends**

263 Fig. 1. The *tmexC3D2-toprJ3* gene cluster in *Pseudomonas alcaligenes* KAM426.
264 (A) Genetic context of the *tmexC3D2-toprJ3* gene cluster in *P. alcaligenes*
265 KAM426 and its surrounding genomic region (the region between 1,977,208 and
266 2,027,209 nt in accession no. AP024354), and structural comparison with the
267 corresponding genomic region in *P. alcaligenes* NEB 585 (the region between
268 2,990,265 and 2,915,762 nt in accession no. CP014784). (B) Structural
269 comparison of the *tmexC3D2-toprJ3* gene cluster in *P. alcaligenes* KAM426 (the
270 region between 1,995,475 and 2,006,928 nt in accession no. AP024354) with that
271 in the chromosome of *P. juntendi* BJP69 (the region between 3,340,041 and
272 3,349,533 nt in accession no. CP041933) and in plasmid pNDTH9845 of *P.*
273 *aeruginosa* NDTH9845 (the region between 225,014 and 215,640 nt in accession
274 no. CP073081). The strain names of *Pseudomonas* species, along with the
275 country and year in which bacteria were isolated, are shown. *tmexC3D2-toprJ3*
276 genes (TRG), other AMR genes (ARG), mobile gene elements (MGE), and other
277 genes (Other) are highlighted in red, yellow, light blue, and gray, respectively.
278 Sequence identity is shown as a color scale with the indicated percentages.

279

280 Fig. 2. Two copies of $bla_{\text{IMP-1}}$ genes in *Pseudomonas alcaligenes* KAM426. (A)
281 Genetic context of the class I integron gene cassette containing $bla_{\text{IMP-1}}$ in *P.*
282 *alcaligenes* KAM426 and its surrounding genomic region (the region between
283 3,757,827 and 4,033,855 nt in accession no. AP024354), and structural
284 comparison with the corresponding genomic region in *P. alcaligenes* NEB 585
285 (the region between 1,159,724 and 1,200,667 nt in accession no. CP014784).

286 (B) Genetic context of the partial integron gene cassette containing the other
287 *bla*$_{IMP-1}$ gene in *P. alcaligenes* KAM426 and its surrounding genomic region (the
288 region between 2,181,279 and 2,188,592 nt in accession no. AP024354), and
289 structural comparison with the corresponding genomic regions in *P. alcaligenes*
290 NEB 585 (the region between 2,758,939 and 2,768,635 nt in accession no.
291 CP014784) and in *P. alcaligenes* ATCC 55044 (super-integron In*55044* in
292 accession no. AY038186). The strain names of *P. alcaligenes*, along with the
293 country and year in which bacteria were isolated, are shown. *bla*$_{IMP-1}$ genes
294 (CRG), other AMR genes (ARG), mobile gene elements (MGE), other genes
295 (Others), and *P. alcaligenes* repetitive DNA (PAR) are highlighted in red, yellow,
296 light blue, gray, and khaki green, respectively. Sequence identity is shown as a
297 color scale with the indicated percentages.
298
299 Fig. S1. Core genome phylogeny constructed by Roary v3.13.0
300 (https://github.com/sanger-pathogens/Roary) with minimum percentage identity
301 for BLASTp=70% and RAxML v8.2.4 (https://github.com/stamatak/standard-
302 RAxML), with 1,000 bootstraps using ceftriaxone-resistant *Pseudomonas*
303 *alcaligenes* isolates in this study and reference strains of *P. alcaligenes* and *P.*
304 *aeruginosa* (NCTC 10367$^{T}$ and NEB 585 for *P. alcaligenes*, and PAO1 for *P.*
305 *aeruginosa*). *P. aeruginosa* was used as the outgroup. Bar lengths represent the
306 number of substitutions per site in the core genome. Genome assembly status
307 (complete or draft genome sequence, contig numbers if draft), sizes, and
308 accession numbers are shown.
309

