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COMPARATIVE TRANSCRIPTOME ANALYSIS OF ADIPOSE TISSUES FROM BACTRIAN CAMEL

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ABSTRACT

The purpose of this study was to reveal the molecular mechanism that regulates fat metabolism in hump of Bactrian camel. The subcutaneous fat (SF), greater omentum (GOM) and hump fat (HF) of Bactrian camel were sequenced by RNA sequencing, and the differentially expressed genes of fat tissue in 3 different parts at transcriptome level were obtained by paired comparison. Genes related to fat metabolism were screened out, among which HF vs. GOM group had the largest number of different genes related to fat metabolism. Some genes such as SCD, FASN, ACACA, ADIPOQ, PLIN1, PLIN4, LPL and HSL were highly expressed in HF. These genes may play an important role in maintaining the energy homeostasis of Bactrian camels in the absence of food. Signaling pathway analysis revealed a number of pathways involved in fat metabolism including AMPK signaling pathway, PPAR signaling pathway, Adipocytokine signaling pathway, ECM-receptor interaction and regulation of lipolysis in adipocytes. These data suggests HF has a greater capacity to modulate the release and storage of triglycerides in adipocytes than GOM.

Key words: Adipose, Bactrion camel, RNA sequence, transcriptome

Fat is not only an important energy storage organ of the body, but also an important endocrine organ, which can secrete adipokines to regulate the energy balance of the body (Unamuno *et al,* 2018). According to the location of fat deposition, adipose tissue can be categorised into visceral adipose tissue (VAT) and subcutaneous adipose tissue (SAT). VAT has more cellular activity than SAT, has more abundant distribution of blood vessels and nerves, and contains more immune and inflammatory cells. VAT has higher metabolic activity and more lipolytic activity than SAT. VAT has a greater capacity to generate free fatty acids (FFA) and to absorb glucose than SAT, while SAT absorbs more circulating FFA and triglycerides (TG) (Ibrahim, 2010, Schoettl *et al,* 2018).

The reason why the camel can adapt to the extremely harsh living environment well is that its body structure and organ function have good adaptability to the desert ecological environment. Camels manage their stores of fat by having enough food. When food is abundant, the body needs to preserve fat and store energy, and when food is insufficient, the body needs to ensure that the camel can resist hunger, adapt to the barren vegetation in desert areas (Wu *et al,* 2014). Camels store fat mainly in hump, kidney, subcutaneous, abdomen, omentum and mesentery. The main component of hump is fat, and early studies have shown that hump and other fat storage sites are rich in fatty acids, phospholipids and TG (Kadim *et al,* 2002).

RNA-Seq approach has been applied to identify gene expression profiles of different types of adipose tissue in pigs, sheep and cattle (Cai *et al,* 2018; Kang *et al,* 2017; Xing *et al,* 2019) and many genes associated with fat metabolism have been identified. However, there has been no transcriptome study of adipose tissues in camel. We therefore, studied the differential gene expression in subcutaneous fat (SF), hump fat (HF) and greater omentum (GOM) by RNA-Seq technology, thus revealing mechanisms in adipose deposition and understanding of differences between adipose depots in Bactrian camel.

Materials and Methods

Ethic statement and tissue collection

All the procedures involving animals were approved by the Institutional Animal Care and Use Committee of the Inner Mongolia Agricultural University (IMAU) (License No. SYXK, Inner Mongolia, 2014–0008) with adherence to IMAU

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guidelines. The study was conducted on castrated Bactrian camel (aged approximately 10 years) obtained from Bayan hot in Inner Mongolia. A total of 3 healthy individuals were selected randomly. The 3 types of adipose tissues i.e., subcutaneous, visceral and hump were taken from the thoracic, greater omentum and hump regions, respectively. Each fat tissue was immediately submerged in liquid nitrogen, and stored at −80°C for RNA-seq analysis.

RNA sequencing

RNA sequencing was performed by Novogene Bioinformatics Technology Co., Ltd, Beijing, China. The main steps are described below. Total RNA was extracted from the sample. The sample quality was tested. The mRNA in the sample was purified with Oligo (dT) attached magnetic beads. The mRNA was then broken into short fragments and used as a template to synthesise double-stranded cDNA. The end was repaired, the A tail was added, and the adaptor was connected, the fragment size was selected. Then the cDNA library was enriched by PCR and library quality was assessed. Finally, High-throughput sequencing was performed on cDNA that passed the library inspection.

