Scanning of selection signature provides a glimpse into important economic traits in goats (*Capra hircus*)

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Goats (*Capra hircus*) are one of the oldest livestock domesticated species, and have been used for their milk, meat, hair and skins over much of the world. Detection of selection footprints in genomic regions can provide potential insights for understanding the genetic mechanism of specific phenotypic traits and better guide in animal breeding. The study presented here has generated 192.747G raw data and identified more than 5.03 million single-nucleotide polymorphisms (SNPs) and 334,151 Indels (insertions and deletions). In addition, we identified 155 and 294 candidate regions harboring 86 and 97 genes based on allele frequency differences in Dazu black goats (DBG) and Inner Mongolia cashmere goats (IMCG), respectively. Populations differentiation reflected by Fst values detected 368 putative selective sweep regions including 164 genes. The top 1% regions of both low heterozygosity and high genetic differentiation contained 239 (135 genes) and 176 (106 genes) candidate regions in DBG and IMCG, respectively. These genes were related to reproductive and productive traits, such as “neurohypophyseal hormone activity” and “adipocytokine signaling pathway”. These findings may be conducive to molecular breeding and the long-term preservation of the valuable genetic resources for this species.

There are over 300 distinct breeds of goat (*Capra hircus*) in the world, which are distributed over all types of ecological areas with more concentrated in the tropics, dry zones and developing countries. Goats have been used for their milk, meat, hair, or cashmere and skins over much of the world. In 2011, there were more than 1.4 billion live goats around the globe, according to the UN Food and Agriculture Organization (http://kids.fao.org/gliph/a/). China is rich in goat genetic resources, and there are about 69 goat breeds in this country, including 58 local breeds, 8 improved breeds and 3 introduced breeds. Especially, Inner Mongolia cashmere goat (IMCG), mainly lived in Alashan, Inner Mongolia, in the north of China (~1304 m) coated white long hair, which produced primarily cashmere and had relatively low fecundity (~105%) compared with Duzu black goat (DBG, ~272%), black short hair, which are raised in Dazu County of Chongqing in the southwest of China (267~934 m) and are primarily used for meat production1 (Fig. 1a).

Goat is one of the earliest animals domesticated by humans. The most recent genetic analysis confirms the archaeological evidence that the wild Bezoar ibex of the Zagros Mountains are the likely origin of almost all domestic goats today. But the morphologicaland behavioral characteristics of modern domestic goats have greatly changed compared with wild progenitor, the Bezoar goat (*Capra aegagrus*)2. Compared with the Bezoar goat, modern goats exhibit a reduction in body size, a more docile demeanor, a series of coat color variants and the ability to adapt after domestication and breed formation, which have left detectable signatures of selection within the genomes3,4. Hence, scanning of selection signature can't only provide straightforward insights into the mechanism of evolution events but also use for identifying functional genes of important economic traits or causative variations of phenotypic diversity.

Based on populations differentiation reflected by Fst statistic, Gibbs et al. detected some genomic regions embracing some SNPs in genes associated with meat quality (*SPOCK1*) and feed efficiency (*ZRB3, RSHDM1*)5.
The differences in allele frequencies were correlated with the effects of those SNPs on various production traits. For instance, Xu et al. identified some of less-known genes under positive selection correlated with milk production traits such as \( \text{LAP3} \) and \( \text{SAR1B} \), associated with hair length, namely, \( \text{FGF5} \), and related to reproduction traits such as \( \text{TSHR}, \text{GHR} \) and \( \text{BMP15} \). However, studies of selection signature on goats are still incipient compared with studies of other livestock. The goal of the present study was to identify a number of candidate genes for available to study based on allele frequency differences and population genetic differentiation.

**Results**

**Sequencing.** The genomes of 12 goats from two genetically diverse and geographically distinct indigenous breeds consists of DBG and IMCG (Fig. 1) were sequenced to average 6.02-fold coverage. A total of 192.74 G raw data generated 191.57 G clean data after a quality check and filtering by removing the adapter of paired reads or low quality reads. The effective rate and the ratio of clean data to raw data were 98.79% to 99.64%, respectively. We also measured the GC content distribution (45.06% of our data versus 41.75% of the reference sequence). Effective sequencing reads were aligned to CHIR_1.0 reference genome, resulting in ~100 million mapped reads. The mapping rate in different individuals were varies from 98.11% to 98.69%. The percentages of reads sequenced once or four times per bp were >97.8% and 62.72%, respectively (Supplementary Table 1).