310 Fig. S2. Circular representation of the chromosome of *Pseudomonas alcaligenes*
311 KAM426 (accession no. AP024354) harboring *tmexC3D2-toprJ3*, along with two
312 copies of $bla_{IMP-1}$ (shown in Figs. 1, 2A, and 2B), isolated in Japan in 2020. This
313 was visualized with the CGView server (http://cgview.ca). Gray, green, purple,
314 black, red, yellow, cyan, light green, and orange indicate coding sequences
315 (CDS), GC skew+, GC skew-, GC content, tigecycline or carbapenem resistance
316 genes (TRG/CRG), other AMR genes (ARG), mobile gene elements (MGE), type
317 IV secretion system (T4SS)-associated genes, and type VI secretion system
318 (T6SS)-associated genes, respectively. T4SS- and T6SS-associated genes were
319 detected by TXSScan v1.0.5 (https://research.pasteur.fr/en/tool/txsscan-models-
320 and-profiles-for-protein-secretion-systems/).
321
322 Fig. S3. Alignment of *Pseudomonas alcaligenes* repetitive DNAs (PARs) in *P.*
323 *alcaligenes* strains. One PAR in *P. alcaligenes* ATCC 55044 (super-integron
324 In*55044* in accession no. AY038186), two PARs in *P. alcaligenes* KAM426
325 (accession no. AP024354), and 11 PARs in *P. alcaligenes* NEB 585 (accession
326 no. CP014784) are shown. The multiple alignment comparison was performed
327 and visualized using MAFFT v7 (https://mafft.cbrc.jp/alignment/software/). The
328 PAR signature sequence and variable region are shown. Open boxes and arrows
329 represent consensus sequences of inverted repeats (1L, 2L, 2R, and 1R), as
330 described previously (16).
331

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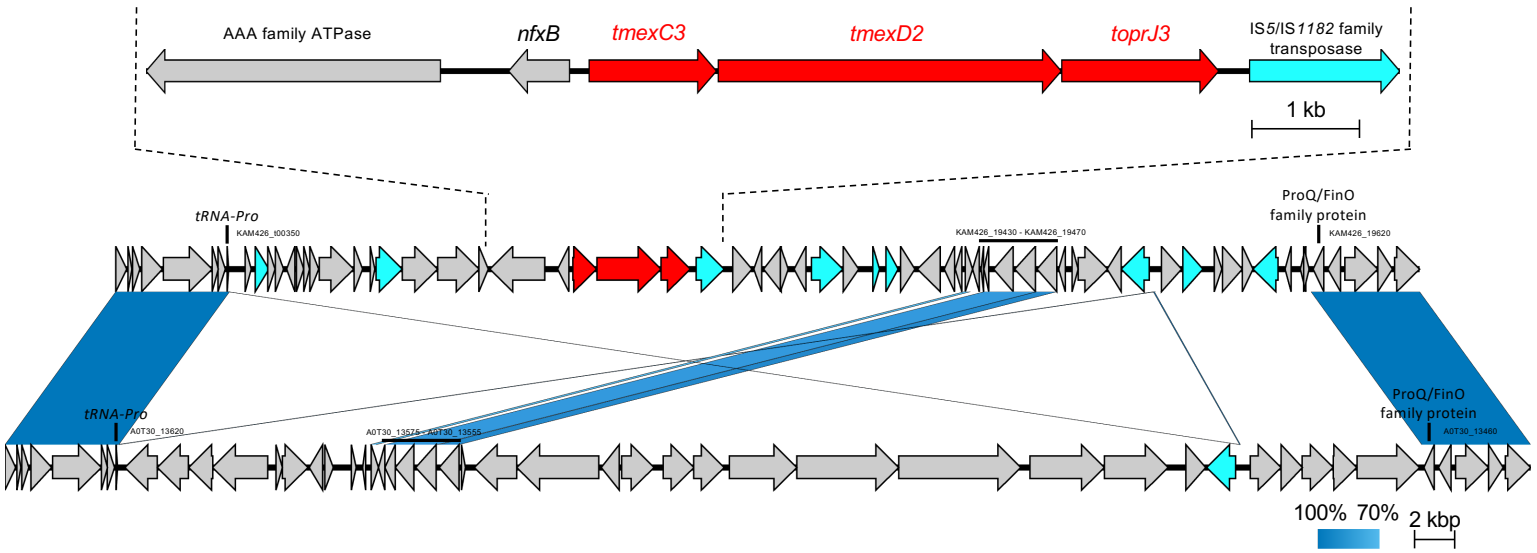
# Fig. 1

