



Detection of Mendelian and Parent-of-origin Quantitative Trait Loci for Meat Quality in a Cross between Korean Native Pig and Landrace

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ABSTRACT : This study was conducted to detect quantitative trait loci (QTL) affecting meat quality in an F₂ reference population of Korean native pig and Landrace crossbreds. The three-generation mapping population was generated with 411 progeny from 38 F₂ full-sib families, and 133 genetic markers were used to produce a sex-average map of the 17 autosomes. The data set was analyzed using least squares Mendelian and parent-of-origin interval-mapping models. Lack-of-fit tests between models were used to characterize the QTL for mode of gene expressions. A total of 10 (32) QTL were detected at the 5% genome (chromosome)-wise level for the analyzed traits. Of the 42 QTL detected, 13 QTL were classified as Mendelian, 10 as paternal, 14 as maternal, and 5 as partial expressed QTL, respectively. Among the QTL detected at 5% genome-wise level, four QTL had Mendelian mode of inheritance on SSCs 5, 10, 12, and 13 for cooking loss, drip loss, crude lipid and crude protein, respectively; two QTL maternal inheritance for pH at 24-h and shear force on SSC11; three QTL paternal inheritance for CIE b and Hunter b on SSC9 and for cooking loss on SSC15; and one QTL partial expression for crude ash on SSC13, respectively. Most of the Mendelian QTL (9 of 13) had a dominant mode of gene action, suggesting potential utilization of heterosis for genetic improvement of meat quality within the cross population via marker-assisted selection. (**Key Words :** QTL, Meat Quality Trait, Korean Native Pig, Landrace, Parent-of-origin)

INTRODUCTION

Consumer satisfaction for meat product is influenced by meat color, leanness, amount of fat tissue, and water holding capacity etc. (Otto et al., 2006). Thus, understanding the genetic regulation of meat quality is becoming more important criteria for better meat production (Duthie et al., 2011). With the development of molecular tools and high throughput genotyping technologies, lots of chromosomal regions were found that harbored genes responsible for production traits in farm animals including pigs. Recent pig QTL database showed that approximately 4,434 QTL affecting meat quality traits have been detected on a variety of pig chromosome regions

by using different experimental populations (<http://www.animalgenome.org>).

Pork is the one of the most important protein sources in Korea. As well-being foods have been more focused on, pork quality is also of great interest to Korean meat consumers. Korean native pigs (KNP) are known to have more redness, less cooking loss and shear force than Yorkshire and Landrace breeds (Cho, 2006), as well as abundant amino acid compositions (*i.e.* threonin, arginin, tryptophan, leucine, lysine, alanin and glutamic acid), which may be associated with high flavor and palatability in KNP (Hwang et al., 2004). Bidanel and Rothschild (2002) reported that the KNP would gain some appreciable characteristics for growth and meat quality if the KNP were crossed with western breeds due to the effect of heterosis and breed complementarity.

Kim et al. (2007) performed genome scans to detect Mendelian and parent-of-origin QTL for growth and body composition traits in a cross population of KNP and Landrace. In this study, we report Mendelian or non-Mendelian QTL that are responsible for meat quality traits using the same experimental population.

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MATERIALS AND METHODS

Animals, phenotypes and genetic map construction

A resource population consisting of three generations was generated by crossing five KNP sires and ten Landrace dams at the National Livestock Research Institute (NLRI), Songhwan, Korea. Ten F_1 boars were randomly chosen for *inter se* mating up to six F_1 sows to produce 38 full-sib F_2 families resulting 411 F_2 progenies in the first ($N = 281$) and second ($N = 130$) parities. Among the F_2 s, 318 individuals were used in this study. Raising conditions and management practices are described in detail in Choy et al. (2002a; 2002b). The F_2 individuals were slaughtered at the age of 201 to 246 days (avg. 216.4 d) at the slaughterhouse of NLRI. The average final (live) weight before slaughter was 88.5 kg with a range of 46 to 138 kg. The animals were slaughtered by flowing 300 volts electric current of 1.25 to 1.50 amperes for one to five seconds. Bleeding was performed at vertical position to minimize post-mortem changes, and the scalding tank was maintained at around 60°C for subsequent carcass processing.