Bioinformatics analysis

First, the quality of the high-throughput raw data obtained by sequencing was evaluated, including sequencing error rate distribution check, GC content distribution check and sequencing data filtering. Hisat2 was then used to align to the reference genome. FKPM (fragments per kilo bases per million reads) was used to estimate gene expression in samples and padj < 0.005 was used as the threshold for screening differentially expressed genes (DEGs). The involved signaling pathways were analysed by comparison with KEGG.

Results and Discussion

Summary of transcriptome sequencing data

We sequenced 9 cDNA libraries from 3 adipose depots from Bactrian camel. Three replicates each of HF, SF and GOM depots, 59, 152, 350, 44, 336, 816 and 65, 552, 914 raw reads were obtained for HF; 57, 151, 528, 50, 973, 870 and 46, 332, 920 raw reads were obtained for SF; 55, 584, 566, 65, 647, 414 and 54, 536, 066 raw reads were obtained for GOM. The raw reads were filtered to obtain clean reads, which were then aligned to the camel reference genome using Hisat2. 88.52%~91.05% of the total sequenced fragments could be mapped to the reference genome (Table 1).

Identification of differentially expressed genes

We identified 723, 1, 460, 1, 757 genes showing differential expression between HF and SF, HF and GOM, SF and GOM, respectively, and were clustered by a visual heat map (Fig 1). Of 723 differentially expressed genes between HF and SF, 371 showed higher expression in the HF versus 352 genes showed higher expression in the SF. Of 1, 460 genes between HF and GOM, 502 expressed higher in the HF versus 958 expressed higher in the GOM. Of 1, 757 genes between SF and GOM, 570 expressed higher in the SF versus 1, 187 expressed higher in the GOM. HF vs. GOM and SF vs. GOM had greater differences than HF vs. SF at the transcriptional level. We found more than 20 genes involved in fat metabolism (Table 2).

Pathway analysis of differentially expressed genes

Pathway annotation of DEGs was performed using the KEGG database. The DEGs of HF vs. SF were significantly enriched in pathways including Cell adhesion molecules and ECM-receptor interaction. The up-regulated genes in HF vs. GOM were significantly 5 most enriched in pathways including AMPK signaling pathway,

Table 1. Statistics for filtering and mapping reads.

Sample	Raw reads	Clean reads	Total map	Clean bases	Error rate	Q20	Q30	GC(%)
HF1	59152350	58138948	52363415(90.07%)	8.72G	0.03	97.57	93.26	52.18
HF2	44336816	43320378	38969395(89.96%)	6.5G	0.03	97.03	92.19	50.5
HF3	65552914	63262250	56365092(89.1%)	9.49G	0.03	97.82	94.07	52.25
SF1	57151528	55824084	49754737(89.13%)	8.37G	0.03	96.75	91.6	49.54
SF2	50973870	49557888	44449340(89.69%)	7.43G	0.03	97.81	94.04	52.54
SF3	46332920	45363498	41304461(91.05%)	6.8G	0.03	97.09	92.15	51.17
GOM1	55584566	54503656	49061874(90.02%)	8.18G	0.03	96.91	91.88	51.04
GOM2	65647414	64780532	58769365(90.72%)	9.72G	0.03	97.78	93.73	52.29
GOM3	54536066	53184776	47077685(88.52%)	7.98G	0.03	96.88	91.85	50.94

