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Genetic Variants on *SLC45A2* Gene Associated with White Coat Color in the Dromedary Camel (*Camelus dromedarius*)

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ABSTRACT

Background: Dromedary camel coat color is an important trait that breeders aim to select for certain coat colors camels. Few efforts showed that *MC1R*, *ASIP*, *TYR* and *KIT* genes are associated with different coat colors in the species. However, *Solute Carrier Family 45 Member 2* (*SLC45A2*) gene is considered as a key factor in pigmentation pathway associated with coat color phenotypes in many domesticated animals but not studied in the dromedary. We hypothesize that *SLC45A2* sequence variants of *SLC45A2* are associated with different color phenotypes in the dromedary camel. Therefore, our current study aims to show the *SLC45A2* gene sequence in the dromedary camel (*Camelus dromedarius*) coat color.

Methods: The study is conducted on samples collected from 135 dromedaries representing 5 coat color groups: white (n=48), light brown (n=28), brown (n=20), dark brown (n=21) and black (n=18).

Result: We identified 2 missense mutations (c.95 C>T; T32M and c.1494 C>G; S498R), 4 synonymous mutations (c.633 G>C, c.783 G>C, c.879 T>C and c.975 C>T) and one variant in intron 4 (g.23719513 C>T). c.1494 C>G; S498R is associated with white phenotype, where the G allele is only found in white phenotype (p-value < 0.001). As far as we know, this is the first report to investigate *SLC45A2* genetic variants and their association with coat color phenotypes in the dromedary. The results might assist in the discovery of a reliable coat color testing in the dromedary.

Key words: Coat color, Dromedary camel, Genetics, *SLC45A2*.

INTRODUCTION

Coat color is a complex trait that is controlled by a few major genes and many spotting and diluted genes. Since the beginning of animal domestication, humans have selected for desirable phenotypic traits such as production and performance. For example, humans have selected for high milk yield in dairy cattle and goats (Miglior *et al*., 2017; Saleh *et al*., 2023). Light coat colors in alpaca have high fiber quality (Pacheco *et al*., 2024) and selecting for production and performance traits in dromedary camels has long been the practice (Khalkhali-Evrigh *et al*., 2022). One of the most desirable phenotypes is coat color for which extensive selection has been made. Dromedary camel coat color is uniform except for the Canary camel which is spotted (2025; Holl *et al*., 2017). Coat color of dromedary camels in the Arabian Peninsula varies from white to black and all shades of brown. Yellow and red coat colors are present in some dromedary camel herds. Majaheem camels are characterized by a black coat color, white and brown camels are called Wodh and Sofor, respectively. Shaul camels are a distinct type of dromedary also characterized by a brown coat that is different from Sofor camels. Sofor camels are characterized by a darker hump, tail and crest (Almathen *et al*., 2018; Al-Swailem *et al*., 2007).

Research efforts have also been directed toward candidate gene association analysis to investigate potential associations between genetic variants and coat color in the dromedary camel. It has been reported that white coat color is dominant at the *Melanocortin 1 receptor* (*MC1R*) gene (c.901 C>T) (Almathe *et al*., 2018; Alshanbari *et al*., 2019). Conversely, a black coat color is a recessive trait. The *Agouti Signaling Protein* (*ASIP*) gene exon 2

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homozygote deletion is responsible for the black phenotype in dromedary camels (Almathen *et al*., 2018; Alshanbari *et al*., 2019). The *tyrosinase* (*TYR*) gene c.200 C>T is associated with light brown dromedaries (Alshanbari 2023) and *TYR* c.523 T>C variant was associated with black dromedaries (Mahmoud *et al*., 2020). Also, the *proto-oncogene c-KIT* (*KIT*) gene is associated with white spotted camels (Holl *et al*., 2017). No association has been determined for the *tyrosinase-related protein 1* (*TYRP1*) (Alshanbari *et al*., 2019).