Several traits such as, moisture, lipid, crude protein, crude lipid, crude ash, shear force, pH at 24-h, drip loss, water holding capacity, cooking loss, CIE L, CIE a, CIE b, Hunter L, Hunter a, Hunter b were considered under the experiment. Table 1 contains the mean and standard deviation for the respective meat quality traits.

For lipid, total fat was obtained from fat trimming of carcasses. Samples from muscle *longissimus dorsi* were taken to measure moisture (%), crude protein (%), crude lipid (%), and crude ash (%) following the protocol of

AOAC (1990). Warner-Bratzler shear force was measured according to Wheeler et al. (2000), and pH was taken with a portable needle-tipped electrode (NWKbinar pH-K21, Germany) at 24-h after slaughter. Drip loss was also measured at 24-h postmortem period by weighing the sample before and after vacuum storage. Cooking loss was calculated from the weight loss after cooking for 40 minutes in an 80°C water bath. Water holding capacity (WHC) was measured after some adaptations from Kristensen and Purslow (2001). One gram (g) of homogenized tissue was placed in a 2 ml centricon tube (VIDAS, France), followed by its placement in a 50 ml centrifugation tube, heated in a 70°C water bath for 30 minutes, and centrifuged at 100 g (Hitachi, SCR20BA, Japan) for 10 min at 18°C room temperature. WHC was measured as the percentage of weight loss of the sample tissues after centrifugation. Objective meat colors CIE (L, a, b) and Hunter (L, a, b) were determined by a Minolta Chroma meter (CR-301, Minolta, Japan) on fresh cut surface after a 30-min blooming at 1°C. Meat color was expressed by commission and the color meter was calibrated against a white tile provided by the manufacturer.

To generate a linkage map a total of 133 genetic (microsatellite) markers were used. The DNA isolation, marker selection, and genotyping were performed as described in detail in Choi et al. (2006). Marker orders and relative locations were determined, such that for all autosomes except for *Sus scrofa* chromosomes (SSC) 2, 17 and 18, linkage maps were constructed using Crimap version 2.4 (Kim et al., 2007).

QTL analysis

For each chromosome, least squares interval mapping models were applied to detect Mendelian and parent-of-origin QTL. According to Kim et al. (2007), a set of QTL models such as Mendelian, paternal, maternal and full model along with a series of lack-of-fit tests between the models were applied to identify QTLs and to classify whether the QTL had Mendelian, paternal, maternal, or partial expression (Figure 1). The base model was a Mendelian line cross model, assuming that alternate QTL alleles were fixed in grand-parental breeds (Haley et al., 1994). The full (partial) model included the probabilities of inheriting KNP and Landrace alleles at a testing position, while the paternal or maternal models included only probabilities of paternal or maternal inheritance. The null model was the simple regression model without parents' allele information.

A paternally expressed QTL was defined as the one which shows a significant allelic effect when inherited from the sires and non-significant allelic effect when inherited from the dams of the progeny, and *vice versa* for maternally expressed QTL. A partially expressed QTL was one that

Table 1. Means and standard deviations for meat composition measured on F_2 animals

Trait	Number of observation	Mean	Standard deviation
Crude ash (%)	318	1.09	0.67
Crude protein (%)	318	22.20	2.01
Crude lipid (%)	318	2.21	2.76
Lipid (kg)	318	10.58	4.98
Drip loss (%)	308	2.75	2.26
Water holding capacity (%)	310	58.30	6.86
Moisture (%)	310	73.93	1.92
Cooking loss (%)	310	33.64	4.78
Shear force (kg)	310	3.84	2.63
pH at 24 h	310	5.62	0.27
CIE L	310	50.78	6.01
CIE a	310	9.88	4.12
CIE b	310	5.51	2.38
Hunter L	310	43.81	5.59
Hunter a	310	8.19	3.58
Hunter b	310	4.19	1.81

