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Escherichia coli O157:H7 and Other *E. coli* Strains Share Physiological Properties Associated with Intestinal Colonization^{∇†}

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***Escherichia coli* isolates (72 commensal and 10 O157:H7 isolates) were compared with regard to physiological and growth parameters related to their ability to survive and persist in the gastrointestinal tract and found to be similar. We propose that nonhuman hosts in *E. coli* O157:H7 strains function similarly to other *E. coli* strains in regard to attributes relevant to gastrointestinal colonization.**

Escherichia coli is well known for its ecological versatility (15). A life cycle which includes both gastrointestinal and environmental stages has been stressed by both Savageau (15) and Adamowicz et al. (1). The gastrointestinal stage would be subjected to acid and detergent stress. The environmental stage is implicit in *E. coli* having transport systems for fungal siderophores (4) as well as pyrroloquinoline quinone-dependent periplasmic glucose utilization (1) because their presence indicates evolution in a location containing fungal siderophores and pyrroloquinoline quinone (1).

Since its recognition as a food-borne pathogen, there have been numerous outbreaks of food-borne infection due to *E. coli* O157:H7, in both ground beef and vegetable crops (6, 13). Cattle are widely considered to be the primary reservoir of *E. coli* O157:H7 (14), but *E. coli* O157:H7 does not appear to cause disease in cattle. To what extent is *E. coli* O157:H7 physiologically unique compared to the other naturally occurring *E. coli* strains? We feel that the uniqueness of *E. coli* O157:H7 should be evaluated against a backdrop of other wild-type *E. coli* strains, and in this regard, we chose the 72-strain ECOR reference collection originally described by Ochman and Selander (10). These strains were chosen from a collection of 2,600 *E. coli* isolates to provide diversity with regard to host species, geographical distribution, and electromorph profiles at 11 enzyme loci (10).

In our study we compared the 72 strains of the ECOR collection against 10 strains of *E. coli* O157:H7 and six strains of *E. coli* which had been in laboratory use for many years (Table 1). The in vitro comparisons were made with regard to factors potentially relevant to the bacteria's ability to colonize animal guts, i.e., acid tolerance, detergent tolerance, and the presence of the Entner-Doudoroff (ED) pathway (Table 2). Our longstanding interest in the ED pathway (11) derives in part from work by Paul Cohen's group (16, 17) showing that the ED pathway is important for *E. coli* colonization of the mouse large intestine. Growth was assessed by replica plating

88 strains of *E. coli* under 40 conditions (Table 2). These included two LB controls (aerobic and anaerobic), 14 for detergent stress (sodium dodecyl sulfate [SDS], hexadecyltrimethylammonium bromide [CTAB], and benzalkonium chloride, both aerobic and anaerobic), 16 for acid stress (pH 6.5, 6.0, 5.0, 4.6, 4.3, 4.2, 4.1, and 4.0), four for the ability to grow in a defined minimal medium (M63 glucose salts with and without thiamine), and four for the presence or absence of a functional ED pathway (M63 with gluconate or glucuronate). All tests were done with duplicate plates in two or three separate trials. The data are available in Tables S1 to S14 in the supplemental material, and they are summarized in Table 2.

Detergent resistance. SDS resistance is a convenient model for resistance to another powerful detergent, gastrointestinal bile salts (2, 7). Strain numbers (1 to 72) are from the ECOR reference collection (10). Aerobically, all strains grew well in SDS, both 1% and 5% SDS, except for ECOR strains 8, 9, and 63 and *E. coli* O157:H7 strains C503 and C535, which grew poorly. Anaerobically, 53 of the ECOR strains, one *E. coli* O157:H7 strain, and two of the lab-adapted *E. coli* strains grew

TABLE 1. *E. coli* strains used in this study

<i>E. coli</i> strain (n)	Source
ECOR strains (72)	Thomas Whittman
Laboratory adapted (6)	
K-12 Davis	Paul Blum
CG5C 4401	Paul Blum
K-12 Stanford	Paul Blum
W3110	Paul Blum
B	Tyler Kokjohn
AB 1157	Tyler Kokjohn
O157:H7 (10)	
FRIK 528	Andrew Benson
ATCC 43895	Andrew Benson
MC 1061	Andrew Benson
C536	Tim Cebula
C503	Tim Cebula
C535	Tim Cebula
ATCC 43889	William Cray, Jr.
ATCC 43890	William Cray, Jr.
ATCC 43888	William Cray, Jr.
ATCC 43894	William Cray, Jr.

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TABLE 2. Physiological comparison of 88 strains of *Escherichia coli*