**Variation discovery.** After assembly and mapping of clean reads, we identified 5.03 million SNPs and 334,151 Indels (insertions and deletions) as average. Furthermore, the distributions of the SNPs were determined in the goat genome that there were 37,684 (0.75%) and 38,976 (0.77%) SNPs in the exon in DBG and IMCG, respectively, while the intronic regions contained 28.39% and 28.04% of the SNPs in DBG and IMCG, respectively. SNPs within intergenic regions accounted for up to 69.51% and 68.09% of the SNPs in DBG and IMCG, respectively (Table 1). The results indicated that similar heterozygosity rates existed between the two populations (1.1622 of the DBG population versus 1.1605 of the IMCG population). The number of SNPs in each category of mutations in the goat genome are shown in Table 2. As shown in Table 2, the ratio of transition (ts) to transversion (tv) was estimated to be 2.3347 in the DBG goats, slightly lower than that in the IMCG goats (2.3552).
detection of variation type showed that the classes of T: A > C: G or C: G > T: A were the primary types of variation (Supplementary Figure 1). In addition, the results showed that intergenic regions contained 66.44% of the Indels, intronic regions contained 30.31% of the Indels, and exons contained only 0.21% of the Indels (Table 1).

Population structure analysis. Population substructure was investigated using Clustering, MEGA and ADMIXTURE softwares based on using genomic SNPs. We ran Admixture 1.22 for determining genetic backgronds of samples and indicated two breeds been almost diverged but there is a little gene introgression in DBG when K = 2 (Fig. 1b). The results of principal component analysis (PCA) analysis showed that three principal components (PC1, PC2 and PC3) differentiated DBG and IMCG individuals (Fig. 1c). The neighbor-joining (NJ) tree confirmed these results and successfully divided into two populations displaying genetically distinct clusters (Fig. 1d). The clear genetic divergence between DBG and IMCG showed that the individuals chosen could be used for further exploring their genomic features.

Analysis of Selective sweeps. Those genomic regions with ZHp value exceeding the empirical threshold level of −5 across the two populations were obtained, that contain 155 and 294 candidate regions in the DBG and IMCG populations, respectively. The top regions were located on chromosome 8 in DBG goats (41890001–41950001 bp) and on chromosome 2 in IMCG goats (113850001–113900001 bp), respectively (Fig. 2a,b, Supplementary Table 2). To obtain the available candidate genes, all candidate regions were annotated using

### Table 1. Characteristics of SNPs and indels identified in the two study cohorts.

| Variationtype | Population | Exonic | Intronic | Intergenic | Total |
|---------------|------------|--------|----------|------------|-------|
| SNPs          | DBG        | 37,684 | 1,414,555| 3,463,597  | 4,915,836|
|               | IMCG       | 38,976 | 1,424,565| 3,458,726  | 4,922,267|
| Indels        | DBG        | 710    | 100,638  | 221,103    | 322,451 |
|               | IMCG       | 702    | 100,493  | 219,789    | 320,984 |

### Table 2. The number of SNPs in the genomes of the two goat breeds. SG, SL, Syno., Non-Syno., Sp, Ts and Tv represent stop gain, stop loss, synonymous, non-synonymous, splicings, transitions and transversions, respectively. Stop gain means that mutations make the gene gain termination codon. Stop loss means that mutations make the gene lose termination codon. Splicings mean mutation is located at the exon/intron border of 2 KB in the intron.

|     | SG | SL | Syno. | Non-Syno. | Sp | Ts | Tv | Total  |
|-----|----|----|-------|-----------|----|----|----|--------|
| DBG | 191| 32 | 19,590| 17,871    | 186| 348,832| 1,494,208| 1,880,910|
| IMCG| 204| 34 | 20,348| 18,390    | 205| 356,865| 1,513,718| 1,909,764|

Figure 2. The Manhattan plot based on allele frequency differences in DBG breeds (a) and IMCG breeds (b).
the first generation goat genome annotation information to identify candidate genes that underwent sweeps. A total of 86 and 97 genes in DBG goats and IMCG goats respectively were identified (Supplementary Table 5). Next, Fst values were measured, which a special statistic was used to detect the selection signature based on genetic differentiation that resulted from genetic drift and selective pressure. The result showed that a total of 368 putative selective sweep regions containing 164 candidate genes exceeding the empirical threshold level of 4.5 were obtained (Fig. 3, Supplementary Tables 3 and 5). To further explore the sweep regions, those regions that contained both low heterozygosity and high genetic differentiation were scanned and contained a total of 239 regions that ranked in the top 1% based on the |ZHp| and ZFst value in both groups. There were 239 and 176 outliers detected in the DBG and IMCG, respectively (Fig. 4a,b, Supplementary Table 4). There are 239 and 176 gene candidates in DBG and IMCG, respectively (Supplementary Table 5). Gene ontology (GO) and pathway analysis (KEGG) for candidate genes under selection were performed in order to further explore the functions of the selective sweep gene candidates in detail. All