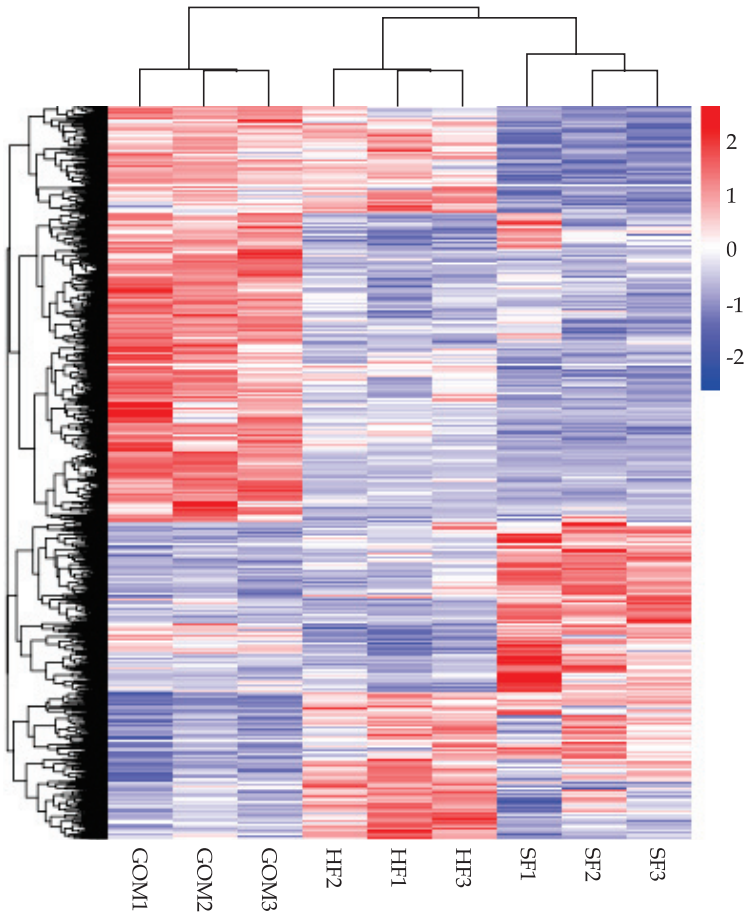

Fig 1. Clustering analysis of DEGs in three adipose depots.

PPAR signaling pathway, Adipocytokine signaling pathway, ECM-receptor interaction and carbon metabolism. The down-regulated genes in HF vs. GOM were significantly 5 most enriched in pathways including cytokine-cytokine receptor interaction, Hippo signaling pathway, Cell adhesion molecules (CAMs), Complement and coagulation cascades and Rap1 signaling pathway. The up-regulated genes in SF vs. GOM were significantly enriched in pathways including ECM-receptor interaction, Fatty acid metabolism, Biosynthesis of unsaturated fatty acids, Fatty acid elongation and glycosaminoglycan biosynthesis-keratan sulfate. The down-regulated genes in SF vs. GOM were significantly 5 most enriched in pathways including cytokine-cytokine receptor interaction, Cell adhesion molecules (CAMs), Chemokine signaling pathway, Epstein-Barr virus infection and Rap1 signaling pathway (Table 3).

In this study, SF, HF and GOM of Bactrian camel were sequenced by transcriptome sequencing technology, and the different genes of fat tissue in 3 different parts at transcriptome level were obtained by paired comparison. Among the differentially expressed genes of HF and GOM, the genes related to fat metabolism in HF were significantly up-regulated.

SCD is a rate-limiting enzyme that dehydrogenates saturated fatty acids to form monounsaturated fatty acids in mammals (Ntambi and Miyazaki, 2004). SCD activity is positively correlated with fat deposition and monounsaturated fatty acids (Jiang *et al,* 2008). The greater accumulation of fat in hump than in omentum may be related to the high expression of SCD. FASN and ACACA are rate-limiting enzymes for novo synthesis of long-chain fatty acids (Smith *et al,* 2003; Zu *et al,* 2013). Feeding carbohydrates to animals after a long period of fasting significantly increased FASN activity (Semenkovich, 1997) The high expression of FASN and ACACA in hump suggests that the Bactrian camel has an important role in the effective synthesis of fatty acids, and the energy storage is very important for Bactrian camel to adapt to the desert environment where food is scarce. ACSS, ACSM and ACSL are involved in the synthesis of fatty acid (van der Sluis and Erasmus, 2016). ELOVL5 and ELOVL6 are involved in the synthesis of monounsaturated fatty acids (Green *et al,* 2010). Monoacylglycerol (MAG) was converted to diacylglycerol (DAG) under the catalysis of MOGAT, and then to TG under the catalysis of DGAT (Liu *et al,* 2012). PPARG is mainly expressed in adipose tissue and liver and is the main regulator of adipogenesis, adipocyte differentiation, proliferation and lipid accumulation (He *et al,* 2013). THRSP plays an important role in fat deposition by regulating the expression of fat-synthesis-related genes such as FASN (Schering *et al,* 2017). The data from this study suggest that these genes involved in fat synthesis play an important role in fat deposition in hump. HSL and LPL mainly catalyse TG to release free fatty acids to participate in the oxidation and energy supply. LPL and HSL are key rate-limiting enzymes that hydrolyse TG in serum and adipocytes, respectively. MGLL hydrolysed MAG into glycerol and fatty acids (Lafontan and Langin, 2009). This suggests that the catabolism of hump is more active than that of omental fat. PLIN has a bidirectional regulation effect on lipolysis and is known as the "molecular switch" in the regulation of lipolysis. In the basal state, the

Table 2. The selected DEGs that were involved in fat metabolism.