Growth medium or condition	Oxygen ^c	No. of strains with type of growth ^b											
		ECOR strains (n = 72)				Laboratory strains (n = 6)				O157:H7 strains (n = 10)			
		Good	Poor	None	Variable	Good	Poor	None	Variable	Good	Poor	None	Variable
LB control ^a	Both	72	0	0	0	6	0	0	0	10	0	0	0
1% SDS	Aerobic	69	3	0	0	6	0	0	0	8	0	0	2
5% SDS	Aerobic	68	4	0	0	6	0	0	0	8	2	0	0
1% SDS	Anaerobic	53	15	4	0	2	3	1	0	1	7	0	2
5% SDS	Anaerobic	0	68	4	0	0	4	2	0	0	7	0	4
CTAB ^d (all)	Both	0	0	72	0	0	0	6	0	0	0	10	0
0.05% BAC	Aerobic	3	11	58	2	0	2	2	2	0	0	9	1
0.2% BAC	Aerobic	0	1	71	0	1	0	5	0	0	0	10	0
0.05% BAC	Anaerobic	2	3	67	0	0	1	5	0	0	0	9	1
0.2% BAC	Anaerobic	0	0	72	0	0	0	6	0	0	0	10	0
pH 6.5	Both	72	0	0	0	6	0	0	0	10	0	0	0
pH 6	Both	72	0	0	0	6	0	0	0	10	0	0	0
pH 5	Both	70	2	0	0	6	0	0	0	9	0	0	1
pH 4.6	Both	70	2	0	0	6	0	0	0	10	0	0	0
pH 4.3	Aerobic	14	0	1	57	3	1	2	0	3	2	0	5
pH 4.3	Anaerobic	69	3	0	0	3	1	2	0	1	1	0	0
pH 4.1 or 4.2	Aerobic	0	0	72	0	ND ^g				ND			
pH 4.0	Both	0	0	72	0	0	0	6	0	0	0	9	1
M63 with supplement ^e													
Glucose	Aerobic ^f	69	1	2	0	5	0	1	0	9	0	1	0
Glucose	Anaerobic ^f	70	0	2	0	5	0	1	0	9	0	1	0
Gluconate	Both	69	1	2	0	5	0	1	0	9	0	1	0
Glucuronate	Aerobic	68	2	2	0	5	0	1	0	9	0	1	0
Glucuronate	Anaerobic	69	1	2	0	5	0	1	0	9	0	1	0

^a Eight LB controls were run, two for each set of LB experiments: SDS, CTAB, benzalkonium chloride (BAC), and pH stress.

^b Growth was measured as either +++, +, or 0 (good, poor, and none, respectively), with +++ being the growth achieved on the LB control plates. "Variable" means that two or three replicates did not agree. All experiments were done at 37°C.

^c "Anaerobic" refers to use of an Oxoid anaerobic chamber. Aerobic and anaerobic growth data are presented together when the results were identical and separately when the results were not the same or the anaerobic set had not been done. LB plates were measured after 1 (aerobic) or 2 (anaerobic) days, and the M63 plates were measured after 2 or 3 days.

^d CTAB used at 0.05, 0.2%, and 0.4%.

^e M63 defined medium (3) was supplemented with glucose, gluconate, or glucuronate, all at 0.2%.

^f Identical results were obtained with and without 0.0001% thiamine.

^g ND, not determined.

well on 1% SDS, but none grew well on 5% SDS (Table 2). It is reasonable that the bacteria grew better on SDS aerobically because SDS resistance is energy dependent; the cells lyse when they run out of energy (2). However, the results were very different with cationic detergents. None of the *E. coli* strains grew on LB agar containing CTAB (Table 2), regardless of the CTAB concentration employed (0.05, 0.2, or 0.4%). This sharp distinction between the effects of anionic and cationic detergents is in agreement with our earlier work on over 200 strains of *Enterobacter cloacae* (7) and our later work showing that *E. coli* MC4100 could tolerate a maximum of only 0.01% CTAB (12). Benzalkonium chloride, another cationic detergent, is less harsh; with 0.05% benzalkonium chloride 14 of the 72 ECOR strains grew aerobically and 5 of those 14 also grew anaerobically (Table 2). None of the *E. coli* O157:H7 strains grew on benzalkonium chloride (0.05 or 0.2%) either aerobically or anaerobically, but four of the six laboratory-adapted strains grew on 0.05% benzalkonium chloride aerobically.

Acid resistance. Acid stress experiments for the ECOR collection show that all of the strains grew well, both aerobically and anaerobically, at pH 4.6 to 6.5 except for strains 8 and 9, which grew poorly at pH 4.6 and 5.0 (Table 2). Similarly, none of the strains grew at pH 4.0, 4.1, or 4.2. Results at pH 4.3 were highly variable, even with three trials. We conclude that, within the limitations of our replica plating method, pH 4.3 is the

acidic threshold of growth for the strains examined, except for strains 8 and 9, for which it is somewhat higher. Our results with the 10 *E. coli* O157:H7 strains were virtually identical (Table 2). Our data are in agreement with the work of Lin et al. (9), who found the minimum growth pH of *E. coli* to be pH 4.4, and of Large et al. (8), who suggested that *E. coli* O157:H7 is not more acid resistant than are other *E. coli* strains. These data are, of course, subject to the caveat that growth in acid is not the same as survival in acid (9).

ED pathway. Only four strains (ECOR 29 and 52, MC1061, and the known auxotroph AB1157) could not grow on M63 with glucose. We did not identify the auxotrophic requirement(s) for these strains. The remaining 84 strains grew well under both aerobic and anaerobic conditions, with the curious exception of ECOR strain 20, which grew much better anaerobically than aerobically with all three carbon sources. In no case did the addition of thiamine permit growth or enhance growth. Significantly, all strains which grew on M63 with glucose also grew on M63 with gluconate or glucuronate. Thus, all strains of *E. coli* have a functional ED pathway. The initial view that *E. coli* possessed the ED pathway was based on only three strains of *E. coli* (5), later increased to 24 strains (18). Clearly, sugar acid metabolism via the ED pathway is important for growth of *E. coli* in intestinal habitats (11).

