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AbaR5, a Large Multiple-Antibiotic Resistance Region Found in *Acinetobacter baumannii*▽†

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A multiply antibiotic-resistant *Acinetobacter baumannii* strain, 3208, contains the *aacC1*-orfP-orfP-orfQ-*aadA1* gene cassette array; *sul1*, *tetA*(A), and *aphA1b* genes; and a *mer* operon in a large region containing a novel transposon, Tn*6020*, and segments of Tn*1696*, Tn*21*, Tn*1721*, and Tn*5393*. This region is part of a genomic resistance island, AbaR5, related to and found in the same chromosomal position as AbaR1. This strain is the first European clone I isolate detected in Australia.

The increase in antimicrobial resistance in *Acinetobacter baumannii* in hospitals is a major concern, and strains that are resistant to almost all currently available antibacterial agents have been observed (17, 18). *Acinetobacter* species are naturally transformable and thus can potentially readily acquire resistance genes from the mobile gene pool, and many different antibiotic resistance genes and combinations of resistance genes have been found in clinical isolates (5, 17, 18). However, there is currently very little detailed information on the locations of these genes and their relationships to one another. Until recently, the multiple-antibiotic resistance regions from only two *A. baumannii* strains had been reported. Strain AYE, which is representative of a clonal line that is epidemic in French hospitals, contains a large cluster of antibiotic and heavy-metal resistance genes in an 86.2-kb resistance island designated AbaR1 (6). The 18 antibiotic resistance genes, some of which are present in multiple copies, confer resistance to most of the known classes of antibiotics. The second strain, ACICU, carries an antibiotic resistance island, AbaR2, consisting of only a small remnant of the AbaR1 region modified by the substitution of an *aacA4*-orf-*oxa1* cassette array for the *aacC1*-orfP-orfP-orfQ-*aadA1* array found in AbaR1 (7). Here, we have examined a cluster of antibiotic resistance genes found in a multiply antibiotic-resistant *A. baumannii* strain isolated in Australia. After this work was completed, a further sequence containing a related region, designated AbaR3, became available (1).

***A. baumannii* strain 3208.** Isolate 32080497, herein called 3208, was isolated in 1997 at a Sydney, Australia, hospital from a blood sample. It was identified as *A. baumannii* with a Vitek 2 compact identification system (bioMérieux, Hazelwood, MO). The sequence of a fragment from the *recA* gene, amplified as described previously (8, 13), was identical to that of *recA* of *A. baumannii* AYE (GenBank accession no. CU459141) (24).

Antibiotic susceptibility for a range of antibiotics was tested using the Vitek 2 system and interpreted using CLSI guidelines (3). 3208 showed intermediate resistance to ceftriaxone, ceftazidime, and cefepime (MIC, 16 μg/ml) as well as ticarcillin-clavulanate (MIC, 32 μg/ml) but was susceptible to piperacillin-tazobactam (MIC, ≤4 μg/ml) and meropenem (MIC, 0.5 μg/ml). It was also resistant to gentamicin (MIC, ≥16 μg/ml) but susceptible to tobramycin (MIC, ≤1 μg/ml). In addition, 3208 was resistant to ciprofloxacin (MIC, ≥4 μg/ml) and trimethoprim-sulfamethoxazole (MIC, ≥320 μg/ml). Additional MICs for antibiotics for which breakpoints for *A. baumannii* have not been established were ≥32 μg/ml for nalidixic acid, ≥16 μg/ml for norfloxacin, ≥16 μg/ml for trimethoprim, and 1 μg/ml for tigecycline.

Identification of resistance genes. The *intI1* gene from the 5′-conserved segment (5′-CS) and the *sul1* sulfonamide resistance gene from the 3′-conserved segment (3′-CS) of a class 1 integron were detected using PCR conditions described previously (19) (see Table S1 in the supplemental material for primers). PCR products were purified using a QIAquick PCR purification kit (Qiagen, Inc., Valencia, CA) or, after separation in an agarose gel, using a QIAquick gel extraction kit. Automated sequencing was performed with an ABI Prism 377 DNA sequencer or a 3130 Exel genetic analyzer (Applied Biosystems, Carlsbad, CA) using the Big Dye system. Amplification of the gene cassettes yielded a 3-kb PCR amplicon that contained the *aacC1*-orfP-orfP-orfQ-*aadA1* gene cassettes (*aacC1* confers resistance to gentamicin, and *aadA1* confers resistance to streptomycin and spectinomycin). Though found first in *Serratia marcescens* (2) (GenBank accession no. AF453999), this cassette array, or a variation of it lacking one copy of the orfP gene cassette, has been found most often in *A. baumannii* isolates (11, 12, 22, 23). It is also present in AbaR1 (GenBank accession no. CT025832 and CU459141) (6).