Solute Carrier Family 45 Member 2 (*SLC45A2*) is a key gene that has been associated with pseudo-albinism and leucism in many species including horses, cattle and dogs (Wijesena and Schmutz, 2015; Rothammer *et al*., 2017; Mariat and Guerin, 2003). However, this gene has not been studied for its association with coat color phenotypes in the dromedary camel. Here, we hypothesize that *SLC45A2* genetic variants are associated with white coat color in the dromedary camel.

MATERIALS AND METHODS

Identification of variants in SLC45A2 from whole genome sequencing data

The whole genome sequencing (WGS) data for 40 dromedary camels from the Arabian Peninsula were obtained from Bahbahani and Almathen (2022) and Bahbahani *et al*. (2024), corresponding to 13 different breeds. The samples were collected from Saudi Arbia, Kweit, Oman and Pakistan from 2018-2023 and samples processing were taken a place at The Camel Research Center, King Faisal University. The raw sequence reads were aligned to the African dromedary reference genome assembly (CamDro3) using the bwa-mem algorithm implemented in the Burrows-Wheeler Aligner version 0.7.17 (Li and Durbin, 2010). The reads were then coordinate-sorted using the SortSam option and PCR duplicates marked and excluded using the MarkDuplicates and REMOVE_DUP LICATES=true options in the Picard tools version 3.0.0 (http://broadinstitue.github.io/picard/index.html).

Single nucleotide polymorphisms (SNPs) on the *SLC45A2* gene were called using the HaplotypeCaller tool in GVCF mode and implemented in the Genome Analysis Toolkit (GATK) version 4.2.5.0 (McKenna *et al*., 2010). The called SNPs were then filtered using the Variant Filtration algorithm in the GATK, following Bahbahani *et al.* (2024). The Fasta files of the *SLC45A2* gene sequence for each dromedary sample were generated using the *Fasta Alternate Reference Maker* algorithm in GATK.

Animal sampling and phenotypes

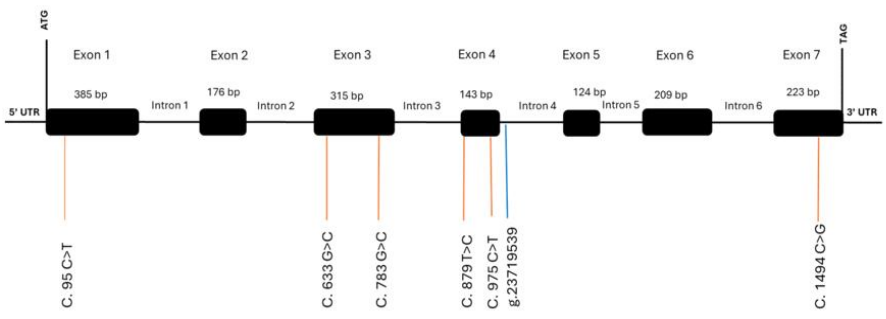
This study used blood samples from 136 dromedary camels of different herds and locations across Saudi Arabia from June, 2023 to January, 2025; the samples were randomly taken from five different coat color groups: white (n=48), light brown (n=28), brown (n=20), dark brown (n=21) and black (n=19). A total of 3 mL of whole blood was collected from the jugular vein of each animal, using vacutainers containing EDTA (Becton Dickinson). All samples were labeled and photographs captured during the sampling to confirm the phenotype. Sample were carried out to the Laboratory of Molecular Genetics, Department of Medical Biosciences, College of Veterinary Medicine, Qassim University. All samples were collected form desert camel breeds that are used for meat and milk production purposes.

DNA isolation

The genomic DNA was isolated from peripheral leukocytes using whole blood and a Gentra Puregene DNA Isolation Kit (Qiagen). DNA quality and quantity were determined using gel electrophoresis in a 1% agarose gel and nano-drop spectrophotometer (Thermo Scientific).