Gene symbol	Gene name	FPKM		Log_2 fold change	*P* value	Padj
		HF	GOM			
MOGAT3	monoacylglycerol O-acyltransferase 3	15.38	0	6.45	2E-04	2E-03
SCD	stearoyl-CoA desaturase	6662.46	150.23	5.47	7E-11	6E-09
MOGAT1	monoacylglycerol O-acyltransferase 1	232.92	16.51	3.82	1E-05	3E-04
LEP	leptin	429.20	34.31	3.64	1E-05	3E-04
FASN	fatty acid synthase	31712.11	3398.73	3.22	7E-07	2E-05
PPARA	peroxisome proliferator-activated receptor α	382.72	48.18	2.99	4E-04	4E-03
ACACA	acetyl-CoA carboxylase α	16139.53	2580.54	2.64	1E-09	8E-08
ADIPOQ	adiponectin	106202.05	17555.19	2.60	5E-09	3E-07
PLIN1	perilipin 1	103254.92	19504.69	2.40	1E-06	4E-05
ACSL1	acyl-CoA synthetase long-chain family member 1	25172.84	5375.09	2.23	9E-05	1E-03
ACSS3	acyl-CoA synthetase short-chain family member 3	1204.72	262.14	2.20	2E-04	3E-03
MGLL	monoglyceride lipase	17906.87	4007.07	2.16	1E-06	4E-05
LPL	lipoprotein lipase	38504.93	8656.04	2.15	2E-06	5E-05
THRSP	thyroid hormone responsive	7338.78	1711.07	2.10	1E-06	4E-05
PLIN4	perilipin 4	233662.47	55569.29	2.07	1E-05	2E-04
ACSM1	acyl-CoA synthetase medium-chain family member 1	6736.44	1680.26	2.00	5E-05	9E-04
ADIPOR2	adiponectin receptor 2	11797.80	2963.55	1.99	2E-06	6E-05
ELOVL6	ELOVL fatty acid elongase 6	724.07	186.80	1.95	2E-06	6E-05
HSL(LIPE)	lipase hormone-sensitive	47290.33	12332.88	1.94	5E-05	9E-04
ACSS2	acyl-CoA synthetase short-chain family member 2	5690.35	1560.15	1.87	3E-07	1E-05
DGAT2	diacylglycerol O-acyltransferase 2	1377.71	414.99	1.73	2E-04	2E-03
PPARG	peroxisome proliferator-activated receptor γ	5185.60	1565.88	1.73	4E-06	1E-04
ELOVL5	ELOVL fatty acid elongase 5	5442.25	1664.24	1.71	9E-12	8E-10
Gene symbol	**Gene name**	**FPKM**		**Log_2 fold change**	***P* value**	**Padj**
		HF	**SF**			
ACACA	acetyl-CoA carboxylase α	13449.13	958.51	3.81	1E-17	2E-14
PLIN5	perilipin 5	1367.20	160.42	3.09	6E-06	3E-04
ACACB	acetyl-CoA carboxylase β	319.44	49.01	2.69	3E-05	1E-03
THRSP	thyroid hormone responsive	6137.50	1051.92	2.54	2E-06	1E-04
Gene symbol	**Gene name**	**FPKM**		**Log_2 fold change**	***P* value**	***P* value**
		SF	**GOM**			
SCD	stearoyl-CoA desaturase	24617.53	130.75	7.56	6E-16	1E-13
ELOVL3	ELOVL fatty acid elongase 3	47.71	0.67	5.95	5E-07	1E-05
ELOVL6	ELOVL fatty acid elongase 6	790.94	162.66	2.28	5E-10	3E-08
MGLL	monoglyceride lipase	13756.66	3484.99	1.98	2E-04	2E-03

PLIN package is placed on the surface of the lipid droplets, forming a molecular barrier that prevents lipase from contacting the TG in the lipid droplets, thus inhibiting lipolysis (Wolins *et al,* 2005). As energy demand increases, PLIN is phosphorylated by protein kinase A (PKA), and the barrier is modified to allow lipase to contact and break down TG (Lafontan and Langin, 2009). In this study, the high expression of PLIN1 and PLIN4 in the hump suggested that PLIN1 and PLIN4 play an important role in the fat deposition and lipolysis of the hump.

