Review

Emerging opportunities for DNA methylation biomarkers in cattle improvement

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Abstract. Improving economically important traits such as productivity, fertility, and health remains a central goal in modern cattle breeding. While genome-wide association studies (GWAS) have revolutionized genomics by identifying numerous trait-associated single nucleotide polymorphisms (SNPs), a significant proportion of phenotypic variation remains unexplained, often referred to as missing heritability. Furthermore, identifying causal genes and regulatory elements within complex GWAS loci is challenging. Population-scale multi-omics studies like FarmGTEx, particularly those focusing on epigenetics, offer new opportunities to uncover regulatory biomarkers beyond static SNPs. DNA methylation (DNAm) has emerged as a promising epigenetic layer that acts as a bridge between the genome and the phenome, mediating environmental and genetic influences on gene expression. Within this landscape, genomic regions containing stable single methylation polymorphisms (SMPs), known as Correlated Regions of Systemic Interindividual Variation (CoRSIVs) are gaining increasing recognition for its emerging potential. CoRSIVs exhibit stability across diverse tissues, high interindividual variability, and partial heritability, making them ideal, tissue-agnostic candidates for scalable and cost-effective epigenetic applications. This review highlights the growing relevance of SMPs, especially CoRSIVs, for improving biomarker discovery, enhancing prediction accuracy, and strengthening cattle management and breeding strategies.

Key words : Biomarker, Cattle, Correlated Regions of Systemic Interindividual Variation (CoRSIVs), DNA methylation, Single methylation polymorphism (SMP)

(**J. Reprod. Dev. 72:** 150–157, 2026)

Introduction

Traditional cattle breeding programs have relied on phenotypic selection and, more recently, genomic selection based on single-nucleotide polymorphisms (SNPs) [1]. Although genomic selection has accelerated genetic gain, its progress is constrained by fundamental limitations of the genome-wide association study (GWAS). A major challenge is missing heritability, as identified SNPs explain only a fraction of phenotypic variance for many complex traits [2, 3]. Most associated variants also fall in non-coding regulatory regions, making it difficult to connect them to specific molecular mechanisms or phenotypic outcomes [4].

Complex traits are shaped not only by DNA sequence but also by regulatory processes that vary across tissues, developmental stages, and environments [5]. These processes are governed by epigenetic marks that influence the activity of enhancers, promoters, and other regulatory elements. Static SNP markers cannot capture these dynamic regulatory states, highlighting the need for an additional functional layer of information.

Epigenetics encompasses heritable changes in gene regulation independent of DNA sequence, including DNA methylation (DNAm), histone modifications, noncoding RNAs, and chromatin remodeling [6]. Among these, DNAm is the most stable and extensively studied, acting as a key mediator between genetic variation, environmental exposures, and gene expression [7]. By integrating both genetic and environmental influences on regulatory function, DNAm provides a valuable complement to SNP-based models, potentially helping to address the current limitations of genomic selection.

DNAm involves the covalent addition of a methyl group (CH_3) to cytosine and plays essential roles in embryonic development, genomic imprinting, gene regulation, and transposon silencing [8–11]. In animals, DNAm occurs primarily at CpG dinucleotides, whose uneven genomic distribution creates distinct functional domains [12, 13]. CpG islands located in promoter regions are typically unmethylated, and increases in methylation are generally associated with transcriptional repression [14]. CpG shores and shelves, extending up to 4 kb from islands, display greater interindividual and tissue-specific variability and often correlate strongly with tissue-specific gene expression, particularly during development. Methylation within gene bodies is usually positively associated with transcription and may influence alternative splicing. In contrast, intergenic regions and repetitive elements are predominantly hypermethylated to maintain genome stability and suppress transposable element activity [15]. These properties make DNAm a powerful tool for studying complex traits, offering regulatory insights that extend beyond genetic variation alone.

The dynamic state of this mark is maintained by a complex enzymatic balance: DNA methyltransferase 3 family (DNMT3A and DNMT3B) enzymes establish new, *de novo* methylation patterns during development, while DNMT1 acts as the primary guardian of the methylome by accurately copying them to the daughter strand after DNA replication, which preserves the cell's epigenetic memory [16]. The active removal of the methyl mark is a multi-step process initiated by Ten-eleven translocation (TET) enzymes (TET1, TET2, TET3), which successively oxidize 5-methylcytosine (5mC) to 5hmC, 5fC, and 5caC. The highly oxidized forms are then excised by base

Received: December 9, 2025
Accepted: March 31, 2026

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excision repair machinery, completing the active demethylation process [17].

