

ORIGINAL ARTICLE

A non-synonymous polymorphism in galectin-3 lectin domain is associated with allergic reactions to beta-lactam antibiotics

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Genetic predictors of beta-lactam (BL) allergy are mostly related to Immunoglobulin E (IgE) synthesis and atopy. Despite this context, little attention has been devoted to genes of IgE/FcεRI pathway, such as galectin-3, a β-galactoside-binding lectin, which binds to IgE. We evaluated the association of *LGALS3* polymorphisms with BL allergy in 395 Spanish and 198 Italian cases, compared with 310- and 339-matched controls, respectively. The rs11125 predicted BL allergy with an odds ratio of 4.0 in Spanish population ($P < 0.0001$). This association was replicated with an odds ratio of 5.1 in Italian population ($P < 0.0001$); rs11125 predicted also increased serum level of total IgE in Spanish controls. These data are consistent with the predicted deleterious influence of Gln > His substitution produced by rs11125 on galactose-binding activity of galectin-3. In conclusion, *LGALS3* is the strongest genetic predictor of BL allergy reported so far. This association reflects the influence of genes of IgE/FcεRI pathway in this pathology.

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INTRODUCTION

Beta-lactam (BL) antibiotics are the most frequent cause of immediate reactions (IR) to drugs.¹ Most of these reactions appear within the first hour after drug intake and are mediated by specific Immunoglobulin E (IgE) antibodies. Both genetic and environmental factors are predictors of IR to BL and may explain differences in its prevalence worldwide.^{2–4} Most genetic associations have been related to the *IL4-IL13* pathway involved in IgE synthesis and atopy.^{2–7} However, less attention has been devoted to the mechanisms related to IgE binding to their high-affinity receptor FcεRI.⁸ Recently, we performed a fine-mapping genome-wide association study of the genetic predictors of BL allergy. We found that gene variants of HLA-DRA and HLA-DRA | HLA-DRB5 inter-region were significant predictors of BL allergy to penicillins, but not to cephalosporins.⁹ These data suggested that HLA-type 2 antigen presentation has a central role in the genetic susceptibility of BL allergy.⁹

Galectin-3 is a secretory β-galactoside-binding lectin, which interacts with IgE and FcεRI on the cell surface of mast cells and B lymphocytes, and influences mediator release from IgE-sensitized mast cells and T-cell functions.^{10–12} *Lgals3*^{−/−} mice have diminished IgE-mediated reactions through enhanced Th2 responses.^{11,12} These data suggest that *LGALS3* could be a genetic predictor of IR to drugs. We could not consider this hypothesis by genome-wide association study, as we performed it with an array, which did not analyze the variants of *LGALS3* gene with predicted functional influence.⁹ Therefore, we aimed to evaluate the potential association between non-synonymous single nucleotide polymorphisms (SNPs) in *LGALS3* exons and IR to BL and their relationship with total IgE levels and atopy, in the two

case-control populations from Spain and Italy investigated in our previous genome-wide association study.

MATERIALS AND METHODS

The study was performed in two already described case-control populations from Spain (discovery) and Italy (replication).^{4,6,9,13} The Spanish population consisted of 395 cases and 310 controls and the Italian population included 198 patients and 339 controls recruited in the Allergy Unit of the Regional University Hospital of Malaga (Spain), the Allergy Units of CI Columbus (Rome, Italy) and Oasi Maria SS (Troina, Italy), respectively. Diagnostic of IR to BL was established according to standard protocols of the European Network for Drug Allergy.¹⁴ We considered as biological criteria of Atopy total serum IgE levels higher than 100 kU l^{−1} (determined by UniCAP, Phadia, Uppsala, Sweden) and presence of serum-specific IgE against prevalent allergens (*Dermatophagoides pteronyssinus*, *Cynodondactylon*, *Lolium perenne*, *Phleum pratense*, *Olea europaea*, *Cupressus sempervirens*, *Plantago lanceolata*, *Chenopodium album*, *Salsola kali* and *Parietaria judaica*). We measured specific IgEs in serum by UniCAPTM (Phadia Diagnostics, Uppsala, Sweden). Controls were healthy individuals recruited in preventive care consultations in the same geographical area than patients. Inclusion criteria were the absence of reported history of drug hypersensitivity and/or any other immunological diseases and an age range similar to that of cases (between 16 and 60 years). The study was approved by institutional review boards and written informed consent was obtained from all participants. We performed DNA extraction and genotyping as described.^{3,6} The four variants on *LGALS3*, rs4652 (T98P), rs4644 (P64H), rs11125 (Q201H) and rs10148371 (R183K) were genotyped by real-time PCR with fluorescence resonance energy transfer in a Light-Cycler 480 Real-Time PCR System (Roche Molecular Biochemicals, Lyon, France). We controlled the fluorescence resonance energy transfer genotyping by direct DNA sequencing of 10% of samples. Demographic and clinical variables, Hardy–Weinberg equilibrium and SNP association were evaluated by Mann–Whitney *U*-test,

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Table 1. Clinical and biological characteristics of controls and patients with beta-lactam allergy, in Spain and Italy

