

## Molecular Characterization of a Prophage of *Salmonella enterica* Serotype Typhimurium DT104

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**Isolates of the *Salmonella enterica* serotype Typhimurium definitive phage type (DT104) were found to contain the same prophage (designated phage ST104). The complete sequence of the DNA genome of prophage ST104 was determined. The entire DNA sequence consisted of 41,391 bp, including 64 open reading frames, and exhibited high similarity to P22 and to phage type conversion phage ST64T.**

Recently, *Salmonella enterica* serotype Typhimurium multi-drug-resistant strain definitive phage type 104 (DT104) has emerged and spread over many countries (4, 9, 14, 15). The organism has a core pattern of resistance to ampicillin, chloramphenicol, streptomycin, sulfonamides, and tetracycline. Previously, we used fluorescent amplified-fragment length polymorphism fingerprinting (FAFLP) analysis for molecular epidemiological investigation of serotype Typhimurium (13). Among 120 isolates from cattle, there were 17 FAFLP profiles that formed four distinct clusters (A to D). The isolates belonging to cluster A, in which all of the isolates of DT104 were included, have become increasingly common since 1992 in the northernmost island of Japan. The sequence of a polymorphic marker that is common to the strains of FAFLP cluster A has homology with the segment of the *eae* gene of phage P22. In this study, we isolated prophage ST104, which is common to isolates of DT104, and determined the whole sequence of this phage. The genomic architecture is similar to that of P22, and a number of regions are very similar to those of P22.

**Isolation of prophage common to serotype Typhimurium DT104.** Forty-two serotype Typhimurium strains, including the 12 isolates of DT104 used in this study, were described previously (13). To investigate whether lysogenic prophages are present in serotype Typhimurium, we cultured the strains in the presence of mitomycin C at a concentration of 0.5 µg/ml as previously described (17). Thirty-four out of 42 strains released phages that produced plaques on lawns of serotype Typhimurium strain LT2. To characterize the isolated phages, the restriction patterns of their DNAs were compared. Endonuclease digestion with EcoRI revealed five DNA types, designated a1, a2, b, c, and d (Fig. 1). All of the phages isolated from strains that belong to FAFLP cluster A (13), including 12 isolates of DT104, show the same restriction pattern, type a1 (Fig. 1). We have named this phage ST104. The restriction

patterns of the prophages from strains NET25 and NET26, both of which belong to FAFLP cluster B, are similar to that of ST104; however, an additional EcoRI site was observed (Fig. 1). Therefore, the DNA type of these phages was designated a2. The restriction patterns of the phages isolated from strains belonging to FAFLP cluster B or C are different from those of ST104. No phage was detected in the two strains that belong to FAFLP cluster D. Schicklmaier et al. (10) suggested that prophage restriction patterns in natural isolates of serotype Typhimurium could serve as markers for the epidemiologic classification of pathogenic strains. Our results suggest that the presence of prophage ST104 could be a marker of DT104 or its related strains.

**Sequence of the ST104 genome.** The entire nucleotide sequence of ST104 was 41,391 bp in size. This sequence was homologous to the genomic sequences of both bacteriophages P22 (41,724 bp) and ST64T (40,679 bp). The overall homology between ST104 and P22 was 70.4%, and that between ST104 and ST64T was 74.5%. The average GC content of ST104 was calculated to be 47.3%, which is a level similar to those of phages P22 (47.1%) and ST64T (47.5%).

Schmieger and Schicklmaier (11) reported that all of the DT104 strains examined harbor a prophage, PDT17, that is related to P22 and is a generalized transducing phage, like P22. Our data show that the nucleotide sequence of prophage ST104 has high similarity to that of P22 and that all of the DT104 strains examined harbored ST104, suggesting that ST104 is the same prophage as PDT17.