Primer design

The genomic region of *SLC45A2*, including seven exons and six introns, was retrieved from the dromedary camel reference genome 4 (mCamDro1.pat) NCBI gene database (Fig 1). Primers were designed using Primer3 software (Untergasser *et al*., 2012) to amplify the coding



The black rectangular boxes represent exons, whereas the horizontal black line indicates introns and the 5′ and 3′ UTRs. The orange lines are SNPs in the coding region, while the blue line is a non-coding SNP. ATG is the start codon and TAG is the termination codon of the coding region

Fig 1: Schematic representation of the *SLC45A2* gene structure and variants distribution in Saudi Arabian dromedary camel breeds.

regions, including the exon-intron boundaries, 5′ untranslated region (UTR) and 3′ UTR (Table 1). A repeat masker was used to check for repetitive sequences (de Koning *et al*., 2011).

PCR sequencing and SNP discovery

We used 25 dromedary camels representing five different coat color phenotypes (five white, five light brown, five brown, five dark brown and five black) to validate the SNPs identified by the WGS data. A PCR test was conducted on a 20 uL reaction using one unit of Dreamtaq DNA polymerase master mix (Therom Fishe Scientific), 50 ng genomic DNA, 10 picomole forward and reverse primers and nuclease-free water. The PCR condition was a 95°C initial denaturation for 3 minutes for 35 cycles, 95°C denaturation for 30 seconds, primer-specific t°C (as shown in Table 1), annealing for 30 seconds and 72°C for 1 minute for extension and a final extension of 72°C for 10 minutes. The PCR products were checked on 2% gel agarose using gel electrophoresis to confirm amplification. Positive amplicons with clear band on the gel were sent to Macrogen for cleaning via the ExoSAP-IT™ Express PCR Product Cleanup (ThermoFisher). Sanger sequencing was preformed using a BigDye (R) Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and an ABI PRISM 3730XL Analyzer (96 capillary type) (Macrogen Inc., Korea). Sequencher v. 5.4.6 (Gene Codes Corp.) was used for the sequence analysis and variants identification.

Further samples were sequenced to validate the association between the discovered variants and coat color phenotypes. We sequenced 117 samples (33 white, 29 light brown, 20 brown, 16 dark brown and 19 black) for exon 1, 61 samples (11 white, 10 light brown, 16 brown, 8 dark brown and 16 black) for exon 3, 62 samples (16 white, 20 light brown, 7 brown, 13 dark brown and 6 black) for exon 4 and 135 samples (44 white, 28 light brown, 20 brown, 21 dark brown and 18 black) for exon 7. Some samples did not have clear sequencing and were removed from the analysis. This explains why we had different numbers of sequencing for each exon. Cohort resequencing was therefore necessary only for significant associations.

Sequence and statistical analysis

The SLC45A2 mRNA sequence from NCBI (XM_ 01097 7623.3) was used to locate variations in the ORF. Briefly, observed sequences were aligned to the mRNA reference to determine their positioning and used in the following step. ExPASy webtools were used to translate mRNA sequences to protein and identify changes in the protein sequences (Gasteiger *et al*., 2003). Every SNP was given a unique name associated with the resulting change in the protein sequence. The BLASTP webtool from NCBI was used to compare the amino acid sequences of the dromedary SLC45A2 protein to other species. Transmembrane protein prediction was performed using TMHMM webtools to show the different structures of the

Table 1: Forward and reverse primers used to amplify the dromedary *SLC45A2* gene.

Primer name	Target region	Forward primer	Reverse primer	Annealing temperature	Product size (bp*)
SLC45A2 exon 1	exon 1	CCAGCCTGACCATCTCTGTT	GTCATTCACGGGTGGGAAATTCA	56°C	659
SLC45A2 exon 2	exon 2	TCTTTTCTGGACATTCACTTGCA	AAAACTCCACACCGGTCA	56°C	559
SLC45A2 exon 3	exon 3	CTCTGTTGCCTCTCCAGTCA	ACTTCACAAAACTCTTCACACCA	56°C	581
SLC45A2 exon 4	exon 4	TTCATGCTAACCTTCGTGCC	GGTGTAGTTAACTTCCCTCTGG	55°C	450
SLC45A2 exon 5	exon 5	GGATGAAACGGGTGACATGG	TGATGGGTCAATTCTAGGGGA	56°C	422
SLC45A2 exon 6	exon 6	AAGCCAGCTGTTTTCAAGCA	GCCAGACCATTGTTACACCTG	55°C	520
SLC45A2 exon 7-1	exon 7-1	GCTGAAAGTATTTATTATCTGGCTTTG	GACGGCTGGATGAGAGTGAG	60°C	497
SLC45A2 exon 7-2	exon 7-2	GTGGAGCACACAGCAAGAAA	CCTCCAGCATGAGATGTTCA	60°C	577

