

Genome-wide selective sweeps providing classic evidence of emotional and behavioural control in *Bos indicus* cattle breeds

S. Vani^{1*}, D. Balasubramanyam¹, S.M.K. Karthickeyan¹, K.G. Tirumurugan², A. Gopinathan¹, B. Jaya Madhuri¹, J. Hepsibah¹, G. Srinivasan³, N.V. Kavith⁴ and P. Ganapathi¹

¹Department of Animal Genetics and Breeding, ²Department of Animal Biotechnology, ³Pulikulam Cattle Research Station, Manamadurai, ⁴Kangayam Cattle Research Station, Sathyamangalam, Tamil Nadu Veterinary and Animal Sciences University, Chennai – 600 051

*Corresponding Author e-mail: vanireddy12786@gmail.com

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Abstract

Diverse genomic selection signatures were identified from whole genome sequencing data of five cattle breeds of Tamil Nadu viz. Alambadi, Bargur, Kangayam, Pulikulam and Umblachery. Two complementary approaches were utilized to detect most recent (CLR) and distant past (F_{ST}) selective sweep regions from a total of 13,90,449 filtered SNPs. A total of 7,250 and 806 genomic regions were found to contain selective sweeps in 1,238 and 101 candidate genes using these methods respectively and were found mostly related to production (*PAIPI*, *NNT*, *OCIAD1*), coat colour (*MC1R*, *KIT*, *KDR*, *PDGFRA*), Disease resistance (*TCF25*, *CDH15*, *SPIRE2*) and adaptation (*SLC22A31*, *SPG7*) of indigenous breeds to tropical climatic conditions and disease resistance (*SPIRE2*, *CHAMP1A*). Of the total candidate genes, 12 were identified by both CLR and F_{ST} methods (e.g. *GABRG1*, *GABRA4*, *CBFA2T3*, *GAS8*, *USP46*, *RASL11B*, *SCFD2*, *FIP1L1*, *LNK1*, *FRYL*, *LOC109560438* and *NNT*) and are related to production, disease resistance and emotional and behavioural control of these cattle. KEGG pathway analysis showed significance ($P < 0.05$) in *GABRG1* and *GABRA4* genes that are responsible for aggressive behaviour in Alambadi and Pulikulam cattle showing their importance in Jallikattu sport. The knowledge about signatures of selection and candidate genes affecting aggressive behaviour in these cattle would facilitate in formulating the selection index and genome-assisted breeding that help in conservation of these native cattle.

Key words: *Bos indicus* cattle, Selection Signatures, F_{ST} , CLR, Jallikattu, Tamil Nadu.

Introduction

It is known that modern cattle breeds have descended from various domestication events from the wild aurochs (*Bos primigenius*). As a result, taurine cattle (humpless) were domesticated around 8,000 to 10,000 years ago in the fertile crescent, while indicine cattle (humped) around 6,000 to 8,000 years ago in the Indus Valley (Loftus *et al.*, 1994; Kumar *et al.*, 2003). Further, these cattle have been selectively bred for desirable traits, especially draft power, milk production and tolerant to hot climate (Biradar *et al.* 2024). Thus, natural selection followed by domestication and subsequently artificial selection had led to an increased genetic differentiation among the cattle breeds (Sharma *et al.*, 2015). These selection strategies are expected to put pressure on specific genomic regions that control breed characteristics like productivity, reproduction, body conformation, behaviour, adaptation to various environmental conditions and disease resistance. These selection strategies left certain unique genetic patterns or footprints in the genome of individuals which are termed now as selection signatures (Jensen *et al.*, 2015).

Several statistical models were developed to determine the signatures of selection in recent years. Variants under selection pressure generate the typical genomic patterns such as (i) change in the allele frequency spectrum (ii) greater number of homozygous genotypes; (iii) long haplotypes (iv) intense differentiation of local population. Several studies were conducted utilizing more than one statistic *viz.* composite likelihood ratio (CLR), integrated haplotype score (iHS), cross-population extended haplotype homozygosity (XP-EHH) and fixation index (F_{ST}) *etc.* to detect the signatures of selection that exploit the advantage of complementarity of methods intending to improve the statistical power (Mastrangelo *et al.*, 2020).