**Analysis and comparison of ORFs.** A search for open reading frames (ORFs) with WebGeneMark.hmm (5) revealed 64 ORFs larger than 144 nucleotides. A complete list of ST104 ORFs is given in Table 1. We labeled these ORFs consecutively from ORF1 to ORF64. Searches for homologous protein sequences were conducted with the BLAST software (2, 3) against the GenBank database. The characteristics of these ORFs and their corresponding predicted proteins are described in Table 1. Genes with functional assignments were named, and the names of equivalent P22 genes were used when

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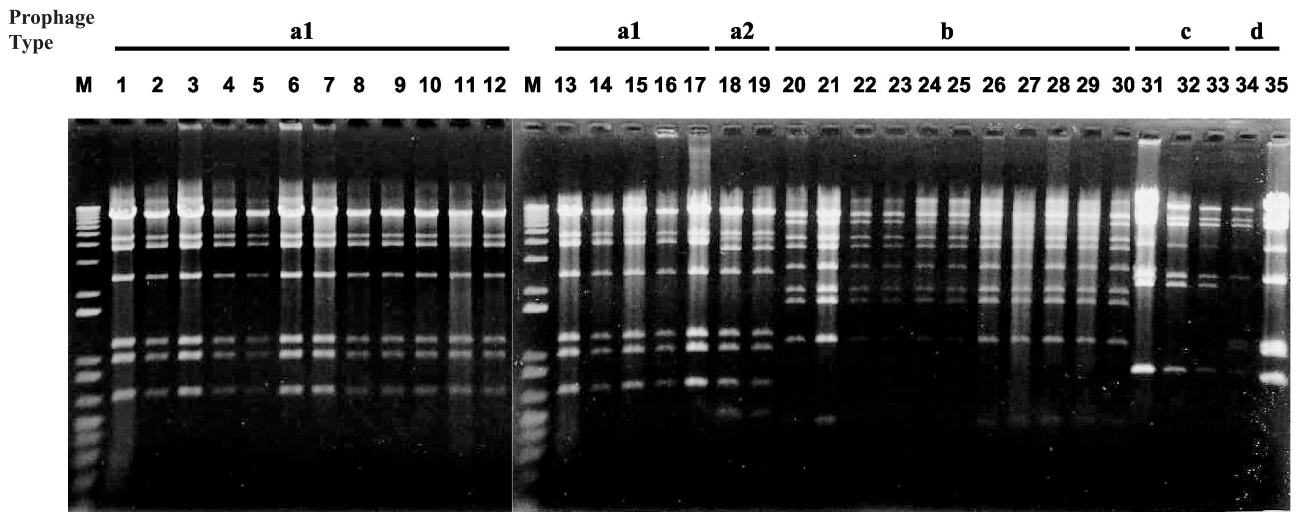


FIG. 1. Electrophoresis of endonuclease digests of phage DNA. Phage DNA was digested with EcoRI and subsequently separated at 10 mV  $\text{cm}^{-1}$  in a 0.8% agarose gel prepared with 89 mM Tris–2.5 M EDTA–89 mM boric acid. Lanes (FAFLP profiles are in parentheses): M, 1-kb ladder; 1, U1 (A2); 2, U2 (A2); 3, U3 (A2); 4, U4 (A2); 5, U5 (A2); 6, U6 (A1); 7, U7 (A2); 8, U8 (A2); 9, U9 (A1); 10, U17 (A2); 11, U18 (A1); 12, U20 (A1); 13, U1 (A1); 14, NET57 (A1); 15, NET2 (A2); 16, NET8 (A3); 17, H6(A4); 18, NET25 (B1); 19, NET26 (B1); 20, KT1 (B2); 21, KT2 (B2); 22, N78 (B2); 23, NET55 (B2); 24, N59 (B5); 25, NET37 (B5); 26, N34 (B5); 27, N79 (B5); 28, N81 (B5); 29, NET48 (B5); 30, NET52 (B6); 31, NET31 (B2); 32, NET40 (C1); 33, KT3 (C1); 34, 478 (B4); 35, N48 (C5).

