National survey of *Escherichia coli* causing extraintestinal infections reveals the spread of drug-resistant clonal groups O25b:H4-B2-ST131, O15:H1-D-ST393 and CGA-D-ST69 with high virulence gene content in Spain

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Objectives: To evaluate the current prevalence of the three clonal groups O25b:H4-B2-ST131, O15:H1-D-ST393 and CGA-D-ST69 (where ST stands for sequence type) among *Escherichia coli* isolates causing extraintestinal infections in Spain and to characterize their virulence background, 500 consecutive non-duplicate *E. coli* isolates causing extraintestinal infections were analysed.

Methods: The 500 isolates were collected during February 2009 from five hospitals in different Spanish regions. Phylogenetic groups, STs, serotypes, virulence genes, PFGE profiles, antimicrobial resistance and extended-spectrum β-lactamase (ESBL) enzymes were determined.

Results: The three clonal groups accounted for 19% of the 500 isolates. Furthermore, they accounted for 37% of the isolates exhibiting trimethoprim/sulfamethoxazole plus ciprofloxacin resistance, 34% of aminoglycoside-resistant isolates and 30% of multidrug-resistant isolates. Clonal group ST131 was the most prevalent, and accounted for 12% of isolates overall and for 23% of multidrug-resistant isolates. The ST131 isolates exhibited a significantly higher virulence score (mean of virulence genes 8.1) compared with the ST393 (6.0) and ST69 (5.4) isolates. The prevalence of ESBL-producing isolates was 7%. Six (10%) of the 59 ST131 isolates were positive for CTX-M-15 and one (6%) of the 16 ST393 isolates was positive for CTX-M-14, whereas none of the 22 ST69 isolates produced ESBL enzymes.

Conclusions: The three clonal groups investigated accounted for 30% of the multidrug-resistant isolates, which gives evidence of an important clonal component in the emergence of resistances among extraintestinal pathogenic *E. coli*. Notably, a single high virulence clonal group (O25b:H4-B2-ST131) causes approximately 1 in every 10 extraintestinal infections in Spain, representing an important public health threat. A new variant of the ST131 clonal group, which is non-ESBL-producing but trimethoprim/sulfamethoxazole resistant and with high virulence content, is reported.

Keywords: E. coli, ExPEC, antimicrobial resistance

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Introduction

The intercontinental *Escherichia coli* clonal group producing CTX-M-15 with a high virulence potential, O25b:H4-B2-ST131 (where ST stands for sequence type), has been reported recently all over the world, representing a major public health problem.^{1,2} This clonal group belongs to the B2 phylogenetic group, to the serotype O25b:H4 and to the multilocus ST131. The O25b:H4-B2-ST131 clonal group is characterized by co-resistance to several classes of antibiotics and is able to acquire different mechanisms of resistance. Although commonly associated with the dissemination of CTX-M-15 extended-spectrum cephalosporin resistance, *E. coli* O25b:H4-B2-ST131 also occurs as a fluoroquinolone-resistant but cephalosporin-susceptible pathogen.³⁻¹²

Since the outbreak of 1986 in London, numerous studies have reported evidence of the continued clinical importance and global distribution of another fluoroquinolone-resistant clonal group that belongs to the D phylogenetic group, to the serotype O15:H1 and to the multilocus ST393.^{4,6,13,14} Olesen *et al.*¹⁵ recently published an epidemiological analysis with the conclusion that the O15:H1-D-ST393 clonal group has maintained a fairly stable virulence profile since its first known appearance, but, in contrast, its antimicrobial resistance profile has become progressively more extensive. Similarly, Mora *et al.*¹⁶ recently reported the emergence of CTX-M-14-producing isolates of this clonal group in Spain.

Clonal group A (CGA) belongs to the D phylogenetic group and to the multilocus ST69, and the isolates exhibit distinctive O groups (O11, O17, O73 and O77). CGA-D-ST69 accounted for up to 50% of trimethoprim/sulfamethoxazole-resistant urinary tract infections (UTIs) due to *E. coli* in the USA in the 1990s and also has a worldwide distribution.^{6,17–20}

Despite the clinical importance and worldwide distribution of these three drug-resistant clonal groups, as far as we know, they have been screened in only one study carried out in Canada from 2002 to 2004.⁶ For this reason, the present study was carried out to evaluate the current prevalence of these three clonal groups among *E. coli* isolates causing extraintestinal infections in Spain and to understand their contribution to the emergence of antimicrobial resistance. This type of study has a special interest due to the dramatic increase in ciprofloxacin and trimetho-prim/sulfamethoxazole resistances observed in Spain during recent years.^{21,22}

Materials and methods

Bacterial isolates

Five hospitals in different Spanish regions (Lugo, LU; Barcelona, BA; Santander, SA; Madrid, MA; and Seville, SE) participated in the present study. In the study period (February 2009), 100 consecutive non-duplicate clinically relevant *E. coli* isolates were obtained in each hospital from ambulatory (71%) and hospital-admitted (29%) patients. Clinical sources included urine (421 isolates), blood (25 isolates), surgical wounds (14 isolates), respiratory tract samples (5 isolates), bile (5 isolates) and other sources (30 isolates).

Antimicrobial susceptibility and extended-spectrum $\beta\text{-lactamase}$ (ESBL) typing

Susceptibility to antibiotics was analysed by broth microdilution and/or disc diffusion. Minimal inhibitory concentrations were determined using

a MicroScan WalkAway automated system (Siemens, Madrid, Spain) according to the manufacturer's instructions. Intermediate susceptibility was not considered as resistant. Resistance was interpreted based on the recommended breakpoints of the CLSI.²³ Multidrug-resistant isolates were those resistant to at least one representative of three or more antimicrobial classes, including fluoroquinolones (ciprofloxacin), trimetho-prim/sulfamethoxazole, aminoglycosides (gentamicin and tobramycin), β -lactam/ β -lactamase inhibitors (amoxicillin/clavulanic acid and piperacillin/tazobactam) and extended-spectrum cephalosporins (cefotaxime, ceftazidime and cefepime).

Suggestive evidence of ESBL production was defined as synergy between amoxicillin/clavulanate and at least one of cefotaxime, ceftazidime, aztreonam or cefepime. To determine the genotype of the ESBLs, PCR was performed using the TEM, SHV, CTX-M-1 and CTX-M-9 groupspecific primers, as reported previously.^{7,24} Sequencing of both strands of amplicons was performed using specific primers.

Detection of clonal groups

For detection of the three drug-resistant clonal groups, all 500 isolates were screened by PCR for the O25b *rfb* variant (O25b:H4-B2-ST131 associated),²⁵ for the O15 *rfb* allele and a single nucleotide polymorphism (SNP) in *fumC* specific for CC31 (where CC stands for clonal complex) (O15:H1-D-ST393 associated),^{6,26} and for an SNP in *fumC* and *gyrB* specific for CC69 (CGA-D-ST69 associated).^{6,27}

Phylogenetic grouping and multilocus sequence typing (MLST)

To confirm the presumptive clonal group assignments, all isolates of the three clonal groups detected by the PCR screening were analysed for their phylogenetic group (A, B1, B2 and D) by the multiplex PCR-based method of Clermont *et al.*²⁸ and MLST. MLST was achieved as previously described by gene amplification and sequencing of the seven housekeeping genes (*adk, fumC, gyrB, icd, mdh, purA* and *recA*) according to the protocol and primers specified at the *E. coli* MLST web site (http://mlst.ucc.ie/mlst/dbs/Ecoli). The allelic profile of the seven gene sequences and the STs were obtained via the electronic database at the *E. coli* MLST web site.²⁹

O and H typing

Determination of O and H antigens was carried out using the method previously described by Guinée *et al.*³⁰ with all available O (O1–O181) and H (H1–H56) antisera. Isolates that did not react with O and H antisera were classified as non-typeable (ONT and HNT, respectively), and those non-motile were denoted as HNM. Additionally, the specific O25a and O25b molecular subtypes were determined by PCR.²⁵

Virulence factors

The presence of 30 virulence genes was analysed as documented previously,³¹⁻³³ using primers specific for genes and operons that encode extraintestinal virulence factors characteristic of extraintestinal pathogenic *E. coli* (ExPEC), i.e. *fimH*, *fimAv*_{MT78}, *papEF* (positive results were tested for *papG I*, *papG II*, *papG III* and *papG IV* alleles), *sfa/focDE*, *afa/draBC* (positive results were tested for *afa* operon FM955459), *bmaE*, *gafD*, *cnf1*, *cdtB*, *sat*, *hlyA*, *iucD*, *iroN*, *kpsM II* (establishing *neuC*-K1, -K2 and -K5 variants), *kpsM III*, *cvaC*, *iss*, *traT*, *ibeA*, *malX*, *usp* and *tsh*.

