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Adherent-Invasive *Escherichia coli* Phenotype Displayed by Intestinal Pathogenic *E. coli* Strains from Cats, Dogs, and Swine[▽]

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The adherent-invasive *Escherichia coli* (AIEC) pathotype, which has been associated with Crohn's disease, shows similar traits to human and animal extraintestinal pathogenic *E. coli* (ExPEC) with respect to their phylogenetic origin and virulence gene profiles. Here, we demonstrate that animal ExPEC strains generally do not share the AIEC phenotype. In contrast, this phenotype is very frequent among animal intestinal pathogenic *E. coli* (InPEC) strains, particularly of feline and canine origin, that genetically resemble ExPEC. These results strengthen the particular identity and disease specificity of the AIEC pathotype and the putative role animals might play in the transmission of AIEC-like strains to humans.

Adherent-invasive *Escherichia coli* (AIEC) is a recently described pathotype that has been repeatedly associated with Crohn's disease (2, 4, 8, 9, 13). Nowadays, this pathotype can be identified only by phenotypical traits, because no specific virulence genes have been discovered to date. The identification of AIEC strains is based on their ability to adhere to and to invade intestinal epithelial cells, as well as their capacity to survive and replicate within macrophages (4). The AIEC strains isolated to date are clonally diverse and belong to distinct serotypes, and even though they primarily fall into the B2 phylogroup, AIEC strains belonging to the A, B1, and D phylogroups have also been isolated (2, 8, 9, 11, 13). Moreover, AIEC strains carry different sets of virulence-associated gene characteristics of extraintestinal pathogenic *E. coli* (ExPEC) strains (2, 4, 9), and some strains, including the prototype strain LF82, have been found to be genetically similar to distinct avian pathogenic *E. coli* (APEC) (2, 3, 10, 14). Due to the similarities observed between these pathotypes, we compared several genotypic and phenotypic characteristics of AIEC and human ExPEC strains in a previous study (10). We observed that although both pathotypes were genetically similar (in terms of virulence gene profiles, phylogenetic backgrounds, and pulsed-field gel electrophoresis profiles), the majority of human ExPEC strains did not share the AIEC phenotype, which gives to the pathotype a particular identity.

It is against this background that we sought to examine the AIEC phenotype among animal strains, either from extraintestinal or intestinal infections, commonly showing an ExPEC-typical genotype in order to (i) evaluate the impact of the similar phylogenetic background and virulence profile among animal strains on their AIEC-like phenotype properties, (ii) study host and disease specificity of the AIEC pathotype, and (iii) seek out a putative zoonotic risk of AIEC strains between humans and animals.

We analyzed the AIEC phenotype of 79 ExPEC strains causing extraintestinal disease (Table 1) and 45 intestinal pathogenic *E. coli* (InPEC) strains causing enteritis to animals (Table 2). Together, these strains were adopted from a larger collection of animal strains with available sequence types (C. Ewers and L. H. Wieler, unpublished data; strains have been deposited in the MLST database [http://mlst.ucc.ie/mlst/mlst/dbs/Ecoli/]). Virulence-associated genes linked with the ExPEC group were determined as described recently (5). Strains were selected with respect to sequence types (STs) that had already been found in AIEC strains from patients with Crohn's disease, including ST131, ST73, ST10, and ST101. A broad range of serotypes was included, and we preferentially chose motile strains with *malX* and *kpsMTII* virulence genes, which are common traits in AIEC strains (10, 15). This strain set is, of course, biased toward strains with characteristics frequently found in AIEC. However, this was intended, as we aimed to increase the chance to identify the AIEC phenotype among strains from different animal species rather than to provide prevalence data.

As for the ExPEC strain collection, the present study includes 49 APEC strains isolated from colibacillosis in poultry; 24 uropathogenic *E. coli* strains (UPEC) from cystitis and pyelonephritis in cats, dogs, and pigs; and six strains causing upper genital tract infections in pigs (Table 1) (7). As determined by STRUCTURE analysis of concatenated sequences of the seven housekeeping genes included in MLST analyses (6), the distribution of ancestral groups was 50.6% B2, 17.7% A, 15.2% B1, and 7.6% D. Seven other strains were catego-

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TABLE 1. Origin and characteristics of the 79 animal ExPEC strains included in this study[a]

