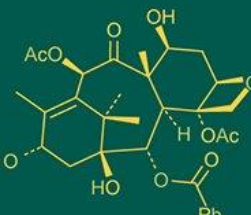
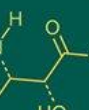
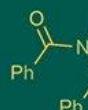
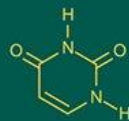


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ABCG2 gene polymorphism and its association with milk traits in Dangi cattle

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Abstract

The bovine ATP-binding cassette subfamily G member 2 (ABCG2) gene is a well-established candidate gene implicated in the regulation of milk yield and composition in dairy cattle. This study aimed to detect genetic variation within selected regions of the ABCG2 gene and assess its association with milk production traits in purebred Dangi cattle. A total of 60 lactating cows maintained under field conditions in the Ahilyanagar district of Maharashtra were screened across four genomic regions: exon-14, intron-3, exon-7, and intron-15. Molecular characterization employing PCR-RFLP and PCR-SSCP techniques revealed a complete absence of polymorphism at all loci examined. All 60 animals exhibited the AA genotype, with an allelic frequency of 1.00, indicating that these genomic regions are highly conserved within the Dangi breed. Consequently, no statistical association between the studied ABCG2 gene regions and milk production traits, including fat, protein, solids-not-fat (SNF), and lactose, could be established. These findings suggest strong genetic conservation in the Dangi breed, consistent with natural selection and long-term adaptation to local agroclimatic conditions.

Keywords: Dangi cattle, ABCG2 gene, genetic polymorphism, monomorphism, milk traits, PCR-RFLP, PCR-SSCP, Marker Assisted Selection

Introduction

Livestock production constitutes a cornerstone of the Indian agrarian economy, with the dairy sector contributing substantially to the national Gross Value Added (GVA). India is the world's largest producer of milk; however, the average daily yield of indigenous cattle breeds remains considerably lower than that of exotic *Bos taurus* breeds and their crossbreds. In this context, the genetic improvement of native breeds through modern molecular tools, particularly Marker Assisted Selection (MAS), represents a promising avenue to enhance productivity without compromising breed integrity or environmental adaptability.

The Dangi breed locally known as "*Kandadi*" is one of the 55 officially recognized indigenous cattle breeds of India. Native to the hilly tracts of the Western Ghats and regions of high rainfall in Maharashtra, Dangi cattle exhibit remarkable adaptive traits, including a distinctive oily skin secretion that protects against heavy precipitation and humid conditions. Despite these ecological advantages, Dangi cows demonstrate modest milk production, with an average lactation yield ranging from 175 to 800 kg.

The ABCG2 gene (ATP-binding cassette subfamily G member 2), located on bovine chromosome 6, encodes a transporter protein involved in the efflux of diverse substrates across cellular membranes. It has been identified as a candidate gene for milk yield and composition, primarily due to its role in the secretory pathway of the mammary gland. A functional missense mutation in exon-14 (Y581S; c.A>C), previously reported in exotic breeds, has been associated with increased milk yield but reduced fat and protein percentages.

The ABCG2 gene is one of the promising genes influencing milk production and its components. The ABCG2 gene variants were reported to be associated with milk production traits and the composition of bovine milk (Bouwman *et al.*, 2011; Leonard *et al.*, 2005). It also affects absorption and distribution, changing the toxicity and efficacy of medications in humans and animals (Sarkadi *et al.*, 2004; Jonker *et al.*, 2005) [4, 11, 17, 8].

Given the potential of ABCG2 as a molecular marker for selective breeding, this investigation was undertaken to characterize allelic variation at key regions of the gene in Dangi cattle and to evaluate any associations with phenotypic milk production traits.

Materials and Methods: Experimental Animals and Sample Collection:

The study was conducted on 60 lactating Dangi cows maintained under farmer herd conditions in the Ahilyanagar district of Maharashtra, India. Animals were selected based on confirmed purebred status, active lactation, and the absence of any known clinical conditions. All sample collection procedures were carried out in accordance with institutional animal ethics guidelines.

Blood samples (5 ml) were collected aseptically from the jugular vein into EDTA-coated vacutainers and stored at -20°C until DNA extraction. Milk samples (10 ml) were collected fortnightly over a period of six months and subjected to compositional analysis for fat, protein, solids-not-fat (SNF), and lactose content using a calibrated LACTOSCAN milk analyzer.