Conclusions. The major conclusion from this study is that the 10 strains of *E. coli* O157:H7 examined are equivalent to the 72 strains of the ECOR collection with regard to a series of in vitro physiological parameters selected because of their relevance to colonization of animal gastrointestinal tracts. Perhaps significant differences would have been found if we had chosen further in vitro tests, and perhaps our in vitro tests are not directly applicable to in vivo colonization. Nevertheless, the results presented show significant similarities between *E. coli* O157:H7 and other *E. coli* strains. Often *E. coli* O157:H7 control measures are primarily targeted to reducing or eliminating an *E. coli* serotype that is thought to be significantly different from those of other commensal *E. coli* strains. Even though *E. coli* O157:H7 can colonize the human gastrointestinal tract and be highly infectious to humans, it does not usually affect the health of other mammals, including cattle, which commonly carry *E. coli* O157:H7 as a normal part of their fecal flora. Thus, we suggest that strategies to address *E. coli* O157:H7 in nonhuman mammals should not be viewed as eliminating a pathogen but rather should be geared toward containing or controlling a naturally occurring commensal organism.

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Table 1. Response of the 72 *E. coli* in the ECOR collection to the anionic detergent SDS under both aerobic (two trials) and anaerobic (two trials) growth conditions.

ECOR Strain #	AEROBIC			ANAEROBIC		
	No SDS	1% SDS	5% SDS	No SDS	1% SDS	5% SDS
1	3	3	2	3	2	1
2	3	3	2	3	2	1
3	3	3	2	3	1	1
4	3	3	2	3	2	1
5	3	3	2	3	2	1
6	3	3	2	3	2	1
7	3	3	2	3	2	1
8	3	1	1	2	0	0
9	3	1	1	2	0	0
10	3	3	2	3	2	1
11	3	3	2	3	2	1
12	3	3	2	3	2	1
13	3	3	2	3	2	1
14	3	3	2	3	2	1
15	3	3	2	3	2	1

16	3	3	2	3	2	1
17	3	3	2	3	2	1
18	3	3	2	3	2	1
19	3	3	2	3	1	1
20	3	3	2	3	0	0
21	3	3	2	3	2	1
22	3	3	2	3	2	1
23	3	3	2	3	2	1
24	3	3	2	3	2	1
25	3	3	2	3	1	1
26	3	3	2	3	2	1
27	3	3	2	3	1	1
28	3	3	2	3	2	1
29	3	3	2	3	2	1
30	3	3	2	3	2	1
31	3	3	2	3	2	1
32	3	3	2	3	2	1
33	3	3	2	3	2	1
34	3	3	2	3	1	1
35	3	3	2	3	1	1
36	3	3	2	3	2	1
37	3	3	2	3	2	1
38	3	3	2	3	1	1

Table 1. (continued)

ECOR Strain #	AEROBIC			ANAEROBIC		
	No SDS ^a	1% SDS	5% SDS	No SDS ^a	1% SDS	5% SDS
39	3	3	2	3	1	1
40	3	3	2	3	1	1
41	3	3	2	3	2	1
42	3	3	2	3	2	1
43	3	3	2	3	1	1
44	3	3	2	3	1	1
45	3	3	2	3	1	1
46	3	3	2	3	2	1
47	3	3	2	3	1	1
48	3	3	2	3	1	1
49	3	3	1	3	2	1
50	3	3	2	3	1	1
51	3	3	2	3	2	1
52	3	3	2	3	2	1
53	3	3	2	3	2	1
54	3	3	2	3	2	1
55	3	3	2	3	2	1

56	3	3	2	3	2	1
57	3	3	2	3	2	1
58	3	3	2	3	2	1
59	3	3	2	3	2	1
60	3	3	2	3	2	1
61	3	3	2	3	2	1
62	3	3	2	3	2	1
63	3	1	1	3	0	0
64	3	3	2	3	2	1
65	3	3	2	3	2	1
66	3	3	2	3	2	1
67	3	3	2	3	2	1
68	3	3	2	3	2	1
69	3	3	2	3	2	1
70	3	3	2	3	2	1
71	3	3	2	3	2	1
72	3	3	2	3	2	1

^{a/} Just LB agar plates. Last plate replicated so it serves as a control for the efficiency of transfer during replica plating. Each trial was done with duplicate replica plates. One number in a column means that the duplicate plates for a given trial agreed with one another and that the multiple trials gave the same result. Multiple numbers indicate disagreement. In the text, values of 0, 1, 2, and 3 are presented as -, +, ++, and +++, respectively. This footnote applies to all 13 Tables.

Table 2. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to the anionic detergent SDS under both aerobic and anaerobic growth conditions.

Lab adapted <i>E. coli</i>	AEROBIC			ANAEROBIC		
	NoSDS ^a	1% SDS	5% SDS	NoSDS	1% SDS	5% SDS
K12 Davis	3	3	3	2	2	1
CG5C 4401	3	3	3	2	0	0
K12 Stanford	3	3	3	2	2	1
W3110	3	2	2	2	1	0
B	3	3	3	2	1	1
AB 1157	3	2	2	2	1	1

<i>E. coli</i> O157:H7s	AEROBIC			ANAEROBIC		
	NoSDS ^a	1% SDS	5% SDS	NoSDS	1% SDS	5% SDS
FRIK 528	3	3	3	2	1	1, 0
ATCC 43895	3	3	3	2	1	1, 0
MC 1061	3	3	2	2	1, 0	1, 0
C536	3	3	3	2	1	1
C503	3	2, 0	1	2	1, 0	1, 0
C535	3	2, 0	1	2	1	1
ATCC 43889	3	3	3	2	1, 2	1

ATCC 43890	3	3	3	2	1, 2	1
ATCC 43888	3	3	3	2	1, 2	1
ATCC 43894	3	3	3	2	2	1

Table 3. Response of the 72 *E. coli* in the ECOR collection to the anionic detergent hexadecyl (cetyl) trimethylammonium bromide under both aerobic (one trial) and anaerobic (one trial) growth conditions.