India has a massive livestock inventory with 193.46 million cattle; of which, 51.36 million are exotic/crossbred and 142.11 million are indigenous/non-descript (Livestock Census, 2019). There are 50 well-defined and registered indigenous cattle breeds reared for milch, dual and draught purpose that make up the large reservoir of cattle genetic resources playing a crucial role in augmenting agrarian economy in the country. Tamil Nadu, the southernmost state of the country has five draught breeds of cattle (Alambadi, Bargur, Kangayam, Pulikulam and Umblachery) with distinct phenotypic characteristics. Apart from their draught capacity, these cattle also possess unique adaptability to hot and humid climate prevailing in their native tract (Biradar *et al.*, 2024), aggressive behaviour and resistance to tropical diseases, ticks and parasites. Among these, Umblachery cattle is known to have specific behavioural fear response whereas, Pulikulam and Alambadi cattle possess very peculiar aggressive behaviour which facilitates them to engage in Jallikattu, an old cultural and traditional religious rite of the Tamil people, which is a bull-taming sport that is held every year during and after the Pongal festival in Tamil Nadu (Priyadharsini *et al.*, 2019).

Due to indiscriminate cross breeding with exotic breeds to increase milk production of these draught cattle to meet the demands of Tamil Nadu people, the native germ plasm has been diluted. If this scenario continues over a long term, the population may come under risk category. Knowing the facts about how the domestication and selection have changed the genomes of these cattle and identifying the regions under selection for their aggressive behavior needed for Jallikattu is of utmost important. Hence, the present study was carried out to identify the regions of selective sweeps responsible for knowing their behavior and emotional control so as to plan strategies for breeding and conservation of these imperative native cattle breeds.

Materials and Methods

A total of 302 representative animals from five draught cattle breeds of Tamil Nadu were utilized in the present study and is shown in figure 1 along with the longitude and latitude of the sampling area in the breeding tract. An amount of three ml of blood sample was collected aseptically from the jugular veins of each animal *viz.* Alambadi (16), Bargur (106), Kangayam (63), Pulikulam (56) and Umblachery (61) cattle breeds. While sampling, care was taken to avoid close relationship among them. The blood samples were carefully brought to the molecular laboratory, Department of Animal Genetics and Breeding, Madras Veterinary College, Chennai and stored at 4°C until further use. Genomic DNA was isolated using standard phenol-chloroform extraction procedure recommended by Sambrook (1989) with slight modifications by using DNAzol reagent, instead of sodium dodecyl sulphate (SDS) and proteinase K.

Of the total samples, 79 DNA samples were selected and pooled into three groups from each breed as bulls, moderately yielding dams and low yielding dams (ACG1, ACG2 and ACG3 for Alambadi; BCG1, BCG2 and BCG3 for Bargur; KCG1, KCG2 and KCG3 for Kangayam; PCG1, PCG2 and PCG3 for Pulikulam; and UCG1, UCG2 and UCG3 for Umblachery cattle). For pooling the samples, the concentration of DNA from selected individuals has been properly balanced to 200 ng/μl with nuclease free water in order to represent each genome equally (Anand *et al.*, 2016). Equal volume of DNA (10 μl) from each selected individual of respective

group were combined to obtain group-specific pools, that would give enough DNA for subsequent process of whole genome sequencing. Thus, a sum of 15 pooled samples three from each breed were prepared and sequenced using paired-end libraries on Illumina Hiseq 2500 and Novoseq 6000 platforms.

Quality filtering of raw sequence reads and alignment

The sequence data was checked for base call quality distribution, phred score quality (Q score), GC percentage and sequencing adapter contamination using FastQC (Andrews, 2017) and MultiQC (Philip *et al.*, 2016) software. The fastp v0.20.1 was used to trim adapter sequences and low-quality bases with a phred score of less than 20. The processed reads were mapped against *Bos indicus* reference genome (GCF_000247795.1_Bos_indicus_1.0) using BWA-MEM algorithm v0.7.17-r1188 with the default parameters. The obtained SAM files were converted into BAM files using SAMtools. The resultant BAM files underwent sorting and filtering for duplicates using PICARD tool v 2.0.1.

