Unveiling A1 and A2 Beta-Casein Gene Variants: Insights into Indian Cattle Breeds

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Abstract

Milk is an essential part of the human diet, containing over 20 different protein types. The main aim of this article is to examine the distribution of A1 and A2 alleles across various regions and breeds. The findings reveal variability in allele frequencies, with indigenous Indian breeds exhibiting a higher prevalence of A2 alleles compared to exotic breeds like Holstein and Jersey. These insights underscore the importance of tailored genetic management strategies to optimize breeding practices, enhance milk quality and address public health concerns. By prioritizing the preservation and promotion of indigenous cattle breeds with a high prevalence of A2 alleles, stakeholders can work towards sustainable breeding programs that support the long-term viability of the dairy industry in India. Continued research and monitoring of beta-casein genetic variants are essential for informing evidence-based breeding decisions and ensuring the continued success of dairy farming operations in the country.

Keywords: Beta-casein; A1/A2 variants; Cattle; Genetic polymorphism; Milk quality; Public health

Introduction

The dairy industry in India is a vital component of the agricultural sector, significantly contributing to the national economy and supporting the livelihoods of millions of farmers. It makes up about 5% of the national economy and gives jobs to more than 80 million farmers (PIB, 2024). India is the biggest milk producer globally, making 239.30 million tonnes yearly, 24% of the world's milk supply (FAOSTAT, 2024). The Gross Value Added (GVA) from milk is reported to constitute 82% of India's livestock GVA, highlighting its dominance within the livestock sector. Cattle constitute 36% of the country's livestock and contribute 54.68% to the nation's total milk production, with indigenous cows accounting for 11.36%, non-descript cows 10.11%, exotic cows 2.10%, and crossbred cows 31.11% (BAHS, 2023).

Milk is a rich source of essential nutrients, with casein being the predominant protein, constituting about 80% of total milk proteins in cattle. Recently interest have increased for the studies on casein content of the milk and its effect on human health (Koloskova et al., 2021; Sharaz & Rabindrakumar, 2024). Casein is a family of phosphoproteins synthesized in mammary tissue, comprising four main subtypes: αs1-casein, αs2-casein, β-casein, and κ-casein (Ramesha et al., 2016). Among these, β-casein is of particular interest due to its genetic variants and potential health implications. The β-casein gene, located on the sixth chromosome in bovines, encodes the β-casein subtype (Barwar et al., 2023). Two major variants of the β-casein protein are recognized in bovine milk, known as A1 and A2. The A1 variant is more prevalent globally, particularly in European cattle breeds, while the A2 variant is more common in Indian cattle (Massella et al., 2017; Adoligbe et al., 2022). The distinction between these variants arises from a single nucleotide polymorphism (SNP) at position 67 (Figure 1) of the β-casein gene (CSN2), where histidine is present in A1 and proline in A2. Cows with proline at this position are classified as A2 cows, and their milk is termed A2 milk, which is predominantly found in indigenous Indian breeds.

Historically, bovine milk primarily contained the A2 variant of β-casein, which is structurally similar to human β-casein. Approximately 5000 years ago, a genetic mutation occurred, leading to the emergence of the A1 variant, which became widespread in European cattle breeds. This base pair mutation occurs in exon-7 of the β-casein gene (CSN2). The A1 variant is more susceptible to enzymatic cleavage, releasing beta-casomorphin-7 (BCM-7), an opioid peptide potentially linked to health issues such as type 1 diabetes, heart disease, and neurological disorders. In contrast, the A2 variant is less likely to form BCM-7 due to its resistance to digestion, making milk from A2 cows generally considered healthier than milk from A1 cows. This mutation alters the protein's structure, affecting micelle characteristics and digestion. This has fueled global consumer interest in A2 milk, particularly in regions where A1 milk is more common, driving demand for dairy products from A2A2 cows. The A2 allele is more prevalent in certain breeds than others. For example, Indian indigenous breeds have a high frequency, frequently over 90%, and some breeds, including Gir, Sahiwal, and Tharparkar, have upto 100% A2A2 genotype (Ramesha et al., 2016; Barwar et al., 2023). In contrast, European breeds such as Holstein-Friesian and Jersey have a higher prevalence of the A1 allele. Notably, pure Asian and African cattle breeds lack the A1 β-casein variant entirely. The high prevalence of A2 β-casein in Indian cattle positions India as a potential leader in the A2 milk market, which is gaining traction globally due to perceived health benefits. However, crossbreeding with exotic breeds carrying the A1 allele poses a risk of increasing A1 prevalence, necessitating careful breeding strategies. Studies suggest that screening sire lines and promoting A2A2 bulls could enhance A2 milk production (Mukesh et al., 2022). The growing demand for A2 milk also presents economic opportunities for Indian dairy farmers, particularly small-scale producers who dominate the sector (IMARC report, 2023). Understanding these variants in India, where milk is a dietary staple, can guide breeding programs and consumer choices.