ECOR Strain #	AEROBIC % CTAB				ANAEROBIC % CTAB			
	0 ^a	0.05	0.2	0.4	0 ^a	0.05	0.2	0.4
1	3	0	0	0	3	0	0	0
2	3	0	0	0	3	0	0	0
3	3	0	0	0	3	0	0	0
4	3	0	0	0	3	0	0	0
5	3	0	0	0	3	0	0	0
6	3	0	0	0	3	0	0	0
7	3	0	0	0	3	0	0	0
8	3	0	0	0	3	0	0	0
9	3	0	0	0	3	0	0	0
10	3	0	0	0	3	0	0	0
11	3	0	0	0	3	0	0	0
12	3	0	0	0	3	0	0	0
13	3	0	0	0	3	0	0	0
14	3	0	0	0	3	0	0	0
15	3	0	0	0	3	0	0	0
16	3	0	0	0	3	0	0	0
17	3	0	0	0	3	0	0	0

18	3	0	0	0	3	0	0	0
19	3	0	0	0	3	0	0	0
20	3	0	0	0	3	0	0	0
21	3	0	0	0	3	0	0	0
22	3	0	0	0	3	0	0	0
23	3	0	0	0	3	0	0	0
24	3	0	0	0	3	0	0	0
25	3	0	0	0	3	0	0	0
26	3	0	0	0	3	0	0	0
27	3	0	0	0	3	0	0	0
28	3	0	0	0	3	0	0	0
29	3	0	0	0	3	0	0	0
30	3	0	0	0	3	0	0	0
31	3	0	0	0	3	0	0	0
32	3	0	0	0	3	0	0	0
33	3	0	0	0	3	0	0	0
34	3	0	0	0	3	0	0	0
35	3	0	0	0	3	0	0	0
36	3	0	0	0	3	0	0	0
37	3	0	0	0	3	0	0	0
38	3	0	0	0	3	0	0	0

Table 3. (continued)

ECOR Strain #	AEROBIC % CTAB				ANAEROBIC % CTAB			
	0^a	0.05	0.2	0.4	0^a	0.05	0.2	0.4
39	3	0	0	0	3	0	0	0
40	3	0	0	0	3	0	0	0
41	3	0	0	0	3	0	0	0
42	3	0	0	0	3	0	0	0
43	3	0	0	0	3	0	0	0
44	3	0	0	0	3	0	0	0
45	3	0	0	0	3	0	0	0
46	3	0	0	0	3	0	0	0
47	3	0	0	0	3	0	0	0
48	3	0	0	0	3	0	0	0
49	3	0	0	0	3	0	0	0
50	3	0	0	0	3	0	0	0
51	3	0	0	0	3	0	0	0
52	3	0	0	0	3	0	0	0
53	3	0	0	0	3	0	0	0
54	3	0	0	0	3	0	0	0
55	3	0	0	0	3	0	0	0
56	3	0	0	0	3	0	0	0
57	3	0	0	0	3	0	0	0

58	3	0	0	0	3	0	0	0
59	3	0	0	0	3	0	0	0
60	3	0	0	0	3	0	0	0
61	3	0	0	0	3	0	0	0
62	3	0	0	0	3	0	0	0
63	3	0	0	0	3	0	0	0
64	3	0	0	0	3	0	0	0
65	3	0	0	0	3	0	0	0
66	3	0	0	0	3	0	0	0
67	3	0	0	0	3	0	0	0
68	3	0	0	0	3	0	0	0
69	3	0	0	0	3	0	0	0
70	3	0	0	0	3	0	0	0
71	3	0	0	0	3	0	0	0
72	3	0	0	0	3	0	0	0

Table 4. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to the cationic detergent hexadecyl (cetyl) trimethylammonium bromide under both aerobic conditions and anaerobic growth conditions.

Lab adapted <i>E. coli</i>	AEROBIC %CTAB				ANAEROBIC %CTAB			
	0 ^a	0.05	0.2	0.4	0 ^a	0.05	0.2	0.4
K12 Davis	3	0	0	0	2	0	0	0
CG5C 4401	3	0	0	0	2	0	0	0
K12 Stanford	3	0	0	0	2	0	0	0
W3110	3	0	0	0	2	0	0	0
B	3	0	0	0	2	0	0	0
AB 1157	3	0	0	0	2	0	0	0

<i>E. coli</i> O157:H7s	AEROBIC %CTAB				ANAEROBIC %CTAB			
	0 ^a	0.05	0.2	0.4	0 ^a	0.05	0.2	0.4
FRIK 528	3	0	0	0	2	0	0	0
ATCC 43895	3	0	0	0	2	0	0	0
MC 1061	3	0	0	0	2	0	0	0
C536	3	0	0	0	2	0	0	0
C503	3	0	0	0	2	0	0	0
C535	3	0	0	0	2	0	0	0
ATCC 43889	3	0	0	0	2	0	0	0
ATCC 43890	3	0	0	0	2	0	0	0

ATCC 43888	3	0	0	0	2	0	0	0
ATCC 43894	3	0	0	0	2	0	0	0

Table 5. Response of the 72 *E. coli* in the ECOR collection to the cationic detergent benzalkonium chloride under both aerobic (one trial) and anaerobic (one trial) growth conditions.