Variant calling

SNP Variants were called using GATK HaplotypeCaller v4.2.0.0-1. The identified raw variants were filtered using default parameters of GATK *viz.* Quality by Depth (QD) of <2.0, Filter Score (FS) of >60, Mapping Quality (MQ) of <40, Symmetric Odds Ratio (SOR) of >4.0, Mapping Quality Rank Sum (MQRS) of <8.0 and Read Pos Rank Sum (RPRS) of <8.0. The filtered variants were subjected for base quality recalibration. The SNPs with more than 95 per cent call rate and MAF>0.05 were only adopted. SNPs on X-chromosome, Y-chromosome, Mitochondrial DNA and SNPs that were not under HWE ($P<0.001$) were removed from further population analysis. Each common and unique SNP was annotated using SnpEff v 5.0e by using .gff (general feature format) annotation file of the *Bos indicus* reference genome.

Identification of Selective Sweeps

Inter-Population Analysis: Distribution of Wright's F_{ST} index in the genome

Fixation index (F_{ST}) was computed according to Weir and Cockerham (1984) to assess degree of genetic differentiation between populations. The genome-wide pair-wise distribution of F_{ST} was scanned using vcftools with window size of 500kb and step size of 50kb for all SNP pairs for individual chromosomes. The SNPs showing negative F_{ST} values were converted to zero, as negative values cannot be interpreted from the biological point of view (Saravanan *et al.*, 2021). The remaining F_{ST} values were then averaged for every ten consecutive SNPs. The distribution of F_{ST} values of the SNPs were categorised into class intervals as low, medium and high degree of genetic differentiation as 0 to < 0.15, ≥ 0.15 to < 0.25 and ≥ 0.25 respectively (Dixit *et al.*, 2021). The pair-wise F_{ST} values of SNPs were plotted against the chromosomal position using Manhattan plot using R platform. The regions having threshold F_{ST} value of ≥ 0.25 (highly differentiated allele frequency at a given locus) were considered to represent the signatures of selection.

Intra-Population Analysis: Composite likelihood ratio method (CLR)

The CLR test detects 'hard sweeps' at genomic regions where beneficial adaptive alleles reached fixation recently. This was done by using SweeD program that run separately for each chromosome by setting the grid parameter at five kb equidistant positions across all the chromosomes. The threshold value for α statistics was taken as the 99th percentile of the empirical distribution. The outliers falling within the top one per cent of the CLR distribution were selected. One kb flanking regions to these outlier sites were considered as regions of selective sweeps.

Annotation and Gene Ontology

Annotation of the candidate regions that exhibited a signal of selection identified using both CLR and F_{ST} methods was performed using SNPEff tool.

Ethical approval

Ethical committee approval has not been taken as it involves only the collection of blood samples aseptically from the jugular veins of live animals which was done by the qualified veterinarians.

Results

Whole genome sequencing data

The quality of the sequence reads obtained after whole genome sequencing are shown in figure 2. On an average, 391.02 million reads per sample had passed quality control; out of which, 380.13 million reads were mapped on to reference genome with a mapping percentage of 97.28 and average depth of coverage as 19.11x