In a significant regulatory development, the Food Safety and Standards Authority of India (FSSAI) issued an advisory on August 21, 2024, directing food business operators (FBOs) and e-commerce platforms to remove all claims related to A1 and A2 milk and milk products from packaging and marketing, citing the absence of recognition for such differentiation under the current Food Safety Standards Act, 2006. The advisory stated that such claims could be misleading, as the distinction between A1 and A2 beta-casein types is not officially validated in Indian food regulations. However, just five days later, on August 26, 2024, FSSAI withdrew the advisory, stating the need for further stakeholder consultations before implementing such a directive. This temporary rollback permits FBOs to continue using A1/A2 claims while discussions are ongoing (FSSAI, 2024). This sequence of events highlights the ongoing regulatory uncertainty surrounding A1 and A2 beta-casein differentiation in India's dairy sector.

There is just one amino acid difference between A1 and A2 milk, which is in the beta-casein protein. However, the health effects of this difference are still unclear, and aggressive marketing frequently makes them seem more important. In India, where cattle breeds are genetically diverse and include a large population of indigenous *Bos indicus* breeds predominantly carrying the A2 allele, there is a pressing need to consolidate existing research. A comprehensive review of the current perspectives on A1 and A2 beta-casein gene variants in Indian

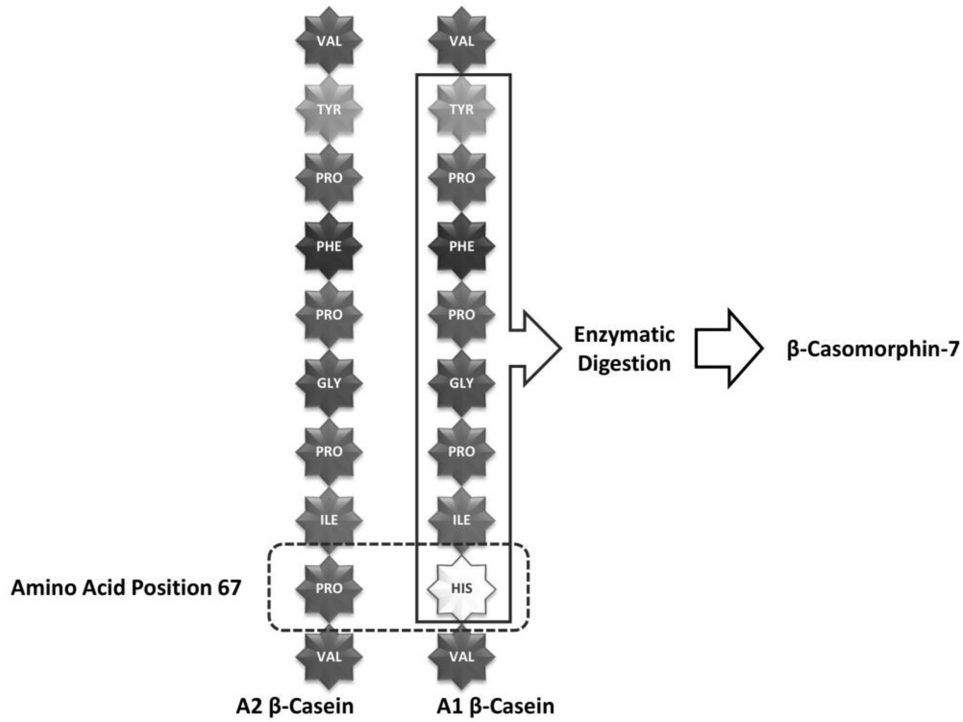

Figure 1. β-casein A1 and A2 variants position

cattle is timely and essential. It would clarify misconceptions, bridge gaps between science and consumer perception and provide valuable insights for researchers, policymakers, and the dairy industry, especially amid regulatory uncertainty and increasing global focus on functional foods and personalized nutrition.