Strain	Host species	Pathotype	Disease	Serotype	ST	ST complex	Ancestral group	ADH_I		INV_I		REPL_I		AIEC phenotype
								Mean	SD	Mean	SD	Mean	SD	
IMT2312	Chicken	APEC	Colibacillosis	O131:NM	10	STC10	A	0.2	0.1	ND		ND		–
IMT2488	Chicken	APEC	Colibacillosis	Ont:H4	10	STC10	A	0.4	0.2	0.048	0.030	ND		–
IMT9238	Chicken	APEC	Colibacillosis	Ont:H6	10	STC10	A	0.4	0.1	0.022	0.011	ND		–
IMT9706	Chicken	APEC	Colibacillosis	O119:Hnt	10	STC10	A	0.3	0.1	0.030	0.014	ND		–
IMT5110	Chicken	APEC	Colibacillosis	O149:Hnt	100	STC165	A	0.1	0.1	0.001	0.001	ND		–
IMT9712	Chicken	APEC	Colibacillosis	O22:H31	373	STC168	A	3.7	3.6	0.031	0.039	ND		–
IMT2358	Chicken	APEC	Colibacillosis	O78:H4	915	None	ABD	0.1	0.1	0.008	0.000	ND		–
IMT5215	Chicken	APEC	Colibacillosis	O5:H10	93	STC168	AxB1	0.3	0.2	0.019	0.003	ND		–
IMT1939	Duck	APEC	Colibacillosis	O78:H51	155	STC155	AxB1	0.3	0.1	0.050	0.049	ND		–
IMT2095	Chicken	APEC	Colibacillosis	O8:H19	162	STC469	AxB1	2.7	2.7	0.038	0.010	ND		–
IMT5475	Duck	APEC	Colibacillosis	O8:H4	359	STC101	AxB1	0.2	0.1	0.004	0.004	ND		–
IMT5494	Duck	APEC	Colibacillosis	O29:H51	359	STC101	AxB1	0.5	0.2	ND		ND		–
IMT2087	Chicken	APEC	Colibacillosis	O78:H9	23	STC23	B1	0.2	0.2	0.088	0.061	ND		–
IMT2125	Chicken	APEC	Colibacillosis	O78:H9	23	STC23	B1	0.1	0.1	0.007	0.005	ND		–
IMT2113	Chicken	APEC	Colibacillosis	Ont:NM	101	STC101	B1	0.2	0.2	0.001	0.001	ND		–
IMT5124	Chicken	APEC	Colibacillosis	O78:Hnt	369	STC23	B1	0.1	0.1	0.001	0.001	ND		–
IMT2097	Chicken	APEC	Colibacillosis	O1:H7	95	STC95	B2	0.3	0.3	0.052	0.015	ND		–
IMT2272	Chicken	APEC	Colibacillosis	O2:Hnt	95	STC95	B2	0.2	0.0	0.018	0.007	ND		–
IMT2297	Chicken	APEC	Colibacillosis	O2:H5	95	STC95	B2	0.2	0.0	0.047	0.016	ND		–
IMT2532	Chicken	APEC	Colibacillosis	O18:H7	95	STC95	B2	0.3	0.2	0.014	0.010	ND		–
IMT2537	Chicken	APEC	Colibacillosis	O18:H7	95	STC95	B2	0.2	0.1	0.015	0.009	ND		–
IMT2545	Chicken	APEC	Colibacillosis	O1:H5	95	STC95	B2	0.1	0.1	0.001	0.001	ND		–
IMT4517	Poultry	APEC	Colibacillosis	O2:H7	95	STC95	B2	0.2	0.2	0.023	0.011	ND		–
IMT4533	Chicken	APEC	Colibacillosis	O18:Hnt	95	STC95	B2	0.4	0.4	0.038	0.008	ND		–
IMT5211	Chicken	APEC	Colibacillosis	O18:H7	95	STC95	B2	0.2	0.1	0.021	0.020	ND		–
IMT5214	Chicken	APEC	Colibacillosis	O1:NM	95	STC95	B2	0.2	0.1	0.001	0.001	ND		–
IMT8989	Chicken	APEC	Colibacillosis	O1:H7	95	STC95	B2	0.2	0.0	0.030	0.043	ND		–
IMT9232	Chicken	APEC	Colibacillosis	O1:H7	95	STC95	B2	0.7	0.1	0.022	0.016	ND		–
IMT9241	Chicken	APEC	Colibacillosis	O2:H4	95	STC95	B2	0.6	0.2	0.018	0.014	ND		–
MT78	Chicken	APEC	Colibacillosis	O2:Hnt	95	STC95	B2	6.1	7.0	0.997	0.859	34.6	25	–