possible. ST104 has similarities to both P22 and ST64T, not only at the sequence level but also at the gene organization level (Table 1; Fig. 2). Most of the ORFs of prophage ST104 are similar to particular ORFs present in these two bacteriophages. Beginning with a counterpart to P22 *gtrC* (92% identity) and ending with the gene 9 protein of P22 (98% identity),

27 of the translated products of these genes showed more than 90% amino acid sequence identity to P22 (Table 1; Fig. 2). These proteins included the functional serotype conversion cassette, integrase, excisionase, Abc1, superinfection exclusion (gp17), antitermination (gp24), Ral, helicase, NinB, NinD, NinE, NinF, NinG, NinY, NinH, packaging (gp3 and gp2),

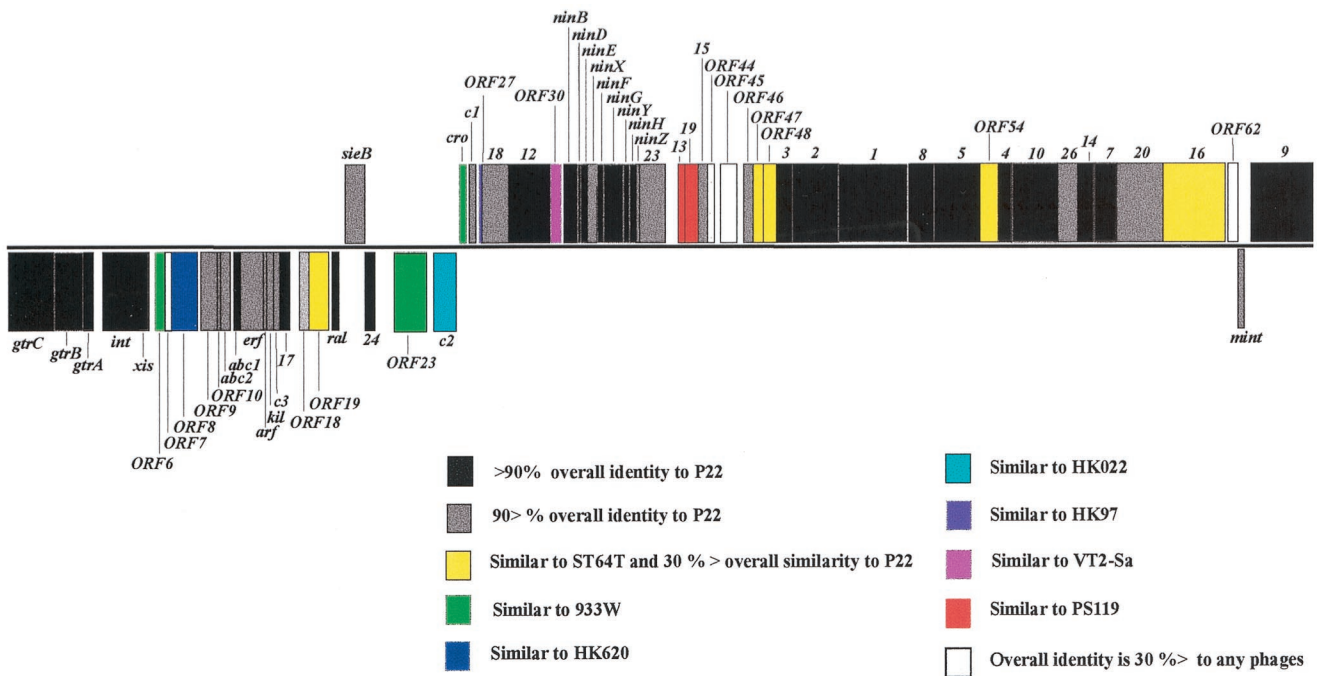


FIG. 2. Schematic illustration of the ST104 genome. The predicted ORFs are illustrated. ORFs with a rightward orientation are above the black line; ORFs with a leftward orientation are below the line. The map was opened adjacent to a stem-loop structure located between gene 9 and *gtrC* as reported in the sequence of P22 (16).