PFGE

XbaI-PFGE analysis was performed as previously described. $^{\rm 31}$ Profiles were analysed with the BioNumerics fingerprinting software (Applied

Maths, St-Martens-Latem, Belgium). Dendrograms were generated by the unweighted pair-group method using arithmetic averages, based on the Dice similarity coefficient with a 1.0% band position tolerance.

Statistical analysis

Comparisons of proportions and scores (continuous variables) were tested using Fisher's exact test and the Mann-Whitney U-test, respectively. For each comparison, a P value of <0.05 was considered to denote significant differences.

Results and discussion

Prevalence of clonal groups

According to molecular typing, the clonal group O25b:H4-B2-ST131 accounted for 59 (12%) of the 500 study isolates, the clonal group O15:H1-D-ST393 accounted for 16 (3%) and CGA-D-ST69 accounted for 22 (4%). Thus, the three clonal aroups collectively accounted for 19% of the total isolates analysed. Hospital Vall d'Hebron in Barcelona city exhibited the highest prevalence (30%) of the three clonal groups. ST131 and ST69 occurred in all five hospitals, and ST393 in four. ST131 was significantly more prevalent than either of the other two groups in the five hospitals (P < 0.001 for each comparison and collectively) (Table 1). The three clonal groups were detected with a similar prevalence among isolates obtained from

ambulatory and hospital-admitted patients: ST131 (12% versus 12%, respectively); ST393 (3% versus 4%, respectively); and ST69 (4% versus 4%, respectively).

In Canada during 2002–04, Johnson *et al.*⁶ found that the three clonal groups contributed substantially to the study population (37%); however, in the Canadian study four subsets of ~50 isolates (all from UTIs) were selected according to combined trimethoprim/sulfamethoxazole and fluoroquinolone phenotypes, and so it is difficult to make a detailed comparison with our results. Nevertheless, *E. coli* ST131, like in Spain, was the most prevalent clonal group in Canada (23%). In another study including mostly invasive isolates, Johnson *et al.*⁸ estimated that ST131 caused 17% of *E. coli* infections in patients hospitalized across the USA in 2007.

Distribution of the three clonal groups by resistance subgroup

In the present study, the three clonal groups accounted for 37% of the isolates exhibiting trimethoprim/sulfamethoxazole plus ciprofloxacin resistance, 34% of the aminoglycoside-resistant isolates and 30% of the multidrug-resistant isolates (Table 2). CGA-D-ST69 was concentrated within the trimethoprim/ sulfamethoxazole-resistant and ciprofloxacin-susceptible group (10 of 81 isolates, 12%), whereas the O25b:H4-B2-ST131 (23%)

 Table 1. Prevalence of the three clonal groups among 500 E. coli isolates from five hospitals

Hospital			Prevalence of clonal groups, number of isolates					
	City	Total isolates	O25b:H4-B2-ST131	015:H1-D-ST393	CGA-D-ST69			
Hospital Lucus Augusti ^a	Lugo	100	8	4	5			
Hospital Vall d'Hebron	Barcelona	100	16	5	9			
Marqués de Valdecilla	Santander	100	9	2	2			
12 de Octubre	Madrid	100	15	0	3			
Virgen Macarena	Seville	100	11	5	3			
Total		500	59 (12%)	16 (3%)	22 (4%)			

^aPreviously named Complexo Hospitalario Xeral-Calde.⁷

Table 2. Distribution of the three clonal groups by resistance subgroup

		Prevalence of clonal groups, number of isolates (%)				
Resistance phenotypes ^a	Total isolates	O25b:H4-B2-ST131	015:H1-D-ST393	CGA-D-ST69	Any	
Trimethoprim/sulfamethoxazole	174	31 (18%)	10 (6%)	14 (8%)	55 (32%)	
Fluoroquinolones	155	41 (26%)	14 (9)	4 (3%)	59 (38%)	
Trimethoprim/sulfamethoxazole plus fluoroquinolones	93	21 (23%)	9 (10%)	4 (4%)	34 (37%)	
Aminoglycosides	61	17 (28%)	0	4 (7%)	21 (34%)	
Amoxicillin/clavulanic acid	39	6 (15%)	0	0	6 (15%)	
Extended-spectrum cephalosporins	38	6 (16%)	1 (3%)	0	7 (19%)	
Any of the above	256	51 (20%)	14 (5%)	14 (5%)	79 (31%)	
Multidrug resistance (three or more of the above drug classes)	61	14 (23%)	1 (2%)	3 (5%)	18 (30%)	

^aFluoroquinolones, resistant to ciprofloxacin; aminoglycosides, resistant to gentamicin, tobramycin and/or amikacin; extended-spectrum cephalosporins, resistant to cefepime, ceftazidime and/or cefotaxime.

Table 3. Virulence genes of the three clonal groups

	Clonal gra	oups, number of isolates	<i>P</i> value ^a			
Virulence genes	O25b:H4-B2-ST131 (n=59)	O15:H1-D-ST393 (n=16)	CGA-D-ST69 (n=22)	ST131 versus ST393	ST131 versus ST69	ST393 versus ST69
Adhesins						
fimH	58 (98%)	16 (100%)	22 (100%)			
, fimAv _{MT78}	0	16 (100%)	0	< 0.001		< 0.001
papEF	15 (25%)	14 (88%)	12 (55%)	< 0.001	0.011	0.029
papG I	0	0	0			
papG II	3 (5%)	14 (88%)	8 (36%)	< 0.001	0.005	< 0.001
papG III	12 (20%)	0	0	0.043	0.016	
papG IV	0	0	3 (14%)		0.018	
sfa/focDE	0	0	0			
afa/draBC	7 (12%)	0	1 (5%)			
afa FM955459	4 (7%)	0	0			
bmaE	0	0	1 (5%)			
gafD	0	0	1 (5%)			
Toxins						
cnf1	10 (17%)	0	0		0.033	
cdtB	6 (10%)	0	0			
sat	39 (66%)	15 (94%)	11 (50%)	< 0.001		0.004
hlyA	10 (17%)	0	0		0.033	
Siderophores						
iucD	52 (88%)	15 (94%)	19 (86%)			
iroN	22 (37%)	0	5 (23%)	0.002		
Capsula						
kpsM II	43 (73%)	16 (100%)	11 (50%)	0.013	0.034	0.001
kpsM II-K2	6 (10%)	0	1 (5%)			
kpsM II-K5	36 (61%)	16 (100%)	10 (45%)	0.001		< 0.001
neuC-K1	1 (2%)	0	0			
kpsM III	0	0	6 (27%)		< 0.001	0.027
Miscellaneous						
cvaC	14 (24%)	0	5 (23%)	0.024		
iss	21 (36%)	0	5 (23%)	0.002		
traT	51 (86%)	3 (19%)	19 (86%)	< 0.001		< 0.001
ibeA	16 (27%)	0	0	0.013	0.003	
malX (PAI)	58 (98%)	0	0	< 0.001	< 0.001	
usp	59 (100%)	0	0	< 0.001	< 0.001	
tsh	1 (2%)	0	2 (9%)			
ExPEC status	38 (64%)	16 (100%)	13 (59%)	0.002		0.003
Strains with ≥8 virulence genes	25 (42%)	0	1 (5%)	<0.001	<0.001	

PAI, pathogenicity island.

^aP values by Fisher's exact test are shown where P < 0.05.

and O15:H1-D-ST393 (10%) clonal groups were concentrated within the trimethoprim/sulfamethoxazole-resistant and cipro-floxacin-resistant group. Notably, clonal group ST131 was the most prevalent in all resistance subgroups and accounted for 23% of multidrug-resistant isolates. Similar results were found by Johnson *et al.*⁶ in the Canadian study (2002–04). In another study, Johnson *et al.*⁸ estimated that clonal group ST131 accounted for >40% of all isolates exhibiting any resistance,

Figure 1. PFGE of XbaI-digested DNA from the 59 O25b:H4-B2-ST131 isolates included in this study. Clusters with ≥85% similarity are indicated in bold. Isolate designation, virulence profile designation-number of virulence genes, virulence genes and associated resistances are shown on the right. Isolates 55SA, 167LU, 6MA, 99SE, 85MA and 29BA of Group II were CTX-M-15 producing. CIP, ciprofloxacin; SXT, trimethoprim/sulfamethoxazole; GEN, gentamicin; TOB, tobramycin.