IMT5112	Chicken	APEC	Colibacillosis	O6:NM	127	STC127	B2	0.1	0.1	0.000	0.000	ND		–
2363	Chicken	APEC	Colibacillosis	Ont:Hnt	135	None	B2	0.62	0.16	0.038	0.000	ND		–
IMT21073	Chicken	APEC	Colibacillosis	O2:H1	135	None	B2	1.83	0.46	0.205	0.092	58	28	–
IMT2295	Chicken	APEC	Colibacillosis	O2:Hnt	135	None	B2	0.04	0.05	0.014	0.003	ND		–
IMT2288	Chicken	APEC	Colibacillosis	O2:H5	140	STC95	B2	0.4	0.4	0.018	0.006	ND		–
IMT4534	Chicken	APEC	Colibacillosis	O2:Hnt	140	STC95	B2	0.2	0.0	0.026	0.005	ND		–
IMT5128	Chicken	APEC	Colibacillosis	O2:H5	140	STC95	B2	0.3	0.3	0.028	0.004	ND		–
IMT2290	Chicken	APEC	Colibacillosis	O2:H6	141	None	B2	1.7	0.2	0.045	0.032	ND		–
IMT2477	Chicken	APEC	Colibacillosis	O2:H6	141	None	B2	0.2	0.2	0.043	0.005	ND		–
IMT5160	Chicken	APEC	Colibacillosis	Orough:H11	141	None	B2	0.3	0.1	0.028	0.024	ND		–
IMT2112	Poultry	APEC	Colibacillosis	O2:H5	355	STC73	B2	0.3	0.1	0.032	0.003	ND		–
IMT9713	Chicken	APEC	Colibacillosis	O125:H10	372	None	B2	0.1	0.1	0.002	0.001	ND		–
IMT4542	Chicken	APEC	Colibacillosis	O2:Hnt	1168	STC95	B2	0.3	0.0	0.044	0.016	ND		–
IMT2111	Chicken	APEC	Colibacillosis	O1:H15	38	STC38	D	1.2	0.4	0.030	0.005	ND		–
IMT2487	Chicken	APEC	Colibacillosis	O77:H18	69	STC69	D	0.2	0.0	0.019	0.007	ND		–
IMT2282	Chicken	APEC	Colibacillosis	O23:H15	70	None	D	0.2	0.0	0.025	0.007	ND		–
K416/97-2	Chicken	APEC	Colibacillosis	O2:Hnt	115	None	D	1.9	2.6	0.043	0.024	ND		–
IMT2294	Chicken	APEC	Colibacillosis	O2:H9	115	None	D	0.0	0.0	0.011	0.006	ND		–
IMT2261	Chicken	APEC	Colibacillosis	O166:H15	349	STC349	D	8.3	3.1	0.066	0.055	ND		–
IMT14972	Dog	UPEC	UTI	Ont:NM	10	STC10	A	0.0	0.0	0.000	0.000	ND		–
VB 973164	Pig	UPEC	UTI	O128:NM	10	STC10	A	0.0	0.0	ND		ND		–
VB 985583	Dog	UPEC	UTI	Ont:NM	10	STC10	A	0.0	0.0	0.000	0.000	ND		–
VB 991926	Cat	UPEC	UTI	O49:H32	10	STC10	A	0.0	0.0	0.004	0.004	ND		–
VB 905336	Cat	UPEC	UTI	Ont:NM	10	STC10	A	0.8	1.0	0.000	0.000	ND		–
VB 993928	Cat	UPEC	UTI	Ont:H35	10	STC10	A	0.1	0.0	0.030	0.013	ND		–
IMT15499	Pig	UPEC	UTI	Unknown	880	STC10	A	0.5	0.6	0.011	0.004	ND		–
IMT15532	Pig	UPEC	UTI	Unknown	891	STC10	A	0.5	0.6	0.050	0.000	ND		–
VB 960678.1	Dog	UPEC	UTI	O19:NM	1254	STC101	AxB1	0.0	0.0	0.000	0.000	ND		–
IMT15513	Pig	UPEC	UTI	O86:Hnt	101	STC101	B1	0.4	0.4	0.046	0.016	ND		–
VB 996714.1	Dog	UPEC	UTI	O15:H10	101	STC101	B1	0.1	0.0	0.047	0.042	ND		–
IMT14958	Cat	UPEC	UTI	O22:H1	73	STC73	B2	0.2	0.3	0.047	0.038	ND		–
IMT14966	Dog	UPEC	UTI	O6:H1	73	STC73	B2	0.4	0.5	0.023	0.024	ND		–
IMT14980	Cat	UPEC	UTI	O6:H1	73	STC73	B2	0.0	0.0	0.004	0.003	ND		–
IMT14995	Cat	UPEC	UTI	O6:H1	73	STC73	B2	0.0	0.0	0.015	0.023	ND		–
IMT15033	Cat	UPEC	UTI	O25:H1	73	STC73	B2	0.1	0.1	0.052	0.003	ND		–