PCR screening for further resistance genes and several insertion sequences (IS) (see Table S1 in the supplemental material for a complete list) detected the *aphA1* (kanamycin and neomycin resistance), *tetA*(A) (tetracycline resistance), and *merA* (mercuric ion resistance) genes as well as IS*6100* and IS*26*.

Structure of the 3208 multiple-antibiotic resistance region. Digestion of the *merA* amplicon with restriction enzyme RsaI identified it as the Tn*1696*-associated gene (14), and IS*6100*

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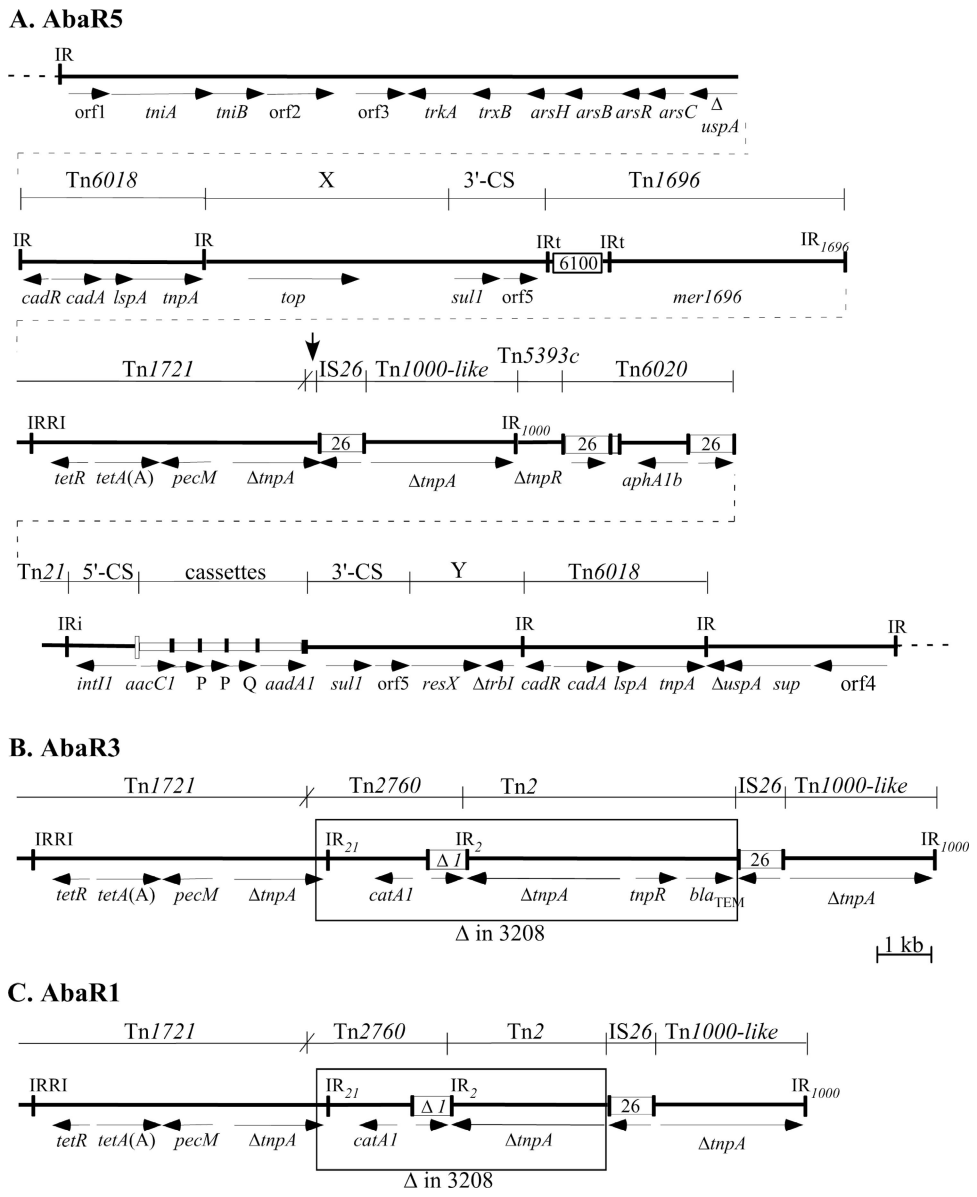