Dice (Tol 1.0%-1.0%) (H>0.0% S>0.0%) [0.0%-100.0%] PFGE-Xbal PFGE-Xbal

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99 55 99 4 fmH tot mak up CP SM GN 15 54 99 5 P46 fmH tot lood tot mak up CP 16 4 15 54 99 5 fmH diddedS tot lood pAM H2 mak up CP SM TOB 16 7 16 7 fmH diddedS tot lood pAM H2 mak up CP SM TOB CP SM TOB 16 7 16 7 fmH diddedS tot lood pAM H2 mak up CP SM TOB CP SM TOB 16 7 16 7 fmH diddedS tot lood pAM H2 mak up CP SM TOB CP SM TOB 16 7 fmH diddedS tot lood pAM H2 mak up CP SM TOB CP SM TOB CP SM TOB 18 8 P3 5 fmH stit lood pAM H2 fmAM m2 up CP SM TOB CP SM TOB CP SM TOB 18 8 P3 5 fmH stit lood pAM H2 fmAM m2 up CP SM TOB CP SM TOB CP SM TOB CP SM TOB 18 8 P3 5 fmH stit lood pAM H2 fmAM m2 up CP SM TOB CP SM TOB <t< td=""><td>89.7</td><td>113 LU</td><td>P3-6</td><td>fimH sat iucD traT malX usp</td><td></td><td>CIP SXT</td><td></td></t<>	89.7	113 LU	P3-6	fimH sat iucD traT malX usp		CIP SXT	
1 1	87.1	42 MA	P3-6	fimH sat iucD traT malX usp		CIP SXT	
1/15: P3-6 (min set lucb Train Max tup) CLP SXT GEN 1/15: P3-6 (min set lucb Train Max tup) CLP SXT GEN 1/15: P3-6 (min set lucb Train Max tup) CLP SXT GEN 1/15: P3-7 (min set lucb Train Max tup) CLP SXT TOB 1/15: P3-7 (min set lucb Train Max tup) CLP SXT TOB 1/15: P3-7 (min set lucb Train Max tup) CLP 1/15: P3-7 (min set lucb Train Max tup) CLP 1/15: P3-7 (min set lucb Train Max tup) CLP 1/15: P3-7 (min set lucb Train Max tup) CLP 1/15: P3-6 (min set lucb Train Max tup) CLP 1/15: P3-6 (min set lucb Train Max tup) CLP 1/15: P3-6 (min set lucb Train Max tup) CLP 1/15: P3-6 (min set lucb Train Max tup) CLP 1/16: P3-6 (min set lucb Train Max tup) CLP 1/16: P3-6 (min set lucb Train Max tup) CLP 1/16:	97.1	59 SE	P4-4	fimH traT malX usp		CIP SXT G	EN
55 S.A. P-7 finitel effetdedE sati LucD lapeM II-K2 mark usp CIP SAT TOB 167 LU P-7 finitel effetdedE sati LucD lapeM II-K2 mark usp CIP SAT TOB 28.A. P-7 finite sati LucD lapeM II-K5 tot T mark usp CIP 28.A. P-7 finite sati LucD lapeM II-K5 tot T mark usp CIP 28.A. P-7 finites sati LucD lapeM II-K5 tot T mark usp CIP 65.S. P-7 finites sati LucD lapeM II-K5 tot T mark usp CIP 66.S.A. P-7 finites tat LucD lapeM II-K5 tot T mark usp CIP 66.S.A. P-7 finites tat LucD lapeM II-K5 tot T mark usp CIP 66.S.A. P-7 finites tat LucD lapeM II-K5 tot T mark usp CIP 67.S.A. P-96 finites tat LucD lapeM II-K5 tot T mark usp CIP EAN 132.UD P-77 finites tat LucD lapeM II-K5 tot T mark usp CIP EAN 132.UD P-77 finites tat LucD lapeM II-K5 tot T mark usp CIP EAN 132.UD P-77 finites tat LucD lapeM II-K5 tot T mark usp CIP EAN 132.UD P-77 finites tat LucD lapeM II-K5 t	84.1	71 SE	P3-6	fimH sat iucD traT malX usp		CIP	
1 1 55.5.A P5-7 fmH dq/ddddS cat luc/b kpM H/42 mak' usp CIP SXT TOB 1 1 P5-7 fmH dq/ddddS cat luc/b kpM H/42 mak' usp CIP SXT TOB 1 1 P5-7 fmH dq/ddddS cat luc/b kpM H/45 traf mak' usp CIP 2 1 P5-7 fmH stat luc/b kpM H/45 traf mak' usp CIP 2 1 P5-7 fmH stat luc/b kpM H/45 traf mak' usp CIP 2 1 A P5-7 fmH stat luc/b kpM H/45 traf mak' usp CIP 2 1	83.6 89.5	18 BA	P3-6	fimH sat iucD traT malX usp		CIP SXT G	EN
167 UU P5-7 finkl eghtedBe set kub kgsM II-K2 tradK kup CIP SKT TOB 28A P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 20 SE P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 20 SE P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 20 SE P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 20 SE P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 20 SE P7-7 finkl set kub kgsM II-K5 trad makK kup CIP 40 SA P9-6 finkl set kub kgsM II-K5 trad makK kup CIP 40 SA P9-6 finkl set kub kgsM II-K5 trad makK kup CIP 15 KA P3-6 finkl set kub kgsM II-K5 trad makK kup CIP II 15 KA P3-6 finkl set kub kgsM II-K5 trad makK kup CIP SKT Finkl set kub kgsM II-K5 trad makK kup CIP SKT 15 KA P3-6 finkl set kub kgsM II-K5 trad makK kup CIP SKT Finkl set kub kgsM II-K5 trad makK kup CIP SKT 16 KA P3-7 finkl set kub kgsM II-K5 trad makK kup CIP SKT Fin		55 SA	P5-7	fimH afa/draBC sat iucD kpsM II-K2 malX usp		CIP SXT TO	DВ
2 BA P7-7 finkt set luck kpsM II-KS trol malk usp CIP 2 0 SE P7-7 finkt set luck kpsM II-KS trol malk usp CIP 2 0 SE P7-7 finkt set luck kpsM II-KS trol malk usp CIP 2 0 SE P7-7 finkt set luck kpsM II-KS trol malk usp CIP 4 0 SA P9-6 finkt set luck kpsM II-KS trol malk usp CIP 4 0 SA P9-6 finkt set luck kpsM II-KS trol malk usp CIP 4 0 SA P9-6 finkt set luck kpsM II-KS trol malk usp CIP 4 0 SA P9-6 finkt set luck kpsM II-KS trol malk usp CIP 1 1 BA P9-6 finkt set luck kpsM II-KS trol malk usp CIP 1 1 SA P3-6 finkt set luck kpsM II-KS trol malk usp CIP 1 1 SA P3-6 finkt set luck kpsM II-KS trol malk usp CIP 1 1 SA P3-6 finkt set luck kpsM II-KS trol malk usp CIP 2 1 SA P3-6 finkt set luck kpsM II-KS trol malk usp CIP 2 1 SA P3-6 finkt set luck kpsM II-KS trol malk usp CIP 2 1 SA <td< td=""><td>82.6</td><td>167 LU</td><td>P5-7</td><td>fimH afa/draBC sat iucD kpsM II-K2 malX usp</td><td></td><td>CIP SXT TO</td><td>OB</td></td<>	82.6	167 LU	P5-7	fimH afa/draBC sat iucD kpsM II-K2 malX usp		CIP SXT TO	OB
20 SE P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 66 SA P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 11 BA P9-6 fmH sat lucb kpsM II-K5 trof malk usp CIP 11 BA P9-6 fmH sat lucb kpsM II-K5 trof malk usp CIP 11 BA P9-6 fmH sat lucb kpsM II-K5 trof malk usp CIP 12 LU P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 13 LW P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 13 LW P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 13 LW P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 14 LW P7-7 fmH sat lucb kpsM II-K5 trof malk usp CIP 15 SA P3-6 fmH sat lucb kpsM II-K5 trof malk usp CIP 16 SA P3-6 fmH sat lucb kpsM II-K5 trof malk usp CIP 17 SBA P3-6 fmH sat lucb kpsM II-K5 trof malk usp CIP StT GEN 17 SBA P3-6 fmH sat lucb kpsM II-K5 trof malk usp CIP StT GEN 18 SA P3-5		6 MA	P6-10	fimH papG II cnf1 sat hlyA iucD kpsM II-K5 traT malX usp		CIP	
0 97-7 fmH stille/bpM H-K5 trof malk usp CIP 66 5A P7-7 fmH stille/bpM H-K5 trof malk usp CIP 66 5A P7-7 fmH stille/bpM H-K5 trof malk usp CIP 66 5A P7-7 fmH stille/bpM H-K5 trof malk usp CIP 66 5A P7-7 fmH stille/bpM H-K5 malk usp CIP 66 5A P7-7 fmH stille/bpM H-K5 malk usp CIP 67 mH stille/bpM H-K5 malk usp CIP FmH stille/bpM H-K5 malk usp CIP 67 mH stille/bpM H-K5 malk usp CIP TI FmH stille/bpM H-K5 malk usp CIP 112 LU P7-7 fmH stille/bpM H-K5 malk usp CIP TI 12 SA P3-6 fmH stille/bpM H-K5 trof malk usp CIP TI 10 SA P3-6 fmH stille/brM malk usp CIP TI 10 SA P3-6 fmH stille/brM malk usp CIP TI 10 SA P3-5 fmH stille/brM malk usp CIP SXT GEN CIP 11 SA fmH stille/brM malk usp CIP SXT GEN CIP SXT GEN CIP SXT GEN	100	2 BA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP	
0 0	97.1	20 SE	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP	
a 11 BA P9-6 fmH sat lucD kpsM II-K5 malX usp CIP a 0 SA P9-6 fmH sat lucD kpsM II-K5 malX usp CIP 13 ZU P7-7 fmH sat lucD kpsM II-K5 trait malX usp CIP II 15 AA P3-6 fmH sat lucD kpsM II-K5 trait malX usp CIP II 15 AA P3-6 fmH sat lucD trait malX usp CIP II 15 AA P3-6 fmH sat lucD trait malX usp CIP SXT GEN CIP II 50 BA P10-9 fmH sat lucD trait malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN CIP SXT GEN 74 AB P3-6 fmH sat lucD trait malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN CIP SXT GEN 75 AP P7-7 fmH sat lucD trait malX usp CIP SXT CIP SXT GEN CIP SXT GEN CIP SXT GEN CIP SXT GEN 75 AP P7-7 fmH sat lucD hapM II-K5 trait malX usp CIP SXT CIP SXT GEN	82 93.2	66 SA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP	