ECOR Strain #	AEROBIC % benzalkonium chloride			ANAEROBIC % benzalkonium chloride		
	0 ^a	0.05	0.20	0 ^a	0.05	0.20
1	3	2	0	3	2	0
2	3	0	0	3	0	0
3	3	0	0	3	0	0
4	3	2	1	3	2	0
5	3	0	0	3	0	0
6	3	1	0	3	1	0
7	3	0	0	3	0	0
8	3	0	0	3	0	0
9	3	0	0	3	0	0
10	3	2	0	3	0	0
11	3	0	0	3	0	0
12	3	1	0	3	0	0
13	3	1	0	3	0	0
14	3	0	0	3	0	0
15	3	1	0	3	0	0
16	3	1	0	3	0	0
17	3	0	0	3	0	0

18	3	1	0	3	1	0
19	3	0	0	3	0	0
20	3	0	0	3	0	0
21	3	0	0	3	0	0
22	3	1	0	3	0	0
23	3	0	0	3	0	0
24	3	0	0	3	0	0
25	3	0	0	3	0	0
26	3	0	0	3	0	0
27	3	0	0	3	0	0
28	3	0	0	3	0	0
29	3	0	0	3	0	0
30	3	1	0	3	0	0
31	3	0	0	3	0	0
32	3	0	0	3	0	0
33	3	0	0	3	0	0
34	3	1	0	3	0	0
35	3	0	0	3	0	0
36	3	0	0	3	0	0
37	3	0	0	3	0	0
38	3	0	0	3	0	0

Table 5. (continued)

ECOR Strain #	AEROBIC % benzalkonium choloride			ANAEROBIC % benzalkonium choloride		
	0^a	0.05	0.2	0^a	0.05	0.2
39	3	0	0	3	0	0
40	3	0	0	3	0	0
41	3	0	0	3	0	0
42	3	0	0	3	0	0
43	3	0	0	3	0	0
44	3	0	0	3	0	0
45	3	1	0	3	0	0
46	3	0	0	3	0	0
47	3	0	0	3	0	0
48	3	0	0	3	0	0
49	3	0	0	3	0	0
50	3	0	0	3	0	0
51	3	0	0	3	0	0
52	3	0	0	3	0	0
53	3	0	0	3	0	0
54	3	0	0	3	0	0
55	3	0	0	3	0	0
56	3	0	0	3	0	0
57	3	0	0	3	0	0

58	3	0	0	3	0	0
59	3	0	0	3	0	0
60	3	0	0	3	0	0
61	3	0	0	3	0	0
62	3	0	0	3	0	0
63	3	0	0	3	0	0
64	3	0	0	3	0	0
65	3	0	0	3	0	0
66	3	0	0	3	0	0
67	3	0	0	3	0	0
68	3	0	0	3	0	0
69	3	0	0	3	0	0
70	3	0	0	3	0	0
71	3	1	0	3	1	0
72	3	0	0	3	0	0

Table 6. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to the cationic detergent benzalkonium chloride under both aerobic and anaerobic growth conditions.

Lab adapted <i>E. coli</i>	AEROBIC %Benzalkonium Chloride			ANAEROBIC %Benzalkonium Chloride		
	0 ^a	0.05	0.2	0 ^a	0.05	0.2
K12 Davis	3	1	0	2	1	0
CG5C 4401	3	0	0	2	0	0
K12 Stanford	3	1	0	2	0	0
W3110	3	0	0	2	0	0
B	3	2, 0	2	2	0	0
AB 1157	3	1, 0	0	2	0	0

<i>E. coli</i> O157:H7s	AEROBIC %Benzalkonium Chloride			ANAEROBIC %Benzalkonium Chloride		
	0 ^a	0.05	0.2	0 ^a	0.05	0.2
FRIK 528	3	0, 1	0	2	0	0
ATCC 43895	3	0	0	2	0	0
MC 1061	3	0	0	2	0	0
C536	3	0	0	2	0	0
C503	3	0	0	2	0, 1	0
C535	3	0	0	2	0	0
ATCC 43889	3	0	0	2	0	0

ATCC 43890	3	0	0	2	0	0
ATCC 43888	3	0	0	2	0	0
ATCC 43894	3	0	0	2	0	0

Table 7. Response of the 72 *E. coli* in the ECOR collection to acid stress under aerobic conditions (two trials).

ECOR Strain #	Culture pH values							
	6.5	6.0	5.0	4.6	4.3 ^a	4.2	4.1	4.0
1	3	3	3	3	2, 2, 2	0	0	0
2	3	3	3	3	2, 0, 2	0	0	0
3	3	3	3	3	2, 0, 2	0	0	0
4	3	3	3	3	2, 2, 2	0	0	0
5	3	3	3	3	0, 0, 2	0	0	0
6	3	3	3	3	0, 0, 2	0	0	0
7	3	3	3	3	2, 0, 2	0	0	0
8	2	2	1	1	0, 0, 0	0	0	0
9	2	2	1	1	1, 0, 0	0	0	0
10	3	3	3	3	2, 0, 2	0	0	0
11	3	3	3	3	0, 0, 2	0	0	0
12	3	3	3	3	0, 0, 2	0	0	0
13	3	3	3	3	0, 0, 2	0	0	0
14	3	3	3	3	2, 0, 2	0	0	0
15	3	3	3	3	2, 0, 2	0	0	0
16	3	3	3	3	2, 2, 2	0	0	0
17	3	3	3	3	2, 1, 2	0	0	0
18	3	3	3	3	0, 0, 2	0	0	0
19	3	3	3	3	0, 0, 2	0	0	0
20	3	3	3	3	0, 0, 2	0	0	0