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TABLE 1—*Continued*

Strain	Host species	Pathotype	Disease	Serotype	ST	ST complex	Ancestral group	ADH_I		INV_I		REPL_I		AIEC phenotype
								Mean	SD	Mean	SD	Mean	SD	
IMT9096	Cat	UPEC	UTI	O2:H1	73	STC73	B2	0.8	0.9	0.035	0.007	ND		−
IMT12556	Dog	UPEC	UTI	O25b:H4	131	None	B2	0.6	0.7	0.041	0.008	ND		−
VB 977549	Dog	UPEC	UTI	O25b:H4	131	None	B2	0.1	0.1	ND		ND		−
VB 999294	Dog	UPEC	UTI	O25b:H4	131	None	B2	0.3	0.2	ND		ND		−
VB 973707	Dog	UPEC	UTI	O25b:H4	131	None	B2	4.3	0.6	ND		ND		−
VB 984674	Dog	UPEC	UTI	O25b:H4	131	None	B2	0.4	0.3	ND		ND		−
BF 187735	Dog	UPEC	UTI	O25b:H4	131	None	B2	0.3	0.2	ND		ND		−
VB 991463	Dog	UPEC	UTI	O2:Hnt	135	None	B2	1.85	0.49	0.103	0.004	976	210	+
IMT15525	Pig	ExPEC	GTI	Ont:H21	101	STC101	B1	0.4	0.5	0.048	0.018	ND		−
IMT15459	Pig	ExPEC	GTI	O114:Hnt	101	STC101	B1	0.9	1.2	0.045	0.002	ND		−
IMT15466	Pig	ExPEC	GTI	Ont:H21	101	STC101	B1	0.2	0.3	0.063	0.039	ND		−
IMT15469	Pig	ExPEC	GTI	Orough:NM	101	STC101	B1	0.5	0.6	0.007	0.006	ND		−
IMT15472	Pig	ExPEC	GTI	Ont:H21	101	STC101	B1	0.3	0.4	0.034	0.015	ND		−
IMT15497	Pig	ExPEC	GTI	Ont:NM	101	STC101	B1	0.1	0.1	0.001	0.001	ND		−

[a] Adhesion index (ADH_I), calculated as the mean number of bacteria per cell, and invasion index (INV_I), calculated as the percentage of intracellular bacteria of total bacteria inoculated, are detailed. Survival/replication index (REPL_I), calculated as the percentage of intracellular bacteria at 24 h postinfection, has been investigated only for those invasive strains. AIEC phenotype is positive (+) if $ADH\_I \geq 1$, $INV\_I \geq 0.1$, and $REPL\_I \geq 100$. Abbreviations: ND, not determined; UTI, urinary tract infection; GTI, genital tract infection.

rized under hybrid groups AxB1 (7.6%) and ABD (1.3%), which resemble highly recombining strains supposed to have acquired genetic material from all four major phylogenetic groups (16). With regard to the InPEC strain collection, we included 22 strains causing enteritis in cats, 17 in dogs, and six in swine. These strains belonged to phylogroups B2 (64.4%) and A (35.6%) (Table 2).

To identify the AIEC phenotype, we determined the ability of strains to adhere to and to invade intestinal epithelial cells, as well as their capacity to survive and replicate within macrophages by performing gentamicin protection assays over intestine-407 epithelial cells (ATCC CCL-6) and murine J774A1.1 macrophages (ATCC TIB-67), respectively (9). Assays for strains resistant to gentamicin were carried out with kanamycin at a final concentration of $100\ \mu g \cdot ml^{-1}$. All assays were performed on 24-well plates in triplicate. AIEC prototype strain LF82 and nonpathogenic *E. coli* strain C600 were used as controls.