0 11 BA P9-6 firmH sot LucD kpsM II-K5 malX usp CIP 0 0.0 A P9-6 firmH sot LucD kpsM II-K5 malX usp CIP 0.1 B 11 BA P9-6 firmH sot LucD kpsM II-K5 torl malX usp CIP 0.2 A 12 LUP P7-7 firmH sot LucD kpsM II-K5 torl malX usp CIP II 11 BA P9-6 firmH sot LucD torl malX usp CIP II III III III III III III III IIII IIII IIII IIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIII	91.4	61 BA	P8-9	fimH iucD iroN kpaM II-K5 cvaC iss tra malX usp		CIP GEN	
0.3 0.3 0.3 0.3 0.3 0.4 0	71	11 BA	P9-6	fimH sat iucD kpsM II-K5 malX usp		CIP	
132 LU P7-7 fmH sat lucD kpM II-K5 traT malX usp CIP SXT 15 MA P3-6 fmH sat lucD kroT malX usp CIP II 15 MA P3-6 fmH sat lucD kroT malX usp CIP II 16 SA P3-6 fmH sat lucD kroT malX usp CIP II 16 SA P3-6 fmH sat lucD kroT malX usp CIP II 17 MA P3-6 fmH sat lucD kroT malX usp CIP SXT ER 18 MA P1-8 fmH sat lucD kroT malX usp CIP SXT ER 17 MA P3-6 fmH sat lucD kroT malX usp CIP SXT ER 18 MA P1-8 fmH sat lucD kroT malX usp CIP SXT ER 19 MA P2-5 fmH sat lucD malX usp CIP SXT ER 19 MA P2-5 fmH sat lucD malX usp CIP SXT ER 19 MA P2-5 fmH sat lucD kpM II-KS traT malX usp CIP SXT ER 19 MA P2-7 fmH sat lucD kpM II-KS traT malX usp CIP SXT ER 19 MA P2-7 fmH sat lucD kpM II-KS traT malX usp CIP SXT ER 19 MA	90 <u>2</u>	40 SA	P9-6	fimH sat iucD kpsM II-K5 malX usp		CIP	
15 MA P3-6 fmH sat lucD traT malX usp CP II 15 KA P3-6 fmH sat lucD traT malX usp CP II 16 SA P3-6 fmH sat lucD traT malX usp CP II 16 SA P3-6 fmH sat lucD traT malX usp CP Stat 17 SA P3-6 fmH sat lucD traT malX usp CP SXT GEN CP SXT GEN 17 SB P3-6 fmH sat lucD traT malX usp CIP SXT GEN CIP SXT GEN 18 AP P3-6 fmH sat lucD traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN 19 AP P3-7 fmH sat lucD traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN 19 AP P3-7 fmH sat lucD kpM II-KS traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN 19 AP P3-7 fmH sat lucD kpM II-KS traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN 19 AP P3-7 fmH sat lucD kpM II-KS traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT GEN 19 AP P3-6 fmH ad lucD kpM II-KS traT malX usp CIP SXT GEN CIP SXT GEN CIP SXT TOB	8. 6	66 BA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP GEN	
16 SA P3-6 fmH sat iucD traT malX usp CIP II 50 BA P10-9 fmH sat iucD traT malX usp CIP Stat 43 BA P11-8 fmH sat iucD traT malX usp CIP SXT GEN 74 SA P3-6 fmH sat iucD traT malX usp CIP SXT GEN 74 SA P3-6 fmH sat iucD traT malX usp CIP SXT GEN 74 SA P3-6 fmH sat iucD traT malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-7 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-7 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-7 fmH sat iucD malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD hasM II-KS traT malX usp CIP SXT GEN 78 BA P3-6 fmH sat iucD hasM II-KS traT malX usp CIP SXT TOB 78 BA P14-8 fmH afa/draBC sat iucD hasM	67.1 81.3	132 LU	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP SXT	
50 BA P10-9 firmH sat iucD iroN kvaC iss traT malX usp CIP 43 BA P11-8 firmH sat iucD iroN kvaC iss traT malX usp CIP SXT GEN 74 SA P3-6 firmH sat iucD traT malX usp CIP SXT 78 BA P3-6 firmH sat iucD traT malX usp CIP SXT 78 BA P3-6 firmH sat iucD traT malX usp CIP GEN 78 BA P3-6 firmH sat iucD traT malX usp CIP SXT 78 BA P3-6 firmH sat iucD traT malX usp CIP SXT 78 BA P3-6 firmH sat iucD malX usp CIP SXT 78 BA P12-5 firmH sat iucD kpsM II-K5 traT malX usp CIP SXT 78 BA P12-5 firmH sat iucD kpsM II-K5 traT malX usp CIP SXT 78 BA P12-5 firmH sat iucD kpsM II-K5 traT malX usp CIP SXT 78 BA P13-6 firmH sat iucD kpsM II-K5 traT malX usp CIP SXT 78 BA P12-8 firmH dot/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 78 BA P12-8 firmH dot/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE <td></td> <td>15 MA</td> <td>P3-6</td> <td>fimH sat iucD traT malX usp</td> <td></td> <td>CIP [</td> <td></td>		15 MA	P3-6	fimH sat iucD traT malX usp		CIP [
43 BA P11-8 fmH sat lucD iroN iss traT malX usp CIP SXT GEN 74 SA P3-6 fmH sat lucD iroN iss traT malX usp CIP SXT 74 SA P3-6 fmH sat lucD iroN iss traT malX usp CIP SXT 74 SA P3-6 fmH sat lucD iroN iss traT malX usp CIP SXT 74 SA P3-6 fmH sat lucD malX usp CIP SXT 74 SA P3-6 fmH sat lucD malX usp CIP SXT 74 SA P3-5 fmH sat lucD malX usp CIP SXT 74 SA P3-5 fmH sat lucD malX usp CIP SXT GEN 75 SA P7-7 fmH sat lucD bpM II-KS traT malX usp CIP SXT GEN 76 MA P3-6 fmH at lucD kpM II-KS traT malX usp CIP SXT GEN 76 MA P3-6 fmH at lucD kpM II-KS traT malX usp CIP SXT TOB 99 SE P14-8 fmH af dr/draBC sat lucD kpM II-KS traT malX usp CIP SXT TOB 97 SE P14-8 fmH af dr/draBC sat lucD kpM II-KS traT malX usp CIP SXT TOB 97 SE P14-8 fmH af dr/draBC sat lucD kpM II-KS traT malX usp CIP SXT TOB 97 SE P14-8 fmH af dr/draBC sat lucD kpM II-KS traT malX usp CIP SXT TOB </td <td>91.4</td> <td>16 SA</td> <td>P3-6</td> <td>fimH sat iucD traT malX usp</td> <td></td> <td>CIP</td> <td>II</td>	91.4	16 SA	P3-6	fimH sat iucD traT malX usp		CIP	II
451 10 10 14 <t< td=""><td></td><td>50 BA</td><td>P10-9</td><td>fimH sat iucD iroN cvaC iss traT malX usp</td><td></td><td>CIP</td><td></td></t<>		50 BA	P10-9	fimH sat iucD iroN cvaC iss traT malX usp		CIP	
98 91-6 fmH sot iucD traT malX usp CIP SXT 98.4 P12-5 fmH sot iucD traT malX usp CIP GEN 98.4 P12-5 fmH sot iucD traT malX usp CIP SXT 98.4 P12-5 fmH sot iucD malX usp CIP SXT 98.4 P12-5 fmH sot iucD kpM II-KS traT malX usp CIP SXT GEN 98.4 P12-5 fmH sot iucD kpM II-KS traT malX usp CIP SXT GEN 98.4 P12-5 fmH sot iucD kpM II-KS traT malX usp CIP SXT GEN 99.5 P1-7 fmH sot iucD kpM II-KS traT malX usp CIP TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP SXT TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP SXT TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP SXT TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP SXT TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp CIP SXT TOB 99.5 P14-8 fmH djd/adBC sot iucD kpM II-KS traT malX usp </td <td>88.4</td> <td>43 BA</td> <td>P11-8</td> <td>fimH sat iucD iroN iss traT malX usp</td> <td></td> <td>CIP SXT G</td> <td>EN</td>	88.4	43 BA	P11-8	fimH sat iucD iroN iss traT malX usp		CIP SXT G	EN
68 5E P12-5 fimH sot lucD malX usp CIP 32 MA P12-5 fimH sot lucD malX usp CIP SXT 45 BA P12-5 fimH sot lucD malX usp CIP SXT 7 MA P7-7 fimH sot lucD kpsM II-K5 traT malX usp CIP GEN TOB 7 MA P7-7 fimH sot lucD kpsM II-K5 traT malX usp CIP GEN TOB 7 MA P7-7 fimH sot lucD kpsM II-K5 traT malX usp CIP SXT 46 SE P14-8 fimH dfoldraBC sot lucD kpsM II-K5 traT malX usp CIP SXT TOB 9 SE P14-8 fimH dfoldraBC sot lucD kpsM II-K2 traT malX usp CIP SXT TOB 9 SE P14-8 fimH dfoldraBC sot lucD kpsM II-K2 traT malX usp CIP SXT TOB 9 SE P14-8 fimH dfoldraBC sot lucD kpsM II-K2 traT malX usp CIP SXT TOB 9 SE P14-8 fimH dfoldraBC sot lucD kpsM II-K3 traT malX usp CIP SXT TOB 9 SE P14-8 fimH afoldraBC sot lucD kpsM II-K3 traT malX usp CIP SXT TOB 9 SE P14-8 fimH afoldraBC sot lucD kpsM II-K5 traT malX usp CIP SXT TOB 9 SE P14-9 fimH sat lucD iroN kpsM II-K5 traT malX usp CIP SXT 9 SE P14-9		74 SA	P3-6	fimH sat iucD traT malX usp		CIP SXT	
32 MA P12-5 fimH sat iucD malX usp CIP SXT 45 BA P12-5 fimH sat iucD kpsM II-KS traT malX usp CIP SXT GEN 77 MA P7-7 fimH sat iucD kpsM II-KS traT malX usp CIP SXT 46 SE P14-8 fimH dia/draBC sat iucD kpsM II-KS traT malX usp CIP SXT TOB 99 SE P14-8 fimH dia/draBC sat iucD kpsM II-KS traT malX usp CIP SXT TOB 57 SF P7-7 fimH sat iucD kpsM II-KS traT malX usp CIP SXT 46 SE P14-8 fimH dia/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 57 SF P14-8 fimH dia/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 57 SF P14-8 fimH dia/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 57 SF P14-8 fimH dia/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 62b MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 62b MA P15-9 fimH iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH iroN kpsM II-K5 iss traT malX usp CIP SXT 91 BA P15-12 fimH papG III citB iucD iroN kpsM ii-K5 cvoc iss traT ibeA malX usp CIP SXT		78 BA	P3-6	fimH sat iucD traT malX usp		CIP GEN	