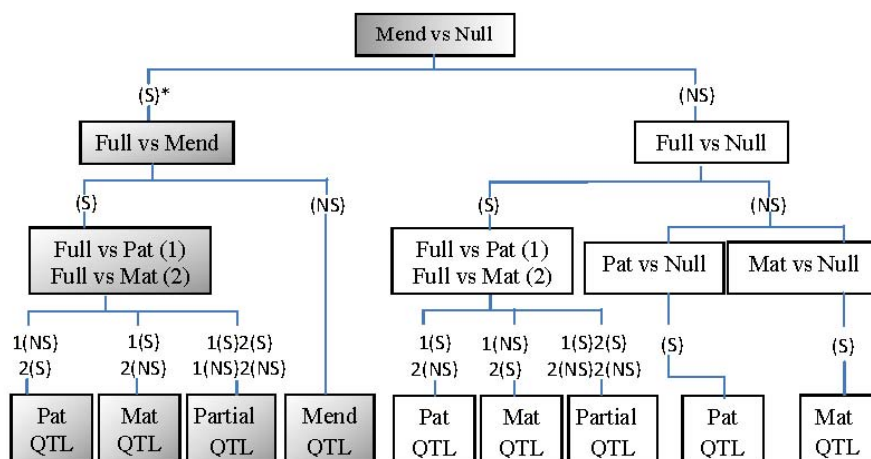


Figure 1. Decision trees to determine classification of QTL type using Mendelian (Mend), full (Full), paternal (Pat) and maternal (Mat) models. * S, F = Significant; NS = Non-significant.

shows an allelic effect when inherited from the sires and dams of progeny, but the magnitude of the effect depends on sex of the parents from which it was inherited.

All models were fitted for the parity, gender and F_1 sire as fixed effects. Additionally, birth-year-season was fitted as a fixed effect for total lipid, crude lipid, crude protein, and crude ash. For the rest of meat quality traits, the date of slaughtering was fitted as another fixed effect. The proportion of phenotypic variance due to a QTL was then estimated from the residual sum of squares with and without fitting QTL in the model. To determine the presence of QTL, permutations ($N = 10,000$) were performed to obtain empirical threshold values (p) at the chromosome-wise (CW) significance level, by randomly shuffling the phenotypes, fixed factors, and covariates to marker genotypes. The p value for a genome-wise (GW) significance level was then obtained based on size of the chromosome relative to the whole genome (Kim et al., 2007).

RESULTS AND DISCUSSION

Overall QTL results

Table 2 illustrates the QTL detected for meat quality traits and inheritance patterns. A total of 10 (32) QTLs were detected at 5% GW (CW) level. Among the ten GW QTLs, four QTL with Mendelian mode of inheritance were located on SSCs 5, 10, 12 and 13 for cooking loss, drip loss, crude lipid and crude protein, respectively. Two GW QTLs that were detected on SSC11 were maternally expressed for pH at 24-h and shear force (Table 2). Three GW QTLs with paternal expression were detected for CIE b (SSC9), Hunter b (SSC9) and cooking loss (SSC15), and one GW QTL for crude ash with partial expression of inheritance was detected on SSC13. Among the 42 QTLs, 13, 10, 14 and 5 QTLs were classified as Mendelian, paternally, maternally

and partially expressed, respectively (Table 2). A small portion of phenotypic variation (2.0-8.0%) was explained by each QTL with the mean of 3.9 ± 1.3 (Table 2).

QTL analyses for meat quality traits

For total lipid, three QTLs were detected in the proximal regions of SSCs 3, 8 and 9, respectively, at the 5% CW level (Table 2). The QTLs on the SSC3 and SSC9 had increasing maternal alleles for KNP. In the similar region of the SSC9 QTL, Li et al. (2011) found one SNP (BV726842_344) that was associated with Lipid (%) in an experimental KNP \times Landrace F_2 cross ($p < 0.01$). However, the QTL was not confirmed in other studies (Malek et al., 2001; Liu et al., 2007; Li et al., 2011). This may be partly due to the use of different markers and genetic backgrounds between breeds.

QTL for crude lipid were detected on SSCs 1, 4, 12 and 13. The two QTL on SSC1 and SSC12 were Mendelian expressed, and the two QTL on SSC4 and SSC13 were partially and maternally expressed, respectively. Li et al. (2011) identified two SNPs on SSC12 (BV726873_76, 117 cM) and SSC13 (BV726906_239, 57 cM) in a KNP \times Landrace F_2 cross population ($p < 0.01$), which resided close to the QTL regions in this study. Rohrer et al. (2005) found fat content (%) QTL at 6 cM and 82-85 cM in SSC1 and SSC4, respectively, in a Duroc \times Landrace cross population, which were located at the similar regions of the crude lipid QTL in this study (Table 2).