DNA Extraction and Quality Assessment

Genomic DNA was isolated from whole blood using the phenol: chloroform:isoamyl alcohol (PCI; 25:24:1) method

following standard protocols. DNA concentration and purity were assessed by spectrophotometric measurement at 260 nm and 280 nm using a NanoDrop ND-2000 spectrophotometer, and only samples with an A260/A280 ratio between 1.8 and 2.0 were selected for downstream molecular analyses. The integrity of the isolated DNA was further verified by electrophoresis on 0.8 percent agarose gel, which showed intact genomic DNA suitable for PCR amplification.

PCR Amplification

Four genomic regions of the bovine ABCG2 gene were amplified at exon-14 (207 bp), intron-3 (207 bp), exon-7 with a partial intronic region (393 bp), and intron-15 (323 bp). The amplification was carried out in a 25 µl reaction mixture containing template DNA, gene-specific forward and reverse primers, 2X PCR master mix, and nuclease-free water. The amplified PCR products were confirmed by electrophoresis on a 1.5 to 2 percent agarose gel stained with ethidium bromide and visualized under UV transillumination. The primer sequences, expected amplicon sizes, are presented in Table 1, while the PCR reaction composition and thermal cycling parameters are given in Tables 2 and 3, respectively. Amplified products were checked on 2 percent agarose gels and showed clear fragments of the expected sizes.

Table 1: Primer sequences

Locus	Primer sequence	Base pairs	Reference
Exon-14	F: 5'CACGAGACTGTCAGGGACTT3'	207 bp	Kowalewska-Luczak <i>et al.</i> (2009) [10]
	R: 5'GGACAATGAACCAGCACGGT3'		
Intron-3	F: 5'AAGAAGGAAGGGGATAAAATTGAAAGT3'	207 bp	Kowalewska-Luczak <i>et al.</i> (2009) [10]
	R: 5'CTT TTAAAA AATTATATGCTATAATCA3'		
Exon-7 and partial Intronic region	F: 5'TAAAGGCAGGAGTAATAAAG-3'	393 bp	Alim <i>et al.</i> (2013) [2]
	R: 5'TAACACCAAACTAACCGA AG-3'		
Intron-15	F: 5'TGTATCAGAGCCCCAAATCC-3'	323 bp	Hemlata Chouhan <i>et al.</i> (2021) [5]
	R: 5'AGCCACTGTGACACTGAACG-3'		

Tables 2: PCR reaction mixture

Component	Volume per reaction
2X PCR master mix	12.5 µl
Nuclease-free water	10.5 µl
Forward primer (10 pmol/µl)	0.5 µl
Reverse primer (10 pmol/µl)	0.5 µl
Template DNA	1.0 µl
Total volume	25.0 µl

Table 3: PCR cycling conditions

Locus	Initial denaturation	Denaturation	Annealing	Extension	Cycles	Final extension
Exon-14	95 °C for 5 min	95 °C for 45 sec	59 °C for 45 sec	72 °C for 1 min	35	72 °C for 10 min
Intron-3	94 °C for 5 min	94 °C for 30 sec	50 °C for 30 sec	72 °C for 30 sec	30	72 °C for 5 min
Exon-7 with partial intronic region	95 °C for 5 min	95 °C for 45 sec	54 °C for 45 sec	72 °C for 1 min	35	72 °C for 10 min
Intron-15	95 °C for 5 min	95 °C for 45 sec	57 °C for 45 sec	72 °C for 1 min	35	72 °C for 10 min

Genotyping by PCR-RFLP and PCR-SSCP

PCR-RFLP analysis was employed for genotyping of exon-14 and intron-3. The PCR amplicon of exon-14 was digested with *Hinf*I, while the intron-3 amplicon was digested with *Hin*1II (*Nla*III). The digested products were separated on 3% agarose gel, stained with ethidium bromide (EtBr), and visualized under UV light, and the banding patterns were recorded for genotype identification.

PCR-SSCP analysis was performed for exon-7 and intron-15. The PCR products were denatured to obtain single-stranded

DNA and separated on non-denaturing polyacrylamide gels. The gels were stained with 1% ethidium bromide (EtBr), and the banding patterns were compared among all samples to detect conformational variants associated with sequence polymorphism.

Result and Discussion

Molecular analysis of all four ABCG2 gene regions revealed a complete absence of genetic polymorphism in the study population.