*bp: product size is in base pair.

protein and amino acids in each structure (Krogh *et al*., 2001). Multiple sequence alignment was conducted using CLUSTALW webtools (Thompson *et al*., 1994). Association analysis was determined by a Chi-squared test and contingency analysis conducted using Graphpad software (Prism version 10.4.1).

RESULTS AND DISCUSSION

SLC45A2 gene variants from the WGS data

The whole genome sequencing (WGS) analysis of the 40 dromedary samples identified a total of four SNPs. Comparison with the SLC45A2 mRNA reference sequence from the NCBI (accession number: XM_010977623.3) revealed that one SNP was located at exon 1 (c.95 C>T), another was identified at exon 3 (c.633 G>A) and two were found at exon 4 (c.879 T>C and c.975 C>T).

Verification of SNPs and structural analysis

Twenty-five dromedary camels were analyzed to validate the SNPs identified from the WGS data, with five samples selected from each of the five phenotypic groups. The analysis confirmed the presence of the four previously identified SNPs and revealed three additional variants: one SNP in exon 3 (cDNA 783 G>C, G>A,), another in intron 4 (g.23719539) and one in exon 7 (cDNA 1494 C>G); the G allele was detected exclusively in white dromedaries. No sequence variation was observed in exons 2, 5, or 6. Preliminary data suggested an association between variants in exons 1, 3 and 4 for the dark brown coat phenotype. Additionally, the c.783 G>C variant had three alleles (G, C and A), though no AA genotype was observed. A unique SNP was identified in exon 7 (c.1494 C>G), found exclusively in a single white dromedary presenting with abnormal hind limb growth and yellow eyes (Fig 2a and 2b). This phenotype differed from the typical white dromedary phenotype, which is characterized by darker skin, the absence of limb abnormalities and dark brown eyes (Fig 2c and 2d).

Functional analysis

To examine the impact of the exon 1 (c.95 C>T) and exon 7 (c.1494 C>G) variants on protein level, various tools were utilized to assess whether these mutations affected protein function and stability. The dromedary camel *SLC45A2* gene encodes a protein of 525 amino acids, characterized by 10 transmembrane domains. A comparative sequence analysis revealed a high degree of conservation within camelid species, with 99%, 98% and 97% sequence identity to *Camelus ferus*, *Camelus bactrianus* and *Vicugna pacos*, respectively. However, sequence identity decreased when compared to other species, including *Bos taurus* (86%), *Ovis aries* (86%), *Capra hircus* (86%), *Equus quagga* (83%), *Canis lupus familiaris* (82%), *Homo sapiens* (81%) and *Felis catus* (81%).

The c.95 C>T resulted in amino acid substitution (Threonine, Thr, T >T32M > Methionine (Met/M)). Furthermore, c.95 C>T was found to be located outside the transmembrane domain at the beginning of the protein structure. Multiple alignment sequences of the SLC45A2 protein sequencing showed that the T was highly conserved across mammalian species and chickens, but the M was different.

Additionally, the c.633 G>A, c. 783 G>C, G>A, c.879 T>C and c.975 C>T variants were silent mutations in which no amino acid changes occurred. These four variants were found in exons 3 and 4.