Variable	Spain study population			Italy study population		
	Controls (n = 310)	Patients (n = 395)	P-value	Controls (n = 339)	Patients (n = 198)	P-value
	Mean $\pm$ s.d.	No. of cases (%)		Mean $\pm$ s.d.	No. of cases (%)	
Age, years	40.0 $\pm$ 13.4	43.5 $\pm$ 14.7	0.423	47.6 $\pm$ 20.6	41.1 $\pm$ 18.8	0.588
Female counts	211 (65.7)	225 (55.3)	0.193	221 (65.1)	137 (69.2)	0.371
<i>Clinical entities</i>						
Anaphylaxis	NA	311 (78.7)		NA	128 (65.3)	
Urticaria/angioedema	NA	84 (21.3)		NA	68 (34.7)	
<i>Culprit drug</i>						
Amoxicillin	NA	312 (79.0)		NA	149 (42.0)	
Benzilpenicillin	NA	50 (12.7)		NA	20 (5.6)	
Amoxicillin-clavulanic acid	NA	6 (1.5)		NA	37 (10.2)	
Cephalosporins	NA	19 (4.8)		NA	91 (25.6)	
Other	NA	0		NA	58 (16.3)	
Positive skin test	NA	206 (52.2)		NA	184 (92.9)	
RAST > 2.5	NA	239 (60.6)		NA	52 (26.7) ^a	
Atopy ^b	63 (20.3)	207 (52.4)	< 0.0001	48 (14.1)	125 (63.5)	< 0.0001
Total IgE (kU l ⁻¹ , mean $\pm$ s.d.)	53.9 $\pm$ 111.2	199.7 $\pm$ 342.5	< 0.0001	68.96 $\pm$ 189.0	170.9 $\pm$ 283.3	< 0.0001
IgE ≥ 100 kU l ⁻¹	36 (11.6)	167 (42.7)	< 0.0001	48 (14.1)	104 (52.7)	< 0.0001
IgE against prevalent allergens	51 (16.5)	87 (26.6)	0.019	NA	NA	
<i>rs4644</i>						
CC	148 (47.7)	195 (49.4)	0.101			
CA	134 (43.1)	147 (37.1)				
AA	28 (9.2)	53 (13.5)				
<i>rs4652</i>						
CC	80 (27.9)	67 (20.4)	0.0790			
CA	170 (59.4)	212 (64.4)				
AA	36 (12.6)	50 (58.1)				
<i>rs11125</i>						
AA	274 (88.9)	232 (60.6)	< 0.0001	279 (83.8)	63 (33.7)	< 0.0001
AT	32 (10.4)	150 (39.2)		49 (14.7)	124 (66.3)	
TT	2 (0.7)	1 (0.2)		5 (1.5)	0 (0.0)	

Abbreviations: NA, not applicable; RAST, radio-allergo-sorbent-test. ^aRAST only for penicillins G and V, and cefaclor. ^bAtopy was defined as the presence of rhinitis, asthma or eczema, or total IgE values ≥ 100 kU l⁻¹.

χ^2 -test and logistic regression, respectively, using SPSS v.15 (SPSS Inc., Chicago, IL, USA).

RESULTS

The 1242 individuals recruited included in the study had no significant age and sex differences between groups (Table 1). Systemic anaphylaxis was the most frequent clinical entity in both populations (78.7% and 65.3%, respectively), and amoxicillin was the predominant culprit drug (79.0% and 42.0%, respectively) (Table 1). Total IgE levels were higher in patients than controls in the two populations ($P < 0.0001$) (Table 1). We performed the genotyping of four non-synonymous SNPs from *LGALS3* in the Spanish population. *LGALS3* rs10148371 deviated significantly from Hardy-Weinberg equilibrium in controls, whereas rs 4644 and rs4652 did not show significant association after correction for multiple testing (Table 1 and Table 2). We excluded therefore these gene variants in the replication study. We extracted also data obtained for two rs of *LGALS3*, which were analyzed already in the Illumina Immunochip array.⁹ No association with BL allergy was found for any of these rs ($P = 0.60$ for rs800918 (Fisher's Exact); rs10137409 was monomorphic). In contrast, we found an association between rs11125 genotypes and BL allergy with the genotype additive model in the Spanish population (Table 1). The

minor allele frequency of rs11125 was significantly increased in Spanish cases compared with controls (Table 2). We replicated these associations in the Italian population (Table 1 and Table 2), with a risk prediction of minor allele higher than in Spain (Table 2). The minor allele frequency of the control populations was similar to that reported for European (0.079) in 1000 genome (www.1000genomes.org). The risk prediction of rs11125 was also observed by genotype analysis with the dominant model in both populations (odds ratio = 5.2, 95% confidence interval: 3.4–8.1 and odds ratio = 10.2, 95% confidence interval: 6.5–15.8, respectively, $P < 0.0001$). The risk prediction of the minor allele of rs11125 was not influenced by total IgE concentration in both Spanish and Italian populations, when considering subjects with a concentration either higher or lower than the 100 kU l⁻¹ threshold (Table 3). In contrast, the minor T allele of rs11125 was associated with increased total IgE level in Spanish controls, compared with A allele (74 $\pm$ 42 vs 53 $\pm$ 5.0, $P = 0.006$).

DISCUSSION

Our study shows a strong influence of rs11125 of *LGALS3* on BL allergy in the Spanish and Italian populations, with much higher odds ratios that those previously reported for all the other already

Table 2. Genotypic frequencies of the non-synonymous SNPs analyzed in the *LGALS3* gene

SNP	Change (allele 1, allele 2)	Location (effect)	Position ^a	Spain study population				Italy study population			
				MAF controls	MAF patients	OR (95% CI)	P _{corr}	MAF controls	MAF patients	OR (95% CI)	P _{corr}
rs4644	C>A	Exon 1 (Pro64His)	55604935	0.306	0.320	1.06 (0.84–1.34)	0.579				
rs4652	C>A	Exon 1 (Thr98Pro)	55605036	0.423	0.472	1.22 (0.97–1.55)	0.072				
rs11125	A>T	Exon 3 (Gln201His)	55611839	0.058	0.199	3.98 (2.70–6.00)	< 0.0001	0.086	0.331	5.1 (3.58–7.31)	< 0.0001

Abbreviations: CI, confidence interval; MAF, minor allele frequency; OR, odds ratio; P_{corr}, corrected P-value after Bonferroni correction; SNP, single nucleotide polymorphism. A corrected P-value of ≤0.05 was considered statistically significant. ^aAccording to NCBI build 37.