Beta casein

Casein is a collection of phosphoproteins synthesized in the mammary glands in response to lactogenic hormones and other stimuli. These proteins are released as big colloidal groups called micelles, which are very important for figuring out milk's physical and functional features (Kumar et al., 2020). In bovine milk, proteins are primarily classified as caseins, constituting about 80% of the total milk proteins. Caseins include four main proteins: Alpha S1 (CSN1S1, 36-46% of total caseins), Alpha S2 (CSN1S2, 8-11%), Beta (CSN2, 25-35%), and Kappa (CSN3, 8-15%). Beta-casein is a major protein in ruminant milk, playing a key role in the nutritional and functional properties of milk. It is encoded by the CSN2 gene located on chromosome 6 and is known to be highly polymorphic, with at least 15 known genetic variants identified to date. Among these, the A1 and A2 variants are the most significant and prevalent in dairy cattle breeds (Massella et al., 2017; Adoligbe et al., 2022). Other variants such as B (less frequent), and A3 and C (rare), have also been reported, but their physiological relevance remains limited compared to A1 and A2.

The key difference between A1 and A2 beta-casein lies in a single amino acid substitution at position 67: histidine in A1 and proline in A2. This seemingly minor variation significantly influences the digestion and health impacts of the milk. In A1 milk, histidine forms a weak bond that is easily broken during enzymatic hydrolysis in the gastrointestinal tract, releasing beta-casomorphin-7 (BCM7), a bioactive peptide with strong opioid-like activity. Conversely, A2 milk contains proline, which forms a strong bond that prevents the hydrolysis of the peptide bond between the 66th and 67th residues in β-casein, thereby inhibiting the production of BCM-7 (Kumar et al., 2020).

A1 and A2 milk

The point mutation at the 67th amino acid position in the β-casein gene, where proline (CCT) is replaced by histidine (CAT) due to an adenine-to-cytosine substitution, alters the protein's secondary structure and digestion properties (EFSA, 2009). Cattle inherit two CSN2 gene copies, resulting in three genotypes: A1A1 (producing only A1 β-casein), A2A2 (only A2 β-casein), and A1A2 (producing both forms equally due to co-dominant expression) (Brooke-Taylor et al., 2017). A2 β-casein is the ancestral variant, structurally closer to human β-casein and easier to digest. It predominates in indigenous Indian cattle and buffaloes, while A1 β-casein is mainly found in taurine breeds like Holstein-Friesian and Jersey, due to genetic mutations and selective breeding. Asian and African cattle typically lack the A1 allele. A significant difference between A1 and A2 β-casein lies in digestion; A1 produces β-casomorphin-7 (BCM-7), an opioid peptide linked to adverse health outcomes, which is absent in A2 digestion (EFSA, 2009). A2 milk is derived from cows with the A2A2 genotype and is expected to be free of A1 β-casein. However, trace amounts of A1 may occasionally be present due to cross-contamination during milking, processing, or transport. Regulatory bodies such as AsureQuality (New Zealand) allow A2 labelling only if A1 β-casein is undetectable or present below validated trace thresholds (e.g., <0.027%) (AsureQuality, 2019). Testing services like Eurofins emphasise that any detectable A1 β-casein disqualifies a product from being labelled A2 (Eurofins, 2021). Reports from New Zealand Food Safety (Swirtburn, 2003) and other independent reviews stress the importance of stringent genotyping and contamination control for maintaining A2 milk integrity.

Animal studies provide unclear, although mostly positive, information about the distinct physiological effects of A1 and A2 milk. Kaminskí et al. (2012) found no cardiovascular or haematological changes in gilts given A1 milk; other rodent studies have shown adverse effects. Barnett et al. (2014) reported gastrointestinal inflammation in rats ingesting A1 milk, in contrast to those receiving A2 milk. Similarly, Haq et al. (2014) illustrated T-helper 2 (Th2)-mediated gut inflammation in mice given A1 milk, which was not seen in A2-fed mice. Chia et al. (2018) observed A1 milk consumption with a heightened incidence of type 1 diabetes in non-obese diabetic mice. In contrast, Yadav et al. (2020) documented A1 milk-induced allergic airway inflammation, with A2 milk providing a protective effect. On the other hand, Guantario et al. (2020) found that A2 milk had a good effect on the immune system and morphology in ageing mice.

Human trials further show digestion-related variations. Ho et al. (2014) and Jianqin et al. (2015) found that A1 milk consumption was associated with increased digestive discomfort, softer stools, gastrointestinal inflammation, delayed intestinal transit, and impaired cognitive function, whereas A2 milk improved stool consistency and preserved cognition. He et al. (2017) and Sheng et al. (2019) observed that mixed A1/A2 milk increased gastrointestinal symptoms, inflammation, and impaired lactase activity in lactose-intolerant persons and children, whereas A2 milk improved these effects. Milan et al. (2020) demonstrated greater digestive comfort with A2 milk in lactose-intolerant women. Additionally, Deth et al. (2015) discovered better antioxidant potential in A2 milk, and Kirk et al. (2017) proposed its preferable usage for persons intolerant to A1 β-casein, although finding no athletic recovery advantage.