TABLE 1. Characteristics of ST104 ORFs and deduced proteins

ORF	Gene	Direction <sup>a</sup>	Start position	Stop position	Product length (amino acids)	Function of deduced protein	Accession no. and sequence similarity	% Identity <sup>b</sup>
ORF1	<i>gtrC</i>	-	17	1474	485	O-antigen conversion	AAF74999; glucosyl transferase, phage P22 ( <i>S. enterica</i> )	92 (485)
							AAL15475; glucosyl transferase; phage ST64T ( <i>S. enterica</i> )	93 (485)
ORF2	<i>gtrB</i>	-	1464	2396	310	O-antigen conversion	AAF75000; bactoprenol glucosyltransferase, phage P22 ( <i>S. enterica</i> )	99 (310)
							AAL15476; bactoprenol glucosyltransferase, phage ST64T ( <i>S. enterica</i> )	100 (310)
ORF3	<i>gtrA</i>	-	2393	2755	120	O-antigen conversion	AAF75001; translocase, phage P22 ( <i>S. enterica</i> )	100 (120)
							AAL15477; translocase, phage ST64T ( <i>S. enterica</i> )	100 (120)
ORF4	<i>int</i>	-	3104	4267	387	Integrase	AAF75002; integrase, phage P22 ( <i>S. enterica</i> )	97 (387)
							AAL15478; integrase, phage ST64T ( <i>S. enterica</i> )	98 (387)
ORF5	<i>xis</i>	-	4144	4494	116	Excisionase	AAF75003; excisionase, phage P22 ( <i>S. enterica</i> )	97 (116)
							AAL15479; excisionase, phage ST64T ( <i>S. enterica</i> )	97 (116)
ORF6		-	4706	4990	94		AAD25409; hypothetical protein, phage 933W ( <i>E. coli</i> )	97 (94)
ORF7		-	4983	5267	94		BAA84361; hypothetical protein, prophage VT2-Sa ( <i>E. coli</i> )	28 (73)
ORF8		-	5267	6058	263		AAK28855; hypothetical protein, phage HK620 ( <i>E. coli</i> )	88 (130)
							AAD25483; hypothetical protein, phage 933W ( <i>E. coli</i> )	38 (316)
							AAF75008; Ead, phage P22 ( <i>S. enterica</i> )	47 (122)
							AAF75006; Eaa, phage P22 ( <i>S. enterica</i> )	39 (78)
							AAL15482; Eaa2, phage ST64T ( <i>S. enterica</i> )	37 (79)
ORF9		-	6128	6637	169		AAK28856; hypothetical protein, phage HK620 ( <i>E. coli</i> )	49 (169)
ORF10		-	6634	6804	56		AAF75010; Eae, phage P22 ( <i>S. enterica</i> )	62 (86)
							AAK28857; hypothetical protein, phage HK620 ( <i>E. coli</i> )	75 (56)
							AAN52173; ORF56; phage ST64 ( <i>S. enterica</i> )	89 (56)
							AAF75011; ORF56, phage P22 ( <i>S. enterica</i> )	60 (55)
ORF11	<i>abc2</i>	-	6815	7108	97	Anti-RecBCD protein	AAF7512; anti-Rec protein Abc2, phage P22 ( <i>S. enterica</i> )	71 (97)
							AAL15488; anti-Rec protein Abc2, phage ST64T ( <i>S. enterica</i> )	72 (97)
ORF12	<i>abc1</i>	-	7155	7439	94	Anti-RecBCD protein	AAF75013; anti-Rec protein Abc1, phage P22 ( <i>S. enterica</i> )	97 (94)
							AAL15489; anti-Rec protein Abc1, phage ST64T ( <i>S. enterica</i> )	97 (94)