Table 3. Genotypes of the non-synonymous SNPs analyzed in the *LGALS3* according to IgE < 100 or ≥ 100 kU l⁻¹

Spain study population						
Gene variant	Controls IgE < 100 kU l ⁻¹ (n = 284)	Controls IgE ≥ 100 kU l ⁻¹ (n = 26)	P-value	Patients IgE < 100 kU l ⁻¹ (n = 258)	Patients IgE ≥ 100 kU l ⁻¹ (n = 137)	P-value
rs4644						
CC	99 (47.1)	5 (62.5)		84 (50.9)	44 (46.8)	
CA	93 (44.3)	1 (12.5)		59 (35.8)	37 (39.4)	
AA	18 (8.6)	2 (25.0)	0.075	22 (13.3)	13 (13.8)	0.792
rs4652						
CC	72 (27.7)	8 (30.8)		48 (22.7)	19 (16.0)	
CA	158 (60.7)	12 (46.1)		131 (62.4)	81 (68.0)	
AA	30 (11.6)	6 (23.1)	0.174	31 (14.8)	19 (16.0)	0.345
rs11125						
AA	251 (89.0)	23 (88.5)		160 (64.3)	72 (53.7)	
AT	29 (10.3)	3 (11.5)		88 (35.3)	62 (46.3)	
TT	2 (0.7)	0 (0.0)	0.785	1 (0.4)	0 (0.0)	0.590
Italian study population						
Gene variant	Controls IgE < 100 kU l ⁻¹ (n = 262)	Controls IgE ≥ 100 kU l ⁻¹ (n = 48)	P-value	Patients IgE < 100 kU l ⁻¹ (n = 94)	Patients IgE ≥ 100 kU l ⁻¹ (n = 108)	P-value
rs4644						
CC	76 (51.7)	15 (42.9)		33 (44.6)	37 (44.6)	
CA	57 (38.8)	17 (48.6)		26 (35.1)	32 (38.5)	
AA	14 (9.5)	3 (8.5)	0.568	15 (20.3)	14 (16.9)	0.852
rs11125						
AA	221 (83.9)	40 (83.3)		30 (34.1)	33 (33.3)	
AT	38 (14.7)	7 (15.6)		58 (65.9)	66 (66.7)	
TT	3 (1.4)	1 (2.1)	0.776	0 (0.0)	0 (0.0)	0.518

known genetic predictors of BL allergy.^{2–9} These high odds ratios suggest evaluating whether this polymorphism can be used as a biomarker in the prediction of BL allergy.

Galectin-3 behaves also as a soluble receptor of IgE in blood and activates mediator release of mast cells or basophiles.^{10–12} The complete list of the gene variants of *LGALS3* is given in supplementary table S1 online. We focused our study on missense variants that potentially influence galectin-3 blood concentration and galectin-3 binding activity, among this large number of polymorphisms. The Gln>His substitution of rs11125 is located in the galactose-binding lectin domain (Figure 1). It may have a deleterious influence on the lectin-binding activity, according to the prediction of two bioinformatic tools, sorting intolerant from tolerant and PolyPhen polymorphism phenotyping. This suggests that the association of rs11125 of *LGALS3* with BL allergy may be related to the binding of galectin-3 with IgE. This is consistent with the association of this polymorphism with the serum concentration of total IgE in the Spanish population. In contrast, rs4644 was not significantly associated with BL allergy in the Spanish

population. This rs produces a Pro>His substitution in the low complexity region and influences the blood level of galectin-3.¹⁵ Taken together, our results and these previous data support the hypothesis that *LGALS3* association with BL allergy is related rather to its lectin-binding activity in the IgE/FcεRI pathway than to galectin-3 level. The involvement of the IgE/FcεRI pathway in BL allergy is also illustrated by the association of a polymorphism in the gene promoter of FcεRIβ with increased IgE sensitization to cephalosporins in exposed health-care workers from Korea.¹⁶

The association of the minor T allele of rs11125 with total IgE level may be also related to its influence on molecular mechanisms that improve B-cell production of IgE. We have previously reported the involvement of genetic variants in the IL4-IL13 pathway in IR to BL in population studies conducted in Italy and Spain^{2–4,6} and the increased expression in IL-4, a key cytokine in IgE synthesis in CD4 lymphocytes from patients.¹⁷ Galectin-3 is involved in IgE production by influencing the IL-4 related Th2 response in *Lgals3*^{-/-} mice.^{11,12} In fact, KO mice have lower levels of serum IgE and IL-4 in broncho-alveolar fluid.¹² These data

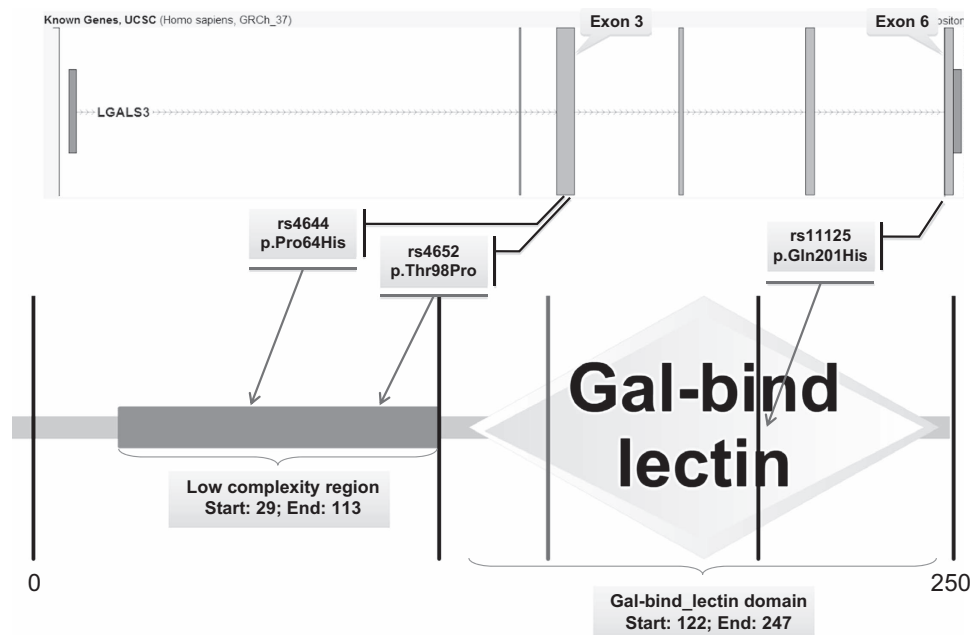


Figure 1. The Pro>His substitution of rs4652 in codon 64 of exon 3 is located in the 'low complexity region' while the Gln>His substitution of rs11125 in codon 201 of exon 6 is located in the galactose-binding lectin domain of galectin-3. Vertical bars represent introns in position 6, 114, 143 and 199, respectively. Adapted from a document available in <http://smart.embl-heidelberg.de/>.