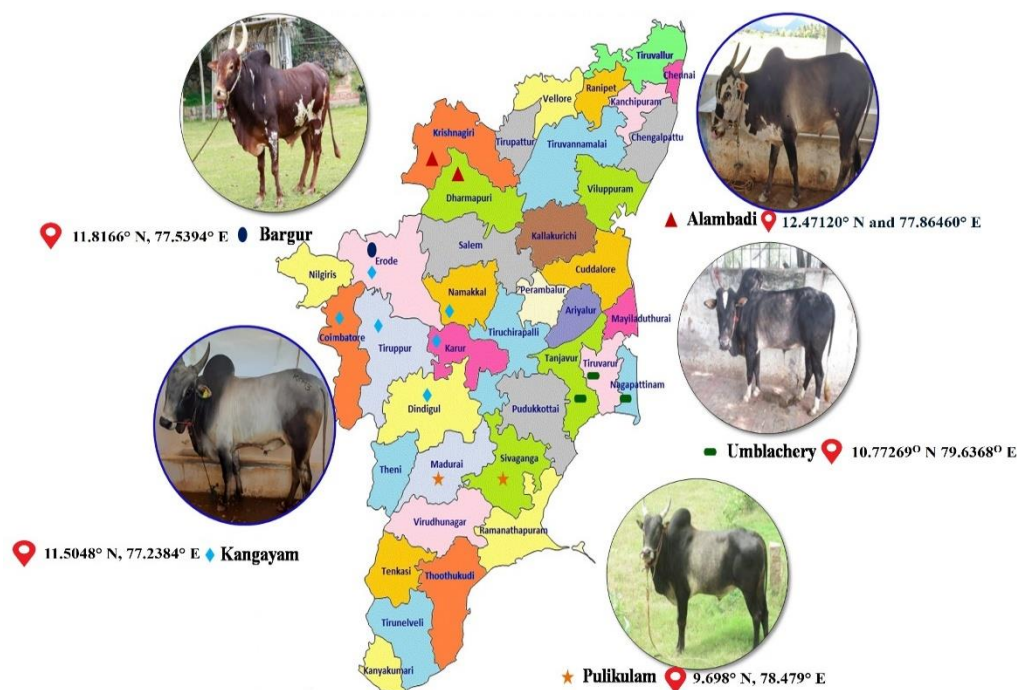


Fig 1: Breeding tract of cattle breeds of Tamil Nadu

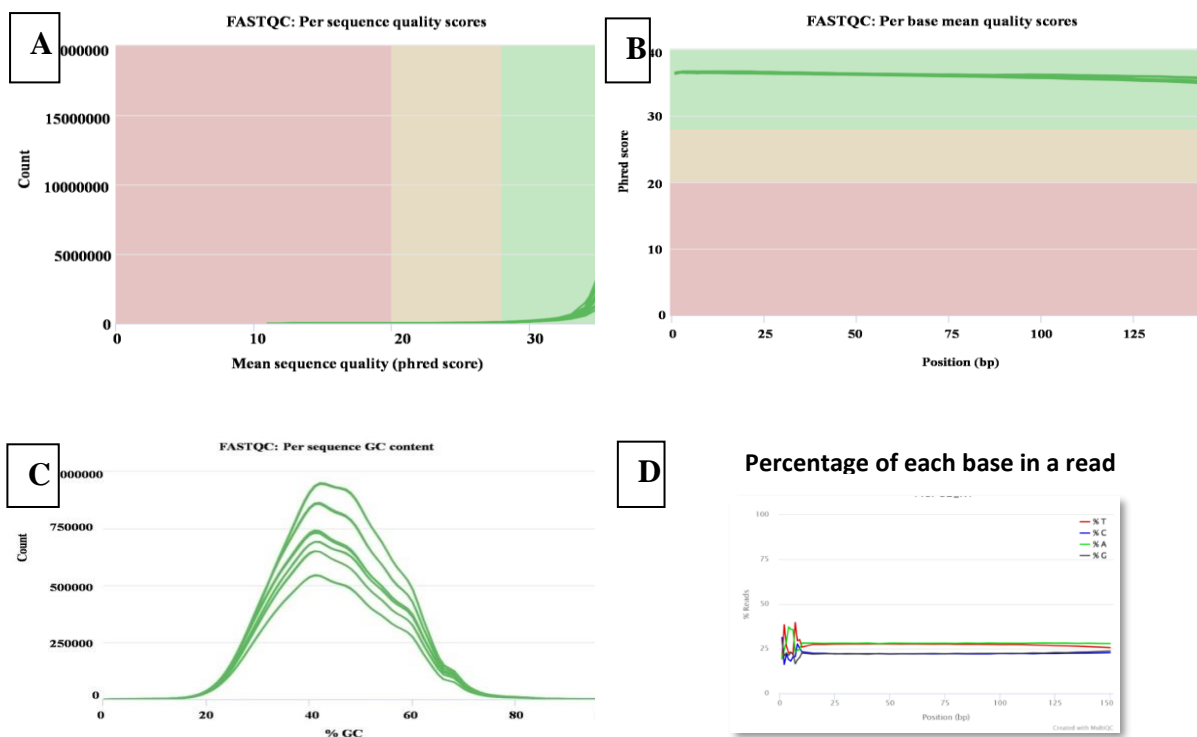


Fig 2. Quality parameters of sequence reads obtained in whole genome sequencing
A: Per sequence quality score; B: Per base mean quality score; C: Per sequence GC content; D: Percentage of each base in a read