DNAm patterns exhibit epigenetic plasticity, changing in response to environmental factors such as nutrition, toxins, and stress [18]. These influences act partly through the one-carbon cycle, which supplies S-adenosylmethionine (SAM) as the methyl donor for DNMT activity [19]. Variations in parental nutritional status during critical developmental windows can alter SAM availability, modulate DNMT activity, and induce persistent changes in offspring methylation patterns relevant to metabolic and growth traits, an important mechanism of developmental programming in livestock. Stressors can also induce rapid, site-specific methylation changes by affecting DNMT or TET activity. This plasticity underscores that phenotype reflects not only genetic variation but also genotype-by-environment (G × E) interactions mediated through the regulatory layer of the methylome.

Epigenome-wide association study (EWAS) and its challenges

Mammalian development features two major waves of epigenetic reprogramming: one in primordial germ cells that erases parental marks, and another after fertilization that resets the zygotic genome while preserving imprints. These waves involve widespread remodeling of DNAm and histone modifications to enable proper gene regulation across generations. Genomic imprinting involves parent-of-origin–specific expression that is established during gametogenesis and is relatively stable across environments, whereas the *agouti* locus represents epigenetic regulation that is sensitive to maternal nutrition and environment [20–22]. Although most DNAm is reset, certain marks, especially those shaped by periconceptional environments, can remain stable. Heritability of CpG methylation varies, with ~10–30% of sites showing moderate to high heritability ($h^2 > 0.5$) [23], reflecting *cis*- and *trans*-genetic regulation as well as genomic features such as CpG density, enhancers, promoters, and repetitive elements, and is further shaped by environmental and tissue-specific factors [24–26]. Additional mechanisms, including germline-transmitted noncoding RNAs, may also contribute [27, 28]. These findings suggest that, under certain biological contexts, particularly within the early embryonic environment, epigenetic states from the germline can influence development and complex traits.

The development of Illumina methylation arrays for humans has fueled epigenome-wide association study (EWAS) [29, 30], which now routinely uses blood as a proxy tissue to identify biomarkers for conditions such as autism, metabolic disease, and smoking [25, 31–35]. Several public databases now catalog human DNAm-trait associations [36, 37]. In non-human species, EWAS has begun to identify DNAm signatures linked to complex traits, as shown in *Arabidopsis* [38], cotton [39], and mouse models [40]. The *Arabidopsis* epigenetic Recombinant Inbred Lines (epiRIL*)* study demonstrated that stably inherited differentially methylated regions (DMRs), independent of DNA sequence, can serve as epigenetic QTL, explaining up to 90% trait heritability and showing responsiveness to selection and overlap with natural methylation variants. Single methylation polymorphisms (SMPs) represent individual CpG sites with interindividual methylation variation, analogous to SNPs but at the epigenetic level [41]. Unlike DMRs, which detect broader regional changes often due to lower coverage, SMPs capture fine-scale regulatory variation and can be distinguished from sequence-based variation like SNPs. SMPs can be quantified by metrics such as minor allele frequency (MAF) and interquartile range (IQR) [41]. Although no universally accepted definition exists, SMPs can be categorized based on methylation percentage (mC%, β-value) into hypomethylated (UU, $0 \le \beta \le 0.3$), intermediate (MU, $0.3 < \beta \le 0.7$), and hypermethylated (MM, $0.7 < \beta \le 1$) "menotypes," analogous to SNP genotypes (Fig. 1a) [39, 41]. In humans, CEU European and YRI African had similar distribution of SMP allele frequency, and shared many Methylation-Demarcated block regions [41]. In cotton, SMPs outnumber SNPs by over 100-fold and show low MAF and short-range methylation disequilibrium (~50 bp) [39]. They are enriched in transposable elements and genic regions, and have been associated with domestication, adaptation, and key agronomic traits. Furthermore, *cis*-mQTLs (methylation Quantitative Trait Locus, where SNPs affect nearby methylation) and eQTMs (expression Quantitative Trait Methylation, where methylation influences gene expression) reveal diverse regulatory architectures, including genetically driven and purely epigenetic patterns. Notably, EWAS and GWAS in cotton show limited signal overlap (~2.1%), emphasizing SMPs as a complementary and functionally rich class of trait markers. However, such comprehensive high-resolution epi-HapMap-like datasets are currently missing in farm animals, including cattle.