Finally, the c.1494 C>G variant led to a serine (Ser/S) to arginine (Arg/R) substitution at position 498 (S498R), occurring within the last transmembrane domain. Moreover, multiple alignment analyses of S498R showed that the S was highly conserved across many species, including chicken and zebrafish. This was followed by poly valine (Val/V); some species differed in the number of Vs (Fig 3). Multiple alignment sequences showed that humans had T instead of S at position 498; however, T and S are both amino acids with polar neutral side chains, whereas R is an amino acid with electrically charged side chains - basic.

Association analysis

A total of 117 dromedary camels were sequenced to assess the association between exon 1 variants and the dark brown coat color phenotype. However, no significant association was observed (p-value > 0.05). Additionally, 61 and 62 dromedaries were analyzed to investigate the potential associations of variants in exon 3, exon 4 and intron 4. Similar to exon 1, no significant associations were detected between these variants and dromedary coat color (p-value > 0.05). To investigate the association of the exon 7 variant (c.1494C>G) with coat color phenotypes, 135 dromedaries were sequenced. The G base was exclusively identified in white dromedaries, while all other coat color groups exhibited the CC genotype. Notably, no individuals with the GG genotype were observed. Statistical analysis revealed a significant association between the G base and white coat phenotype (p-value <0.001) (Table 2). No further sequencing was performed for exon1, exon3 and exon 4 because insignificant associations were determined. The different number of samples corresponding to different individuals was due to a failure of sequencing.

We studied the *SLC45A2* gene, identified several variants in the coding region and associated one variant with a white coat color in the dromedary camel from Saudi Arabia. Our data shows that *SLC45A2* variants are diverse,

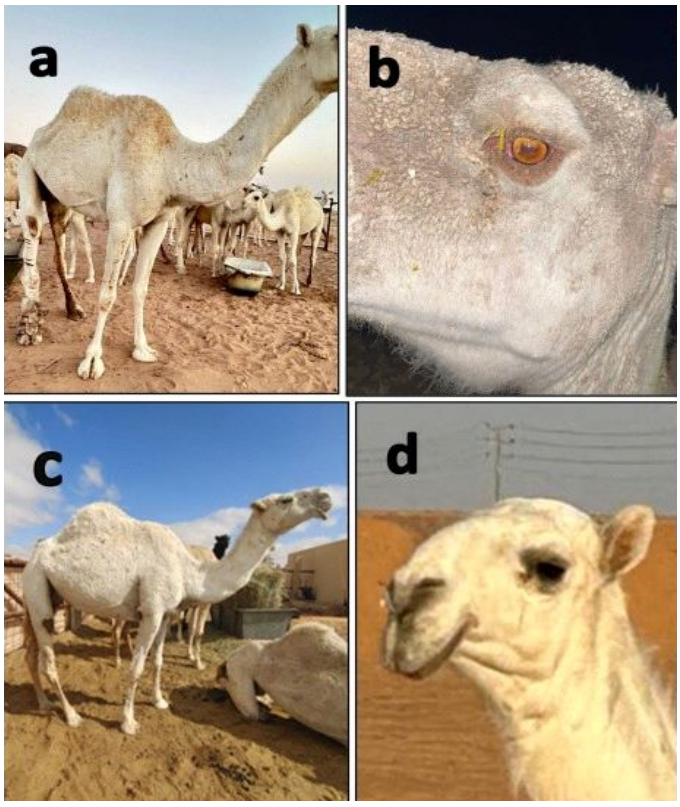
Table 2: Genotypic distribution of exon 7 for 135 dromedaries across all sequenced groups.

Exon 7	CC	CG	GG	Total
Black	18	0	0	18
Brown	20	0	0	20
Light brown	28	0	0	28
Dark brown	21	0	0	21
White	32	16	0	48
Total	119	16	0	135

suggesting that there is gene flow between dromedary populations. Also, our data indicates that the *SLC45A2* region is where crossover events occur and in particular, exon 4 variants.