Exon-14 (PCR-RFLP with *HinfI*)

HinfI digestion of the 207 bp exon-14 amplicon consistently produced two fragments of 151 bp and 56 bp in all 60 animals, corresponding exclusively to the AA genotype. No undigested or alternative restriction patterns indicative of the AB or BB genotype were detected (Figure 1). The present study revealed complete monomorphism at the ABCG2 exon-14 locus in Dangi cattle, with only the AA genotype and A allele (frequency = 1.00). Similar monomorphic patterns with fixation of the A allele were reported by *Chouhan et al.* (2021), *Tantia et al.* (2006), *Sharma et al.* (2016), *Singh et al.* (2019), *El Nahas et al.* (2018), *Ahmed et al.* (2020), *Mömke et al.* (2011), and *Valenti et al.* (2019) [5, 26, 19, 23, 7, 1, 14, 28]. In contrast, polymorphism with predominance of the AA

genotype and A allele but low frequencies of the AC/CC genotypes and C allele was reported by *Komisarek and Dorynek* (2009), *Kowalewska Łuczak and Kulig* (2009), *Yildirim and Şahin* (2010), *Mousavizadeh et al.* (2013), *Ateş et al.* (2014), *Soltani Ghombavani et al.* (2016), *Li et al.* (2016), *Rezaei et al.* (2016), *Mashhadi et al.* (2017), *Singh et al.* (2020), *Sun et al.* (2022), and *Zhou et al.* (2023), with A allele frequencies ranging from 0.63-0.99 and C allele frequencies from 0.01-0.37. *Cohen-Zinder et al.* (2005) further identified the A allele as the ancestral allele and the C allele as a derived variant predominantly found in *Bos taurus* populations, which supports the complete fixation of the A allele observed in the present Dangi cattle [9, 10, 15, 3, 24, 12, 16, 13, 21, 25, 6].

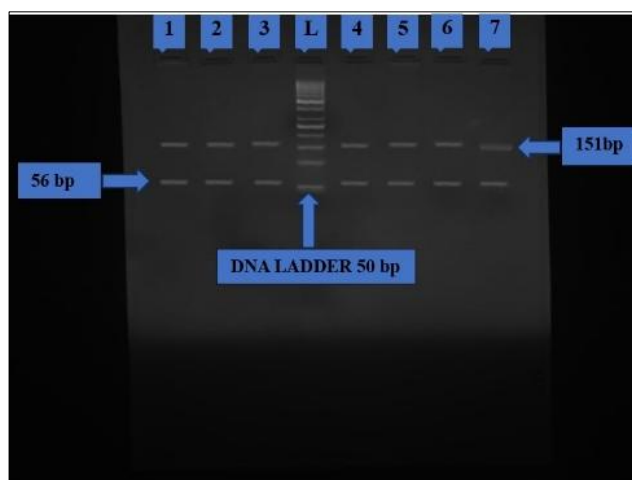


Fig 1: *HinfI*/PCR-RFLP of the ABCG2 gene exon-14

Lane L: DNA Ladder (50 bp) Lane no. 1, 3, 4, 5, 6 and 7: Consists of AA genotype (56 bp and 151 bp).

Intron-3 (PCR-RFLP with *Hin1II*)

Restriction digestion of the intron-3 amplicon with *Hin1II* yielded a single, undigested 207 bp fragment across the entire sample. This pattern confirmed the presence of only the AA genotype and the absence of any restriction site variation (Figure 2).

The present study revealed complete monomorphism at the ABCG2 intron-3 locus in Dangi cattle, with only the AA genotype and A allele (frequency = 1.00). Similar findings were reported by *Kowalewska Łuczak et al.* (2009) [10] in Jersey cattle, where only the AA genotype was observed,

indicating monomorphism at this locus. Likewise, *Cohen-Zinder et al.* (2005) identified an A→T SNP in intron-3 in Israeli and U.S. Holstein cattle but reported no significant association of this polymorphism with milk production traits, suggesting that the exon-14 Y581S mutation is the causal quantitative trait nucleotide (QTN). In contrast, *Kowalewska Łuczak et al.* (2009) [6, 10] also reported polymorphism in Holstein Friesian cattle, detecting AA, AT, and TT genotypes with both A and T alleles, indicating breed-specific variation in the distribution of ABCG2 intron-3 polymorphism. These findings suggest that the complete fixation of the A allele observed in the present Dangi cattle is consistent with several indigenous populations but differs from certain *Bos taurus* breeds exhibiting intron-3 polymorphism.