EWAS is especially valuable for detecting environmentally responsive and regulatory signals that SNP-based GWAS may miss. Methodological advances such as epigenetic relationship matrices (ERMs), principal component adjustment, and mixed models have improved control of confounding and boosted reproducibility [42, 43]. Simulations show that with sufficient sample size and optimized design, EWAS can detect genome-wide signals even with modest effect sizes [44–47]. However, conventional EWAS still faces some challenges. DNAm is highly tissue- and cell-type-specific, making replication difficult. Methylation varies with age, environment (e.g., diet, heat stress), and genetic background [48], reducing power and increasing confounding from cell-type heterogeneity, batch effects, and population structure. These issues are particularly pronounced in livestock populations, where strong relatedness and population stratification, limited sample sizes, restricted access to biologically relevant tissues, and substantial environmental and management heterogeneity are common. Consequently, careful study design and robust modeling are critical to ensure reliable and biologically meaningful results.

Studies of CoRSIVs in humans and other model organisms

Unlike other SMPs, Correlated Regions of Systemic Interindividual Variation (CoRSIVs) are remarkably stable across tissues and time, yet variable across individuals, making them well-suited for tissue-agnostic and cost-effective epigenetic screening. As a functionally enriched subset of SMPs, CoRSIVs address key limitations of traditional EWAS by providing biologically meaningful and replicable signals. The CoRSIV concept builds on earlier mammalian studies of metastable epialleles, such as *agouti viable yellow* and *axin-fused* in mice, where DNA methylation is established early in development and influenced by maternal nutrition [20, 21]. Similar CoRSIV-like patterns have been observed near transposable elements like Intracisternal A-particles (IAPs) [49] and in post-twinning stochastic epigenetic variation among monozygotic twins, particularly in clustered protocadherin regions [50]. A landmark study identified 9,926 CoRSIVs using deep Whole-Genome Bisulfite Sequencing (WGBS) across three tissues from 10 humans [51]. These regions captured interindividual methylation variation at kilobase resolution with short-range correlation. CoRSIVs are enriched near transposable elements, conserved across human ethnic groups, and measurable

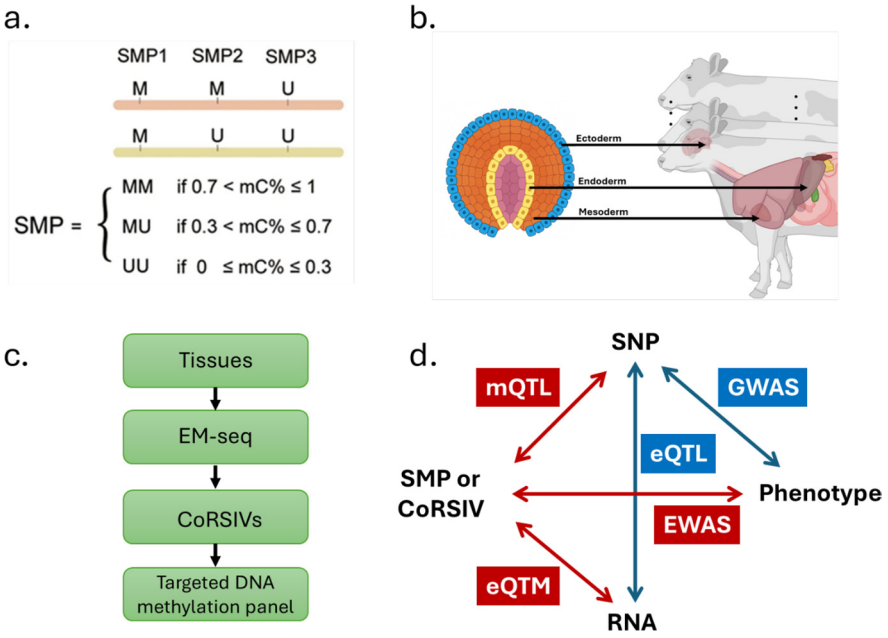

Fig. 1. Investigating DNA methylation variation in cattle. (a) Single methylation polymorphisms (SMPs) can be classified by methylation levels into fully methylated (MM), heterogeneous (MU), or unmethylated (UU) categories (adopted from Zhao *et al*. 2024 [41]). (b) Representative tissue samples from the three germ layers (Ectoderm: spinal cord, brainstem, cerebellum, or mammary gland; Endoderm: liver; Mesoderm: blood, muscle, or heart) illustrate tissue-specific methylation landscapes, with high-coverage EM-seq enabling the identification of CoRSIVs. (c) Targeted methylation capture panels, designed using Agilent or Twist technologies, allow systematic profiling of CoRSIVs in accessible tissues and facilitate their evaluation as potential biomarkers for cattle improvement. (d) Overview of integrating DNA methylation with multi-omics and phenotypic data to study regulatory variation, where SMPs and CoRSIVs are analyzed alongside SNP genotypes, RNA expression, and complex trait records (eQTL, mQTL, and eQTM). EWAS using SMPs or CoRSIVs can be compared with GWAS and array-based EWAS to highlight the added value of methylation markers.