$P < 0.05$

GO terms and KEGG pathways were deposited in Supplementary Tables 6 and 7, respectively. In total, we annotated 386 GO entries (Supplementary Table 6) and 31 KEGG pathways (Supplementary Table 7).

**Candidates affecting goat reproduction.** Reproduction trait is an important component of efficiency in goat production system$^{24}$. A plurality of reproduction-related categories were identified, such as, (1) Hp values: "neurohypophysial hormone activity" (3 genes, PAIP2B, CCDC64, EPB41L5), "photoreceptor activity" and "blue light photoreceptor activity" (BIRC6, C6H4orf22, SGOL1, SLCE33A1), "meiosis I" (3 genes, SLCE33A1, C6H4orf22, TAOK1, C6H4orf22, SGOL1, SLCE33A1), "meiosis I" (3 genes, SLC33AC1, C6H4orf22, TAOK1), (2) Fst values: "sex determination" and "mating type determination" (2 genes, PAIP2, CLEC16A), "pheromone activity" (4 genes, ZNF280D, CLEC16A, ARID1B, PAIP2), (3) Combination [ZHp] with Fst values: "gamete generation" (8 genes, SBF1, PRTG, PARD3B, KDM4C, FAT1, DMD, TPPP3, DACH2), "neurohypophysial hormone activity" (4 genes, KDM4C, RYBP, FARP1, CELF2), "spermatid development" (3 genes, PARD3B, FAT1, KDM4C), "spermatid nucleus differentiation", "spermatid differentiation", "spermatid differentiation" (3 genes, PARD3B, FAT1, KDM4C), "spermatogenesis" and "male gamete generation" (5 genes, FAT1, KDM4C, TPPP3, SBF1, PARD3B) (Supplementary Tables 6 and 7).

**Candidates related to productive traits.** The rumen, which is the largest compartment, encompasses numerous symbiotic microbial floras to ferment the feed for lipid metabolism$^{15}$. We identified a total of 3 pathways, as followings: "adipocytokine signaling pathway" (2 genes, IKBKG, LOC102190823), "ether lipid
metabolism” (2 genes, **PLD2, PLA2G1B**), “Glycosphingolipid biosynthesis-ganglio series” (**SLC33A1**), and 8 GO terms, such as, glycosphingolipid/galactolipid metabolic process (**LOC102171901**), galactolipid/glycolipid/sphingolipid/membrane lipid/glycosylceramide/glycosphingolipid catabolic process (**LOC102171901**) associated with putative lipid metabolic pathways. In addition, there were “Ras signaling pathway” (5 genes, **RASGRF2, RRAS, PLA2G1B, KDR, IKBKG**), “ubiquitin mediated proteolysis” (4 genes, **STUB1, MID2, LOC102174728, BIRC6,UBE3B**), “VEGF signaling pathway” (2 genes, **PXN, KDR**), “MAPK signaling pathway” (4 genes, **RASGRP2, RRAS, PTPN7, IKBKG**), “thiamine thiolase-mediated thiamine biosynthesis” (2 genes, **LOC102188087, ID1H**), “ribosome” (10 genes, **LOC102178382, RPLP0, LOC102181054, LOC102173128, MROH8, LOC102190542, LOC102175291, LOC102176839, LOC102176407, LOC102181499**), “RNA polymerase” (2 genes, **POLR3F, POLR2C**), “purine metabolism” (3 genes, **AK3, POLR3F, POLR2C**), “biosynthesis of amino acids” (2 genes, **PYCR1, LOC102171894**), “pyrimidine metabolism” (2 genes, **POLR3F, POLR2C**) and “metabolic pathways” (19 genes, **LOC102179840, PANK2, LOC102178836, COX2, COX3, CYPB, COX1, ATP6, NFS1, NDI4L, ATP8, LOC102171894, GLDC, NDI1, NDI3, ND2, NDS, ND4, ND6**) (Supplementary Tables 6 and 7). Our study suggests that the genes included these terms or pathways may be most likely related to productive traits.