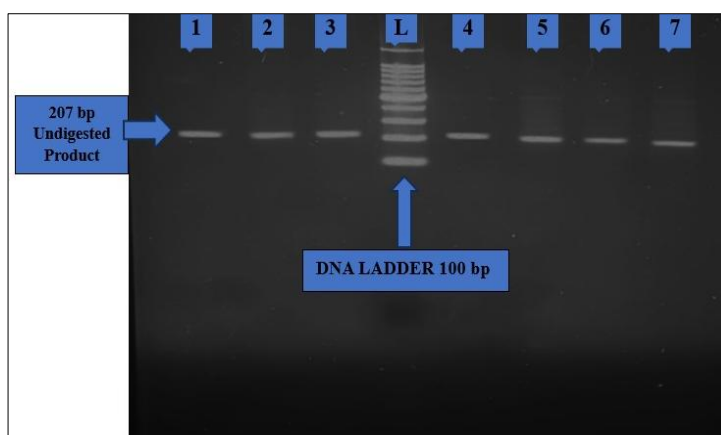


Fig 2: *HinfI* (*NlaIII*)/PCR-RFLP of the ABCG2 gene intron-3

Lane L: DNA Ladder (100 bp) Lane no. 1, 3, 4, 5, 6 and 7: Consists of AA genotype (207 bp undigested product).

Exon-7 (PCR-SSCP)

SSCP analysis of exon-7 revealed a single, uniform banding pattern (designated P1) in all 60 animals (Figure 3). The present study demonstrated complete monomorphism at exon-7 and the partial intronic region of the ABCG2 gene in Dangi cattle, with only the AA genotype and A allele (frequency = 1.00). Similar findings were reported by Chouhan *et al.* (2021) in Rathu cattle, where all animals exhibited a single SSCP pattern (P1) with fixation of the A

allele. In contrast, Zhang *et al.* (1998), Yue *et al.* (2011), and Li *et al.* (2016) reported polymorphism at this locus, detecting three genotypes (AA, AB, and BB) with segregation of A and B alleles in Chinese Holstein cattle. Likewise, Ateş *et al.* (2014) observed polymorphism in South Anatolian Red and East Anatolian Red cattle, with A allele frequencies of 0.63-0.64 and C allele frequencies of 0.36-0.37, and the presence of AA, AC, and CC genotypes. These findings indicate that, unlike several taurine and crossbred populations, the exon-7 and partial intronic region of the ABCG2 gene is highly conserved in Dangi cattle, suggesting breed-specific genetic stability at this locus [5, 29, 12].

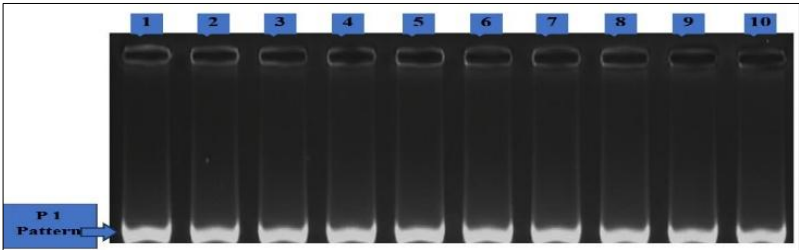


Fig 3: PCR SSCP analysis of the ABCG2 gene exon-7 and partial intronic region showing a similar (P1) SSCP pattern

Lane no. 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 consists similar (P1) SSCP pattern, corresponding to the AA genotype.

Intron-15 (PCR-SSCP)

Similarly, intron-15 exhibited a single conformational pattern (P2) (Figure 4) with no evidence of alternative conformers. The genotypic and allelic frequencies for all four loci were AA = 1.00 and A = 1.00, respectively, confirming complete fixation of the ancestral A allele within this Dangi population. The present study revealed complete monomorphism at the intron-15 locus of the ABCG2 gene in Dangi cattle, with only the AA genotype and A allele (frequency = 1.00). In contrast, Chouhan *et al.* (2021) [5] reported polymorphism in Rathu cattle, identifying two SSCP patterns (P1 and P2) corresponding to AA and AB genotypes, with genotypic frequencies of 0.70 and 0.30, respectively,

and herd-wise variation between LRS Nohar and LRS Bikaner. The absence of polymorphism in the present study indicates lower genetic diversity at this locus in Dangi cattle than in Rathu cattle. Similar monomorphic patterns have also been reported in indigenous cattle by Kumar *et al.* (2020) and Sharma *et al.* (2015), suggesting conserved genetic structure due to breed-specific selection and adaptation. Furthermore, Upadhyay *et al.* (2017) and FAO (2015) [20, 27, 18, 6] emphasized that identifying such fixed loci is important for assessing genetic diversity and developing effective marker-assisted selection and conservation strategies. Owing to the limited number of published reports on ABCG2 polymorphisms in intron-3, exon-7 (with a partial intronic region), and intron-15, the present findings provide valuable baseline information for future genetic studies in indigenous cattle.