## A

***P. alcaligenes***
**KAM426**
**(1,977,208 - 2,027,209 nt)**
**Japan, 2020**

***P. alcaligenes***
**NEB 585**
**(2,990,265 - 2,915,762 nt)**
**USA, 1989**

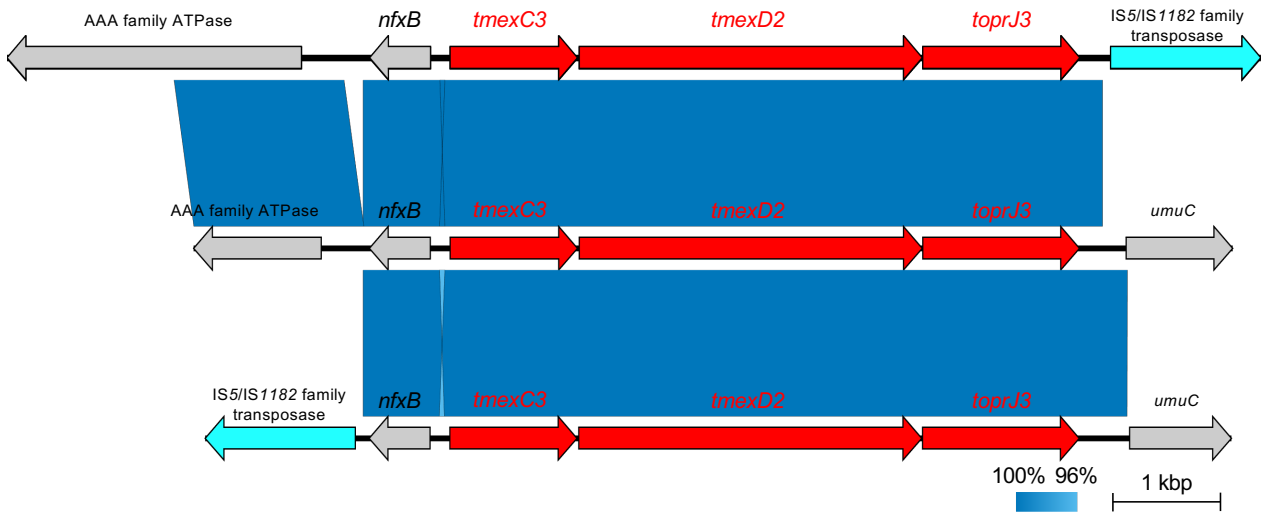



## B

***P. alcaligenes***
**KAM426**
**(1,995,475 - 2,006,928 nt)**
**Japan, 2020**

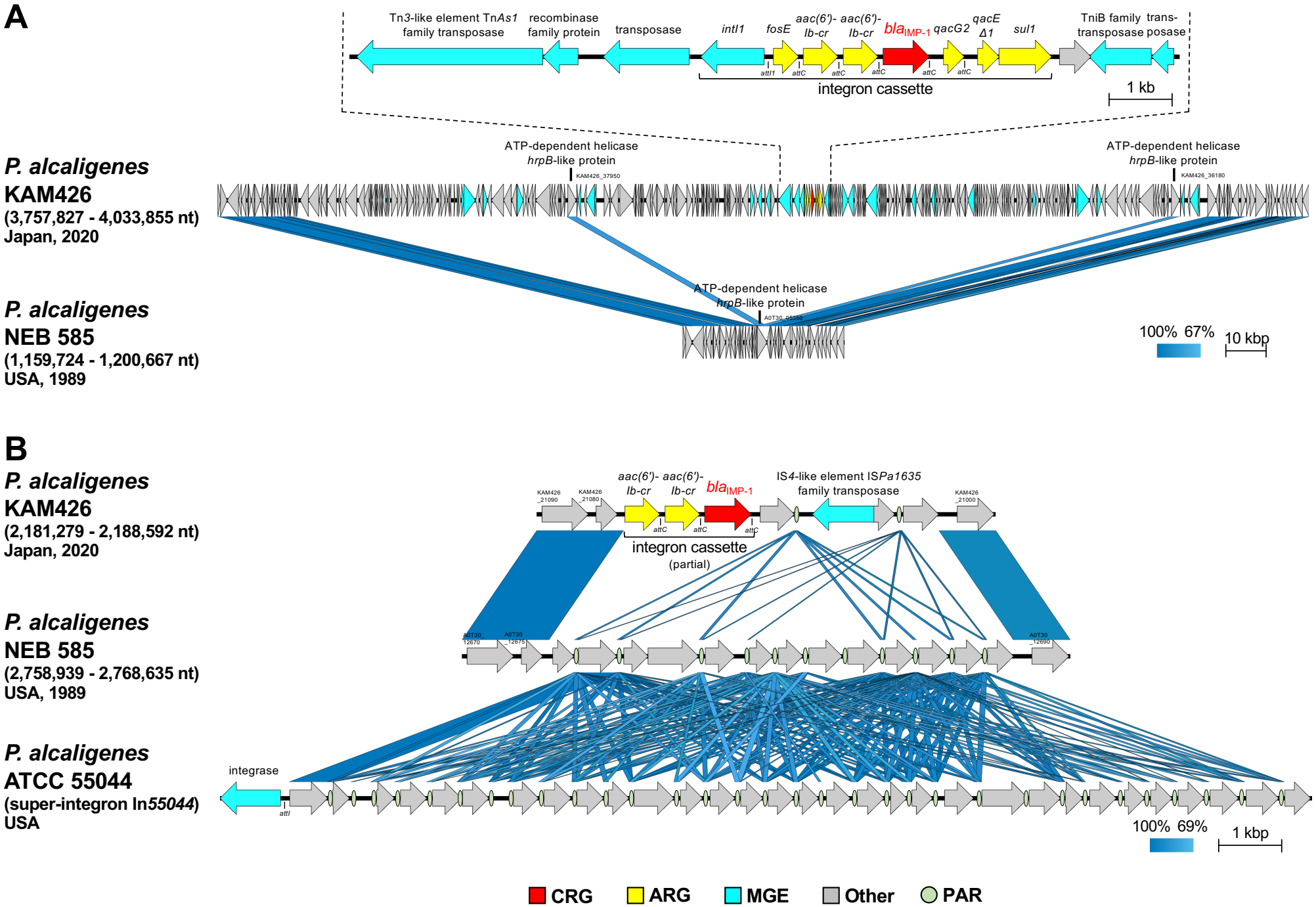
***P. juntendi***
**BJP69**
**(3,340,041 - 3,349,533 nt)**
**China, 2015**

***P. aeruginosa***
**pNDTH9845**
**(225,014 - 215,640 nt)**
**China, 2018**




**TRG** **ARG** **MGE** **Other**

# Fig. 2


A
Tn3-like element TnAs1 family transposase
recombinase family protein
transposase
intI1
fosE
aac(6')-Ib-cr
aac(6')-Ib-cr
blaIMP-1
qacG2
qacE Δ1
sul1
TniB family transposase
trans-posase
attI1
attC
integron cassette
1 kb
P. alcaligenes
KAM426
(3,757,827 - 4,033,855 nt)
Japan, 2020
ATP-dependent helicase
hrpB-like protein
KAM426_37950
ATP-dependent helicase
hrpB-like protein
KAM426_36180
P. alcaligenes
NEB 585
(1,159,724 - 1,200,667 nt)
USA, 1989
ATP-dependent helicase
hrpB-like protein
A0T30_05350
100% 67%
10 kbp
B
P. alcaligenes
KAM426
(2,181,279 - 2,188,592 nt)
Japan, 2020
KAM426_21090
KAM426_21080
aac(6')-Ib-cr
aac(6')-Ib-cr
blaIMP-1
IS4-like element ISPa1635 family transposase
KAM426_21000
attC
integron cassette
(partial)
P. alcaligenes
NEB 585
(2,758,939 - 2,768,635 nt)
USA, 1989
A0T30_12670
A0T30_12675
A0T30_12690
P. alcaligenes
ATCC 55044
(super-integron In55044)
USA
integrase
attI
100% 69%
1 kbp
CRG
ARG
MGE
Other
PAR