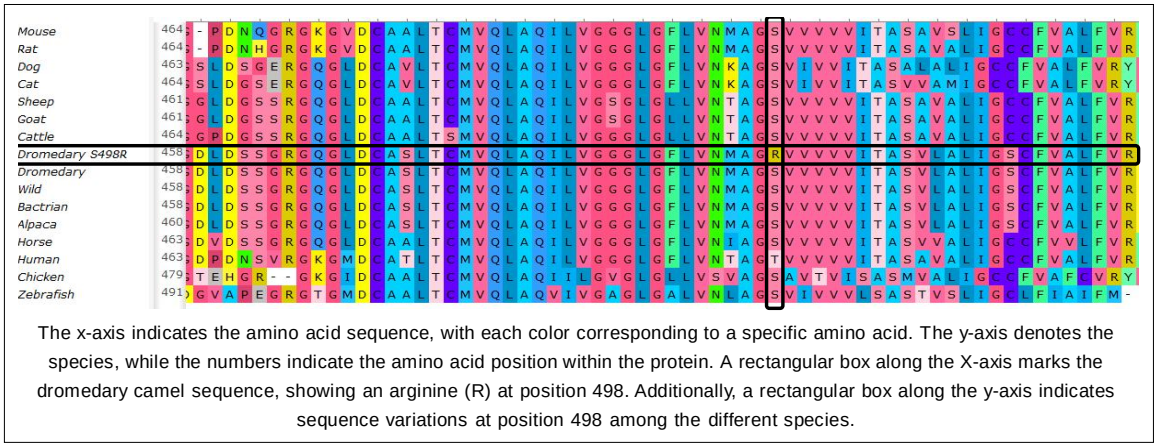
Exon 1 c.95 C>T resulted in amino acid substitution T32M. Although about 44% of the dark brown camels studied carried the TT genotype, the large cohort analysis did not confirm this association. It is possible that increasing the sample size of dark brow dromedary would increase the significance level. However, as the TT genotype is present in all dromedary populations, it is possible that this variant is involved in regulating other genes that might increase the intensity of darker pigmentation production. Threonine is highly conserved across mammalian species, suggesting that it might lead to a functional effect on protein level. Though, as it is located on the outside of the transmembrane domain, it may cause only insignificant damage to protein function. It has been noted that SLC45A2 is highly expressed in black-headed goats and black skin biopsies (Xiong *et al*., 2020). Dark brown dromedaries have darker wool on their humps, necks and tails, which could be due to higher SLC45A2 expression in these regions. Further, contribution of other coat color genes such as *MC1R*, *ASIP* and *TYR* genes together with *SLC45A2* will lead to have a more comprehensive answer of how these gene can correlate to produce a final melanin product. Yang *et al*. (2019) identified more genetic loci in *MC1R*, *ASIP* and *TYRP1* genes in wild boar that was not discovered in domesticated pigs; however, these genetic bases were underlying the coat color variations in wild boar and domesticated pigs.

The exon 7 c.1494 C>G missense mutation was found only in the white population; thus, this variant was determined to be significantly associated with the white phenotype (p-value < 0.001). The variant replaces serine with arginine at position 498 (S498R). S498R is located in the transmembrane domain suggestion that it may lead to affect the protein function. Furthermore, multiple alignment sequencing shows that the S is highly conserved across mammalian species, chicken and zebrafish (Fig 3). It has been found that c.1478 G>A G493D is responsible for oculocutaneous albinism in dogs and is located in exon 7, where homozygote deletion is lethal (Wijesena and Schmutz, 2015). Our findings show that the CG genotype is responsible for the white phenotype in dromedary camels and the GG genotype is lethal. It must be noted that 19 white dromedaries were sampled from one herd, 15 of which were heterozygotes. Most of these animals had



(a) Camels exhibiting abnormal hind limb growth. (b) Yellow-tinged eyes. (c) A normal camel with typical limb development. (d) A white dromedary with dark-colored eyes.

Fig 2: Four white dromedary camels with varying phenotypic traits.