914 45 BA P12-5 fimH sat traT malX usp CIP SXT GEN 914 914 57 SA P7-7 fimH sat ucD kpsM II-K5 traT malX usp CIP GEN TOB 7 MA P7-7 fimH sat ucD kpsM II-K5 traT malX usp CIP SXT 43 SA P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT 43 SA P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT 45 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT TOB 99 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT TOB 90 SE P14-8 fimH afa/arbaC sat ucD kpsM II-K5 traT malX usp CIP SXT TOB 91 SU P15-9 fimH sat ucD		68 SE	P12-5	fimH sat iucD malX usp		CIP	
38.5 97.7 fmH sat iucD kpsM II-K5 traT malX usp CIP GEN TOB 7 MA 97.7 fmH sat iucD kpsM II-K5 traT malX usp CIP 24 BA P13-6 fmH sat iucD kpsM II-K5 traT malX usp CIP SXT 43 SA P14-8 fmH afa/draBC sat iucD kpsM II-K5 traT malX usp CIP TOB 99 SE P14-8 fmH afa/draBC sat iucD kpsM II-K5 traT malX usp CIP SXT 99 SE P14-8 fmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 fmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 62b MA P15-9 fmH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 62b MA P15-9 fmH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 92 SE P14-8 fmH hopG III sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 92 BA P17-10 fmH hopG III sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 92 BA P12-12 fmH hopG III catIB iucD iroN kpsM II-K5 iss traT ibeA malX usp	75.6 87.2	32 MA	P12-5	fimH sat iucD malX usp		CIP SXT	
384 91-2 7 MA P7-7 firmH sat iucD kpsM II-K5 traT malX usp CIP 44 BA P13-6 firmH sat iucD kpsM II-K5 traT usp CIP SXT 43 SA P14-8 firmH afa/draBC sat iucD kpsM II-K5 traT malX usp CIP TOB 99 SE P14-8 firmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 99 SE P14-8 firmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 97 SE P14-8 firmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 97 SE P14-8 firmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 97 SE P14-8 firmH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 62b MA P15-9 firmH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 62b MA P15-9 firmH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 firmH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 85 MA P16-7 firmH page III cdtB iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 95 IU P20-9 firmH page III cdtB iucD iroN kpsM II-K5 iss traT ibeA malX usp SXT 92 BA P19-12		45 BA	P12-5	fimH sat traT malX usp		CIP SXT G	EN
38.5 ²⁴ BA ^{21.4} P13-6 ^{17mH} sat iucD kpsM II-K5 traT usp (IP SXT ⁴³ SA ^{21.4} P14-8 ^{17mH} afa/draBC sat iucD kpsM II-K5 traT malX usp (IP TOB ^{45.5} P14-8 ^{17mH} afa/draBC sat iucD kpsM II-K2 traT malX usp (IP SXT TOB ^{57.5} E ^{14.8} ^{17mH} afa/draBC sat iucD kpsM II-K2 traT malX usp (IP SXT TOB ^{57.5} E ^{14.9} ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ^{11.5} ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ^{11.5} ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ¹⁰⁰ ^{11.5} ^{11.5} ^{11.5} ^{11.5} ¹⁰⁰ ^{11.5}	91.4	57 SA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP GEN T	OB
38.5 91.9 - 6 firmH sat lucD kpsM II-K5 tra1 usp CIP SXT 43 SA P14-8 firmH afa/draBC sat lucD kpsM II-K5 tra1 malX usp CIP SXT 46 SE P14-8 firmH afa/draBC sat lucD kpsM II-K5 tra1 malX usp CIP SXT TOB 99 SE P14-8 firmH afa/draBC sat lucD kpsM II-K2 tra1 malX usp CIP SXT TOB 57 SE P14-8 firmH afa/draBC sat lucD kpsM II-K2 tra1 malX usp CIP SXT TOB 64 H P14-8 firmH afa/draBC sat lucD kpsM II-K5 tra1 malX usp CIP SXT TOB 64 H P15-9 firmH sat lucD kpsM II-K5 tra1 malX usp CIP SXT TOB 64 H P15-9 firmH sat lucD kpsM II-K5 iss tra1 malX usp CIP SXT 77 MA P15-9 firmH sat lucD iroN kpsM II-K5 iss tra1 malX usp CIP SXT 81 MA P16-7 firmH pag6 II sat lucD iroN kpsM II-K5 iss tra1 malX usp CIP SXT 91 BA P19-12 firmH pag6 III sat lucD iroN kpsM II-K5 iss tra1 malX usp CIP SXT 91 BA P19-12 firmH pag6 III cdtB iucD iroN kpsM II-K5 iss tra1 ibeA malX usp SXT 92 BA P19-12 firmH pag6 III cdtB iucD iroN kpsM II-K5 iss tra1 ibeA malX usp SXT 92 BA P21-8 firmH pag6	84.4	7 MA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP	
651 9 3-4 6 SE P14-8 fimH dfa/draBC sat iucD kpsM II-K2 traT malX usp CIP TOB 99 SE P14-8 fimH dfa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB CIP SXT TOB 57 SE P14-8 fimH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT GEN TOB CIP SXT GEN TOB 64 Deg 99 SE P14-8 fimH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT GEN TOB 64 Deg 99 SE P14-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT GEN TOB 62b MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 85 MA P16-7 fimH iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 99 BA P17-10 fimH pago III cdtB iucD iroN kpsM ii-K5 iss traT malX usp CIP SXT 90 BA P19-12 fimH pago III cdtB iucD iroN kpsM ii-K5 iss traT ibeA malX usp SXT 91 BA P19-12 fimH pago III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 92 BA P21-8	/ ^{3.2} 82.3	24 BA	P13-6	fimH sat iucD kpsM II-K5 traT usp		CIP SXT	
99 SE P14-8 fimH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 64 99 SE P14-8 fimH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 64 97 SE P14-8 fimH afa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 64 97 SE P14-8 fimH afa/draBC sat iucD kpsM II-K5 traT malX usp CIP SXT GEN TOB 62b MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH pap6 II sat iucD iroN kpsM ii-K5 iss traT malX usp CIP SXT 78 MA P16-7 fimH pap6 II sat iucD iroN kpsM ii-K5 cvoC iss traT ibeA malX usp CIP SXT 99 BA P17-10 fimH pap6 III cdtB iucD iroN kpsM ii-K5 cvoC iss traT ibeA malX usp SXT 90 BA P19-12 fimH pap6 III cdtB iucD iroN kpsM ii-K5 cvoC iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss iba A malX usp SXT 92 BA P21-8 fimH pap6 III cdtB iucD iroN kpsM II-K5 iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss iba A malX usp III <td></td> <td>43 SA</td> <td>P14-8</td> <td>fimH afa/draBC sat iucD kpsM II-K5 traT malX usp</td> <td></td> <td></td> <td></td>		43 SA	P14-8	fimH afa/draBC sat iucD kpsM II-K5 traT malX usp			
585 F7 SE P14-8 fimH qfa/draBC sat iucD kpsM II-K2 traT malX usp CIP SXT TOB 64 64 64 P7-7 fimH sat iucD kpsM II-K2 traT malX usp CIP SXT GEN TOB 62b MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT CIP SXT 64 91-9 FimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH ast iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 77 MA P15-9 fimH ast iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 85 MA P16-7 fimH papG II sat iucD iroN kpsM ii-K5 iss traT malX usp CIP SXT 9 BA P17-10 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp CIP SXT 9 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 9 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibaA malX usp SXT 9 CIP 92 BA P21-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp SXT 92 BA P21-18 fimH cdtB iroN kpsM II-K5 iss ibaA malX usp SXT III 92 BA P21-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss	65.171.5 92.3	46 SE	P14-8	fimH afa/draBC sat iucD kpsM II-K2 traT malX usp		CIP TOB	