in accessible tissues like blood. Other studies confirmed that their methylation levels are influenced by periconceptional environment (e.g., maternal nutrition) yet remain stable across tissues and life stages, and correlate with gene expression [52, 53]. Additionally, human studies show that CoRSIVs produce 72-fold more mQTLs [54] and up to 100–200-fold greater EWAS power [55] compared to CpGs on Illumina 450k or EPIC arrays.

DNA methylation studies and EWAS in cattle

Over the past decade, cattle DNAm studies have grown rapidly. As of July 2025, NCBI lists 283 genome-wide WGBS or Enzymatic Methyl-seq (EM-seq) datasets (≥ 40 Gb) from untreated/normal cattle tissues, including 174 (61.5%) from Holsteins, spanning 51 sperm, 16 liver, 16 blood, 15 muscle, 13 mammary gland, and other samples across fetal, neonatal, calf, and adult stages. These efforts have advanced our understanding of DNAm's role in development, reproduction, immunity, environmental adaptation, and evolution [7, 56–69]. Evidence also suggests intergenerational inheritance and environmentally responsive methylation [65, 66, 70]. In a preliminary EWAS of 19 bulls, we identified 46 out of 17,323 variably methylated regions (VMRs) associated with fertility traits, including daughter pregnancy rate [71]. Of these, 9 VMRs (~20%) overlapped local SNPs, highlighting the interaction between genetic variation and methylation. Genes involved included *ZFP36L1*, *CRISP2*, and *HGF*, key regulators of sperm function. One candidate mQTL SNP (rs109326022 on chr18) was linked to methylation near *JOSD2* and *ASPDH*, with possible effects on reproduction. With ~50 Gb (~17×) WGBS coverage, we computed 31,272 methylation haplotype blocks (MHBs) by applying pairwise methylation linkage disequilibrium ($r^2 \geq 0.5$) across CpGs with ≥ 10 × coverage, as described before [72]. These MHBs averaged 52 bp with ~12 CpGs per 100 bp and allowed partitioning of the genome into coordinated methylation domains. Later, by integrating methylation data with SNP genotypes, gene expression, and phenotypes from the Farm Genotype Tissue Expression (FarmGTEx) - Cattle project [73], we showed that DNAm at regulatory regions correlates with both gene expression and genetic variation, enabling functional annotation. In a study of feed efficiency (n = 48 Holsteins), 421 CpG sites were identified as being associated with residual feed intake, implicating pathways involved in energy metabolism and nutrient utilization [74]. DNAm changes in immune genes following parasite infection also suggest roles in host defense [75]. As in humans, studies in cattle using the HorvathMammalMethylChip40 Chip (the Horvath Chip in short) found that age-related methylation shifts affected only ~1% of CpGs, just a few hundred sites, indicating minimal aging effects and supporting the use of most SMPs in trait association analyses without age-related confounding [76–79]. An unpublished study further explored the genetic control of sperm methylation in 405 Holstein bulls using RRBS and imputed SNPs (PAG32 Abstract 1) [80]. Of ~160,000 CpGs, 76% showed heritability > 0.1; 33% and 5% were associated with *cis*- and *trans*-mQTLs, respectively. Eight *trans*-mQTL hotspots were enriched in promoters, CpG-rich regions, ATAC-seq peaks, and epigenetic regulators (e.g., histone modifiers, DNA methyltransferase interactors).

Despite promising results, early cattle EWAS were limited by high costs and small sample sizes. Scalable methods like methylation arrays and targeted bisulfite sequencing now enable more efficient profiling but depend on selecting informative targets. To disentangle epigenetic from genetic effects, SMPs have been proposed, but require

deep coverage (~90 Gb or 30 ×) to reliably call, estimate MAF, and assess variability [41]. Thus, platform design and sequencing depth are critical for developing practical DNAm tools for cattle.