Three QTL for crude protein were detected on SSCs 1, 12, and 13, respectively, and all of the QTL had Mendelian mode of gene action. The two QTL on SSC1 and SSC13 had dominance effects with increasing Landrace alleles (Table 2). Three QTL for crude ash were identified on SSCs 6, 9 and 13, respectively, and the two QTL on SSC6 and SSC13 were partially expressed (Table 2).

Table 2. Quantitative trait loci for meat composition detected at least at 5% chromosome-wise evidence for linkage

SSC	Trait	cM ^a	$-\log_{10}P^b$	% σ_p^{2c}	QTL type ^d	QTL effect (standard errors) ^e		
1	Crude lipid (%)	0	2.29	3.4	Mend	0.196 (0.271)	1.310 (0.421)	
1	Crude protein (%)	0	2.70	4.0	Mend	-0.104 (0.208)	-1.120 (0.323)	
1	pH at 24-h	49	3.10	4.7	Mend	-0.050 (0.026)	0.170 (0.051)	
1	CIE b	77	2.67	3.1	Mat	0.551 (0.178)		
1	Hunter L	87	2.49	2.9	Pat	1.311 (0.442)		
3	Lipid (kg)	0	2.37	2.7	Mat	0.820 (0.285)		
4	Water holding capacity (%)	0	2.83	4.3	Mend	-2.021 (0.647)	1.795 (0.968)	
4	Crude lipid (%)	102	2.65	4.8	Partial	0.528 (0.206)	-0.412 (0.206)	
5	Shear force (kg)	77	2.88	5.2	Partial	0.460 (0.191)	-0.496 (0.191)	
5	Cooking loss (%)	139	3.61	**	5.5	Mend	1.067 (0.379)	-1.823 (0.576)
5	CIE b	152	2.94	3.5	Pat	-0.530 (0.161)		
5	Hunter b	157	2.58	3.0	Pat	-0.400 (0.132)		
6	Crude ash (%)	179	2.65	4.8	Partial	0.170 (0.066)	-0.158 (0.066)	
7	pH at 24-h	0	3.32	*	5.0	Mend	-0.109 (0.027)	0.014 (0.045)
8	Lipid (kg)	11	2.39	3.6	Mend	1.068 (0.395)	-1.150 (0.677)	
8	Moisture (%)	21	3.46	*	5.2	Mend	-0.733 (0.187)	0.175 (0.275)
9	Crude ash (%)	0	3.43	5.1	Mend	-0.256 (0.079)	-0.359 (0.121)	
9	Lipid (kg)	0	2.62	4.7	Partial	-0.437 (0.326)	0.870 (0.326)	
9	Cooking loss (%)	35	2.48	*	2.9	Pat	1.022 (0.345)	
9	CIE b	125	3.16	***	3.8	Pat	0.602 (0.176)	
9	Hunter b	126	2.89	***	3.4	Pat	0.439 (0.135)	
9	Drip loss (%)	127	2.24	2.5	Pat	0.485 (0.175)		
10	Drip loss (%)	165	4.29	**	6.5	Mend	-0.269 (0.231)	-1.719 (0.393)
11	pH at 24-h	38	3.93	***	4.9	Mat	-0.072 (0.018)	
11	Hunter a	92	2.38	2.7	Mat	0.812 (0.281)		
11	Shear force (kg)	102	3.90	***	4.8	Mat	0.928 (0.239)	
11	Water holding capacity (%)	108	2.62	3.0	Mat	-1.899 (0.621)		
11	Cooking loss (%)	112	2.33	2.7	Mat	1.177 (0.413)		
12	Crude lipid (%)	117	5.26	***	7.7	Mend	1.057 (0.221)	-0.521 (0.347)
12	Crude protein (%)	118	3.47	*	5.1	Mend	-0.670 (0.167)	0.116 (0.256)
13	Cooking loss (%)	0	2.93	*	3.5	Mat	-1.311 (0.400)	
13	Water holding capacity (%)	0	2.15	2.4	Mat	1.625 (0.599)		
13	Crude protein (%)	18	2.35	**	3.5	Mend	0.199 (0.193)	-1.042 (0.340)
13	Crude ash (%)	36	2.76	**	4.9	Partial	-0.144 (0.051)	-0.127 (0.051)
13	Crude lipid (%)	45	2.09	2.3	Mat	-0.471 (0.177)		
15	Moisture (%)	0	2.49	2.9	Mat	-0.395 (0.133)		
15	Hunter L	9	2.02	2.2	Mat	1.142 (0.438)		
15	CIE L	12	2.25	2.5	Mat	1.304 (0.468)		
15	Shear force (kg)	19	2.01	2.2	Mat	-0.528 (0.203)		
15	Cooking loss (%)	138	3.65	**	4.5	Pat	1.549 (0.415)	
15	CIE a	143	2.32	2.6	Pat	1.017 (0.358)		
15	Hunter a	144	2.26	2.6	Pat	0.863 (0.309)		