FIG. 1. Map of AbaR5, showing the origins of different segments. (A) AbaR5. In the central line, the dotted lines represent chromosomal DNA flanking AbaR5, and IR of transposons are indicated with vertical lines. IR within the MARR between the Tn*6018* regions have an identifying notation, IRi and IRt for class 1 integron ends and IR_{1696}, IR_{21}, IR_2, and IR_{1000} for IR from Tn*1696*, Tn*21*, Tn*2*, and Tn*1000*-like, respectively. Numbered open boxes represent the IS, with the number indicating the identity of the IS. The *attI1* site of the class 1 integron is shown as a tall open box, and cassettes are represented by an open box with a vertical bar representing the *attC* site. The lines above indicate the extents of the regions derived from known transposons, with vertical lines indicating the boundaries between segments and X indicating a recombination crossover. The *mer* region of Tn*1696*, encoding the *merEDACTPR* genes, is represented by *mer1696*. The extents of other genes are shown by horizontal arrows with the gene names underneath. The genes named *resX*, *sup*, and orf4 potentially encode a resolvase, a sulfate permease, and a protein of unknown function, respectively. The *sup* gene was incorrectly identified as *sul1* in earlier publications (6, 20). The vertical arrow indicates the position of the deletion. (B and C) Portions of AbaR3 and AbaR1, respectively, that contain the *catA1* and bla_{TEM} genes. Only the region flanked by the segments from Tn*1721* and Tn*1000*-like is shown, and the segment missing from AbaR5 is boxed. AbaR3 is otherwise identical to AbaR5, except that only one copy of the orfP cassette is present. AbaR1 contains a large segment replacing the region between Tn*6018* and *sul1*, marked X in the in the top line of panel A. The structure of most of this region can be found in reference 8. Gene Construction Kit (version 2.5; Textco, West Lebanon, NH) was used to create the figure to scale.

was found to be linked to the *mer* module and to the *sul1* gene, as it is in Tn*1696* (GenBank accession no. U12338) (14, 16). However, the gene cassettes could be linked to the *intI1* gene and the *sul1* gene but not to IS*6100*, indicating that there are at least two copies of the *sul1* gene.

The *aphA1* gene was shown to be flanked by directly oriented copies of IS*26*, as is *aphA1a* in transposon Tn*4352* (26) or Tn*4352B* (15). However, the sequence revealed an *aphA1b* gene within a longer central fragment of 1,254 bp, whose sequence diverges from that of Tn*4352* immediately downstream

TABLE 1. Modules in AbaR5

Region[a]	Length (bp)	Progenitor				Region(s)/gene(s)	% Identity
		Name	Length (bp)	GenBank accession no.[b]	Part present (position, in bp)[c]		
1	4,421	X	4,421	CP001182		*top*	100
2	7,322	Tn*1696*	16,318	U12338	8675–16318[d]	Δ3′-CS -IS*6100-mer1696*	100
3	5,157[e]	Tn*1721*	11,139	X61367[f]	5560–10727	Δ*tnpA-tetR-tetA-pecM-*Δ*tnpA*	99.7
4	154[e]	Tn*21*	19,672	AF071413	282–435	Δ*tnpA*	100
5	820	IS*26*	820	AY123253	Complete	IS*26*	100
6	2,883[g]	Tn*1000*	5,981	X60200	1–2883	Δ*tnpA*	74.9
7	685	Tn*5393c*	5,470	AF313472	2968–3652	Δ*tnpR*	99.9
8	820	IS*26*[h]	820	AY123253	Complete	IS*26*	100
9	175	IS*26*[h]	820	AY123253	645–820	ΔIS*26*	100
10	3,069	Tn*6020*	3,069	CT025832	1–3069	*aphA1b*	
11	820	IS*26*	820	AY123253	Complete	IS*26*	100
12	446	Tn*21*	19,672	AF071413	3594–4039	Δ*tnpM*	100
13	1,371	5′-CS[i]	1,371	U12338	Complete	5′-CS	99.6
14	2,962	Cassettes	2,962	AF453999	1–2962	*aacC1*-orfP-orfP-orfQ-*aadA1*[j]	99.6
15	1,987	3′-CS[i]	2,239	U12338	1–1987	3′-CS	100
16	2,025	Y		CT025832[k]		*resX-*Δ*trbI*	
17	3,372	Tn*6018*[l]	3,372	AY128707	Complete	*cadR-cadA-lspA-tnpA*	96.7
18	4,003			CT025832[k]		Δ*uspA-sup*-orf4[m]	