585 81 MA P7-7 fimH sat iucD kpsM II-K5 traT malX usp CIP SXT GEN TOB 585 62b MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 585 77 MA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT 585 91.9 91.9 FimH iroN kpsM II-K1 cvaC traT ibeA malX usp CIP SXT 585 91.9 91.9 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp CIP SXT 586 91.9 91.9 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp CIP SXT 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp SXT SXT 103 LU P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 cvaC iss traT ibeA malX usp III 111 122 LU P22-10 fimH cdtB iroN kpsM II-K5 traT malX usp CIP 48 SA P24-7 afa/dtaBC sat iucD kpsM II-K5 tra malX usp CIP 26 MA P3-6 fimH sat iucD iroT malX usp CIP 26 MA		99 SE	P14-8	fimH afa/draBC sat iucD kpsM II-K2 traT malX usp		CIP SXT TO	DB
585 ⁶² ¹⁰⁰		57 SE	P14-8	fimH afa/draBC sat iucD kpsM II-K2 traT malX usp		CIP SXT TO	OB
58.5 91.9 88.7 100 BA P15-9 fimH sat iucD iroN kpsM II-K5 iss traT malX usp CIP SXT CIP GEN TOB 58.5 91.9 88.7 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp CIP SXT 58.5 91.9 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp CIP SXT 100 BA P18-12 fimH papG III cdtB iucD iroN kpsM ii-K5 iss traT ibeA malX usp SXT 100 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 100 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 100 BA P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 iss ibeA malX usp SXT 101 LU P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 iss traT ibeA malX usp SXT 111 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh IIII 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 26 MA P3-6 fimH sat iucD traT malX usp	69.7	81 MA	P7-7	fimH sat iucD kpsM II-K5 traT malX usp		CIP SXT G	EN TOB
631 85 MA P16-7 fimH iucD iroN iss traT malX usp CIP GEN TOB 29 BA P17-10 fimH pap6 II sat iucD iroN kpsM ii-K5 iss traT malX usp CIP SXT 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp CIP SXT 100 BA P18-8 fimH pap6 III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 19 BA P19-12 fimH pap6 III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 95 LU P20-9 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 103 LU P19-12 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 111 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp IIII 30 SE P19-12 fimH pap6 III cdtB iucD iroN kpsM II-K5 iss traT ibeA malX usp IIII 31 BA P23-8 fimH pap6 III cdtB iucD iroN kpsM II-K5 tra malX usp CIP 48 SA P24-7 ofa/draBC sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 ofa/draBC sat iucD kpsM II-K5 tra malX usp CIP 26 MA P3-6 fimH sat iucD traT ma	100	62b MA	P15-9	fimH sat iucD iroN kpsM II-K5 iss traT malX usp		CIP SXT	
58.5 85 MA P16-7 fimH iucD iroN iss traT malX usp CIP GEN TOB 29 BA P17-10 fimH papG II sat iucD iroN kpsM ii-K5 iss traT malX usp CIP SXT 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp CIP SXT 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp SXT 91.9 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 91.0 P20-9 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp SXT IIII 103 LU P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp IIII 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp IIII 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp IIII 726 31 BA P23-8 fimH papG III cdtB iucD iroN kpsM II-K5 tra malX usp CIP 48 SA P24-7 efa/draBC sat iucD kpsM II-K5 tra malX usp CIP CIP GEN TOB	692 87.2	77 MA	P15-9	fimH sat iucD iroN kpsM II-K5 iss traT malX usp		CIP SXT	
58.5 100 BA P18-8 fimH iroN kpsM II-K1 cvaC traT ibeA malX usp 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp 95 LU P20-9 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp 103 LU P19-12 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp 111 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 iss traT ibeA malX usp 122 LU P22-10 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp CIP 48 SA P24-7 ofa/draBC sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 ofa/draBC sat iucD kpsM II-K5 tra malX usp CIP 26 MA P3-6 fimH sat iucD traT malX usp TU CIP GEN TOB		85 MA	P16-7	fimH iucD iroN iss traT malX usp		CIP GEN T	OB
58.5 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp 95 LU P20-9 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp 95 LU P20-9 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp IIII 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh IIII 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 75 26 MA P3-6 fimH sat iucD traT malX usp CIP GEN TOB		29 BA	P17-10	fimH papG II sat iucD iroN kpsM ii-K5 iss traT malX usp		CIP SXT	
385 19 BA P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp 95 LU P20-9 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp 95 LU P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp IIII 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp IIII 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp IIII 31 BA P23-8 fimH papG II sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 75 26 MA P3-6 fimH sat iucD traT malX usp CIP GEN TOB		100 BA	P18-8	fimH iroN kpsM II-K1 cvaC traT ibeA malX usp			
84.7 103 LU P19-12 fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA malX usp SXT 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp III 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp III 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp III 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh III 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp III 718 31 BA P23-8 fimH papG III cdtB iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 75 26 MA P3-6 fimH sat iucD traT malX usp TV		19 BA	P19-12	fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA mo			
82.7 92 BA P21-8 fimH cdtB iroN kpsM II-K5 iss ibeA malX usp III 76.4 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh III 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp CIP 74.8 31 BA P23-8 fimH papG II sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 75 26 MA P3-6 fimH sat iucD traT malX usp TIV		95 LU	P20-9	fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp			
764 122 LU P22-10 firmH cdtb iroN kpsM II-K5 iss traT ibeA malX usp tsh 122 LU P22-10 firmH cdtb iroN kpsM II-K5 iss traT ibeA malX usp tsh 30 SE P19-12 firmH papG III cdtb iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp 718 31 BA P23-8 firmH papG II sat iucD kpsM II-K5 tra malX usp 75 26 MA P3-6 firmH sat iucD traT malX usp		103 LU	P19-12	fimH papG III cdtB iucD iroN kpsM ii-K5 cvaC iss traT ibeA ma	alX usp	SXT r	
76.4 122 LU P22-10 fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh 30 SE P19-12 fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA malX usp 7L8 31 BA P23-8 fimH papG II sat iucD kpsM II-K5 tra malX usp 7L8 26 MA P3-6 fimH sat iucD traT malX usp CIP TV	82.7	92 BA	P21-8	fimH cdtB iroN kpsM II-K5 iss ibeA malX usp			III
71.8 31 BA P23-8 fimH papG II sat iucD kpsM II-K5 tra malX usp CIP 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp CIP 75 26 MA P3-6 fimH sat iucD traT malX usp TV		122 LU	P22-10	fimH cdtB iroN kpsM II-K5 iss traT ibeA malX usp tsh		L	
7L8 48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp 75 26 MA P3-6 firmH sat iucD traT malX usp	72.6	30 SE	P19-12	fimH papG III cdtB iucD iroN kpsM II-K5 cvaC iss traT ibeA m	alX usp		
48 SA P24-7 afa/draBC sat iucD kpsM II-K5 tra malX usp 26 MA P3-6 fimH sat iucD traT malX usp CIP GEN TOB	77.8	31 BA	P23-8	fimH papG II sat iucD kpsM II-K5 tra malX usp		CIP	
26 MA P3-6 fimH sat iucD traT malX usp CLP GEN TOB		48 SA	P24-7				
95 SE P3-6 fimH sat iucD traT malX usp IV CIP SXT	75	26 MA	P3-6	fimH sat iucD traT malX usp		CIP GEN T	ÖВ
		95 SE	P3-6	fimH sat iucD traT malX usp	1.0	CIP SXT	