However, not all studies reveal a causal relationship. Crowley et al. (2013) demonstrated no β-casein-type-specific effects in children with cardiofaciocutaneous syndrome, suggesting that other milk constituents may contribute to reported unfavourable responses. This underscores the need for further mechanistic and population-based research to appropriately understand the health impacts of A1 and A2 milk consumption.

Molecular Techniques for Genotyping Beta-Casein

Accurate identification of A1 and A2 beta-casein genotypes is critical for breeding programs aimed at increasing A2 milk production. Several molecular techniques are employed to genotype the CSN2 gene, each offering specific advantages: PCR-RFLP (Polymerase Chain Reaction-Restriction Fragment Length Polymorphism): A cost-effective method that amplifies the CSN2 gene region and uses restriction enzymes to distinguish A1 and A2 alleles based on fragment patterns. AS-PCR (Allele-Specific PCR): Utilizes primers specific to A1 or A2 alleles, enabling rapid and accurate detection, widely used in Indian cattle studies (Malarmathi et al., 2014). Real-Time PCR and TaqMan Assays: High-throughput methods offering precise allele discrimination, suitable for large-scale screening (Miluchová et al., 2023). DNA Sequencing: Provides definitive genotype confirmation by sequencing the CSN2 gene, though it is more costly and typically used for identifying novel variants (Kumar et al., 2020). Isoelectric Focusing Electrophoresis (IEF): A protein-based method that separates beta-casein variants based on their isoelectric points, useful for milk sample analysis (Caroli et al., 2016). These techniques support marker-assisted selection in breeding programs, enabling dairy farmers to select A2A2 cattle efficiently. In India, PCR-RFLP and AS-PCR are particularly prevalent due to their affordability and applicability in local research settings.

Genetic Variants of Beta-casein in Indian Cattle Breeds

The frequency of A1 and A2 beta-casein genetic variants across various breeds of Indian cattle presents a detailed examination and distribution of these genotypes (A1A1, A1A2, A2A2) and alleles (A1, A2) in different locations (Table 1).

In Gir cattle, studies conducted at IVRI, Izatnagar, reported no A1A1 genotypes, with 13% A1A2 and 87% A2A2, resulting in allele frequencies of 6.5% for A1 and 93.5% for A2 (Kumar et al., 2018). In Gujarat, the frequency of A1A2 dropped to 7%, and A2A2 rose to 93%, corresponding to 4% for A1 and 96% for A2 (Khan et al., 2023). Similarly, complete absence of the A1 allele was observed in Gir cattle from Narmada Puram and Mhow in Madhya Pradesh (Barwar et al., 2023; Yadav et al., 2023).

For the Sahiwal breed, results varied by location. At NDRI, Karnal, all individuals were A2A2, suggesting 100% A2 allele frequency (Haq et al., 2012). However, in Madhya Pradesh and Chhattisgarh, 30% of cattle were

Table 1. Genotypic and allelic frequency at beta-casein locus in different Indian cattle breeds