Genome-wide identification of cattle CoRSIVs

In a recent cattle CoRSIV study [81], we analyzed WGBS data from three germ layers, lung (endoderm), blood (mesoderm), and brain (ectoderm), from two Holsteins [58], dividing the genome into ~6 million 100 bp bins containing ≥1 CpG (Fig. 1b). Using a two-step pipeline adapted from human studies [51], we first identified bins with ≥ 10% methylation difference between animals, then calculated a systemic interindividual variation index (SIVI). Applying thresholds of SIVI ≥ 20 and ≥ 5 CpGs per region, we identified 217 candidate CoRSIVs (median length ~200 bp, ~3 CpGs per region), after masking CpG-SNPs. Relaxing the CpG filter yielded > 1,200 candidates. The lower number compared to humans (~9,926) likely reflects the reduced sequencing depth (18 × *vs*. 30–40 ×) and sample size (2 *vs*. 10). These CoRSIVs were enriched near transcription start sites ($P = 2.1 \times 10^{-3}$) and more likely to harbor discordant SNPs. To assess environmental sensitivity, we analyzed WGBS data from *In Vitro* Production (IVP) and Multiple Ovulation and Embryo Transfer (MOET) calves [60]. CoRSIVs were 5–10 × more likely than control regions to overlap DMRs and consistently showed higher methylation in IVP animals across tissues, supporting their systemic and environment-responsive nature. CpG-SNP densities were comparable to controls, and a read-level chi-square test confirmed significantly greater methylation differences at CoRSIVs ($P = 0.025$), further supporting their sensitivity to periconceptional conditions.

Translating epigenomics to cattle improvement

Translating epigenomics into practical applications requires a detailed understanding of the bovine methylome, particularly during critical developmental windows that shape heritable traits.

Bovine methylome structure and critical developmental windows

Comparative whole-genome DNAm profiling across bovine tissues reveals both global and tissue-specific methylation patterns. Sperm serves as a key model, displaying the globally hypomethylated landscape characteristic of the male germline while retaining essential methylation marks at regulatory regions such as imprinted gene promoters. These paternal epigenetic marks are transmitted directly to the zygote and may influence offspring phenotypes. Mammalian cells undergo two major waves of methylation reprogramming: one during spermatogenesis and another during early embryogenesis [82–86]. In cattle, a substantial demethylation event occurs after fertilization, followed by *de novo* remethylation during pre-implantation development, a stage highly sensitive to environmental perturbation. Genomic imprinting, governed by methylation at imprinting control regions to ensure monoallelic expression, is especially vulnerable during Assisted Reproductive Technologies [87]. Suboptimal culture conditions can disrupt this balance, leading to developmental abnormalities such as Large Offspring Syndrome, underscoring the value of DNAm markers as quality-control tools for reproductive technologies.

Utility of systemic methylation markers in cattle breeding

CoRSIVs hold significant potential due to their tissue-agnostic stability, high interindividual variability, and partial heritability [51, 54]. Their application is particularly advantageous for traits historically difficult to measure, such as feed efficiency. As a metabolic trait, feed efficiency can be informed by CoRSIVs detected in accessible tissues like blood, providing stable systemic biomarkers that reflect regulatory states in key metabolic organs and reducing reliance on costly phenotyping. For fertility, sperm-based CoRSIVs may predict sire conception rate by indicating the integrity of methylation marks transmitted at fertilization, while blood-derived markers in cows may reflect the regulatory status of genes essential for reproductive performance. Epigenetic markers are also highly responsive to immune function, stress, health, and resilience. CoRSIVs linked to inflammatory cytokines or heat-shock protein regulation can support the selection of animals with more robust stress-response systems.

Integrating epigenetic information into selection models

The so-called "estimated epigenetic value" (EEV) or epigenetic estimated breeding value (EGEBV) framework could extend traditional genomic selection by incorporating biologically meaningful epigenetic signals [88]. Classical genomic selection, based solely on SNP markers, captures only part of the variation underlying traits influenced by genetics. EEV/EGEBV integrates the additional, heritable information embedded in stable DNAm differences such as CoRSIVs, helping to explain variation not accounted for by genetics alone. When combined with traditional genetic evaluations, EEV/EGEBV can provide a more complete assessment of an animal's potential, improving prediction accuracy for environmentally responsive traits and enabling more informed selection decisions.