suggest that the associations of *LGALS3* with BL allergy and serum IgE levels could reflect also an influence of galectin-3 on IL4-IL13 pathway, beside its interaction with FcεRI and IgE.^{10,18}

In conclusion, our data in two European populations show that rs11125 of *LGLS3* is the strongest genetic predictor of BL allergy reported so far. Previous experimental data and the predicted influence of this polymorphism on lectin activity of Galectin-3 suggest that the underlying mechanisms could be related to the IgE/FcεRI and IL4-IL13 pathways.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Supplementary Information accompanies the paper on the The Pharmacogenomics Journal website (<http://www.nature.com/tpj>)

Supplementary Table 1S. List of single nucleotide polymorphisms found on the *LGALS3* gene and its 5'- and 3'-flanking regions (Chr14: 55,595,431 to 55,612,808) according to the SNP 137 UCSC annotation track ('Start' and 'Stop' positions are reported according to the Genome Reference Consortium Human genome build 37, GRCh37)

Chr	Start	Stop	Name	Observed	Strand	RefNCBI	RefUCSC	Class	Function
14	55595431	55595431	rs113301825	A/C	+	A	A	single	near-gene-5
14	55595457	55595456	rs138561351	-/TA	+	-	-	insertion	near-gene-5
14	55595471	55595470	rs140714161	-/TA	+	-	-	insertion	near-gene-5
14	55595589	55595589	rs182226220	C/T	+	C	C	single	near-gene-5
14	55595595	55595595	rs140438666	A/G	+	A	A	single	near-gene-5
14	55595807	55595807	rs150413624	C/T	+	T	T	single	near-gene-5
14	55595817	55595817	rs113273087	A/T	+	T	T	single	near-gene-5
14	55595839	55595839	rs3742566	A/T	+	T	T	single	near-gene-5
14	55596212	55596212	rs118083722	A/G	+	G	G	single	intron
14	55596222	55596222	rs8012397	A/C	+	A	A	single	intron
14	55596388	55596388	rs61975412	C/T	+	C	C	single	intron
14	55596564	55596564	rs117993245	A/T	+	T	T	single	intron
14	55596631	55596631	rs186763001	A/T	+	A	A	single	intron
14	55596677	55596677	rs190473697	A/G	+	G	G	single	intron
14	55596777	55596777	rs12161901	C/T	+	C	C	single	intron
14	55596815	55596818	rs143586467	-/CTGT	+	CTGT	CTGT	deletion	intron
14	55597105	55597105	rs10149038	A/G	+	A	A	single	intron
14	55597116	55597116	rs191718066	A/T	+	T	T	single	intron
14	55597165	55597165	rs76817099	A/G	+	A	A	single	intron
14	55597166	55597166	rs79153423	G/T	+	G	G	single	intron
14	55597168	55597168	rs75449637	A/T	+	A	A	single	intron
14	55597176	55597176	rs117803845	C/T	+	T	T	single	intron
14	55597182	55597182	rs149206631	A/C	+	C	C	single	intron
14	55597193	55597193	rs182982061	A/G	+	G	G	single	intron

14	55597195	55597195	rs115549949	A/G	+	G	G	single	intron
14	55597203	55597203	rs146907658	A/C	+	C	C	single	intron
14	55597215	55597215	rs61160305	C/T	+	T	T	single	intron
14	55597282	55597281	rs60310677	-/TT	+	-	-	insertion	intron
14	55597348	55597348	rs187283380	A/G	+	G	G	single	intron
14	55597371	55597371	rs55710823	G/T	+	G	G	single	intron
14	55597469	55597468	rs201394501	-/G	+	-	-	insertion	intron
14	55597470	55597471	rs201506443	-/GT	+	GT	GT	deletion	intron
14	55597471	55597471	rs56126187	G/T	+	T	T	single	intron
14	55597471	55597471	rs61677952	-/T	+	T	T	deletion	intron
14	55597472	55597472	rs75585784	G/T	+	G	G	single	intron
14	55597632	55597632	rs79109213	A/G	+	G	G	single	intron
14	55597875	55597875	rs7157768	C/G	+	G	G	single	intron
14	55597931	55597931	rs181606509	C/T	+	C	C	single	intron
14	55597953	55597953	rs140323747	-/C	+	C	C	deletion	intron
14	55597982	55597982	rs147372402	C/T	+	T	T	single	intron
14	55598030	55598030	rs2147972	A/G	-	T	T	single	intron
14	55598091	55598091	rs190233052	C/T	+	T	T	single	intron
14	55598143	55598143	rs148016254	C/G	+	C	C	single	intron
14	55598473	55598473	rs182453206	A/G	+	G	G	single	intron
14	55598615	55598615	rs187726652	A/G	+	G	G	single	intron
14	55598617	55598617	rs78793419	G/T	+	G	G	single	intron
14	55598736	55598736	rs150521419	C/T	+	C	C	single	intron
14	55598743	55598743	rs116163094	A/G	+	G	G	single	intron
14	55598839	55598839	rs74669285	G/T	+	T	T	single	intron
14	55599097	55599097	rs193103505	A/G	+	G	G	single	intron
14	55599156	55599156	rs185581854	G/T	+	T	T	single	intron
14	55599181	55599181	rs78733901	A/C	+	A	A	single	intron
14	55599287	55599286	rs10629194	-/CTTTT	+	-	-	insertion	intron
14	55599288	55599287	rs35624648	-/CTTTT	+	-	-	insertion	intron
14	55599289	55599288	rs72369482	-/TTTTC	+	-	-	insertion	intron