[a] The analysis begins with the first base of the multiple-antibiotic resistance region, i.e., after the left-hand Tn*6018* in AbaR5.
[b] Accession numbers used are either the earliest complete sequences or the complete and annotated sequences.
[c] Numbering for IS is with the transposase gene from left to right; for class II Tn, the *tnpA* gene is on the left, except for Tn*1721*, which is as in X61367.
[d] The first base of this region corresponds to bp 391 of the 3′-CS, and AbaR5 lacks the partial copy of IS*6100* (bp 11527 to 11974) in Tn*1696*.
[e] Regions 3 and 4 overlap by 23 bp that are identical in Tn*21* and Tn*1721* and could be derived from either.
[f] This sequence has several single base differences and a short deletion which are not present in other published sequences of this region and might be errors in the Tn*1721* complete sequence (X61367).
[g] A portion (1,209 bp) was 99.6% identical to a partially sequenced Tn*1000*-like element found in GenBank accession no. AY598759.
[h] Part of IS*15*.
[i] 5′-CS and 3′-CS are the 5′ conserved segment and 3′ conserved segment, respectively, of a class 1 integron.
[j] Open reading frames orfP and orfQ have also been called orfX and orfX′, respectively.
[k] Found only in *A. baumannii* strains AYE and ACICU.
[l] Was described as IS*Pu12*-like but is not an IS and was therefore renamed.
[m] *sup* (*su*lfate *p*ermease) is incorrectly labeled *sul1* (sulfonamide-resistant dihydropteroate synthase) in previous publications (1, 6, 20); orf4 encodes an open reading frame of unknown function.
[n] Chromosomal gene found in *A. baumannii* strains AYE, ACICU, and ATCC 17978.

of the *aphA1* gene, and a complete copy and a partial copy of IS*26* were found on one side (Fig. 1A, line 3). This structure was named Tn*6020*, and the only sequence in GenBank identical to that of Tn*6020* was the *aphA1* region in AbaR1. In AbaR1, the class 1 integron containing the *aacC1*-orfP-orfP-orfQ-*aadA1* cassette array is next to Tn*6020*, with a short piece of the Tn*21 urf2M* gene separating the IRi integron end from Tn*6020*. PCR was used to link these two regions, followed by sequencing of the PCR amplicon, the same configuration was shown to be present in strain 3208 (Fig. 1A, lines 3 and 4). This finding suggested that there may be a single multiple-antibiotic resistance region in 3208 that is related to or derived from AbaR1. Using the latter part of the AbaR1 sequence as a guide, we mapped and sequenced a continuous region of 36,153 bp from strain 3208 that includes all of the identified antibiotic resistance genes. All of the junctions between adjacent regions (see below for definitions of the regions) were confirmed by PCRs overlapping one or more boundaries, and sequences were assembled using Sequencher, version 4.8 (Gene Codes Corporation, Ann Arbor, MI). The left-hand copy of the *sul1* gene, which is separated from a cadmium/zinc resistance transposon, here designated Tn*6018*, by a region of 29 kb in AbaR1, was linked to Tn*6018* by long-range PCR, and a further 5,986 bp of sequence that includes the region marked X in Fig. 1A was obtained. This 3208 sequence (total of 42,139 bp) commences within the left-hand copy of transposon Tn*6018* (Fig. 1A) and extends to within the chromosomally located ATPase gene that was interrupted by the insertion of AbaR1 (6) (see below for details).