21	3	3	3	3	0, 0, 2	0	0	0
22	3	3	3	3	0, 0, 2	0	0	0
23	3	3	3	3	2, 0, 2	0	0	0
24	3	3	3	3	1, 0, 2	0	0	0
25	3	3	3	3	2, 0, 2	0	0	0
26	3	3	3	3	2, 2	0	0	0
27	3	3	3	3	2, 2	0	0	0
28	3	3	3	3	0, 2	0	0	0
29	3	3	3	3	0, 2	0	0	0
30	3	3	3	3	0, 2	0	0	0
31	3	3	3	3	2, 2	0	0	0
32	3	3	3	3	2, 2	0	0	0
33	3	3	3	3	1, 2	0	0	0
34	3	3	3	3	0, 2	0	0	0
35	3	3	3	3	2, 2	0	0	0
36	3	3	3	3	1, 2	0	0	0
37	3	3	3	3	2, 2	0	0	0
38	3	3	3	3	0, 2	0	0	0

Table 7. (continued)

ECOR Strain #	Culture pH values							
	6.5	6.0	5.0	4.6	4.3^a	4.2	4.1	4.0
39	3	3	3	3	0, 2	0	0	0
40	3	3	3	3	2, 2	0	0	0
41	3	3	3	3	0, 2	0	0	0
42	3	3	3	3	0, 2	0	0	0
43	3	3	3	3	0, 2	0	0	0
44	3	3	3	3	2, 2	0	0	0
45	3	3	3	3	2, 2	0	0	0
46	3	3	3	3	0, 2	0	0	0
47	3	3	3	3	0, 2	0	0	0
48	3	3	3	3	0, 2	0	0	0
49	3	3	3	3	0, 2	0	0	0
50	3	3	3	3	0, 2	0	0	0
51	3	3	3	3	0, 0, 2	0	0	0
52	3	3	3	3	2, 2, 2	0	0	0
53	3	3	3	3	0, 1, 2	0	0	0
54	3	3	3	3	2, 2, 2	0	0	0
55	3	3	3	3	0, 1, 2	0	0	0
56	3	3	3	3	1, 0, 2	0	0	0
57	3	3	3	3	0, 0, 2	0	0	0
58	3	3	3	3	0, 2, 2	0	0	0
59	3	3	3	3	0, 2, 2	0	0	0

60	3	3	3	3	0, 2, 2	0	0	0
61	3	3	3	3	0, 0, 2	0	0	0
62	3	3	3	3	0, 0, 2	0	0	0
63	3	3	3	3	0, 0, 2	0	0	0
64	3	3	3	3	0, 2, 2	0	0	0
65	3	3	3	3	0, 0, 2	0	0	0
66	3	3	3	3	0, 0, 2	0	0	0
67	3	3	3	3	0, 0, 2	0	0	0
68	3	3	3	3	0, 0, 2	0	0	0
69	3	3	3	3	0, 0, 2	0	0	0
70	3	3	3	3	0, 0, 2	0	0	0
71	3	3	3	3	0, 0, 2	0	0	0
72	3	3	3	3	0, 0, 2	0	0	0

^a/ pH 4.3 = three trials

Table 8. Response of the 72 *E. coli* in the ECOR collection to acid stress under anaerobic conditions (two trials).

ECOR Strain #	Culture pH values					
	6.5	6.0	5.0	4.6	4.3	4.0
1	3	3	3	3	2	0
2	3	3	3	3	2	0
3	3	3	3	3	2	0
4	3	3	3	3	2	0
5	3	3	3	3	2	0
6	3	3	3	3	2	0
7	3	3	3	3	2	0
8	2	2	1	1	1	0
9	2	2	1	1	1	0
10	3	3	3	3	2	0
11	3	3	3	3	2	0
12	3	3	3	3	2	0
13	3	3	3	3	2	0
14	3	3	3	3	2	0
15	3	3	3	3	2	0
16	3	3	3	3	2	0
17	3	3	3	3	2	0
18	3	3	3	3	2	0
19	3	3	3	3	2	0
20	3	3	3	3	2	0

21	3	3	3	3	2	0
22	3	3	3	3	2	0
23	3	3	3	3	2	0
24	3	3	3	3	2	0
25	3	3	3	3	2	0
26	3	3	3	3	2	0
27	3	3	3	3	2	0
28	3	3	3	3	2	0
29	3	3	3	3	2	0
30	3	3	3	3	2	0
31	3	3	3	3	2	0
32	3	3	3	3	2	0
33	3	3	3	3	1	0
34	3	3	3	3	2	0
35	3	3	3	3	2	0
36	3	3	3	3	2	0
37	3	3	3	3	2	0
38	3	3	3	3	2	0

Table 8. (continued)