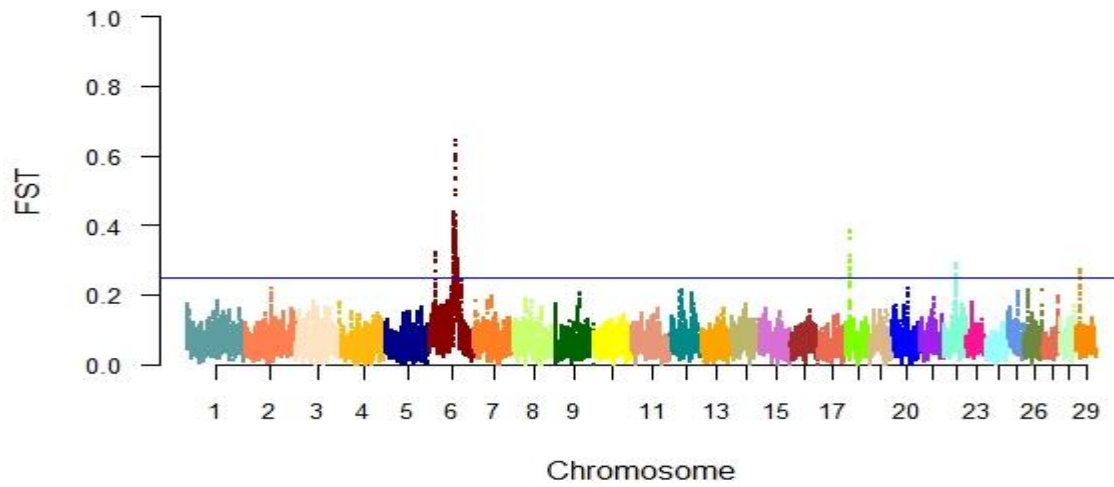


Fig 3. Manhattan plot showing distribution of F_{ST} shared among the individuals across the chromosomes among cattle breeds of Tamil Nadu

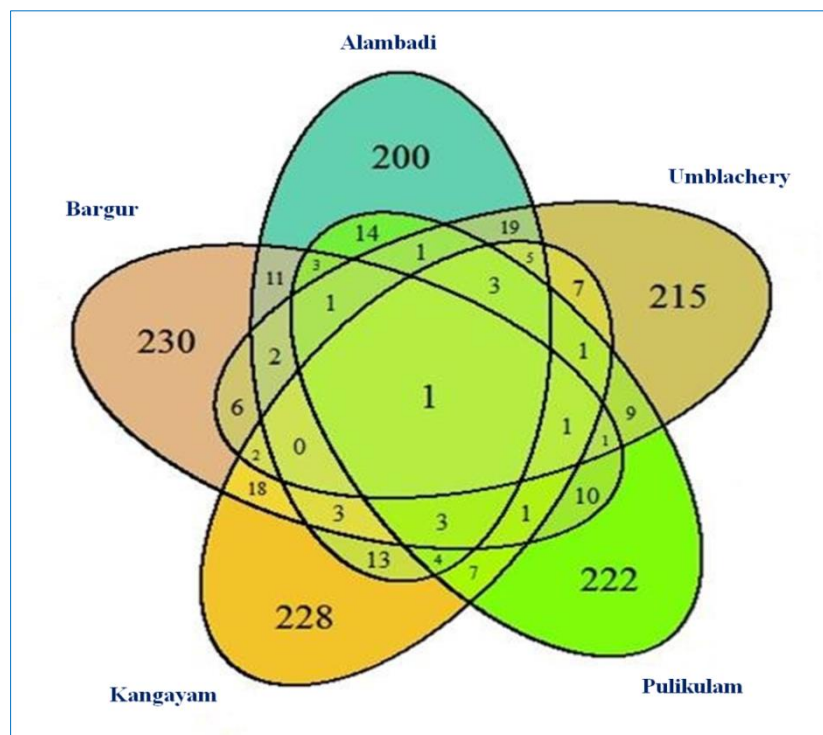
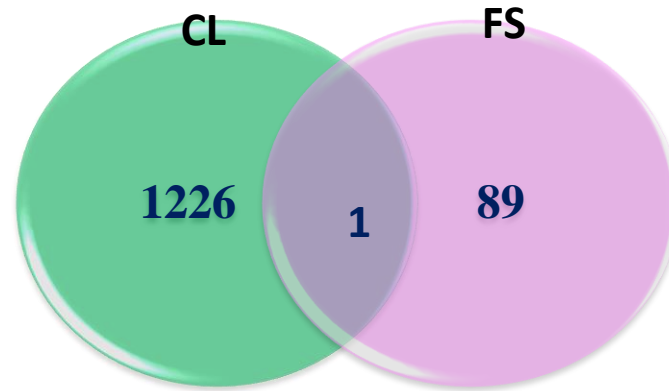