Breed	Location	Frequency					Reference
		Genotype			Allele		
		A1A1	A1A2	A2A2	A1	A2	
Gir	IVRI, Izatnagar	0.000	0.130	0.870	0.065	0.935	Kumar et al., 2018
	Gujarat	0.000	0.070	0.930	0.040	0.960	Khan et al., 2023
	Narmadapuram, Madhya Pradesh	0.000	0.000	1.000	0.000	1.000	Barwar et al., 2023
	Mhow, Madhya Pradesh	0.000	0.000	1.000	0.000	1.000	Yadav et al., 2023
Sahiwal	NDRI, Karnal	0.000	0.000	1.000	0.000	1.000	Haq et al., 2012
	Madhya Pradesh & Chhattisgarh	0.000	0.300	0.700	0.150	0.850	Pandey et al., 2019
	Rajasthan	0.040	0.124	0.871	0.067	0.933	Saran et al., 2019
	Andhra Pradesh	0.000	0.750	0.250	0.370	0.630	Srinivas et al., 2019b
	Rajasthan/Punjab	0.000	0.150	0.850	0.075	0.925	Khan et al., 2023
Tharpakar	NDRI, Karnal	0.000	0.000	1.000	0.000	1.000	Haq et al., 2012
	IVRI, Izatnagar	0.000	0.110	0.890	0.055	0.945	Kumar et al., 2018
		0.000	0.090	0.910	0.040	0.960	Kumar et al., 2020
	Rajasthan	0.000	0.000	1.000	0.000	1.000	Saran et al., 2019
	Haryana	0.000	0.134	0.860	0.067	0.930	Khan et al., 2023
Ongole	Project Directorate on Cattle, Meerut	0.000	0.110	0.890	0.060	0.940	Ganguly et al., 2013b
	Andhra Pradesh	0.000	0.080	0.920	0.040	0.960	Srinivas et al., 2019a
Kangeyam	Tamil Nadu	0.000	0.000	1.000	0.000	1.000	Malarmathi et al., 2014
Bargur		0.000	0.125	0.875	0.062	0.938	Raja et al., 2023
Umblachery		0.000	0.048	0.952	0.024	0.976	
Pulikulam		0.020	0.14	0.840	0.090	0.910	Selvaramesh & Narmatha, 2024
Dangi	Cow Research Station, Igatpuri	0.000	0.000	1.000	0.000	1.000	Jawane et al., 2018
Punganur	Andhra Pradesh	0.000	0.170	0.83	0.080	0.920	Srinivas et al., 2019a
Rathi	Rajasthan	0.000	0.000	1.000	0.000	1.000	Saran et al., 2019
Kankrej		0.000	0.000	1.000	0.000	1.000	
Deoni	Andhra Pradesh	0.000	0.580	0.420	0.290	0.710	Srinivas et al., 2019b
Malnad Gidda		0.000	0.400	0.600	0.200	0.800	
Malvi	Cattle Breeding Farm, Aagar, M.P.	0.000	0.000	1.000	0.000	1.000	Pandey et al., 2020
Nimari	Cattle Breeding Farm Rodiya, Khargon, M.P.	0.000	0.000	1.000	0.000	1.000	
Kosali	Chhattisgarh	0.000	0.260	0.730	0.140	0.860	Khan et al., 2023
Gangatiri	Goa/Maharashtra	0.000	0.310	0.690	0.153	0.850	
Khariar	Odisha	0.000	0.280	0.710	0.140	0.860	
Motu	Andhra Pradesh/ Chhattisgarh/ Odisha	0.000	0.151	0.850	0.070	0.930	
Vechur	KVASU, Kerala	0.000	0.340	0.660	0.200	0.800	Muhammed and Stephen, 2012
Kasargode		0.000	0.790	0.210	0.390	0.610	
Ladakhi	Ladakh	0.000	0.790	0.210	0.100	0.900	Sodhi et al., 2018
Badri	Uttarakhand	0.000	0.240	0.760	0.880	0.120	Dar et al., 2018
Mulki (non-descript)	Narmadapuram, Madhya Pradesh	0.000	0.000	1.000	0.000	1.000	Barwar et al., 2023

A1A2 and 70% A2A2 (Pandey et al., 2019). Rajasthan populations showed 4% A1A1, 12.4% A1A2, and 87.1% A2A2, yielding 6.7% A1 and 93.3% A2 allele frequencies (Saran et al., 2019). In Andhra Pradesh, the A1A2 genotype reached 75%, leading to a relatively high A1 allele frequency of 37% (Srinivas et al., 2019b). Meanwhile, studies in Rajasthan and Punjab observed 15% A1A2 and 85% A2A2, with corresponding allele frequencies of 7.5% for A1 and 92.5% for A2 (Khan et al., 2023).

The Tharparkar breed showed a consistent absence of the A1A1 genotype across all locations. At NDRI, Karnal, all sampled individuals were A2A2 (Haq et al., 2012). At IVRI, Izatnagar, 11% of individuals were A1A2 and 89% were A2A2, giving allele frequencies of 5.5% for A1 and 94.5% for A2 (Kumar et al., 2018). A similar study in Rajasthan reported all individuals as A2A2 (Saran et al., 2019). In Haryana state, the A1A2 genotype was observed in 13.4% of individuals, resulting in allele frequencies of 6.7% for A1 and 93% for A2 (Khan et al., 2023).

In Ongole cattle, 11% A1A2 and 89% A2A2 genotypes were observed at the Project Directorate on Cattle, Meerut (Ganguly et al., 2013b). Andhra Pradesh populations showed slightly lower A1A2 frequency at 8% (Srinivas et al., 2019a).