The x-axis indicates the amino acid sequence, with each color corresponding to a specific amino acid. The y-axis denotes the species, while the numbers indicate the amino acid position within the protein. A rectangular box along the X-axis marks the dromedary camel sequence, showing an arginine (R) at position 498. Additionally, a rectangular box along the y-axis indicates sequence variations at position 498 among the different species.

Fig 3: Multiple sequence alignment of the SLC45A2 protein, highlighting the region containing the S498R variant across 16 different species.

abnormal tumor-like development in the legs that was neither identified nor investigated (Fig 2a). Furthermore, the breeder noticed that 50% of the offspring died in the first week after delivery, suggesting that the GG genotype is in fact lethal.

We also identified two silent mutations in exon 3 and another two in exon 4. None of these variants were associated with coat color variations in the dromedary. Also, the intron 4 variant was not linked to coat color variations in the sample. It must be noted that c.879 T>C and c.975 C>T were not linked suggesting that exon 4 could likely be a site of crossover events. This may also be related to extensive selection in coat color phenotypes, as differences in haplotypes indicates recent changes in the genome (Slatkin, 2008).

It has been reported that *MC1R* c901 C>T is associated with white coat color in dromedary camels (Almathen *et al*., 2018; Alshanbari *et al*., 2019). However, not all white dromedaries carry the T allele, which is probably due to the involvement of other gene regulation processes such as transcriptional regulation process of microRNAs. It has been shown that melanogenesis signaling pathway involved the transcriptional regulation process of microRNAs in white phenotype of yak (Basang Wang Dui *et al*., 2018). This supports our conclusion that *SLC45A2* exon 7 is responsible for white coat color. Also, *SLC45A2* is associated with diluted phenotypes in horses (Holl *et al*., 2019). In addition, *SLC45A2* is associated with albinism in cattle and dogs (Wijesena and Schmutz, 2015; Rothammer *et al*., 2017). Furthermore, it has been reported that *SLC45A2* is associated with white coat color in pigs (Bâlteanu *et al*., 2021).

Other phenotypes were observed in the dromedaries with a G base in c.1494 C>G, including yellow eyes and tumor-like growths in the hind limbs (Figure 2). It has been determined that *SLC45A2* genetic variants are involved in iris pigmentation in quail (Huo *et al*., 2024). Furthermore, *SLC45A2* haplotypes have been associated with the Brazilian population's dark/light pigmentation in the eyes and skin (de Aguiar Fracasso *et al*., 2017). The other phenotypic observation in the present study was abnormal tumor-like growths in the hind limbs of dromedaries with the G base. Due to restrictions by the camel owner, we were not able to take a biopsy from the tumor-like growth. Also, only older camels had this type of growth (older than 7 years), whereas younger dromedaries did not. It appeared like a fibroma with soft tissue overgrowth. It has been determined that *SLC* gene family in general and *SLC45A2* in particular are linked to cancer (Lavoro *et al*., 2023). In addition, some coat color genes are associated with cancer growth and cancer development. More particularly, melanoma is associated with *SLC45A2* genetic variants (Ibarrola-Villava *et al*., 2012).

CONCLUSION

In conclusion, this is the first study investigating *SLC45A2* genetic variants and their association with dromedary coat color. Exon 7 c.1494 C>G S498R is significantly associated with white coat color in dromedary camels. As the G base is linked to abnormal tumor-like development in the hind limbs, it is highly recommended that dromedaries carrying the G base be removed from reproduction. These variants and others discovered in genes associated with coat color (such as *MC1R*, *ASIP* and *TYR*) could be used to investigate further correlations between them and coat color phenotypes in dromedary camels. Furthermore, more genes need to be discovered to answer the question of why coat color varies in dromedary camels. The findings will improve our knowledge of coat color genetics in the dromedary camel and lead to the development of a coat color test for the species.

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Disclaimers

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Informed consent

Ethical review and approval for this study was waived because we did not conduct our experiment on laboratory animals or on animals under our direct care, but rather on camels from local markets and camel breeders in the Qassim region.

Conflict of interest

The authors declare that they have no conflict of interest.

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