ORF13	<i>erf</i>	-	7439	8146	235	Recombination protein	AAF75014; recombination protein Erf, phage P22 ( <i>S. enterica</i> )	75 (71)
							AAL15490; ORF235, phage ST64T ( <i>S. enterica</i> )	95 (235)
ORF14	<i>arf</i>	-	8143	8286	47	Recombination protein	AF217253; recombination protein Arf, phage P22 ( <i>S. enterica</i> )	87 (47)
ORF15	<i>kil</i>	-	8276	8464	62	Unknown	AAF75016; Kil, phage P22 ( <i>S. enterica</i> )	78 (62)
ORF16	<i>c3</i>	-	8445	8603	52	Regulatory protein	AAF75017; regulatory protein C3, phage P22 ( <i>S. enterica</i> )	75 (52)
							AAL15492; regulatory protein C3, phage ST64T ( <i>S. enterica</i> )	93 (45)
ORF17	<i>17</i>	-	8688	9002	104	Superinfection exclusion protein	AAF75018; superinfection exclusion protein, phage P22 ( <i>S. enterica</i> )	91 (103)
							AAL15493; superinfection exclusion protein, phage ST64T ( <i>S. enterica</i> )	99 (104)
ORF18		-	9278	9565	95		AAF75020; ORF78, phage P22 ( <i>S. enterica</i> )	46 (48)
ORF19		-	9599	10243	214		AAL15494; ORF232, phage ST64T ( <i>S. enterica</i> )	76 (213)
ORF20	<i>ral</i>	-	10327	10521	64	Antirestriction protein	AAF75021; antirestriction protein Ral, phage P22 ( <i>S. enterica</i> )	96 (63)
							AAL15495; antirestriction protein Ral, phage ST64T ( <i>S. enterica</i> )	98 (64)
ORF21	<i>sieB</i>	+	10735	11322	195	Superinfection exclusion protein	AAF75022; superinfection protein, phage P22 ( <i>S. enterica</i> )	88 (192)
ORF22	<i>24</i>	-	11335	11637	100	Antitermination protein	AAF75023; antitermination protein, phage P22 ( <i>S. enterica</i> )	98 (100)
							AAL15496; antitermination protein, phage ST64T ( <i>S. enterica</i> )	96 (75)
ORF23		-	12244	13323	359		CAB39294; hypothetical protein, phage 933W ( <i>E. coli</i> )	34 (357)
ORF24	<i>c2</i>	-	13488	14177	229	Regulatory protein	CAA34222; regularoty protein CI, phage HK022 ( <i>E. coli</i> )	41 (234)
ORF25	<i>cro</i>	+	14288	14503	71	Antirepressor	AAD25431; regulatory protein Cro, phage 933W ( <i>E. coli</i> )	32 (61)
ORF26	<i>c1</i>	+	14614	14895	93	Transcriptional activator	AAL15499; regulatory protein C1, phage ST64T ( <i>S. enterica</i> )	100 (93)
							AAF75026; transcriptional protein, phage P22 ( <i>S. enterica</i> )	49 (93)
ORF27		+	14930	15091	53		AAf31131; gp53, phage HK97 ( <i>E. coli</i> )	100 (53)
ORF28	<i>18</i>	+	15078	15899	273	DNA replication protein	AAF31132; gp54, prophage HK97 ( <i>E. coli</i> )	98 (273)
							AAF75028; DNA replication protein, phage P22 ( <i>S. enterica</i> )	51 (259)
ORF29	<i>12</i>	+	15896	17272	458	Helicase	AAF75029; helicase, phage P22 ( <i>S. enterica</i> )	98 (458)