Adiponectin is one of the adipokines secreted by adipose tissue, which can regulate the energy homeostasis, glucose metabolism and fat metabolism of organisms. By binding to its receptors, AdipoR1 and AdipoR2, adiponectin can activate AMPK, PPAR and p38MAPK, promote the oxidation of fatty acids, and thus reduce the deposition of fat (Fang and Judd, 2018). The high expression of ADIPOQ and ADIPOR2 in hump in this study suggests that ADIPOQ and ADIPOR2 play an important role in maintaining the energy homeostasis of Bactrian camel in the absence of food. Leptin is mainly synthesised and secreted by white adipose tissue, which has the function of regulating fat storage and maintaining energy balance in the body. It can directly act on fat cells, inhibit the synthesis of fat, promote lipolysis, and avoid obesity (Triantafyllou *et al,* 2016). The study has reported that the plasma leptin concentration of camels decreased under the

Table 3. Pathway analysis of differentially expressed genes.

Pathway	**HF vs. SF**	**Gene name**	***P* value**	**Padj**
Cell adhesion molecules	Up	ICAM3/SELL/LOC105076320/CD8A/LOC105064235/SIGLEC1/CLDN15/CD6/CDH5/SELP	8E-05	0.016
ECM-receptor interaction	Down	COMP/FN1/CD44/THBS3/ITGA11/SDC4/THBS4/ITGA9/TNXB/TNC/SV2B	5E-07	9E-05
Pathway	**HF vs. GOM**	**Gene name**	***P* value**	**Padj**
AMPK signaling pathway	Up	SCD/ACACA/LOC105062383/ADIPOQ/HNF4A/FASN/SLC2A4/ADIPOR2/PPARG/LEP/LIPE/PPP2R1B/PCK1	6E-06	6E-04
PPAR signaling pathway	Up	SCD/LOC105062383/ADIPOQ/PLIN1/LPL/PPARG/SORBS1/PLIN4/AQP7/ACSL1/PCK1/PPARA	9E-08	2E-05
Adipocytokine signaling pathway	Up	LOC105062383/ADIPOQ/SLC2A4/ADIPOR2/MAPK10/LEP/SLC2A1/ACSL1/PCK1/PPARA	9E-06	6E-04
ECM-receptor interaction	Up	LOC105062383/LAMB1/COL4A3/COL4A1/COL4A2/HSPG2/TNC/COL1A1/LAMB3/LAMC1	3E-05	1E-03
Carbon metabolism	Up	ACSS2/CS/GPT2/HAO2/PCCA/SUCLA2/GPI/MCEE/PC	2E-03	0.033
Regulation of lipolysis in adipocytes	Up	PTGER3/MGLL/PLIN1/ADCY2/ADORA1/LIPE/AQP7/GNAI1	2E-05	1E-03
Glycerolipid metabolism	Up	GPAM/MGLL/LPL/PNPLA3/MOGAT1/LPIN2/MOGAT3/DGAT2	5E-05	1E-03
Cytokine-cytokine receptor interaction	Down	IL33/IL1RL1/TNFSF13/CXCL8/TGFB2/BMP7/IL1B/TGFB3/CD4/BMP4/IL18R1/IL36G/AMHR2/CLCF1/NGF/IL27RA/CX3CR1/EDAR/IL10RA/CCL21/TNFRSF18/IL1A/CCL24/CXCR3/LOC105064293/CD27/OSM	7E-05	2E-03
Hippo signaling pathway	Down	WNT2B/FZD10/WNT4/CRB2/TGFB2/WNT16/WWC1/WNT10A/BMP7/FZD2/TGFB3/BMP4/ID2/PRKCZ/TEAD3/LEF1/FZD9/ITGB2/WNT10B/CDH1/WNT6/AJUBA/LOC105075564/AMOT/DLG4	2E-07	1E-05
Cell adhesion molecules	Down	ICOSLG/CD4/SIGLEC1/CD8A/CLDN1/SELPLG/ITGA9/ITGB2/PDCD1LG2/CDH1/NTNG2/LOC105064249/LOC105064245/LOC105064248/MADCAM1/SELL/CLDN4/ITGAL/SPN/CADM1/CNTNAP2/LOC105064250	1E-06	7E-05
Complement and coagulation cascades	Down	C3/C4BPA/C4A/BDKRB1/F12/C1R/C1S/LOC105074040/SERPING1/CR2/LOC105062185/CFI/C7/CLU/PROS1/C1QB/ITGB2/VSIG4/C5AR1/F5/CD55	2E-11	5E-09
Rap1 signaling pathway	Down	RGS14/SKAP1/NGF/PRKCZ/PRKCB/ITGB2/PDGFRA/FGF16/RAC2/PDGFC/CDH1/PDGFA/FYB/TIAM1/ADCY7/LOC105079217/FGFR2/PLCB2/ITGAL/LOC105075564/PFN3	2E-03	0.021