The antibiotic resistance genes all lie between the two copies of Tn*6018*, and we have designated this the multiple-antibiotic resistance region (MARR). To examine how the MARR arose, the various discrete regions of DNA (e.g., gene cassettes, 5′-CS, 3′-CS, and IS*6100*, etc.) that make up the assembled sequence were delineated by matching the sequence with known complete examples of these regions (listed in Table 1) by using the BLAST paired alignment facility (http://blast.ncbi.nlm.nih.gov). Most of the boundaries between independently derived segments (Fig. 1, vertical lines in top line) coincide with one of the inverted repeats (IR) of one of the transposons, and the overall configuration clearly arose by insertion of one transposon into the next, leaving none of them complete. One boundary (marked with a cross in the top line of Fig. 1A) arose by homologous recombination within a short region of identity in the *tnpA* genes of Tn*1721* and Tn*21* to create a hybrid. There are two copies of the *sul1* gene, both located within partial copies of the 3′-CS. The regions to the left and right of these 3′-CS segments, marked X and Y in the top and bottom lines of Fig. 1A, are found only in other AbaR regions (see Table 1 and below), and there are no identifiable features at the boundaries.

The region of 3208 found to the left of the left-hand Tn*6018*

was mapped using overlapping PCRs with primers (see Table S1 in the supplemental material) designed using the sequence of the corresponding region of AbaR1, which contains an arsenate resistance region (Fig. 1A, line 1). The PCR products were digested with restriction enzyme DdeI or HindIII and yielded fragments of the sizes predicted from the AbaR1 sequence, indicating that this region is the same as that in AbaR1. Sequencing revealed that the boundaries with the left-hand part of the ATPase gene and with the left-hand Tn*6018* were identical to those in AbaR1. Because of the similarities to both AbaR1 and AbaR3 (see below), the 3208 region shown between the dashed lines in Fig. 1A was named AbaR5.

Relationship of AbaR5 to AbaR1 and AbaR3. AbaR1 was the first AbaR region identified, and it was defined as the region that has inserted into an ATPase gene in the *A. baumannii* genome, creating a 5-bp duplication (6). AbaR1 is actually a large (86.2-kb) composite transposon that is bounded by imperfect IR of 26 bp (19/26 matches). Our analysis of this sequence revealed that the MARR and the two flanking copies of Tn*6018* together constitute a compound transposon that creates a duplication of 8 bp when inserted into the *uspA* gene in the backbone transposon. AbaR5 has the same general structure. However, none of the resistance genes [*veb1*, *oxa10*, *arr2*, *aadB*, an unnumbered *aacA* gene, *aadA1*, *strA* and *strB*, *cmlA1*, *cmlA5*, *cmlA9*, *tetA*(G), *dfrA1*, and *dfrA10*] found in the first part of the MARR segment of AbaR1 were detected in 3208. Most of this 29-kb region was reanalyzed recently (9) and was shown to consist of a very complex class 1 integron. AbaR1 also carries a *catA1* gene that is missing from AbaR5, and this can be accounted for by an IS*26*-induced deletion of 5,287 bp relative to AbaR1 (boxed in Fig. 1C).

The configuration of the AbaR5 region from strain 3208 is largely identical to that of AbaR3 (GenBank accession no. CP001182). The only difference is that AbaR5 lacks the *catA1* and bla_{TEM} genes found in AbaR3 (Fig. 1B), and this was accounted for by an IS*26*-induced deletion of 7,324 bp (boxed in Fig. 1B). Thus, it is possible that the AbaR5 configuration arose from AbaR3 or that both have a common ancestor.

Clonality. In Europe, much of the increase in resistance is due to the spread of a small number of clones, designated European clones I, II, and III (4, 12, 21, 25). However, these clones have not been reported in Australia (17). As the *A. baumannii* strain AYE, carrying AbaR1, was recently shown to belong to European clone I (21) and as strain AB0057 (AbaR3) is very closely related to it (1) but strain ACICU (AbaR2) belongs to European clone II (7), we examined the possibility that 3208 was a member of one of these clones. By use of a recently described discriminatory PCR assay (21), 3208 was found to belong to European clone I. This is therefore the first report of a European clone I strain in Australia, indicating that the clonal identity of other Australian multiply resistant *A. baumannii* isolates (10, 23), particularly those that carry the same cassette array as AbaR1, AbaR3, and AbaR5 and also the *aphA1b* gene, should be investigated.

Nucleotide sequence accession number. The sequence of the MARR of *A. baumannii* strain 3208 has been deposited in GenBank under accession no. FJ172370.

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