In parallel, we performed correspondence analysis to determine whether or not a particular distribution of virulence-associated genes correlated with each pathotype (Canoco software version 4.5 for Windows; biplot scaling). We compared the 124 animal strains included in the present study with 22 human intestinal AIEC and 37 human mucosa-associated *E. coli* (non-AIEC) strains from a previous study (10). Fifty-two virulence genes were included in the analysis after removing genes that were present in all the strains or in a single strain.

Only one out of the 79 animal ExPEC strains analyzed shared the AIEC phenotype despite the mindful selection of strains. Approximately 16% of APEC strains were adherent to intestine-407 cells, but only two were invasive (IMT21073 and BEN2332, formerly named MT78). These results are in agreement with those of a previous study that described the adhesion and invasion ability of the MT78 strain to avian heterophils and macrophages (12). Among the UPEC and genital tract infection-associated strains, 10.2% were classified as adherent, but only UPEC strain VB 991463, which belonged to the same phylogroup (B2) and sequence type (ST135) as the LF82 strain, presented the complete AIEC phenotype. These results provided evidence for a particular identity of the AIEC pathotype, since animal ExPEC strains, although being genetically similar to AIEC strains, did not share the AIEC phenotype.

Contrary to animal ExPEC, up to 57.7% of preselected animal InPEC strains phenotypically resembled the AIEC pathotype, and a higher proportion (72.4%) was observed among B2 isolates. These InPEC strains caused enteritis to animals but genetically resembled ExPEC strains rather than classical intestinal pathogenic *E. coli*. Similarly, the AIEC pathotype is genetically similar to ExPEC but different from diarrheagenic *E. coli* pathovars and has been particularly related to ileal Crohn's disease and granulomatous colitis in boxer dogs, a disease which highly resembles ulcerative colitis and Crohn's disease in humans (2, 4, 9, 15). To our knowledge, this is the first study demonstrating the occurrence of AIEC in cats, even though these animals also suffer from inflammatory bowel disease (1). Although the nonarbitrary strain selection might have accounted for the exceptional high frequency of AIEC among intestinal strains from cats (81.8%), it stays a matter of concern that warrants future investigations.

Correspondence analysis of virulence gene (VG) profiles showed that no particular VG distribution was associated to a certain group of strains (see Fig. 1). Strains clustered with regard to their phylogenetic affiliation (data not shown) but not by their extraintestinal/intestinal origin, human/animal host source, or AIEC phenotype. Human and animal AIEC strains appeared scattered in the plot, indicating their genetic diversity and the lack of a genetic marker for the identification of that pathotype. However, we found *malX* and *kpsMTII* more prevalent in animal and human strains with the AIEC phenotype (71.4% of AIEC-like versus 47% of non-AIEC [$P = 0.003$] and 71.4% versus 52% [$P = 0.013$], respectively, taking into account a total of 173 strains used for correspondence analysis). These virulence genes have

TABLE 2. Origin and characteristics of 45 animal intestinal pathogenic strains included in this study[a]