14	55599291	55599290	rs35652569	-/TTCTT	+	-	-	insertion	intron
14	55599292	55599291	rs72376797	-/TCTTT	+	-	-	insertion	intron
14	55599298	55599297	rs10629608	-/TTTTC	+	-	-	insertion	intron
14	55599302	55599301	rs59685999	-/CTTTT	+	-	-	insertion	intron
14	55599302	55599302	rs199584761	C/T	+	T	T	single	intron
14	55599303	55599303	rs79892150	C/T	+	C	C	single	intron
14	55599331	55599331	rs139463984	A/G	+	G	G	single	intron
14	55599384	55599384	rs188446522	C/T	+	C	C	single	intron
14	55599627	55599627	rs192228303	C/T	+	C	C	single	intron
14	55599670	55599670	rs184253710	A/G	+	A	A	single	intron
14	55599914	55599913	rs146503467	-/A	+	-	-	insertion	intron
14	55599914	55599914	rs117502961	G/T	+	T	T	single	intron
14	55599920	55599920	rs188718564	C/T	+	T	T	single	intron
14	55599968	55599968	rs114145651	A/T	+	T	T	single	intron
14	55600035	55600035	rs181161051	C/T	+	T	T	single	intron
14	55600101	55600101	rs143441173	A/T	+	T	T	single	intron
14	55600155	55600155	rs184385433	A/C	+	C	C	single	intron
14	55600172	55600172	rs146277113	A/G	+	G	G	single	intron
14	55600282	55600282	rs1047556	A/T	+	A	A	single	intron
14	55600339	55600339	rs139275100	A/G	+	G	G	single	intron
14	55600351	55600351	rs189264993	C/G	+	C	C	single	intron
14	55600386	55600386	rs182207532	C/G	+	G	G	single	intron
14	55600391	55600391	rs144115619	A/T	+	A	A	single	intron
14	55600405	55600405	rs57970196	C/T	+	C	C	single	intron
14	55600410	55600410	rs187617760	A/G	+	G	G	single	intron
14	55600430	55600430	rs73271727	G/T	+	G	G	single	intron
14	55600500	55600500	rs148967547	C/T	+	T	T	single	intron
14	55600536	55600536	rs142874155	C/T	+	T	T	single	intron
14	55600587	55600591	rs141652522	-/ATCTT	+	ATCTT	ATCTT	deletion	intron
14	55600602	55600602	rs77320652	A/G	+	G	G	single	intron
14	55600796	55600796	rs190951264	C/T	+	T	T	single	intron

14	55600939	55600939	rs76426991	A/G	+	G	G	single	intron
14	55601027	55601027	rs181752111	C/T	+	C	C	single	intron
14	55601092	55601092	rs115890944	C/G	+	G	G	single	intron
14	55601138	55601138	rs114284476	G/T	+	T	T	single	intron
14	55601231	55601231	rs111935382	C/T	+	C	C	single	intron
14	55601263	55601263	rs79936440	C/T	+	T	T	single	intron
14	55601278	55601278	rs151026604	C/T	+	T	T	single	intron
14	55601352	55601352	rs142351455	C/T	+	T	T	single	intron
14	55601371	55601371	rs186059578	C/G	+	C	C	single	intron
14	55601577	55601577	rs190292371	A/C	+	A	A	single	intron
14	55601617	55601617	rs1130118	A/G	+	A	A	single	intron
14	55601653	55601653	rs1130119	A/G	+	A	A	single	intron
14	55601657	55601657	rs183086742	C/G	+	G	G	single	intron
14	55601659	55601659	rs3188651	A/G	+	A	A	single	intron
14	55601702	55601702	rs117131718	A/G	+	G	G	single	intron,near-gene-5
14	55601708	55601707	rs11399383	-/A	+	-	-	insertion	intron,near-gene-5
14	55601709	55601708	rs59465607	-/A	+	-	-	insertion	intron,near-gene-5
14	55601918	55601921	rs151200276	-/CTGA	+	CTGA	CTGA	deletion	intron,near-gene-5
14	55601920	55601920	rs34665681	-/GACT	+	G	G	in-del	intron,near-gene-5
14	55601969	55601969	rs187675496	A/G	+	G	G	single	intron,near-gene-5
14	55602061	55602061	rs117305457	C/T	+	T	T	single	intron,near-gene-5
14	55602201	55602201	rs190906978	A/G	+	A	A	single	intron,near-gene-5
14	55602277	55602276	rs202132153	-/G	+	-	-	insertion	intron,near-gene-5
14	55602279	55602279	rs66950466	-/T	+	T	T	deletion	intron,near-gene-5
14	55602279	55602279	rs113070927	G/T	+	T	T	single	intron,near-gene-5
14	55602280	55602279	rs71963225	-/T	+	-	-	insertion	intron,near-gene-5
14	55602313	55602313	rs182501950	C/T	+	C	C	single	intron,near-gene-5
14	55602323	55602323	rs189161026	C/T	+	C	C	single	intron,near-gene-5
14	55602326	55602326	rs192467939	A/G	+	A	A	single	intron,near-gene-5
14	55602358	55602358	rs184467201	C/T	+	C	C	single	intron,near-gene-5
14	55602421	55602421	rs117744883	C/T	+	C	C	single	intron,near-gene-5