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TABLE 1—Continued

ORF	Gene	Direction <sup>a</sup>	Start position	Stop position	Product length (amino acids)	Function of deduced protein	Accession no. and sequence similarity	% Identity <sup>b</sup>
ORF30		+	17269	17538	89		BAA84311; ORF28, phage VT2-Sa ( <i>E. coli</i> )	95 (89)
ORF31	<i>ninB</i>	+	17612	18049	145	Unknown	AAF75030; NinB, phage P22 ( <i>S. enterica</i> )	97 (145)
ORF32	<i>ninD</i>	+	18046	18219	57	Unknown	AAL15506; NinB, phage ST64T ( <i>S. enterica</i> ) AAF75031; NinD, phage P22 ( <i>S. enterica</i> )	46 (102) 96 (57)
ORF33	<i>ninE</i>	+	18186	18362	58	Unknown	AAL15507; NinD, phage ST64T ( <i>S. enterica</i> ) AAF75032; NinE, phage P22 ( <i>S. enterica</i> )	96 (57) 98 (58)
ORF34	<i>ninX</i>	+	18359	18706	115	Unknown	AAL15508; NinE, phage ST64T ( <i>S. enterica</i> ) AAF75033; NinX, phage P22 ( <i>S. enterica</i> )	98 (58) 57 (125)
ORF35	<i>ninF</i>	+	18699	18875	58	Unknown	AAL15509; NinX, phage ST64T ( <i>S. enterica</i> ) AAF75034; NinF, phage P22 ( <i>S. enterica</i> )	100 (115) 96 (58)
ORF36	<i>ninG</i>	+	18868	19479	203	Unknown	AAL15510; NinF, phage ST64T ( <i>S. enterica</i> ) AAF75035; NinG, phage P22 ( <i>S. enterica</i> )	85 (57) 94 (203)
ORF37	<i>ninY</i>	+	19476	19700	74	Unknown	AAF75036; NinY, phage P22 ( <i>S. enterica</i> )	97 (74)
ORF38	<i>ninH</i>	+	19697	19900	67	Unknown	AAF75037; NinH, phage P22 ( <i>S. enterica</i> ) AAL15514; NinH, phage ST64T ( <i>S. enterica</i> )	98 (67) 98 (67)
ORF39	<i>ninZ</i>	+	19881	20060	59	Unknown	CAA55166; NinZ, phage P22 ( <i>S. enterica</i> ) AAL15515; NinZ, phage ST64T ( <i>S. enterica</i> )	89 (59) 93 (59)
ORF40	23	+	20057	20830	257	Antitermination protein	AAG55478; antitermination protein, phage CP-933W ( <i>E. coli</i> ) AAA96595; antitermination protein, phage lambda ( <i>E. coli</i> )	43 (272) 42 (256)
ORF41	13	+	21261	21464	67	Holin	AAF75038; antitermination protein, phage P22 ( <i>S. enterica</i> ) CAA09709; holin, phage PS119 ( <i>S. enterica</i> )	39 (256) 100 (67)
ORF42	19	+	21436	21939	167	Lysozyme	CAA09710; lysozyme, phage PS119 ( <i>S. enterica</i> ) AAF75040; lysozyme, phage P22 ( <i>S. enterica</i> )	100 (167) 35 (131)
ORF43	15	+	21936	22403	155	Endopeptidase	CAA09711; endopeptidase, phage PS119 ( <i>S. enterica</i> ) AAF75041; endopeptidase, phage P22 ( <i>S. enterica</i> )	100 (155) 55 (156)
ORF44		+	22156	22362	68		AAL15519; endopeptidase, phage ST64T ( <i>S. enterica</i> ) BAB34244; putative lipoprotein precursor ( <i>E. coli</i> )	39 (151) 95 (68)
ORF45		+	22616	23146	176		CAA33655; KilA, phage P1 ( <i>E. coli</i> )	31 (104)
ORF46		+	23369	23611	80		AAL15520; ORF118, phage ST64T ( <i>S. enterica</i> ) AAF7506; ORF80, phage P22 ( <i>S. enterica</i> )	100 (80) 42 (80)
ORF47		+	23615	24004	129		AAK28888; HkbM, prophage HK620 ( <i>E. coli</i> ) AAL15521; ORF129, phage ST64T ( <i>S. enterica</i> )	43 (80) 100 (117)
ORF48		+	24004	24408	134		AAL15522; ORF134, phage ST64T ( <i>S. enterica</i> )	100 (134)
ORF49	3	+	24412	24900	162	Terminase (small subunit)	AAF75043; terminase small subunit, phage P22 ( <i>S. enterica</i> ) AAL11524; terminase small subunit, phage ST64T ( <i>S. enterica</i> )	96 (162) 100 (162)
ORF50	2	+	24878	26377	499	Terminase (large subunit)	AAF75044; terminase large subunit, phage P22 ( <i>S. enterica</i> ) AAL15523; terminase large subunit, phage ST64T ( <i>S. enterica</i> )	99 (441) 99 (499)
ORF51	1	+	26377	28554	725	Portal protein	AAF75045; portal protein, phage P22 ( <i>S. enterica</i> ) AAL15525; portal protein, phage ST64T ( <i>S. enterica</i> )	98 (705) 99 (725)
ORF52	8	+	28568	29479	303	Scaffolding protein	AAF75046; scaffolding protein, phage P22 ( <i>S. enterica</i> ) AAL15526; scaffolding protein, phage ST64T ( <i>S. enterica</i> )	99 (303) 99 (303)
ORF53	5	+	29479	30771	430	Coat protein	AAF75047; coat protein, phage P22 ( <i>S. enterica</i> ) AAL15527; coat protein, phage ST64T ( <i>S. enterica</i> )	99 (430) 100 (430)
ORF54		+	30812	31372	186		AAL15528; ORF186, phage ST64T ( <i>S. enterica</i> ) AAF75048; ORF69, phage P22 ( <i>S. enterica</i> )	95 (186) 36 (44)
ORF55	4	+	31356	31856	166	DNA stabilization	AAF75049; DNA-stabilizing protein, phage P22 ( <i>S. enterica</i> ) AAL15529; DNA-stabilizing protein, phage ST64T ( <i>S. enterica</i> )	99 (166) 96 (166)
ORF56	10	+	31816	33234	472	Packaged DNA stabilization	AAF75050; packaged DNA stabilization protein, phage P22 ( <i>S. enterica</i> ) AAL15530; packaged DNA stabilization protein, phage ST64T ( <i>S. enterica</i> )	95 (472) 98 (472)
ORF57	26	+	33238	33939	233	Packaged DNA stabilization	AAF75051; packaged DNA stabilization protein, phage P22 ( <i>S. enterica</i> ) AAL15531; packaged DNA stabilization protein, phage ST64T ( <i>S. enterica</i> )	80 (233) 54 (233)