>50% of trimethoprim/sulfamethoxazole- plus ciprofloxacinresistant, aminoglycoside-resistant and multidrug-resistant isolates, and 67%–69% of extended-spectrum cephalosporinresistant and fluoroquinolone-resistant isolates from patients hospitalized across the USA in 2007. Therefore, although the ST131 clonal group is highly prevalent among Spanish resistant isolates, its frequency in 2009 was significantly lower than that estimated in the USA during 2007. In the US study, however, 73% of isolates were obtained from blood cultures, while in our study blood isolates represented only 5% of the isolates studied. In view of our results, we cannot discount the existence of other successful clonal groups in Spain.

In the present study, the prevalence of ESBL-producing isolates was 7% (35 of 500 isolates). This prevalence is higher than that observed in a multicentre study performed in 2006 in Spain (4%).²¹ Six (10%) of the 59 ST131 isolates were positive for CTX-M-15 (55SA, 167LU, 6MA, 99SE, 85MA and 29BA isolates) and one (6%) of the 16 ST393 isolates was positive for CTX-M-14 (114LU isolate), whereas none of the 22 ST69 isolates produced ESBL enzymes. Thus, in Spain in 2009, the ST131 clone occurred frequently as a fluoroquinolone-resistant but cephalosporin-susceptible pathogen. Cagnacci *et al.*⁴ characterized 148 *E. coli* isolates displaying reduced susceptibility to ciprofloxacin and causing uncomplicated UTIs in eight European countries during 2003 to 2006. About one-third (51 isolates) belonged to two clonal groups (ST131 and ST393), but only 12 (6%) were ESBL positive.

Virulence factors

ExPEC strains have specialized virulence factors that enable them to colonize host surfaces, injure host tissues and avoid host defence systems. The 97 isolates belonging to the clonal groups (O25b:H4-B2-ST131, O15:H1-D-ST393 and CGA-D-ST69) of the present study were analysed by PCR for the presence of 30 genes encoding virulence factors typical of ExPEC that cause UTIs, sepsis and meningitis. Comparisons of the virulence gene prevalence values among the three clonal groups identified significant differences (Table 3).

The virulence gene profiles identified in each clonal group were different, with 24 profiles (P1–P24) among the 59 ST131 isolates (Figure 1), 4 profiles (P25–P28) among the 16 ST393 isolates (Figure 2) and 16 profiles (P29–P44) among the 22 ST69 isolates (Figure 3). However, isolates belonging to the same clonal groups showed similar virulence gene profiles. Among the 28 ESBL-producing isolates not belonging to the three clonal groups, 18 different virulence profiles (P45–P62) were identified (Figure 4) and only 4 isolates showed virulence profiles (P25, P35 and P36) previously observed.

Notably, the ST131 isolates exhibited a significantly higher virulence score (mean/median/range 8.1/7/4-13) compared with the ST393 (6.0/6/3-7; P=0.01), ST69 (5.4/6/2-9; P<0.001) and ESBL-producing isolates belonging to other clonal groups (4.0/4/1-7; P<0.001). In particular, the ST131 isolates carrying the *ibeA* gene showed the highest virulence score (11.4/13/8-13). In contrast, Johnson *et al.*⁶ studying Canadian *E. coli* isolates from UTIs (2002-04) observed that the virulence scores differed only slightly among the three clonal groups. In the present study, 16 (27%) of 59 ST131 isolates carried the *ibeA* gene associated with a high virulence score, whereas in the Canadian study only 1 (2%) of 46 ST131 was positive for

the *ibeA* gene. This could explain the differences observed in both studies with respect to the virulence scores.

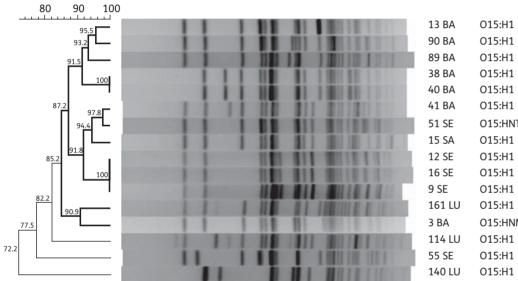
Sixty-seven (69%) of the 97 isolates belonging to the three clonal groups analysed in this study satisfied the criteria for ExPEC status according to the definition of Johnson *et al.*³⁴ Thus, the prevalence of ExPEC status was higher within the three clonal groups (69%) than within the 28 ESBL-producing isolates not belonging to them (14%) (P<0.001).

Macrorestriction profiles by PFGE

Figure 1 shows a dendrogram with the XbaI macrorestriction profiles obtained by PFGE of the 59 ST131 isolates with a similarity of 58.5%. The strains remained distributed in four groups (I–IV) having identities of 67.6%, 71.5%, 72.6% and 75.0%, respectively, characteristically defined by the virulence and resistance profiles of their isolates. Among the 59 ST131 isolates, a total of 11 clusters with \geq 85% similarity were observed. Interestingly, two of these clusters included CTX-M-15-positive and -negative isolates. Previously, Nicolas-Chanoine *et al.*¹ studied the virulence genotypes of 36 CTX-M-15-producing ST131 isolates from eight countries and three continents, and found similar pathotypes to those observed in the present study among the ST131 isolates of Group II.

The novelty of our findings is shown by the eight ST131 ibeA isolates of Group I, all of them with identical high virulence gene content and co-trimoxazole resistance. These eight isolates were obtained from each of the five hospitals included in the study. The virulence profile of this group had been previously described only in seven ESBL-producing strains isolated in the hospital of Barcelona in 2008¹² and one human ST131 strain non-ESBL producer isolated in the hospital of Lugo in 2009.¹¹ Comparing the PFGE profiles of those strains with the eight strains of the present study (Group I), the seven ESBL-producing strains from Barcelona formed a cluster having 88.5% similarity with three ST131 strain non-ESBL producers of Group I (28MA, 8MA and 143LU) and clustered with 82.1% similarity with three other isolates of Group I (18SE, 54BA and 84MA) (dendrogram not shown). Thus, we report for first time the spread of a new variant of the ST131 clonal group with high virulence content and that is non-ESBL-producing but co-trimoxazole resistant. The similarity of the PFGE profiles and the same virulence profile would be indicative of recent emergence. In fact, among a collection of 28 non-ESBL-producing ST131 strains with the ibeA gene obtained from 2464 E. coli blood cultures of patients admitted to the Hospital Lucus Augusti (previously named Complexo Hospitalario Xeral-Calde) from 1998 to 2009 (prevalence of 1.1%),¹¹ only one strain isolated in 2009 showed the same virulence profile as the eight ST131 isolates of Group I from the present study.

Figure 2 shows a dendrogram obtained by PFGE of the 16 O15:H1-D-ST393 isolates identified in the present study that showed a similarity of 72.2%, with a cluster of \geq 85% similarity that includes 13 isolates. Comparing the PFGE profiles of these 16 isolates with seven CTX-M-14-producing strains of this clonal group isolated in Spanish hospitals between 2005 and 2008,^{12,16} five of the seven CTX-M-14-producing strains formed a cluster having 85.8% similarity with the 13 isolates of the present study (dendrogram not shown). The virulence profiles of this clonal group



Dice (Tol 1.0%-1.0%) (H>0.0% S>0.0%) [0.0%-100.0%]

PFGE-Xbal

PFGE-Xbal

015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP
015:H1	P25-3	fimH fimAv _{MT78} kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP
O15:HNT	P27-7	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5 traT	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP
O15:HNM	P27-7	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5 traT	CIP
015:H1	P27-7	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5 traT	CIP SXT
015:H1	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
015:H1	P28-6	fimH fimAv _{MT78} sat iucD kpsM II-K5 traT	

Figure 2. PFGE of XbaI-digested DNA from the 16 O15:H1-D-ST393 isolates included in this study. Clusters with \geq 85% similarity are indicated in bold. Isolate designation, serotype, virulence profile designation-number of virulence genes, virulence genes and associated resistances are shown on the right. Isolate 114LU was positive for CTX-M-14. CIP, ciprofloxacin; SXT, trimethoprim/sulfamethoxazole.