14	55602432	55602432	rs146897116	A/G	+	G	G	single	intron,near-gene-5
14	55602443	55602443	rs187230197	C/T	+	C	C	single	intron,near-gene-5
14	55602450	55602450	rs191694554	A/T	+	T	T	single	intron,near-gene-5
14	55602528	55602528	rs184774675	C/T	+	C	C	single	intron,near-gene-5
14	55602626	55602626	rs189231950	C/T	+	C	C	single	intron,near-gene-5
14	55602686	55602686	rs79074150	A/G	+	G	G	single	intron,near-gene-5
14	55602688	55602688	rs75040142	A/G	+	G	G	single	intron,near-gene-5
14	55602781	55602780	rs57117110	-/C	+	-	-	insertion	intron,near-gene-5
14	55602784	55602784	rs76984155	A/G	+	G	G	single	intron,near-gene-5
14	55602854	55602854	rs181014001	A/G	+	A	A	single	intron,near-gene-5
14	55602914	55602915	rs143294604	-/CT	+	CT	CT	deletion	intron,near-gene-5
14	55602960	55602960	rs139376852	C/T	+	C	C	single	intron,near-gene-5
14	55602980	55602980	rs141732289	A/C	+	C	C	single	intron,near-gene-5
14	55603002	55603002	rs1009977	G/T	+	T	T	single	intron,near-gene-5
14	55603041	55603041	rs79618905	A/G	+	A	A	single	intron,near-gene-5
14	55603042	55603042	rs77482253	A/G	+	G	G	single	intron,near-gene-5
14	55603061	55603061	rs1009978	C/G	+	C	C	single	intron,near-gene-5
14	55603188	55603188	rs150466255	G/T	+	G	G	single	intron,near-gene-5
14	55603195	55603195	rs77031867	A/C	+	C	C	single	intron,near-gene-5
14	55603220	55603220	rs34489143	-/C	+	C	C	deletion	intron,near-gene-5
14	55603462	55603462	rs184343020	C/T	+	C	C	single	intron,near-gene-5
14	55603574	55603574	rs189620702	A/C	+	A	A	single	intron,near-gene-5
14	55603633	55603633	rs77870073	A/T	+	T	T	single	intron,near-gene-5
14	55603696	55603696	rs79565299	A/T	+	T	T	single	intron,near-gene-5
14	55603794	55603794	rs79834356	A/C	+	C	C	single	intron,ncRNA
14	55603795	55603795	rs77139802	A/C	+	A	A	single	intron,ncRNA
14	55603825	55603825	rs137979468	A/G	+	G	G	single	intron,ncRNA
14	55603827	55603827	rs201060113	G/T	+	G	G	single	intron,ncRNA
14	55603874	55603874	rs77419946	C/T	+	C	C	single	intron,ncRNA
14	55603902	55603902	rs149471573	A/G	+	G	G	single	intron,ncRNA
14	55603991	55603991	rs45509294	A/T	+	A	A	single	intron,ncRNA

14	55604011	55604011	rs181801745	A/G	+	G	G	single	intron,ncRNA
14	55604020	55604020	rs61975413	A/G	+	G	G	single	intron,ncRNA
14	55604109	55604109	rs78001930	A/G	+	G	G	single	coding-synon,ncRNA
14	55604116	55604116	rs115891972	A/G	+	G	G	single	intron,ncRNA
14	55604146	55604146	rs199699629	C/T	+	C	C	single	intron,ncRNA
14	55604185	55604185	rs116659993	A/G	+	G	G	single	intron,ncRNA
14	55604223	55604223	rs114186444	C/T	+	T	T	single	intron,ncRNA
14	55604237	55604237	rs36059179	C/T	+	C	C	single	intron,ncRNA
14	55604240	55604240	rs74050920	C/T	+	T	T	single	intron,ncRNA
14	55604308	55604308	rs28415601	A/G	+	G	G	single	intron,ncRNA
14	55604353	55604353	rs2075598	C/T	+	C	C	single	intron,ncRNA
14	55604402	55604402	rs186115963	C/T	+	C	C	single	intron,ncRNA
14	55604454	55604454	rs78054476	C/T	+	C	C	single	intron,ncRNA
14	55604711	55604713	rs10606761	-/CTG	+	CTG	CTG	deletion	intron,ncRNA
14	55604713	55604713	rs201605915	A/C	-	G	G	single	intron,ncRNA
14	55604713	55604715	rs60179062	-/GCT	+	GCT	GCT	deletion	intron,ncRNA
14	55604768	55604768	rs188973411	C/T	+	T	T	single	coding-synon,ncRNA
14	55604773	55604773	rs202159462	C/T	+	C	C	single	ncRNA,missense
14	55604774	55604774	rs11538648	A/G	+	G	G	single	coding-synon,ncRNA
14	55604816	55604816	rs181337247	C/T	+	C	C	single	coding-synon,ncRNA
14	55604856	55604856	rs199980622	C/G	+	G	G	single	ncRNA,missense
14	55604881	55604881	rs200440596	C/G	+	C	C	single	ncRNA,missense
14	55604883	55604883	rs201423229	A/G	+	G	G	single	ncRNA,missense
14	55604902	55604902	rs201924703	A/C	+	C	C	single	ncRNA,missense
14	55604904	55604904	rs11538647	C/T	+	T	T	single	ncRNA,missense
14	55604935	55604935	rs4644*	A/C	+	C	C	single	ncRNA,missense
14	55604957	55604957	rs61735588	C/T	+	C	C	single	coding-synon,ncRNA
14	55604998	55604998	rs201462121	G/T	+	G	G	single	ncRNA,missense
14	55605024	55605024	rs148184206	C/G	+	C	C	single	ncRNA,missense
14	55605036	55605036	rs4652*	A/C	+	A	A	single	ncRNA,missense
14	55605038	55605038	rs78964872	C/T	+	C	C	single	coding-synon,ncRNA