Strain	Host species	Serotype	ST	ST complex	Ancestral group	ADH_I		INV_I		REPL_I		AIEC phenotype
						Mean	SD	Mean	SD	Mean	SD	
IMT15384	Dog	O6:H1	10	STC10	A	0.28	0.17	0.008	0.006	ND		−
IMT15419	Dog	Ont:H32	10	STC10	A	1.50	0.42	0.015	0.014	ND		−
VB 900719	Dog	Ont:Hnt	10	STC10	A	15.25	4.60	0.445	0.049	449	410	+
VB 903359	Dog	Ont:NM	10	STC10	A	0.08	0.07	0.002	0.003	ND		−
BF 137999	Dog	Ont:NM	10	STC10	A	0.06	0.05	0.001	0.001	ND		−
VB 904411	Dog	Ont:Hnt	10	STC10	A	0.18	0.11	0.028	0.003	ND		−
VB 904860	Dog	Ont:H37	10	STC10	A	7.93	1.52	1.975	0.177	439	212	+
VB 905637	Dog	Ont:NM	10	STC10	A	0.28	0.05	0.002	0.002	ND		−
IMT 13347	Swine	Unknown	10	STC10	A	20.25	11.67	0.178	0.018	259	95	+
IMT 13359	Swine	Unknown	10	STC10	A	1.48	0.11	0.678	0.315	942	138	+
IMT 13398	Swine	Unknown	10	STC10	A	3.55	1.39	0.063	0.036	ND		−
IMT 13425	Swine	Unknown	10	STC10	A	0.01	0.01	0.001	0.001	ND		−
IMT 13497	Swine	Unknown	10	STC10	A	0.00	0.00	0.001	0.001	ND		−
IMT 13473	Swine	Unknown	10	STC10	A	0.00	0.00	0.000	0.000	ND		−
VB 934275	Dog	Ont:NM	617	STC10	A	0.02	0.02	0.005	0.001	ND		−
IMT15422	Dog	Ont:H37	1238	STC10	A	9.08	2.67	0.235	0.115	609	97	+
IMT15383	Cat	O6:Hnt	73	STC73	B2	0.34	0.22	0.310	0.014	477	85	+
IMT15401	Cat	O25:NM	73	STC73	B2	4.93	0.39	0.423	0.180	1,153	159	+
IMT15407	Cat	O25:H1	73	STC73	B2	3.03	1.66	0.163	0.067	1,399	535	+
IMT15412	Cat	O6:H1	73	STC73	B2	1.43	0.67	0.370	0.021	658	169	+
IMT15417	Cat	O6:H1	73	STC73	B2	1.60	1.35	0.242	0.173	980	60	+
IMT15418	Cat	O25:H1	73	STC73	B2	0.16	0.21	0.040	0.001	ND		−
IMT15423	Cat	O6:H1	73	STC73	B2	1.17	0.64	0.292	0.183	1,541	190	+
IMT15430	Cat	O25:H1	73	STC73	B2	6.39	1.05	0.155	0.000	2,074	1,081	+
IMT15444	Cat	O6:H1	73	STC73	B2	1.43	0.18	2.350	0.212	1,013	985	+
IMT15445	Cat	Unknown	73	STC73	B2	3.28	0.81	0.238	0.138	741	494	+
IMT15447	Cat	O25:H1	73	STC73	B2	1.04	0.24	1.450	0.424	91	14	−
IMT15448	Cat	O6:H1	73	STC73	B2	1.08	0.55	0.580	0.312	777	456	+
VB 900990	Cat	O6:H1	73	STC73	B2	4.70	1.20	0.463	0.187	604	61	+
VB 901947	Cat	O22:Hnt	73	STC73	B2	2.23	0.25	0.150	0.035	1,060	603	+
VB 901857	Cat	O6:H1	73	STC73	B2	0.16	0.22	0.390	0.156	762	408	+
VB 902289	Cat	O25:H1	73	STC73	B2	1.35	0.14	1.375	0.247	1,287	409	+
VB 902302	Cat	O6:H1	73	STC73	B2	5.20	3.32	0.248	0.032	83	23	−
VB 902827	Cat	O25:H1	73	STC73	B2	1.03	0.32	0.245	0.127	647	286	+
VB 903648	Cat	O25:H1	73	STC73	B2	4.45	3.61	1.378	0.735	345	138	+
BF 138088	Cat	O6:H1	73	STC73	B2	3.68	0.53	0.145	0.014	757	324	+
VB 905481	Cat	O25:H1	73	STC73	B2	1.93	0.53	1.268	0.848	522	349	+
BF 138148	Cat	O25:NM	73	STC73	B2	0.12	0.06	0.018	0.004	ND		−
IMT15380	Dog	O6:H1	73	STC73	B2	1.52	0.77	0.395	0.085	1,504	548	+
IMT15424	Dog	O22:H1	73	STC73	B2	1.04	0.09	0.234	0.164	639	17	+
IMT15441	Dog	O6:NM	73	STC73	B2	0.12	0.09	0.004	0.002	ND		−
VB 900402	Dog	Ont:H1	73	STC73	B2	2.18	1.10	0.039	0.024	ND		−
VB 900782	Dog	O25:H1	73	STC73	B2	1.50	0.28	0.830	0.844	1,159	847	+
VB 901616	Dog	O25:H1	73	STC73	B2	0.37	0.39	0.079	0.075	ND		−
VB 903606	Dog	O6:H1	73	STC73	B2	2.38	0.95	0.026	0.006	ND		−

[a] Adhesion index (ADH_I), calculated as the mean number of bacteria per cell, and invasion index (INV_I), calculated as the percentage of intracellular bacteria of total bacteria inoculated, are detailed. Survival/replication index (REPL_I), calculated as the percentage of intracellular bacteria at 24 h postinfection, has been investigated only for those invasive strains. AIEC phenotype is positive (+) if ADH_I ≥ 1, INV_I ≥ 0.1, and REPL_I ≥ 100. ND, not determined.

already been detected in the LF82 strain and four other AIEC strains from human intestine, two human UPEC and two sepsis-causing *E. coli* strains also with the AIEC phenotype, and three AIEC strains from boxer dogs (10, 15).