Technological and computational requirements for epigenetic application

The application of epigenetic selection depends on overcoming both technological and computational challenges. This requires moving beyond expensive WGBS to cost-effective, high-throughput targeted assays, achieving similar cost with current SNP arrays. Multiple platforms are available for DNAm profiling, each with distinct advantages and limitations. Short-read sequencing (e.g., Illumina) remains the dominant platform for WGBS and EM-seq, while long-read platforms (Pacific Biosciences and Oxford Nanopore Technologies) provide full CpG context and base modifications but remain too costly for routine use [89]. WGBS is the gold standard but degrades DNA and is expensive; EM-seq offers similar coverage with improved molecular integrity and is better suited for low-input samples. RRBS provides reduced coverage (~2M CpGs) with a bias toward promoters and CG islands.

Array-based approaches offer scalable, cost-effective alternatives. The Horvath Chip targets 37,492 conserved CpGs across mammals for aging and disease studies [90, 91]. The cattle-specific RUMIGEN EpiChip (43,420 CpGs), modeled and designed after early human arrays [29, 30], targets markers related to fertility, health, stress, and regulatory elements such as promoters and CTCF sites (PAG32 Abstract 2) [89]. It has been shown to have high repeatability across > 6,000 samples and is expected to become commercially available soon. In humans, targeted DNA methylation capture panels offer greater power, reproducibility, and functional relevance than conventional arrays. Agilent SureSelect, based on phosphoramidite chemistry, is well-established and has been used in designs such as the Baylor Human CoRSIV Panels. Twist Bioscience's silicon-based synthesis provides high precision, low error rates, and efficient scalability [92], particularly advantageous for large or complex designs (Fig. 1c). However, no such panel currently exists for farm animals, including cattle, representing a major opportunity for innovation. In

short, scalable targeted assays, whether array- or sequencing-based, targeting validated SMPs will be key to enhancing utilization and biological interpretation of DNAm in cattle.

Bioinformatic analyses are equally critical for the reliable identification of SMP and for mapping relationships among SNPs, methylation, and gene expression (expression Quantitative Trait locus or eQTL, mQTL, and eQTM, as shown in Fig. 1d) [4]. Such analyses ensure a clear distinction between genetically driven and purely epigenetic effects. Intergenerational and transgenerational analyses represent an additional priority [93, 94]. Existing livestock studies already indicate that some epigenetic marks and associated phenotypic effects persist across generations, supporting the concept that nutritional or developmental programming can exert long-lasting influence. Demonstrating that SMPs function as carriers of such epigenetic memory in cattle is a critical next step for advanced breeding programs.

Biomarker discovery focuses on identifying trait-associated, biologically meaningful methylation sites of practical relevance for management and genetic improvement, not on establishing direct causation. These markers extend beyond what SNPs or current DNAm arrays can capture. In the short term, CoRSIV profiles from early-life samples could inform heifer culling or bull selection decisions before phenotypes emerge. Over the long term, stable SMPs may complement SNP-based genomic models, improve prediction accuracy, and help clarify components of missing heritability. These insights could also guide further optimization of platforms such as the RUMIGEN EpiChip and the Horvath Chip.

Conclusions

DNA methylation is a key regulatory layer underlying phenotypic diversity in cattle, influencing health, productivity, fertility, and overall performance. Advances in whole-genome bisulfite sequencing, long-read methylome profiling, and population-scale epigenome resources have greatly improved the ability to detect and interpret methylation variation across individuals and tissues. These developments highlight the growing potential of epigenomic research to complement traditional genomics in cattle management and breeding. Integrating DNA methylation profiles, particularly stable, partially heritable SMPs and tissue-agnostic regions such as CoRSIVs, offers new opportunities to improve selection accuracy, identify regulatory biomarkers, and capture environmental and management effects on key traits. Emerging computational tools and multi-omics datasets are facilitating the translation of these discoveries into practical applications, supporting more precise decision-making in breeding and herd management. Continued progress will depend on coordinated, data-driven strategies. By leveraging multi-omics resources and advanced epigenetic profiling, improved selection efficiency and sustained genetic progress can be achieved while safeguarding the long-term integrity of cattle populations.

Conflict of interests: The author declares no competing interests.

Acknowledgements

Ransom L. Baldwin VI, Li Ma, Moran Gershoni, Eyal Seroussi, and Nayan Bhowmik provided valuable comments and feedback. The author is supported in part by AFRI grant numbers 2019-67015-29321 and 2021-67015-33409 from the USDA National Institute of Food and Agriculture (NIFA). This research used resources provided by the SCINet project of the USDA ARS project number 0500-00093-001-00-D. The publication fee of this article was covered by JSPS KAKENHI Grant Number 22HP2009.

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