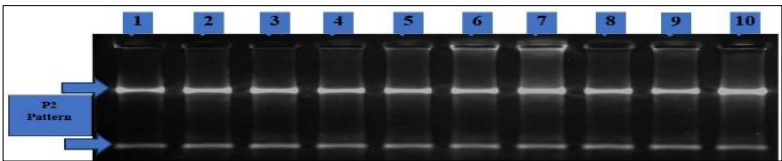


Fig 4: PCR SSCP analysis of the ABCG2 gene intron-15 showing a similar (P2) SSCP pattern

Lane no. 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 consists similar (P2) SSCP pattern, corresponding to the AA genotype.

Milk Composition Traits

Milk samples collected from 60 lactating Dangi cows were analyzed for various milk composition traits. The average

estimates for milk fat, solids-not-fat (SNF), milk protein, and lactose percentage were computed based on repeated milk sampling during the study period. The average milk fat percentage, milk protein percentage, solid-not-fat (SNF) percentage, and lactose percentage were 4.28 ± 0.14 , 3.28 ± 0.03 , 8.94 ± 0.07 , and 4.87 ± 0.05 , respectively.

Table 4: Descriptive statistics for milk composition traits in Dangi cattle (n = 60)

Milk Trait	Mean $\pm$ SE
Milk Fat (%)	4.28 ± 0.14
Milk Protein (%)	3.28 ± 0.03
Solids-Not-Fat (SNF) (%)	8.94 ± 0.07
Lactose (%)	4.87 ± 0.05

Association between ABCG2 Genotype and Milk Traits

Due to the monomorphic nature of all four ABCG2 loci, comparison of milk composition traits across genotypic classes was not statistically feasible. Consequently, no association between variation in the studied ABCG2 gene regions and milk fat, protein, SNF, or lactose percentages could be established in this population.

The complete monomorphism observed at exon-14, intron-3, exon-7 with a partial intronic region, and intron-15 of the ABCG2 gene prevented statistical association analysis between genotypes and milk composition traits in Dangi cattle. Consequently, no association could be established between the analyzed loci and milk fat, protein, SNF, or lactose percentages. In contrast, *Cohen-Zinder et al.* (2005)^[6] and subsequent studies in Holstein, Jersey, and Brown Swiss cattle reported significant associations between functional ABCG2 polymorphisms, particularly the Y581S variant, and milk production traits. The absence of polymorphism in the present study may be attributed to breed-specific genetic uniformity, natural selection, adaptation to local environmental conditions, limited gene flow, or traditional breeding practices in Dangi cattle. Similar monomorphic patterns have also been reported in other indigenous cattle breeds. Overall, the findings indicate that the analyzed ABCG2 regions are conserved in Dangi cattle, and further studies involving larger populations, additional indigenous breeds, and other functional SNPs are needed to clarify their role in milk production traits and their usefulness in marker-assisted selection programmes.

Conclusion

This study demonstrates that exon-14, intron-3, exon-7, and intron-15 of the ABCG2 gene are monomorphic in the sampled Dangi cattle population, with all animals fixed for the ancestral A allele. The absence of allelic variation at these loci precluded any association analysis with milk composition traits. These findings contribute to the foundational genomic characterization of the Dangi breed and reinforce the notion that certain ABCG2 regions subject to diversifying selection in exotic dairy breeds are highly conserved in Indian zebu cattle, likely as a consequence of evolutionary adaptation to local environments and management systems.

Future research should involve larger, geographically diverse Dangi populations and extend molecular analysis to additional functional regions of the ABCG2 gene and other candidate loci. Integration of high-throughput genotyping platforms with phenotypic data on milk yield and extended composition profiles will be essential to develop evidence-based Marker Assisted Selection strategies tailored to the genetic background of Dangi and other indigenous Indian breeds.

Conflict of Interests

Authors declare no Conflict of interest for this article.

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