The detection of AIEC strains in the intestinal tracts of cats, dogs, and swine provides further support for the absence of host specificity of this pathotype, which has already been observed by Simpson et al. in boxer dogs (15). They show that the AIEC pathotype is disease specific rather than host specific. We hold up this hypothesis because the InPEC strains included in the present study were isolated from animals with enteritis. Unfortunately, detailed data on the clinical history of the strains were not available, and thus it was not possible to correlate the presence of AIEC with the type or severity of intestinal disease. Nevertheless, our data support the association of AIEC with an altered intestinal state possibly linked to inflammatory bowel disease. Finally, the presence of AIEC in the intestine of several animal species suggests a putative zoonotic risk. Further studies analyzing the real prevalence of AIEC in well-characterized diseased animals are needed in order to detect putative reservoirs of AIEC strains, even in the intestine of asymptomatic carriers, and

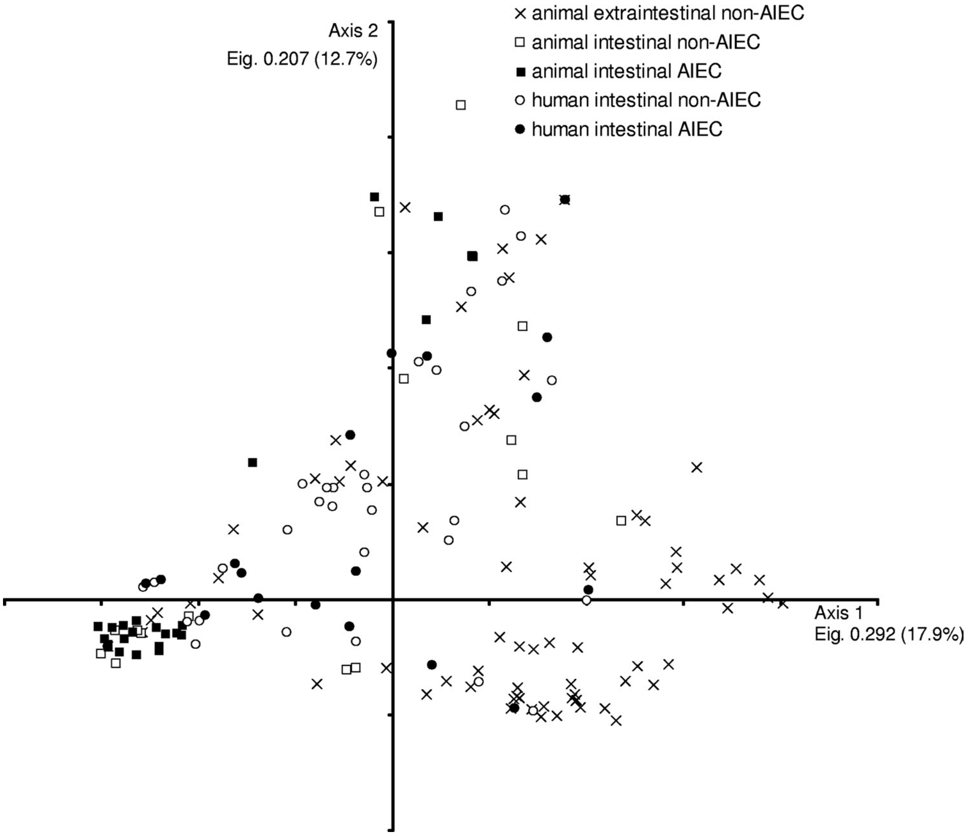

FIG. 1. Correspondence analysis of the distribution of 52 virulence-associated genes in 79 animal ExPEC, 45 animal InPEC (this study), 22 human AIEC, and 37 human mucosa-associated non-AIEC strains (data obtained from reference 10). Eigenvalues (Eig.) and percentages of variance are provided for each axis.

to evaluate the dimension of the risk with respect to the implementation of prevention and control measures and thus to public health.

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