The Kangeyam and Dangi breeds displayed complete fixation for the A2A2 genotype, with no A1 allele detected (Malarmathi et al., 2014; Jawane et al., 2018). Other Tamil Nadu breeds like Bargur (12.5% A1A2), Umblachery (4.8% A1A2), and Pulikulam (2% A1A1, 14% A1A2) showed low A1 allele frequencies ranging from

2.4% to 9% (Raja et al., 2023; Selvaramesh and Narmatha, 2024). The Punganur breed of Andhra Pradesh had 17% A1A2 and 83% A2A2 genotypes, yielding an 8% A1 allele frequency (Srinivas et al., 2019a). Deoni and Malnad Gidda breeds showed relatively higher A1 allele frequencies at 29% and 20%, respectively (Srinivas et al., 2019b). Breeds such as Rathi and Kankrej (Rajasthan) and Malvi and Nimari (Madhya Pradesh) consistently showed 100% A2A2 genotypes, indicating complete absence of the A1 allele (Saran et al., 2019; Pandey et al., 2020). In non-descript Mulki cattle from Narmada Puram, all animals were A2A2, confirming absence of the A1 allele (Barwar et al., 2023). The Kosali breed (Chhattisgarh), Gangatiri (Uttar Pradesh), and Khariar (Odisha) showed moderate A1A2 frequencies (26-31%) with A1 allele frequencies around 14-15% (Khan et al., 2023). The Motu breed, found across Andhra Pradesh, Chhattisgarh, and Odisha, exhibited a 15.1% A1A2 genotype frequency and 7% A1 allele frequency. In southern India, Vechur (Kerala) cattle showed 34% A1A2 and 66% A2A2 genotypes, corresponding to a 20% A1 allele frequency. The Kasargode breed had a high A1A2 frequency (79%), resulting in a 39% A1 allele frequency (Muhammed and Stephen, 2012). The Ladakhi breed showed a similar genotype distribution (79% A1A2), yet with only 10% A1 allele frequency, possibly due to small sample size or population structure (Sodhi et al., 2018). Lastly, the Badri breed of Uttarakhand showed 76% A2A2 and 24% A1A2 genotypes, with a predominant A2 allele frequency of 88% (Dar et al., 2018).

Most Indian cattle breeds (Gir, Sahiwal, and Kangeyam) show a high prevalence of the A2 beta-casein variant (80% A2A2 genotype frequency), suggesting suitability for A2 milk production. Most of Indian cattle breeds have A2 allele frequencies above 0.94 (Mukesh et al., 2022). The frequency of A1 and A2 variants varies by region within breeds, possibly due to local breeding practices or crossbreeding with exotic breeds. Some breeds (Kasargode and Ladakhi) have high A1A2 frequencies (79%), suggesting a balanced presence of both alleles, possibly due to crossbreeding or genetic drift. Whereas, The A1A1 genotype is rare, appearing only in Pulikulam (2%) and Sahiwal in Rajasthan (4%).

Genetic polymorphism of beta casein genes in crossbred or synthetic cattle population in India

In India, crossbreeding of indigenous Indian cattle with exotic breeds such as Holstein Friesian, Jersey and Brown Swiss has been widely practiced to enhance milk yield. This practice, however, introduced genetic variants of beta-casein. A comprehensive overview depicted the frequency distribution of A1 and A2 alleles of beta casein variants in various crossbred and synthetic cattle breeds across different locations in the country showed that they vary significantly, influenced by the proportion of exotic versus indigenous inheritance (Kumar et al., 2025) and regional breeding practices (Table 2).

In the Karan Fries breed at NDRI, Karnal, a significant predominance of the A2 allele was observed, with genotypic frequencies of 12.5% (A1A1), 16.6% (A1A2), and 70.9% (A2A2), corresponding to allele frequencies of 20.8% for A1 and 79.2% for A2 (Haq et al., 2012). Additional studies by Jaiswal et al. (2014) and Mohan et al. (2021) across other locations further confirmed genetic heterogeneity in this breed.

The Karan Swiss population, also at NDRI, showed an even stronger bias toward the A2 allele, with 21.4% A1A2 and 78.6% A2A2 genotypes, resulting in allele frequencies of 10.7% (A1) and 89.3% (A2) (Haq et al., 2012).

In the Frieswal breed, studied at the Project Directorate on Cattle (Meerut) and Military Farms (Bareilly and Lucknow), genotype distributions were 15% A1A1, 41% A1A2, and 44% A2A2. This translates to allele frequencies of 35% for A1 and 65% for A2 (Ganguly et al., 2013a), indicating intermediate variability.

The Vrindavani breed at IVRI, Izatnagar, demonstrated moderate presence of both alleles: 12.3% A1A1, 48.1% A1A2, and 39.6% A2A2, giving allele frequencies of 36.4% (A1) and 63.6% (A2) (Kumar et al., 2022). In contrast, the Hardhenu breed at LUVAS, Hisar, showed high A1 allele frequency, with genotypic frequencies of 32% A1A1 and 68% A1A2, and absence of A2A2 genotype, resulting in allele frequencies of 66% (A1) and 34% (A2) (Ramkaran et al., 2017).