**Discussion**
Selection, which appear to have left detectable signatures of selection within the animal genomes is a vital driving force of evolution. Since the dawn of agriculture, artificial selection has continuously added to the existing pool of phenotypic variation as same as natural selection fuels the generation of biodiversity on earth. The programs of selection signature have identified hundreds of regions or genes targeted by important traits that formed by “artificial selection” (5 genes, **RASGRF2, RRAS, PTPN7, IKBKG**), “ubiquitin mediated proteolysis” (4 genes, **STUB1, MID2, LOC102174728, BIRC6,UBE3B**), “VEGF signaling pathway” (2 genes, **PXN, KDR**), “MAPK signaling pathway” (4 genes, **RASGRP2, RRAS, PTPN7, IKBKG**), “thiamine thiolase-mediated thiamine biosynthesis” (2 genes, **LOC102188087, ID1H**), “ribosome” (10 genes, **LOC102178382, RPLP0, LOC102181054, LOC102173128, MROH8, LOC102190542, LOC102175291, LOC102176839, LOC102176407, LOC102181499**), “RNA polymerase” (2 genes, **POLR3F, POLR2C**), “purine metabolism” (3 genes, **AK3, POLR3F, POLR2C**), “biosynthesis of amino acids” (2 genes, **PYCR1, LOC102171894**), “pyrimidine metabolism” (2 genes, **POLR3F, POLR2C**) and “metabolic pathways” (19 genes, **LOC102179840, PANK2, LOC102178836, COX2, COX3, CYPB, COX1, ATP6, NFS1, NDI4L, ATP8, LOC102171894, GLDC, NDI1, NDI3, ND2, NDS, ND4, ND6**) (Supplementary Tables 6 and 7). Our study suggests that the genes included these terms or pathways may be most likely related to productive traits.

**Materials and Methods**

**Experimental samples.** This study was carried out in strict accordance with the recommendations in the Guide for the International Cooperation Committee of Animal Welfare (ICCAW), which is responsible for...
animal care and use in China. The experimental conditions were approved by the Committee on the Ethics of Animal Experiments of Southwest University (No. [2007] 3). All experimental goats were fed a daily ration of 300–500 g concentrate and were allowed to an unrestricted access to straw, mineral salt lick and water.

We collected a total of 12 blood samples of unrelated individuals from 6 Dazu black female goats (DBG) and 6 Inner Mongolia cashmere female goats (IMCG) (Fig. 1a). All the goats were housed in Dazu Black Goat Farm at Southwest University, Chongqing, China. Genomic DNA was extracted using a Tiangen DNA isolation kit (Tiangen Biotech, Beijing, China). In addition, we calculated the average hair length of 20 IMCG and 5 DBG, respectively with software SPSS 19.0.

Sequencing and variation calling. Each DNA sample was used to construct 350 bp paired-end sequencing libraries. Each library was sequenced with Illumina HiSeq PE150 platform according to the manufacturer’s instructions at Novogene (Tianjin, China). Raw data were processed to filter out the adapters and low quality reads resulted in clean reads using BWA software [24]. After alignment, variation calling was performed per individual using SAMtools package [25]. All the called variants were annotated using the ANNOVAR package with the gene-based, or region-based, or filter-based options for further analysis [26].

Population structure analysis. We used the Cluster 3.0 software for performing PCA analysis with the population scale SNPs [27,28]. Genetic structure was estimated using the program ADMIXTURE Version 1.2.2 [29], which was run at K = 2 on the basis of the whole SNP dataset. The neighbor-joining (NJ) tree was constructed using MEGA 5.2 procedure based on genome-wide SNPs [30,31].

Analysis of selective sweep. Selective sweep analyses were performed by calculating heterozygosity (Hp) and population differentiation (Fst). The Hp and Fst values, respectively were converted to a standard normal distribution, denoted as ZHp and ZFst as described [32,33]. In addition, those regions that have low ZHp value and high ZFst value were scanned as candidates. To know the biological function of genes within candidate regions, the analysis of Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways were performed using Goseq (Bioconductor 2.12) and KOBAS (kobas2.0–20120208), respectively.

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Author Contributions
The work presented here was carried out in collaboration between all authors. Y.Z., J.Z., Y.H. and D.G. defined the research theme. D.G., N.L. and X.T. designed methods and experiments, carried out the laboratory experiments, analyzed the data, interpreted the results and wrote the paper. Z.Z. and R.N. provided the experimental animals, Y.Z. and D.G. co-worked on associated data collection and their interpretation. All authors reviewed the manuscript.

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