14	55605046	55605046	rs200922957	A/C	+	A	A	single	ncRNA,missense
14	55605268	55605268	rs72716688	A/G	+	A	A	single	intron
14	55605328	55605328	rs3837609	-/G	+	G	G	deletion	intron
14	55605355	55605355	rs11850516	C/T	+	T	T	single	intron
14	55605358	55605358	rs186712521	C/T	+	C	C	single	intron
14	55605381	55605381	rs191083721	A/G	+	A	A	single	intron
14	55605383	55605383	rs183027644	C/T	+	C	C	single	intron
14	55605403	55605403	rs75187058	A/T	+	A	A	single	intron
14	55605490	55605490	rs4901555	C/T	+	C	C	single	intron
14	55605655	55605655	rs185032635	A/T	+	T	T	single	intron
14	55605692	55605692	rs141552895	A/C	+	C	C	single	intron
14	55605884	55605884	rs146268003	A/T	+	A	A	single	intron
14	55605909	55605909	rs117433848	A/G	+	G	G	single	intron
14	55606015	55606015	rs139454969	A/G	+	A	A	single	intron
14	55606044	55606044	rs77869590	A/C	+	A	A	single	intron
14	55606121	55606121	rs142560725	A/G	+	G	G	single	intron
14	55606241	55606241	rs190918908	A/G	+	G	G	single	intron
14	55606294	55606294	rs183071338	C/T	+	T	T	single	intron
14	55606333	55606333	rs150550029	C/T	+	C	C	single	intron
14	55606368	55606368	rs187446146	G/T	+	G	G	single	intron
14	55606432	55606432	rs199521216	A/G	+	A	A	single	intron
14	55606601	55606601	rs139575422	A/C	+	C	C	single	intron
14	55606629	55606629	rs72716690	A/G	+	A	A	single	intron
14	55606767	55606767	rs17128230	C/T	+	C	C	single	intron
14	55606802	55606801	rs10657270	-/ATT	+	-	-	insertion	intron
14	55606803	55606802	rs67202714	-/ATT	+	-	-	insertion	intron
14	55606808	55606807	rs3832943	-/ATT	+	-	-	insertion	intron
14	55606823	55606822	rs36087671	-/C	+	-	-	insertion	intron
14	55606902	55606902	rs115078998	C/T	+	C	C	single	intron
14	55606926	55606926	rs115213423	A/G	+	G	G	single	intron
14	55606952	55606952	rs200234222	C/T	+	C	C	single	intron

14	55606972	55606972	rs79515515	G/T	+	T	T	single	intron
14	55607036	55607036	rs201398647	A/G	+	G	G	single	ncRNA,missense
14	55607101	55607101	rs191939424	C/T	+	C	C	single	intron
14	55607366	55607366	rs8004787	C/T	+	C	C	single	intron
14	55607559	55607558	rs138577753	-/T	+	-	-	insertion	intron
14	55607560	55607560	rs183343180	A/T	+	T	T	single	intron
14	55607564	55607564	rs73271737	A/G	+	G	G	single	intron
14	55607781	55607781	rs72716692	A/G	+	A	A	single	intron
14	55608002	55608002	rs144650494	C/T	+	C	C	single	intron
14	55608016	55608016	rs74050921	A/G	+	G	G	single	intron
14	55608028	55608028	rs188455672	A/C	+	C	C	single	intron
14	55608154	55608154	rs147953855	A/G	+	A	A	single	intron
14	55608205	55608205	rs141903952	A/G	+	G	G	single	intron
14	55608246	55608245	rs34079008	-/T	+	-	-	insertion	intron
14	55608365	55608365	rs192679373	A/G	+	G	G	single	intron
14	55608376	55608376	rs35566145	-/A	+	A	A	deletion	intron
14	55608444	55608444	rs56358335	C/G	+	G	G	single	intron
14	55608458	55608458	rs77886871	A/G	+	A	A	single	intron
14	55608479	55608479	rs184514675	C/T	+	T	T	single	intron
14	55608492	55608492	rs151078791	C/G	+	G	G	single	intron
14	55608538	55608538	rs80057912	C/T	+	T	T	single	intron
14	55608604	55608604	rs141052359	C/T	+	C	C	single	intron
14	55608695	55608695	rs188111572	A/G	+	A	A	single	intron
14	55608809	55608809	rs150106586	C/T	+	C	C	single	intron
14	55608868	55608868	rs138609366	C/G	+	G	G	single	intron
14	55609160	55609164	rs143968645	-/TGATT	+	TGATT	TGATT	deletion	intron
14	55609191	55609191	rs192595339	C/T	+	C	C	single	intron
14	55609234	55609234	rs2075601	C/T	+	C	C	single	intron
14	55609318	55609318	rs199729394	C/G	+	C	C	single	ncRNA,missense
14	55609329	55609329	rs184778469	C/T	+	T	T	single	coding-synon,ncRNA
14	55609332	55609332	rs145296140	C/T	+	T	T	single	coding-synon,ncRNA

14	55609355	55609355	rs201865041	A/G	+	G	G	single	ncRNA,missense
14	55609368	55609368	rs201301078	C/T	+	C	C	single	coding-synon,ncRNA
14	55609371	55609371	rs137885280	C/T	+	C	C	single	coding-synon,ncRNA
14	55609381	55609381	rs189412756	A/G	+	A	A	single	ncRNA,missense
14	55609418	55609418	rs10148371	A/G	+	G	G	single	intron,ncRNA,missense
14	55609433	55609433	rs200686001	C/T	+	C	C	single	intron,ncRNA,missense
14	55609468	55609468	rs113169810	A/G	+	G	G	single	intron,splice-5
14	55609502	55609502	rs201941412	A/G	+	A	A	single	intron
14	55609532	55609532	rs142627260	C/T	+	C	C	single	intron
14	55609673	55609673	rs112870736	A/C	+	C	C	single	intron
14	55609690	55609690	rs182081011	C/T	+	C	C	single	intron
14	55609774	55609774	rs2075602	A/G	+	A	A	single	intron
14	55609848	55609848	rs80331783	C/G	+	G	G	single	intron
14	55609912	55609912	rs186736601	C/T	+	T	T	single	intron
14	55609955	55609955	rs2075603	A/C	+	C	C	single	intron
14	55610001	55610001	rs71412667	C/T	+	T	T	single	intron
14	55610106	55610106	rs144162477	A/G	+	G	G	single	intron
14	55610146	55610145	rs72186710	-/T	+	-	-	insertion	intron
14	55610203	55610203	rs189994172	A/G	+	G	G	single	intron
14	55610242	55610242	rs6573005	A/C	+	C	C	single	intron
14	55610285	55610285	rs181119573	A/G	+	G	G	single	intron
14	55610328	55610328	rs8011980	C/T	+	C	C	single	intron
14	55610373	55610373	rs150636420	C/T	+	C	C	single	intron
14	55610398	55610398	rs140857310	A/G	+	A	A	single	intron
14	55610406	55610406	rs34217836	A/G	+	G	G	single	intron
14	55610432	55610432	rs6573006	C/T	+	T	T	single	intron
14	55610517	55610517	rs112726235	C/T	+	C	C	single	intron
14	55610575	55610574	rs72111382	lengthTooLong	+	-	-	in-del	intron
14	55610586	55610585	rs149795113	lengthTooLong	+	-	-	in-del	intron
14	55610708	55610708	rs116032533	C/T	+	C	C	single	intron
14	55610725	55610725	rs185088551	C/T	+	T	T	single	intron