Fig 4. Venn diagram showing breed-specific and overlapped genes in selective sweep regions as identified by SweeD in Cattle breeds of Tamil Nadu

Fig 5. No. of selective sweeps overlapped between CLR and F_{ST} methods**Table 1.** Details of selection signatures identified by two (CLR, F_{ST}) approaches

Gene	Chr. No.	SNP window (Start-end) (Mb)	Breeds reported		Phenotype
			CLR	F_{ST}	
<i>GABRG1</i>	6	67.03-67.24	Alambadi	AU, KU, PU	Emotional and behavioural control
<i>GABRA4</i>	6	67.96-68.07	Pulikulam	AU, BU, KU, PU	Emotional and behavioural control
<i>USP46</i>	6	71.01-71.07	Umblachery	BU, KU	Behavioural fear response
<i>RASL11B</i>	6	71.24-71.24	Umblachery	BU, KU	-
<i>SCFD2</i>	6	71.25-71.63	Alambadi Umblachery	AU, BU, KU, PU	Initial milk yield
<i>FIP1L1</i>	6	71.65-71.70	Alambadi	AU, BU, KU, PU	Disease resistance
<i>LNK1</i>	6	71.71-71.85	Alambadi	AU, BU, KU, PU	Marbling
<i>FRYL</i>	6	69.83-70.09	Umblachery	AU, BU, KU, PU	Cytoskeleton
<i>LOC109560438</i>	6	67.80-67.88	Pulikulam	AU, BU, KU, PU	-
<i>GAS8</i>	18	13.84-13.88	Alambadi	AB, BK, BU, BP, PU	Myogenesis
<i>CBFA2T3</i>	18	13.05-13.11	Bargur	BU	Immune response
<i>NNT</i>	20	33.10-33.19	Bargur	PU	Milk fat percentage

AU- Alambadi-Umblachery; BU- Bargur-Umblachery; KU-Kangayam-Umblachery; PU- Pulikulam-Umblachery; AB- Alambadi-Bargur; BK- Bargur-Kangayam; BP- Bargur-Pulikulam

Table 2 Enriched GO terms of candidate genes identified by both CLR and F_{ST} methods

Gene	Molecular function	Cellular component	Biological processes
<i>GABRG1</i>	GABA-A receptor activity	Cytoplasmic vesicle membrane	Chloride transport
<i>GAS8</i>	Microtubule binding	Cytoskeleton	Cell motility
<i>CBFA2T3</i>	Transcription corepressor activity	Nucleus	Transcription
<i>NNT</i>	NAD(P) ⁺ transhydrogenase activity	Integral component of membrane	Proton transmembrane transport
<i>GABRA4</i>	GABA-A receptor activity	Post-synaptic membrane	Chloride transport
<i>LOC109560438</i>	Cytochrome-c oxidase activity	Integral component of membrane	Oxidative phosphorylation
<i>RASL11B</i>	GTPase activity	Mitochondrial respirasome	-
<i>USP46</i>	Thiol-dependent deubiquitinase	-	Protein deubiquitination
<i>LNK1</i>	Metal ion binding	-	-
<i>FIP1L1</i>	-	Nucleus	-
<i>SCFD2</i>	-	-	Vesicle-mediated transport
<i>FRYL</i>	-	-	Cell morphogenesis

Table 3 Gene ontology and pathway analysis of *GABRA4*, *GABRG1* genes responsible for emotional behaviour in cattle breeds of Tamil Nadu

Category	Term	Processes involved	p-value
Biological process	GO:7214	Gamma-aminobutyric acid signalling pathway	0.010
	GO:6821	Chloride transport	0.049
Cellular component	GO:34707	Chloride channel complex	0.022
	GO:45211	Postsynaptic membrane	0.039
Molecular functions	GO:4890	GABA-A receptor activity	0.012
	GO:5230	Extracellular ligand-gated ion channel activity	0.019
	GO:5254	Chloride channel activity	0.023
KEGG pathways	biu05033	Nicotine addiction	0.018
	biu04727	GABAergic synapse	0.04
	biu05032	Morphine addiction	0.042
	biu04723	Retrograde endo cannabinoid signalling	0.045
INTERPRO Protein domains	IPR006028	GABA receptor	0.013
	IPR018000	Neurotransmitter-gated ion-channel, conserved site	0.026
	IPR006029		
	IPR006202		
	IPR006201		

across all samples. On an average, 97.76 percent fold coverage rate was observed across 15 samples with respect to *Bos indicus* reference genome.