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TABLE 1—Continued

ORF	Gene	Direction <sup>a</sup>	Start position	Stop position	Product length (amino acids)	Function of deduced protein	Accession no. and sequence similarity	% Identity <sup>b</sup>
ORF58	<i>14</i>	+	33939	34394	151	Unknown	AAF75052; gp14, phage P22 ( <i>S. enterica</i> )	92 (151)
							AAL15532; gp14, phage ST64T ( <i>S. enterica</i> )	98 (151)
ORF59	<i>7</i>	+	34397	35086	229	DNA transfer protein	AAF75053; DNA transfer protein, phage P22 ( <i>S. enterica</i> )	96 (229)
							AAL15533; DNA transfer protein, phage ST64T ( <i>S. enterica</i> )	61 (230)
ORF60	<i>20</i>	+	35097	36533	478	DNA transfer protein	AAF75054; DNA transfer protein, phage P22 ( <i>S. enterica</i> )	78 (495)
							AAL15534; DNA transfer protein, phage ST64T ( <i>S. enterica</i> )	58 (449)
ORF61	<i>16</i>	+	36533	38509	658	DNA transfer protein	AAL15535; DNA transfer protein, phage ST64T ( <i>S. enterica</i> )	100 (658)
							AAF75055; DNA transfer protein, phage P22 ( <i>S. enterica</i> )	31 (618)
ORF62		+	38642	38941	99		ZP00032952; hypothetical protein ( <i>Burkholderia fungorum</i> )	42 (87)
ORF63	<i>mnt</i>	−	38962	39210	82	Regulatory protein	AAL15536; regulatory protein, phage ST64T ( <i>S. enterica</i> )	100 (82)
							AAF75057; regulatory protein, phage P22 ( <i>S. enterica</i> )	60 (81)
ORF64	<i>9</i>	+	39346	41349	667	Tailspike protein	AAF75060; tailspike protein, phage P22 ( <i>S. enterica</i> )	98 (667)
							AAL15537; tailspike protein, phage ST64T ( <i>S. enterica</i> )	99 (667)