Pathway	SF vs. GOM	Gene name	*P* value	Padj
ECM-receptor interaction	Up	COMP/TNC/THBS4/SDC4/COL9A1/COL6A3/CD44/LAMC2/CHAD/COL6A2	1E-04	0.017
Fatty acid metabolism	Up	SCD/ELOVL6/ACSL3/PTPLA/HSD17B12/ELOVL3/TECR	2E-04	0.019
Biosynthesis of unsaturated fatty acids	Up	SCD/ELOVL6/PTPLA/HSD17B12/ELOVL3/TECR	1E-04	0.017
Fatty acid elongation	Up	ELOVL6/PTPLA/HSD17B12/ELOVL3/TECR	9E-04	0.042
Glycosaminoglycan biosynthesis-keratan sulfate	Up	CHST2/LOC105078680/LOC105065926/B4GALT1	8E-04	0.042
Cytokine-cytokine receptor interaction	Down	IL1B/ACKR4/IL1RL1/IL33/AMHR2/LOC105064293/CX3CR1/IL2RG/CD27/LOC105064292/IL10RA/IL18R1/IL36G/CCL16/CD4/CXCR6/ACVRL1/BMP4/EDAR/OSM/TNFSF14/LEPR/CX3CL1/XCL1/NGF/CXCR3/CCR2/IL20RA/CXCL10	3E-04	5E-03
Cell adhesion molecules	Down	CD8A/SIGLEC1/SELL/LOC105064235/SPN/CLDN1/LOC105064249/CLDN15/CD6/LOC105064250/ITGB7/SELP/ITGB2/ITGAM/ICAM3/CDH1/CD4/CD2/LOC105064239/SELPLG/ITGAL/CLDN11/MADCAM1/LOC105064248/LOC105074084/PDCD1LG2	2E-07	1E-05
Chemokine signaling pathway	Down	JAK3/ARRB2/SHC2/RAC2/PLCB2/LOC105064293/CX3CR1/NCF1/RASGRP2/LOC105064292/CCL16/CXCR6/PIK3CG/HCK/WAS/PIK3R6/CX3CL1/ITK/XCL1/PRKCB/PTK2B/CXCR3/CCR2/GNB5/PIK3R5/CXCL10	3E-05	8E-04
Epstein-Barr virus infection	Down	JAK3/LOC105064235/CD3E/CCNA2/LOC105064249/BLNK/LOC105064250/CD19/CD3G/CCND3/BTK/MAPK12/LOC105064239/ITGAL/CD247/MAPK14/LOC105064248/LOC105074084/IKBKE/BAK1/ENTPD1/PLCG2/CXCL10	2E-03	0.023
Rap1 signaling pathway	Down	RAC2/SIPA1/PLCB2/RASGRP2/ITGB2/ITGAM/CDH1/TEK/LOC105079217/LCP2/RGS14/FYB/MAPK12/ITGAL/FLT4/ARAP3/PRKCB/MAPK14/NGF/PFN3/LOC105075564/CALML4/PRKD2	5E-03	0.043

condition of insufficient feed and increased under the condition of overfeeding. This suggests that leptin plays an important role in maintaining the energy balance of Bactrian camel.

In HF vs. GOM, genes with increased HF than GOM expression were enriched in several pathways involved in lipid metabolism. These proved that HF metabolism is more active than omental fat metabolism. In the Cytokine-cytokine receptor interaction, cytokine genes and their receptors were expressed significantly higher in GOM than HF and SF. These data suggests that GOM is more likely to cause inflammatory response than HF and SF.

In conclusion, we sequenced the transcriptome of the 3 sources of adipose tissues in Bactrian camel using Illumina Hiseq sequencing platform. DEGs were identified between subcutaneous, visceral and hump fat tissues. The KEGG enrichment were analysed. Our results provide new insight into understanding of differences between adipose depots and providing new insight into exploring the specific fat deposition in hump. Some genes related to fat metabolism in HF may play an important role in maintaining the energy homeostasis of Bactrian camels in the absence of food. These data suggests the hump fat has a greater capacity to modulate the release and storage of TG in adipocytes than omentum.

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