SNP variant calling

A total of 26,406,037 numbers of SNPs were identified across the five breeds investigated. Of these, a final set of 13,90,449 SNPs were utilized for further downstream analysis after removing those SNPs not meeting the quality criteria.

Identification of Selective Sweeps

In the present study, the average pair-wise F_{ST} estimates ranged from low level of genetic differentiation as 0.024 (between Bargur and Pulikulam cattle) to high level of genetic differentiation as 0.083 (between Kangayam and Umblachery cattle) with an average of 0.048 across all the loci. To visualize the genome-wide distribution of selection signatures for the 10 breed pairs (five breeds), the pair-wise F_{ST} values of SNP windows were plotted against the genomic position using Manhattan plot as shown in Figure 3. Using this approach, 806 genomic regions under divergent selection were recognized, which were annotated to 101 different candidate genes across all the breed pairs. Using composite log likelihood method, out of 13,90,449 filtered SNPs, a total of 1450 selective regions were identified in each breed based on top one percentile outliers of CLR value (>3.0). These were annotated to 1238 candidate genes as shown in figure 4. These genes identified with selective sweeps by both CLR and F_{ST} methods are mainly associated with coat colour, production, adaptability, disease resistance. Out of these total genes identified by both the methods, 12 genes (*GABRG1*, *GABRA4*, *USP46*, *RASL11B*, *SCFD2*, *FIPIL1*, *LNX1*, *FRYL*, *LOC109560438*, *GAS8*, *CBFA2T3* and *NNT*) were shared between both the methods as illustrated in Figure 5. Chromosome-wise location of these 12 genes along with their reported QTLs is presented in Table 1.

Gene enrichment and Pathway analysis

The gene enrichment and pathway analysis of the 12 candidate genes identified by both CLR and F_{ST} methods revealed molecular functions (MF), cellular components (CC) and biological processes (BP) as presented in Table 2. Out of these 12 genes, two genes (*GABRG1* and *GABRA4*) were responsible for emotional and behavioural control in indigenous cattle breeds of Tamil Nadu and BP, CC, MF and KEGG pathway analysis of these two genes showed that they were involved in the neuronal activities of the brain responsible for emotional and behavioural control in cattle as shown in Table 3.

Discussion

Variant Calling

The number of SNPs identified in the present study (26,406,037) was higher than that reported by Bhati *et al.* (2020) in Braunvieh cattle (15,722,811 SNPs). The variant richness observed in the present study is attributed

to the pooling of samples in equal proportions prior to sequencing. This was supported by earlier studies on whole genome sequencing by Liao *et al.* (2013) in Gir cattle breed of Brazil.

Selective Sweep Analysis

In this study, we found wide-spread signals of selection in all five cattle populations of Tamil Nadu and generated the first genome-wide incomplete map of selective sweeps.

F_{ST} Approach

The comparable estimates of F_{ST} values were reported by Makina *et al.* (2014) among the South African cattle breeds, where F_{ST} values varied from 0.043 (Nguni - Drakensberger) to 0.081 (Afrikaner-Drakensberger). Tijjani *et al.* (2021) reported pair-wise genetic differentiation values that ranged from 0.015 to 0.342 among 17 cattle indicine and taurine breeds of Africa. The low level of genetic differentiation (F_{ST}) among the breeds of Tamil Nadu in this study reflects the existence of gene flow between the breeds of adjoining breeding tracts as all of them were selected for draft quality and endurance power over the years. The threshold (F_{ST}≥0.25) set in the present study was lower than that reported by Zhang *et al.* (2020) in Chinese indigenous cattle, where the value was 0.40. whereas,

Smetko *et al.* (2015) reported a lower threshold F_{ST} value of 0.20 to identify regions of selection signatures. Singh *et al.* (2020) used mean ± 3 standard deviation as threshold for identifying selection signatures in Vrindavani cattle breed.

Signals of selection identified in 806 genomic regions in all five cattle populations of Tamil Nadu are generally from distant past that might have occurred preceding the separation of these five populations. Lesser selection signatures obtained in our study may be influenced by several factors as opined by Saravanan *et al.* (2021) viz. sample size, the density of SNPs, and ascertainment bias in the genomic data.