^a Position at which the test-statistic value was maximized for the inferred QTL model.

^b Negative logarithm of the comparison-wise p-value of the test statistic against the null hypothesis of no QTL at the most likely position for the inferred QTL model. * Significant at the 0.1 genome-wise level. ** Significant at the 0.05 genome-wise level. *** Significant at the 0.01 genome-wise level.

^c Proportion (%) of phenotypic variance explained by QTL $((RSS_{noQTL} - RSS_{QTL}) / RSS_{noQTL})$, where RSS is residual sum of squares for the model with or without QTL.

^d Declared QTL type: Mend = Mendelian expressed QTL; Pat = QTL with paternal expression; Mat = QTL with maternal expression; Partial = Parent-of-origin QTL with expression of both parental alleles.

^e Estimates of additive and dominance effects for Mend QTL; paternal, maternal and dominance effects for Partial QTL; paternal effect for Pat QTL; Maternal effects for Mat QTL.

Two QTL for moisture were detected on SSC8 and SSC15. The former was Mendelian expressed with additive effect and the latter was maternally expressed, both of which had increasing Landrace alleles (Table 2). Ma et al. (2009) detected two QTL for the trait at 83 and 138 cM of SSC8 in a White Duroc×Chinese Erhualian cross population. Edwards et al. (2008) found one QTL for the trait at 152 cM of SSC8 in a Duroc and Pietrain cross. Duthie et al. (2008) showed a QTL for protein content in loin at 37 cM of SSC8 in a Pietrain-sired F₂ cross population. All the locations of the QTL in the reports were not close to the QTL detected in this study. Therefore, there may be different QTL on SSC8 for protein content between breeds.

Three QTL for shear force were detected on SSCs 5, 11, and 15, respectively. The SSC5 QTL was partially expressed, while the rest two QTL were maternally expressed with increasing KNP and Landrace alleles, respectively (Table 2). Malek et al. (2001) found a QTL for Star Probe Force at 42 cM of SSC15 in an experimental cross population between Berkshire and Yorkshire, which was distal to the QTL location (19 cM) in this study. However, Thomsen et al. (2004) detected a maternally expressed QTL for tenderness at 13 cM of the same chromosome in the same population of Malek et al. (2001), which was very close to the QTL position in this study.

Three QTL for pH at 24-h were detected on SSCs 1 (49 cM), 7 (0 cM), and 11 (38 cM), respectively. The two QTL on SSC1 and SSC7 had Mendelian inheritance mainly with dominance and additive effects, respectively, while the QTL on SSC11 was maternally expressed with an increasing KNP allele (Table 2). Jennen et al. (2007) reported two QTL for loin and ham pH in the SSC1 regions flanked by SW1515-S0155 and S0312-S0113, respectively, in a Duroc-Pietrain cross population. The intervals represented 16~93.9 cM and 59.1 to 80.5 cM in the current NCBI database. Duthie et al. (2011) detected one QTL at 45 cM of SSC1 for loin pH at 45 minutes in a Pietrain-sired cross population, which was close to the QTL in this study. Duan et al. (2009) found a QTL for pH 4.5 m-24 h at 3 cM of SSC7 in a White Duroc×Chinese Erhualian population.

Two QTL for drip loss were detected at 129 cM of SSC9 and 165 cM of SSC10, respectively (Table 2). The latter QTL had dominance effect, explaining 6.5% of phenotypic variation with 5% GW significance of linkage evidence. Thomsen et al. (2004) found a QTL for drip loss between SW2401 and SW174 on SSC9 (57-123 cM in current NCBI database) in a Berkshire and Yorkshire cross population, which was overlapped with the QTL position in this study (109.5-137.6 cM, SW0295-SW174, NCBI).