ECOR Strain #	Culture pH values					
	6.5	6.0	5.0	4.6	4.3	4.0
39	3	3	3	3	2	0
40	3	3	3	3	2	0
41	3	3	3	3	2	0
42	3	3	3	3	2	0
43	3	3	3	3	2	0
44	3	3	3	3	2	0
45	3	3	3	3	2	0
46	3	3	3	3	2	0
47	3	3	3	3	2	0
48	3	3	3	3	2	0
49	3	3	3	3	2	0
50	3	3	3	3	2	0
51	3	3	3	3	2	0
52	3	3	3	3	2	0
53	3	3	3	3	2	0
54	3	3	3	3	2	0
55	3	3	3	3	2	0
56	3	3	3	3	2	0
57	3	3	3	3	2	0
58	3	3	3	3	2	0
59	3	3	3	3	2	0

60	3	3	3	3	2	0
61	3	3	3	3	2	0
62	3	3	3	3	2	0
63	3	3	3	3	2	0
64	3	3	3	3	2	0
65	3	3	3	3	2	0
66	3	3	3	3	2	0
67	3	3	3	3	2	0
68	3	3	3	3	2	0
69	3	3	3	3	2	0
70	3	3	3	3	2	0
71	3	3	3	3	2	0
72	3	3	3	3	2	0

Table 9. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to acid stress under aerobic growth conditions.

Culture pH values						
Lab adapted <i>E. coli</i>	6.5 ^a	6	5	4.6	4.3	4.0
K12 Davis	3	3	3	3	2	0
CG5C 4401	3	3	3	3	0	0
K12 Stanford	3	3	3	3	2	0
W3110	3	3	3	3	1	0
B	3	3	3	3	3	0
AB 1157	3	3	3	2	0	0

Culture pH values						
<i>E. coli</i> O157:H7s	6.5 ^a	6	5	4.6	4.3	4.0
FRIK 528	3	3	3	3	1, 2	0
ATCC 43895	3	3	3	3	2	0
MC 1061	3	3	2, 3	2	0, 1	0
C536	3	3	3	3	1, 3	0, 1
C503	3	3	3	3	0, 1	0
C535	3	3	3	3	0, 1	0
ATCC 43889	3	3	3	3	0, 2	0
ATCC 43890	3	3	3	3	0, 2	0
ATCC 43888	3	3	3	3	1	0
ATCC 43894	3	3	3	3	1, 3	0

Table 10. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to acid stress under anaerobic growth conditions.

Lab adapted <i>E. coli</i>	Culture pH values					
	6.5^a	6	5	4.6	4.3	4.0
K12 Davis	2	2	2	2	1	0
CG5C 4401	2	2	1	0	0	0
K12 Stanford	2	2	2	1	0	0
W3110	2	2	2	1	0	0
B	2	2	2	0	0	0
AB 1157	2	2	2	0	0	0

<i>E. coli</i> O157:H7s	Culture pH values					
	6.5^a	6	5	4.6	4.3	4.0
FRIK 528	2	2	2	1, 2	0, 1	0
ATCC 43895	2	1, 2	2	1, 2	0, 2	0
MC 1061	2	2	1, 2	1, 2	0	0
C536	2	2	2	1, 2	0, 1	0, 1
C503	2	2	2	1, 2	0, 1	0
C535	2	2	2	1, 2	0	0
ATCC 43889	2	2	2	1, 2	0, 1	0
ATCC 43890	2	2	2	1, 2	0, 1	0
ATCC 43888	2	2	2	1, 2	0	0
ATCC 43894	2	2	2	2	0, 1	0

Table 11. Response of the 72 *E. coli* in the ECOR collection to M63 glucose, a minimal defined growth medium, under both aerobic (three trials) and anaerobic (three trials) growth conditions.

ECOR Strain #	AEROBIC		ANAEROBIC	
	LB ^a	M63 glucose	LB ^a	M63 glucose
1	3	3	3	3
2	3	3	3	3
3	3	3	3	3
4	3	3	3	3
5	3	3	3	3
6	3	3	3	3
7	3	3	3	3
8	3	3	2	2
9	3	3	2	2
10	3	3	3	3
11	3	3	3	3
12	3	3	3	3
13	3	3	3	3
14	3	3	3	3
15	3	3	3	3
16	3	3	3	3
17	3	3	3	3
18	3	3	3	3
19	3	3	3	3
20	3	1	3	3
21	3	3	3	3
22	3	3	3	3

23	3	2	3	2
24	3	3	3	3
25	3	3	3	3
26	3	3	3	3
27	3	3	3	3
28	3	3	3	3
29	3	0	3	0
30	3	3	3	3
31	3	3	3	3
32	3	3	3	3
33	3	3	3	3
34	3	3	3	3
35	3	3	3	3
36	3	3	3	3
37	3	3	3	3
38	3	3	3	3

Table 11. (continued)

ECOR Strain #	AEROBIC		ANAEROBIC	
	LB^a	M63 glucose	LB^a	M63 glucose
39	3	3	3	3
40	3	3	3	3
41	3	3	3	3
42	3	3	3	3
43	3	3	3	3
44	3	3	3	3
45	3	3	3	3
46	3	2	3	3
47	3	3	3	3
48	3	3	3	3
49	3	3	3	3
50	3	3	3	3
51	3	3	3	2
52	3	0	3	0
53	3	3	3	3
54	3	3	3	3
55	3	3	3	3
56	3	3	3	3
57	3	3	3	3
58	3	3	3	3
59	3	3	3	3
60	3	3	3	3
61	3	3	3	3
62	3	3	3	3

63	3	3	3	2
64	3	3	3	3
65	3	3	3	3
66	3	3	3	3
67	3	3	3	3
69	3	3	3	3
70	3	3	3	3
71	3	3	3	3
72	3	3	3	3

Table 12. Response of the 6 lab adapted *E. coli* and the 10 *E. coli* O157:H7s to M63 glucose, a minimal defined growth medium, under both aerobic (two trials) and anaerobic (two trials) growth conditions.