CLR Approach

The total selective events (7,250) are considered as very recent, falling mainly within the holocene era. Similar to the present study, Xia *et al.* (2021) reported selective sweep regions using CLR approach in top one per cent of the genome Jiaxian Red cattle breed.

Selective sweeps shared between CLR and F_{ST} methods

There was a substantial overlap between the list of genes identified by F_{ST} and CLR, reflecting the fact that the two tests capture the advantage of different, but correlated patterns of a selective sweep. The regions solely identified by either metric possibly indicate that these statistics identify selection acting at different time scales (recent divergence by CLR and past by F_{ST}) according to the features of the genetic polymorphism data.

Out of 1,238 and 101 candidate genes identified under positive selection by CLR and F_{ST} methods independently, 12 genes were shared by both the methods. The number shared between methods is comparatively less than that reported by Taye *et al.* (2017) who had employed XP-EHH and XP-CLR tests to detect signals of selection and reported 238 and 213 genes respectively; of which 98 were overlapping; Bhati *et al.* (2020) identified 136 and 157 genes through CLR and iHS methods in Braunvieh cattle; of which 35 were shared between them; and Xia *et al.* (2021) identified 1,199 and 351 genes by nucleotide diversity ($\theta\pi$) and CLR methods; of which 171 were shared between them in Jiaxian Red cattle. The discrepancy between the results might be due to variations in the methodology used.

Gene enrichment and pathway analysis

Functional enrichment analysis using KEGG pathways and Gene Ontology (GO) for overlapped genes revealed significance (P<0.05) only for two GABA-A subunit receptor genes (*GABRA1* and *GABRG1*) in Alambadi and Pulikulam cattle in the present study. GABA is the major inhibitory neurotransmitter in the mammalian brain where it acts at GABA-A receptors, which are ligand-gated chloride channels. These genes have been found to mediate anxiolytic activity, which plays a key role in emotional and behavioural control and in the level of neural excitation (Shen *et al.*, 2022). This could be considered as an intriguing result as also identified by Jivanji *et al.* (2019) and Mastrangelo *et al.* (2020) in Holstein-Friesian and three Valdostana cattle breeds respectively. In fact, these findings may be linked to the traditional sport event, “Jallikattu,” a bloodless bull-baiting or bull-taming tournament in which bulls from Pulikulam cattle are used for fighting (Priyadharshini *et al.*, 2019). All the indigenous cattle breeds of Tamil Nadu are well-known as draught cattle and are characterized by their lower milk production but they are well-developed and very strong and quite aggressive. Bulls that are able to participate successfully in the Jallikattu event are used as studs for breeding. The success of “Jallikattu” could be exploited and inclusion of fighting ability of these animals within the selection index may be suggested. Therefore, it is likely that this selection signature is the result of selection efforts on bull fighting ability that had been happened since 400-100BC. Since the population of cattle breeds of Tamil Nadu has dwindled over the years, conservation efforts need to be emphasized meticulously to protect this valued germplasm.

Selection signal on one more unusual gene located on chromosome 6 (*USP46*) identified in Umblachery cattle is known to have behavioural fear response solely observed in these cattle. The same gene was also reported by Jivanji *et al.* (2019) and Mastranglo *et al.* (2020) in Holstein–Friesian and Valdostana cattle breeds respectively.

Conclusion

A total of 26,406,037 genome-wide SNP variants were identified through WGS in cattle breeds of Tamil Nadu of which 13,90,449 were utilized for identification of selective sweeps through F_{ST} and CLR approaches. Among the total genes containing selective sweeps, 12 genes were shared between F_{ST} and CLR methods. Of these 12 genes, selective signatures present in *GABRA1* and *GABRG1* genes in Alambadi and Pulikulam cattle breeds are responsible for their aggressive behaviour which is being used for the Jallikattu event. Hence, having the importance for these breeds in the traditional sport, conservation efforts need to be undertaken by planning appropriate breeding strategies to protect these animals.

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Conflict of interest

The authors declare that there is “no conflict of interest”.

Availability of data

The datasets generated in the study have been deposited in the NCBI (PRJNA893588). SNP genotype data and list of selective sweeps and their candidate genes are available upon request for research purposes.

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