HF crossbreds, examined across multiple regions-Tamil Nadu, Maharashtra, Madhya Pradesh, Andhra Pradesh, and Mhow-exhibited wide-ranging variation in A1 and A2 allele frequencies, reflecting the diversity of breeding strategies and genetic backgrounds (Malarmathi et al., 2014; Shende et al., 2017; Pandey et al., 2019; Srinivas et al., 2019a; Vyas et al., 2025).

In Rajasthan, Rathi × HF crossbreds exhibited a low A2A2 frequency (10%), indicating a predominance of the A1 allele and resulting in an A2 allele frequency of 10% (Saran et al., 2019). Conversely, the Jersey × Local Kashmiri crossbred population studied at SKUAST, Srinagar, had predominantly A2 genotypes: 11.4% A1A2 and 88.5% A2A2, corresponding to allele frequencies of 5.7% (A1) and 94.2% (A2) (Bhat et al., 2017).

At the Cattle Breeding Farm in Kopargaon, Zebu × HF crossbreds with varying exotic inheritance (62.5% and 75.0%) showed differential frequencies of A1 and A2 alleles, again emphasizing the genetic diversity in crossbred populations (Jawane et al., 2018). The observed variability reflects differing breed compositions, geographic selection pressures and breeding goals, underscoring the importance of incorporating beta-casein genotyping in selection programs.

Genetic polymorphism of beta casein genes in exotic cattle populations of India

In India to enhance milk yield for growing population exotic cattle breeds like Jersey and Holstein Friesian was introduced which exhibit a higher prevalence of the A1 allele compared to indigenous breeds (Mukesh et al., 2022). The comprehensive review depicted considerable variation in beta-casein allele frequencies among Jersey and Holstein cattle breeds across various locations in the country (Table 3). The Jersey breed has been studied across several states including Kerala, Rajasthan, Himachal Pradesh, Haryana, Western Uttar Pradesh, Punjab, and Jammu & Kashmir, revealing significant variation in beta-casein allele frequencies.

In a multi-location study, Sodhi et al. (2012) reported genotypic frequencies of 2.5% (A1A1), 60% (A1A2), and 37.5% (A2A2), corresponding to allele frequencies of 32.5% A1 and 67.5% A2. Contrasting results were observed by Khan et al. (2023) in Punjab, where genotypic frequencies were 39% (A1A1), 58% (A1A2), and only 2% (A2A2), leading to a high A1 allele frequency of 68.2% and A2 at 31%. In a study conducted at SKUAST, Srinagar, Bhat et al. (2017) reported equal distribution of A1A2 and A2A2 genotypes, with no A1A1 animals, resulting in allele frequencies of 25% A1 and 75% A2.

Similar variability is noted in the Holstein Friesian breed, one of the most commonly used exotic dairy breeds in India. According to Sodhi et al. (2012), the Holstein population exhibited genotypic frequencies of 21.6% (A1A1), 45.1% (A1A2), and 33.3% (A2A2), yielding allele frequencies of 44.1% A1 and 55.9% A2. In Punjab, Khan et al. (2023) reported a higher incidence of the A1 allele, with genotypic frequencies of 42% (A1A1), 52% (A1A2), and only 4% (A2A2), corresponding to A1 and A2 allele frequencies of 69% and 31%, respectively. These findings suggest that the Holstein population in India generally harbors a higher proportion of the A1 allele compared to Jersey cattle, although regional differences persist.

Table 2. Genotypic and allelic frequency at beta-casein locus in different crossbred and synthetic cattle breeds in India

Breed	Location	Frequency					Reference
		Genotype			Allele		
		A1A1	A1A2	A2A2	A1	A2	
Karan Fries	NDRI, Karnal	0.125	0.166	0.709	0.208	0.792	Haq et al., 2012
		0.080	0.190	0.730	0.175	0.825	Jaiswal et al., 2014
		0.090	0.620	0.290	0.400	0.600	Mohan et al., 2021
Karan Swiss	NDRI, Karnal	0.000	0.214	0.786	0.107	0.893	Haq et al., 2012
Frieswal	CIRC, Meerut	0.150	0.410	0.440	0.350	0.650	Ganguly et al., 2013a
	Military Farm, Bareilly Military Farm, Lucknow	0.175	0.515	0.310	0.432	0.568	Kumar et al., 2019
	Military Farm, Bareilly	0.170	0.390	0.440	0.370	0.630	Kumar et al., 2020
Vrindavani	IVRI, Izatnagar	0.123	0.481	0.396	0.364	0.636	Kumar et al., 2022
Hardhenu	LUVAS, Hisar	0.320	0.680	0.000	0.660	0.340	Ramkaran et al., 2017
HF Crossbred	Tamil Nadu	0.170	0.460	0.370	0.405	0.595	Malarmathi et al., 2014
	Satara, Maharashtra	0.280	0.720	0.000	0.638	0.362	Shende et al., 2017
	Jabalpur, Madhya Pradesh	0.000	0.640	0.360	0.320	0.680	Pandey et al., 2019
	Andhra Pradesh	0.000	1.000	0.000	0.500	0.500	Srinivas et al., 2019a
	Mhow, Madhya Pradesh	0.000	0.600	0.400	0.300	0.700	Yadav et al., 2023
Rathi x Holstein Friesian	Rajasthan	0.000	0.000	0.100	0.000	0.100	Saran et al., 2019
Jersey x Local Kashmiri	SKUAST, Srinagar	0.000	0.114	0.885	0.057	0.942	Bhat et al., 2017
Zebu x HF (62.5%)	Cattle Breeding Farm, Kopargoan	0.000	0.060	0.940	0.030	0.970	Jawane et al., 2018
Zebu x HF (75.0%)		0.060	0.130	0.810	0.130	0.860	