14	55610798	55610800	rs10598317	-/ACA	+	ACA	ACA	deletion	intron
14	55610820	55610820	rs147863612	C/T	+	T	T	single	intron
14	55610826	55610826	rs139881408	C/T	+	C	C	single	intron
14	55610829	55610829	rs111367178	A/G	+	G	G	single	intron
14	55610854	55610854	rs10498474	A/G	+	A	A	single	intron
14	55610856	55610856	rs189604436	A/C	+	A	A	single	intron
14	55610858	55610858	rs150052724	C/T	+	C	C	single	intron
14	55610932	55610932	rs183327578	C/T	+	C	C	single	intron
14	55610940	55610940	rs8013027	C/G	+	C	C	single	intron
14	55611008	55611008	rs73271745	A/T	+	A	A	single	intron
14	55611013	55611013	rs186404595	A/G	+	A	A	single	intron
14	55611031	55611030	rs79712470	G/T	+	-	-	single	intron
14	55611054	55611053	rs35040620	-/G	+	-	-	insertion	intron
14	55611109	55611109	rs145418208	A/G	+	G	G	single	intron
14	55611246	55611246	rs35563148	-/A	+	A	A	deletion	intron
14	55611286	55611286	rs10137382	C/T	+	C	C	single	intron
14	55611318	55611318	rs191959187	G/T	+	T	T	single	intron
14	55611327	55611327	rs201955822	A/G	+	G	G	single	intron
14	55611413	55611413	rs149185462	C/G	+	C	C	single	intron
14	55611431	55611431	rs143363745	C/T	+	C	C	single	intron
14	55611441	55611441	rs10137409	A/C	+	A	A	single	intron
14	55611457	55611457	rs111423667	-/T	+	T	T	deletion	intron
14	55611484	55611484	rs146694848	A/G	+	G	G	single	intron
14	55611510	55611510	rs140263361	C/T	+	C	C	single	intron
14	55611528	55611528	rs145357316	C/T	+	C	C	single	intron
14	55611529	55611529	rs55757365	A/G	+	G	G	single	intron
14	55611535	55611535	rs34719952	G/T	+	G	G	single	intron
14	55611574	55611574	rs137866364	A/G	+	G	G	single	intron
14	55611702	55611702	rs183825869	C/T	+	T	T	single	intron
14	55611748	55611748	rs188215112	A/G	+	A	A	single	intron
14	55611768	55611768	rs140734039	A/G	+	G	G	single	intron

14	55611809	55611809	rs192920279	A/C	+	A	A	single	intron
14	55611834	55611834	rs201096256	A/G	+	A	A	single	intron,ncRNA,missense
14	55611839	55611839	rs11125*	A/T	+	A	A	single	intron,ncRNA,missense
14	55611894	55611894	rs11001	C/T	+	C	C	single	intron,ncRNA,nonsense
14	55611946	55611946	rs1042869	C/T	+	C	C	single	intron,ncRNA,missense
14	55611955	55611955	rs150161752	C/T	+	T	T	single	intron,ncRNA,missense
14	55611975	55611975	rs138668217	C/T	+	T	T	single	intron,ncRNA,missense
14	55611991	55611991	rs1042896	C/T	+	C	C	single	intron,ncRNA,untranslated-3
14	55612005	55612005	rs61975414	A/T	+	T	T	single	intron,ncRNA,untranslated-3
14	55612007	55612007	rs71659941	-/A	+	A	A	deletion	intron,ncRNA,untranslated-3
14	55612007	55612007	rs74959172	A/T	+	A	A	single	intron,ncRNA,untranslated-3
14	55612024	55612024	rs1042906	C/T	+	C	C	single	intron,ncRNA,untranslated-3
14	55612056	55612056	rs1042918	A/C	+	A	A	single	ncRNA,missense,untranslated-3
14	55612086	55612086	rs182580267	C/T	+	T	T	single	ncRNA,missense,untranslated-3
14	55612141	55612142	rs149894805	-/AT	+	AT	AT	deletion	ncRNA,untranslated-3
14	55612178	55612178	rs111992841	G/T	+	G	G	single	intron,near-gene-3
14	55612442	55612442	rs80241027	A/C	+	C	C	single	intron,near-gene-3
14	55612458	55612458	rs17128252	C/T	+	C	C	single	intron,near-gene-3
14	55612480	55612480	rs10498475	C/T	+	C	C	single	intron,near-gene-3
14	55612573	55612573	rs76424323	A/G	+	A	A	single	intron,near-gene-3
14	55612579	55612579	rs138113889	C/T	+	T	T	single	intron,near-gene-3
14	55612744	55612744	rs7140872	C/T	+	C	C	single	unknown
14	55612761	55612761	rs199816740	A/G	+	G	G	single	unknown
14	55612787	55612787	rs1815316	A/G	-	C	C	single	unknown
14	55612798	55612798	rs10141323	A/G	+	G	G	single	unknown
14	55612808	55612808	rs186860936	A/G	+	A	A	single	unknown

* Variants evaluated in the study.