	AEROBIC		ANAEROBIC	
Lab adapted <i>E. coli</i>	LB ^a	M63 glucose	LB ^a	M63 glucose
K12 Davis	3	3	2	2
CG5C 4401	3	3	2	2
K12 Stanford	3	3	2	2
W3110	3	3	2	2
B	3	3	2	2
AB 1157	3	0	2	0

	AEROBIC		ANAEROBIC	
<i>E. coli</i> O157:H7s	LB ^a	M63 glucose	LB ^a	M63 glucose
FRIK 528	3	3	2	2
ATCC 43895	3	3	2	2
MC 1061	3	0	2	0
C536	3	3	2	2
C503	3	3	2	2
C535	3	3	2	2
ATCC 43889	3	3	2	2
ATCC 43890	3	3	2	2
ATCC 43888	3	3	2	2
ATCC 43894	3	3	2	2

Table 13. Response of the 72 *E. coli* in the ECOR collection to M63 gluconate and M63 glucuronate under both aerobic (two trials) and anaerobic (two trials) growth conditions.

ECOR Strain #	AEROBIC			ANAEROBIC		
	LB ^a	M63 gluconate	M63 glucuronate	LB ^a	M63 gluconate	M63 glucuronate
1	3	3	3	3	3	3
2	3	3	3	3	3	3
3	3	3	3	3	3	3
4	3	3	3	3	3	3
5	3	3	3	3	3	3
6	3	3	3	3	3	3
7	3	3	3	3	3	3
8	3	3	3	2	2	2
9	3	3	3	2	2	2
10	3	3	3	3	3	3
11	3	3	3	3	3	3
12	3	3	3	3	3	3
13	3	3	3	3	3	3
14	3	3	3	3	3	3
15	3	3	3	3	3	3
16	3	3	3	3	3	3
17	3	3	3	3	3	3
18	3	3	3	3	3	3
19	3	3	3	3	3	3
20	3	1	1	3	3	3
21	3	3	3	3	3	3
22	3	3	3	3	3	3
23	3	2	1	3	3	3
24	3	3	3	3	3	3

25	3	3	3	3	3	3
26	3	3	3	3	3	3
27	3	3	3	3	3	3
28	3	3	3	3	3	3
29	3	0	0	3	0	0
30	3	3	3	3	3	3
31	3	3	3	3	3	3
32	3	3	3	3	3	3
33	3	3	3	3	3	3
34	3	3	3	3	3	3
35	3	3	3	3	3	3
36	3	3	3	3	3	3
37	3	3	3	3	3	3
38	3	3	3	3	3	3

Table 13. (continued)

ECOR Strain #	AEROBIC			ANAEROBIC		
	LB ^a	M63 gluconate	M63 glucuronate	LB ^a	M63 gluconate	M63 glucuronate
39	3	3	3	3	3	3
40	3	3	3	3	3	3
41	3	3	3	3	3	3
42	3	3	3	3	3	3
43	3	3	3	3	3	3
44	3	3	3	3	3	3
45	3	3	3	3	3	3
46	3	2	2	3	3	3
47	3	3	3	3	3	3
48	3	3	3	3	3	3
49	3	3	3	3	1	1
50	3	3	3	3	3	3
51	3	3	3	3	3	3
52	3	0	0	3	0	0
53	3	3	3	3	3	3
54	3	3	3	3	3	3
55	3	3	3	3	3	3
56	3	3	3	3	3	3
57	3	3	3	3	3	3
58	3	3	3	3	3	3
59	3	3	3	3	3	3
60	3	3	3	3	3	3
61	3	3	3	3	3	3
62	3	3	3	3	3	3
63	3	3	3	3	3	3
64	3	3	3	3	3	3

65	3	3	3	3	3	3
66	3	3	3	3	3	3
67	3	3	3	3	3	3
69	3	3	3	3	3	3
70	3	3	3	3	3	3
71	3	3	3	3	3	3
72	3	3	3	3	3	3

Table 14. Response of the 6 lab adapted *E. coli* (one trial) and the 10 *E. coli* O157:H7s (two trials) to M63 gluconate and M63 glucuronate under both aerobic and anaerobic growth conditions.

AEROBIC				ANAEROBIC		
Lab adapted <i>E. coli</i>	LB ^a	M63 gluconate	M63 glucuronate	LB ^a	M63 gluconate	M63 glucuronate
K12 Davis	3	3	3	2	2	2
CG5C 4401	3	3	3	2	2	2
K12 Stanford	3	3	3	2	2	2
W3110	3	3	3	2	2	2
B	3	3	3	2	2	2
AB 1157	3	0	0	2	0	0

AEROBIC				ANAEROBIC		
<i>E. coli</i> O157:H7s	LB ^a	M63 gluconate	M63 glucuronate	LB ^a	M63 gluconate	M63 glucuronate
FRIK 528	3	3	3	2	2	2
ATCC 43895	3	3	3	2	2	2
MC 1061	3	0	0	2	0	0
C536	3	3	3	2	2	2
C503	3	3	3	2	2	2
C535	3	3	3	2	2	2
ATCC 43889	3	3	3	2	2	2
ATCC 43890	3	3	3	2	2	2
ATCC 43888	3	3	3	2	2	2
ATCC 43894	3	3	3	2	2	2