Table 3. Genotypic and allelic frequency at beta-casein locus in different exotic cattle breeds in India

Breed	Location	Frequency					Reference
		Genotype			Allele		
		A1A1	A1A2	A2A2	A1	A2	
Jersey	Kerala, Rajasthan, Himachal Pradesh, Haryana and Western Uttar Pradesh	0.025	0.600	0.375	0.325	0.675	Sodhi et al., 2012
	SKUAST, Srinagar	0.000	0.500	0.500	0.250	0.750	Bhat et al., 2017
	Punjab	0.390	0.580	0.020	0.682	0.310	Khan et al., 2023
Holstein	Kerala, Rajasthan, Himachal Pradesh, Haryana and Western Uttar Pradesh	0.216	0.451	0.333	0.441	0.559	Sodhi et al., 2012
	Punjab	0.420	0.520	0.040	0.690	0.310	Khan et al., 2023

Breeding Strategies and Policy Recommendations

India's indigenous cattle breeds, with A2 allele frequencies often exceeding 0.95, offer a genetic advantage for A2 milk production (Mukesh et al., 2022). To capitalize on this, the following breeding strategies and policy recommendations are proposed: Selective Breeding: Prioritize A2A2 bulls in artificial insemination programs to increase A2 allele frequency, as demonstrated by high A2 prevalence in breeds like Gir (0.93) (Khan et al., 2023). Genomic Selection: Integrate beta-casein genotyping into genomic evaluation frameworks to enhance selection accuracy, leveraging techniques like PCR-RFLP and AS-PCR (Kumar et al., 2020). Preservation of Indigenous Breeds: Conserve native breeds such as Sahiwal and Tharparkar, which naturally exhibit high A2 frequencies, to maintain genetic diversity and support A2 milk production. Screening of Sire Lines: Regularly test breeding bulls for A2A2 genotypes to reduce A1 allele introgression, particularly in crossbred populations (Mukesh et al., 2022). Labeling and Market Differentiation: Develop A2-certified milk marketing channels to meet consumer demand, supported by policy incentives for A2 milk production. Policy Support: Policymakers should fund research on A2 milk benefits, establish national genotyping programs, and promote indigenous breed conservation to align with global A2 milk market trend. These strategies require careful implementation to balance A2 milk production with genetic diversity, ensuring the resilience of Indian cattle populations.

Conclusion

The A1 and A2 β-casein gene variants illustrate functional genetic diversity in cattle, with potential implications for dairy production, breeding strategies, and consumer health perceptions. Indigenous *Bos indicus* breeds in India predominantly have the A2 allele, providing a natural advantage for A2 milk production, whereas crossbreeding with exotic cattle breeds has introduced various levels of the A1 allele into crossbred and synthetic populations. Although some animal and human studies suggest differences in digestive comfort and specific physiological responses between A1 and A2 milk, evidence remains inconclusive and genetic, dietary, and environmental factors may influence outcomes. Genotyping for β-casein variants can support selective breeding and market differentiation, but such programs should be balanced with genetic diversity preservation and overall productivity goals. Regulatory discussions in India underline the need for robust, peer-reviewed evidence before formalizing labelling or marketing claims based on β-casein type. Future research combining genomics, nutrition science, and epidemiology is important to elucidate the biological importance of these variations and their public health consequences. Until better data comes, consumer communication should remain transparent and fact-based, highlighting milk's nutritious benefits and maintaining India's rich cow genetic heritage.

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Data availability

The data used and analyzed during this study are available from the corresponding author upon reasonable request.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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