<sup>a</sup> A plus sign indicates rightward orientation of the gene, and a minus sign indicates leftward orientation of the gene.

<sup>b</sup> Each value in parentheses is the number of amino acids from which the sequence identity is calculated. The GenBank database was used for homology searches.

head (with the exception of gp26, gp20, and gp16), and tail proteins. Three corresponding ORFs, namely, ORF19, ORF47, and ORF48, are present in ST64T but absent in P22.

P22 belongs to the formal tailed-phage family *Podoviridae* because its virions have very short tails (1). This phage also belongs to the informal category known as lambdoid phages. Originally, lambdoid phages were classified as such because they formed recombinant hybrids with phage lambda DNA. Lambdoid phages are often found to have mosaic structures (8). Sequencing of the complete ST104 genome revealed that the ST104 genome is a genetic mosaic composed of gene modules (Table 1; Fig. 2). The morphopoeitic gene products (gp3 through gp9) and some other segments are almost identical to those of P22, whereas lysis genes *13*, *19*, and *15* resemble those of phage PS119. The immunity C (*immC*) region of P22 consists of the repressor gene (*c2*), antirepressor gene (*cro*), and transcriptional activator (*cI*). The deduced product of the *c2* gene of ST104 exhibits no homology to that of P22 but 41% identity to the *cI* gene product of *Escherichia coli* lambdoid phage HK022, which is the most similar protein in the database. The deduced product of the *cro* gene shows a low-level similarity (32% identity) to that of *E. coli* phage 933W. The gene product of *cI* is identical to that of ST64T. The product of replication protein gene *18* shows high similarity (98% identity) to gp54 of *E. coli* phage HK97. Indeed, ST104 is composed of genome segments typical of at least eight different members of the lambdoid phage family.

The genomic architecture of ST104 is similar not only to that of P22 but also to that of ST64T, which is a temperate phage induced by mitomycin C from DT64. The complete genome of ST64T was only found in DT64. ST64T is a generalized transducing phage, is heteroimmune to P22, and mediates phage type conversion (7). ST64T sequence analysis has confirmed that this bacteriophage has an immunity region different from that of P22 (6). It is likely that the phage type is primarily

determined by the carriage of a template phage or the presence or absence of potential receptors on the bacterial cell surface, and it was proposed that integration of ST64T into the chromosome results in phage type conversion by changing immunity to the panel of the typing phage (7). As stated above, the products of *c2* and *cro*, which consists of the *immC* region of ST104, are different from those of P22 and ST64T. In contrast to phage lambda and most other known lambdoid phages, P22 carries, in addition to the *immC* region, a second region, *immI*, that expresses an antirepressor, Ant, and two repressors, Arc and Mnt, that regulate the expression gene *ant* (12). ST104 has the *mint* gene; however, the ORFs corresponding to *arc* and *ant* are not present in ST104. Although we did not examine if ST104 mediates phage type conversion, ST104 might be resident as a prophage within DT104, and the expression of phage immunity proteins then influences the phage typing results. Further studies are needed to elucidate the function of ST104.

**Nucleotide sequence accession numbers.** The DNA sequence data presented here have been submitted to the DDBJ database and appear under accession number AB102868.

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