For water holding capacity, three QTL were detected on SSCs 4, 11, and 13, respectively. The SSC4 QTL had Mendelian inheritance of gene action, while the rest two

QTL were maternally expressed with increasing Landrace and KNP alleles, respectively (Table 2). Malek et al. (2001) reported a QTL for the trait on SSC13. However, the QTL position (43 cM) was distal to the QTL (0 cM) in this study.

Five QTL for cooking loss were identified on SSCs 5, 9, 11, 13, and 15, respectively. Among the QTL, four QTL had parent-of-origin effects, while only one QTL on SSC5 had Mendelian mode of gene action (Table 2).

For CIE and Hunter traits as meat color measures, five and six QTL were detected, respectively. The QTL that were detected both for the two types of meat color on each of SSCs 1, 5, 9, and 15, were located at the similar regions, e.g. at 152 cM and 157 cM of SSC5 for CIE b and Hunter b, respectively (Table 2). Also, all of the QTL had the same mode of gene action, except the SSC1 QTL, for which maternal and paternal expression was observed for CIE b at 77 cM and for Hunter L at 87 cM, respectively (Table 2). Liu et al. (2007) and Jennen et al. (2007) detected QTL for color measurements on SSC1 around 44.6 to 110.5 cM, which flanked the QTL position in this study.

A comprehensive set of Mendelian and parent-of-origin models were used, which was based on the least squares framework. Application of the set of QTL models provided robustness in detection and characterization of QTL type (Thomsen et al., 2004; Kim et al., 2007). We found lots of QTL (42) for carcass and meat quality that are segregating between KNP and Landrace in many chromosomal regions. For Landrace, intensive selection programs for growth and leanness have been implemented, whereas breed restoration program for KPN was prioritized (Kim et al., 2005; Kim et al., 2007). Consequently, it is very likely that many genes for meat quality have different genotype or allele frequencies between the two breeds, part of which were identified in this QTL study (Table 2).

Many Mendelian QTL with complete or over-dominance mode of gene action were detected in this study. These findings are in a similar fashion with our previous study (Kim et al., 2007), in which many dominance QTL were found for growth and body composition traits. These results support the utilization of heterosis by crossing pig breeds with divergent characteristics as in McLaren et al. (1987) and Edwards et al. (2003).

For several Mendelian QTL, favorable alleles were originated from the Korean native pigs, e.g. for crude lipid on SSC1 and SSC12, cooking loss on SSC5, total lipid on SSC8 and crude protein on SSC10, for which increasing effects were observed for KNP alleles (Table 2). Furthermore, most of the paternally expressed QTL detected in this study, except for CIE b and Hunter b on SSC5, had effects with increasing KNP alleles (Table 2). Such findings of cryptic alleles in KNP indicate further possibilities to select genes for meat quality in breed crosses.

Our QTL analyses also suggest that many QTL for meat

quality are pleiotropic, *i.e.* one QTL influencing multiple traits. For example, we detected QTL at 0 cM on SSC1 for crude lipid and crude protein, at 152 to 157 cM on SSC5 for CIE b and Hunter b, at 11 to 21 cM on SSC8 for lipid and moisture, at 0 cM on SSC9 for crude ash and lipid, at 125 to 127 cM on SSC9 for drip loss, CIE b, and Hunter b, at 102 to 112 cM on SSC11 for shear force, cooking loss, and water holding capacity, at 117 to 118 cM on SSC12 for crude lipid and crude protein, at 0 cM on SSC13 for cooking loss and water holding capacity, at 138 to 144 cM on SSC15 for CIE a, Hunter a, and cooking loss (Table 2). These results may reflect the nature and characteristics of genes for meat quality, which is taken into account to efficiently implement programs of marker assisted selection for genetic improvement of meat quality in the cross population of KNP and Landrace.

We identified many QTL for meat quality in this study. These results can provide the first stage toward the development of molecular breeding plans such as fine mapping, marker-assisted selection, and characterization of causal mutation for the meat quality QTL, specifically to exploit favorable alleles in Korean native pigs.

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