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Dice (Opt:0.25%) (Tol 1.0%-1.0%) (H>0.0% S>0.0%) [0.0%-100.0%] PFGE-Xbal PFGE-Xbal

70 80 90 100

	58 MA	O44:HNM	P29-5	fimH papG IV sat kpsM II-K5 traT	CIP SXT
	64 BA	O15:H18	P30-4	fimH iucD kpsM III traT	SXT
82.4	24 SE	O15:H18	P31-5	fimH papG II sat iucD kpsM II-K5	SXT
79.4	4 BA	015:H7	P32-6	fimH papG II sat iucD kpsM II-K5 traT	
75.9 71.8	53 BA	ONT:HNM	P33-3	fimH kpsM III traT	SXT GEN
	16 BA	011:H4	P34-7	fimH papG II afa/draBC sat iucD kpsM II-K5 traT	
100	26 SA	017,77:H18	P35-2	fimH iucD	CIP SXT GEN
91.4	4 SA	017,77:H18	P35-2	fimH iucD	CIP SXT GEN
76.9	91 MA	017,77:H18	P36-3	fimH iucD traT	CIP SXT GEN TOB
	87 LU	ONT:H18	P37-8	fimH papGNT iucD iroN kpsM III cvaC iss traT	SXT
91.9	59 BA	017,77:H18	P38-5	fimH papG II sat iucD traT	SXT
	98 BA	017,77:H18	P38-5	fimH papG II sat iucD traT	SXT
	96 LU	017,77:H18	P39-7	fimH iucD iroN kpsM III cvaC iss traT	
18.6 87.2	37 MA	017,77:HNM	P40-6	fimH papG II sat iucD kpsM II-K5 traT	SXT
	97 SE	O44:H18	P40-6	fimH papG II sat iucD kpsM II-K5 traT	
86.6	50 SE	ONT:HNM	P41-3	fimH kpsM II-K5 traT	SXT
8.2 882 4	75 BA	017,77:H18	P42-6	fimH papG IV sat iucD kpsM II-K5 traT	SXT
	128 LU	073,77:H18	P42-6	fimH papG IV sat iucD kpsM II-K5 traT	
	70 BA	011:H4	P32-6	fimH papG II sat iucD kpsM II-K5 traT	
	181 LU	017,77:H18	P43-9	fimH bamE gafD iucD iroN kpsM II-K5 cvaC iss traT	SXT
89.5	106 LU	015:H4	P44-8	fimH iucD iroN kpsM III cvaC traT tsh	
	60 BA	O15:HNT	P44-8	fimH iucD iroN kpsM III cvaC iss traT tsh	

Figure 3. PFGE of XbaI-digested DNA from the 22 CGA-D-ST69 isolates included in this study. Clusters with ≥85% similarity are indicated in bold. Isolate designation, serotype, virulence profile designation-number of virulence genes, virulence genes and associated resistances are shown on the right. CIP, ciprofloxacin; SXT, trimethoprim/sulfamethoxazole; GEN, gentamicin; TOB, tobramycin.

60 80 100							
62.9	33 BA	08	CTX-M-15	А	P35-2	fimH iucD	CIP SXT GEN TOB
60.4	69 SE	07	CTX-M-14	А	P45-5	fimH iucD kpsM II-K5 iss traT	CIP SXT
54.9	63 MA	09	CTX-M-15	А	P46-7	fimH iucD iroN cvaC iss traT tsh	CIP SXT GEN TOB
	47 BA	ONT	CTX-M-14	B2	P47-4	fimH kpaM II-K2 malX usp	
72.2	12 MA	ONT	CTX-M-14	B1	P48-4	fimH iroN iss traT	CIP SXT
62.7	75 MA	08	CTX-M-15	А	P36-3	fimH iucD traT	CIP SXT GEN TOB
	9 MA	09	CTX-M-1	А	P49-6	fimH iucD iroN cvaC iss traT	CIP SXT GEN TOB
76.2	179 LU	05	SHV-12	А	P50-7	iucD iroN kpsM II-K2 cvaC iss trat tsh	CIP
60.5	57 MA	011	CTX-M-14	D	P25-6	fimH fimAv _{MT78} papG II sat iucD kpsM II-K5	CIP SXT
64.7	99 BA	017	SHV-12	B1	P51-1	fimH	CIP
	90 SA	033	CTX-M-14b	D	P51-1	fimH	CIP SXT
97.8	6 SA	O25(a)	CTX-M-14	B1	P52-5	fimH iroN cvaC iss traT	CIP SXT
50.1 689 57.8 72.3	61 SA	O25(a)	CTX-M-14	B1	P52-5	fimH iroN cvaC iss traT	CIP
	86 LU	0139	CTX-M-14	А	P53-2	fimH fimAv _{MT78}	
58.9 6 8.2 81.8	25 SA	O101:H9	SHV-12	А	P53-2	fimH fimAv _{MT78}	CIP GEN
78.1	66 MA	053	SHV-12	А	P48-4	fimH iroN iss traT	CIP
73.6	15 BA	O101:H9	CTX-M-14	А	P54-2	traT malX	CIP SXT GEN
833	147 LU	0101:HNM	CTX-M-14	А	P55-2	iucD traT	CIP SXT GEN
57.7	90 LU	014	CTX-M-1	B1	P46-7	fimH iucD iroN cvaC iss traT tsh	CIP
3.2 70.3	27 BA	06	CTX-M-14	А	P56-7	fimH fimAv _{MT78} ircD iroN kpsM III iss traT	CIP STX
	70 SA	08	CTX-M-15	А	P57-1	iucD	CIP GEN
5.8 69.8	44 MA	ONT	CTX-M-14	А	P36-3	fimH iucD traT	CIP STX
	95 MA	0139	CTX-M-15	D	P58-3	iucD traT malX	CIP SXT TOB
100	14 SE	ONT	CTX-M-14	B1	P59-4	fimH iucD iss traT	CIP
62.9	15 SE	045	CTX-M-14	B1	P59-4	fimH iucD iss traT	CIP STX
59 <u>.8</u>	26 SE	0112	CTX-M-14	B1	P60-2	fimH traT	CIP STX
	90 MA	020	CTX-M-14	D	P61-8	fimH fimAVMT78 papG II sat iucD kpsM II-K5 traT malX	CIP GEN TOB
	82 SA	0148	SHV-12	D	P62-4	fimH kpsm II-K5 ibeA usp	CIP GEN

Dice (Opt:0.25%) (Tol 1.0%-1.0%) (H>0.0% S>0.0%) [0.0%-100.0%]
PFGE-Xbal
PFGE-Xbal

Figure 4. PFGE of XbaI-digested DNA from the 28 ESBL-producing isolates not belonging to clonal groups O25b:H4-B2-ST131, O15:H1-D-ST393 and CGA-D-ST69. Clusters with \geq 85% similarity are indicated in bold. Isolate designation, serotype, type of ESBL enzyme produced, phylogenetic groups, virulence profile designation-number of virulence genes, virulence genes and associated resistances are shown on the right. CIP, ciprofloxacin; SXT, trimethoprim/sulfamethoxazole; GEN, gentamicin; TOB, tobramycin.

 \geq

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were very similar, including the fimH, fimAv_{\rm MT78}, pagG II, sat, iucD and kpsM II-K5 genes.

Figure 3 shows a dendrogram with the profiles obtained by PFGE of the 22 isolates belonging to CGA-D-ST69, which showed a similarity of 68.2%, with four clusters having \geq 85% similarity.

In contrast, the 28 ESBL-producing isolates not belonging to any of the three clonal groups showed 48.2% similarity, with only two clusters of \geq 85% similarity (Figure 4).

Conclusions

The three clonal groups investigated in this study accounted for 37% of isolates exhibiting trimethoprim/sulfamethoxazole plus ciprofloxacin resistance, 34% of aminoglycoside-resistant isolates and 30% of multidrug-resistant isolates, which gives evidence of an important clonal component in the emergence of resistance among ExPEC. Notably, a single high virulent clonal group (O25b:H4-B2-ST131) causes approximately 1 in every 10 extraintestinal infections in Spain. The ST131 clonal group was significantly more prevalent than the other two clonal groups characterized in this study, and exhibited a significantly higher virulence score compared with the ST393 and ST69 isolates. This is consistent with its high virulence potential in a mouse model of septicaemia³⁵ and perhaps partly explains the higher epidemiological success of the ST131 clonal group. Interestingly, a new variant of the ST131 clonal group, which is non-ESBLproducing but trimethoprim/sulfamethoxazole resistant and with high virulence content, is reported.

The high prevalence of the ST131 clonal group, particularly among multidrug-resistant isolates, has important clinical and public health implications, due to the real risk of treatment failure. Especially problematic is the dual fluoroquinolone and trimethoprim/sulfamethoxazole resistance (36% of the ST131 isolates), and these drugs constitute the empirical oral UTI therapy. Hence, alternative prophylactic strategies, such as the development of vaccines against successful clonal groups, are urgently needed.

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Transparency declarations

None to declare.

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