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获奖项目： 基于电子鼻、HS-SPME-GC-MS 和脂质组学的羊肉风味表征

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Integrated electronic nose and multi-omics reveal changes in flavour characterization of cashmere goats and tan sheep meat

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ABSTRACT

This study aimed to employ a multi-omics method to identify key compounds contributing to the sensory flavour of mutton and to investigate the internal correlation between volatile metabolites and lipids in Cashmere goats and Tan sheep. The results demonstrate that the electronic nose can effectively and quickly distinguish goats and sheep meat. A total of 18 volatile metabolites and 314 lipids were identified as significant contributors to the flavour difference between goats and sheep meat, as determined by HS-SPME-GC–MS and lipidomic respectively. Specifically, TG(18:1/20:4/20:4), TG(18:1/18:2/20:4), TG(18:1/18:1/20:4), DG(18:0/20:4), and dodecanoic acid influence flavour by participating in key KEGG pathways such as the "fat digestion and absorption", "cholesterol metabolism" and "lipid and atherosclerosis". This study lays the groundwork for understanding the sources and mechanisms of mutton flavour compounds, providing valuable insights to support the growth and development of the mutton industry.

1. Introduction

Goats and sheep play a significant role in meeting the growing global demand for meat consumption, largely due to their unique physicochemical composition, nutritional properties, and sensory characteristics. The widespread acceptance of goats and sheep meat can be attributed not only to their nutritional benefits but also to their distinct flavours, which set them apart from other meats (Teixeira, Silva, & Rodrigues, 2019). The complex volatile flavour profiles and sensory attributes of goats and sheep-derived products are key factors in differentiating them in the market. Flavour perception, which arises from the integration of aroma (detected by the olfactory senses) and taste (experienced during consumption), is crucial to the consumer's overall eating experience (Ponnampalam, Holman, & Scollan, 2016). However, the flavour variation in goats and sheep products often results in inconsistent consumer experiences, which can lead to both positive and negative sensory reactions. Such inconsistencies may discourage repeat purchases, ultimately limiting the potential growth of the market for goats and sheep meat products (Hoffman et al., 2016). Given these challenges, it is crucial to further investigate the substances that contribute to the flavour of goats and sheep meat. Understanding which compounds are common to both species and which are species-specific is essential not only for improving product consistency and quality but also for enhancing consumer satisfaction.

Tan sheep and Shanbei Cashmere goats are renowned local breeds, known for their high-quality meat. Both are certified geographic indication products, celebrated for their distinctive, low-odor, and delicious taste. Although Tan sheep and Shanbei Cashmere goats have different origins, they are equally favored by consumers, particularly in the local areas. The breeding regions of those two species are geographically close and share a similar ecological environment. Studying the specific substances that determine the difference in flavour between Tan sheep and Shanbei Cashmere goat is of great significance for understanding consumers' preferences for mutton flavour and developing sheep and goat-

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derived products.

Mutton is known for its distinctive flavour profile, often referred to as the characteristic "mutton flavour", which sets it apart from other red meats. This flavour is a combination of both taste and smell. Taste is perceived by the taste organs, while smell is detected by the olfactory cells. The defining feature of "mutton flavour" based on its characteristic odor, which is one of the key factors influencing consumers' choice of mutton. The formation of this unique flavour is linked to the interaction of various chemical substances. Long-chain fatty acids (FAs) with 8–10 carbon atoms and branched-chain fatty acids (BCFAs), specifically 4-methyl-octanoic acid and 4-methyl-nonanoic acid, are primarily responsible for the distinct sweaty-sour note associated with mutton (Wong, Nixon, & Johnson, 1975). Other fatty acids, such as octanoic acid, 2-methyloctanoic acid, three isomers of octanoic acid, nonanoic acid, 6-methyloctanoic acid, 4,6-dimethyloctanoic acid, two isomers of nonenoic acid, and 8-methylnonanoic acid may also contribute to the flavour and aroma of mutton. Additionally, fatty acids like oleic acid and linoleic acid, which were found in goat by-product hydrolysates, significantly influence the generation of volatile compounds that shape the aroma of goat meat (de Araújo Cordeiro et al., 2020). Can Xiang's study on the taste of Chinese native sheep breeds identified several key compounds as the major contributors to the aroma of sheep meat, such as —1-octen-3-ol, 1-pentanol, octanal, nonanal, and hexanal (Xiang et al., 2023). Previous research has also highlighted the increasing interest in the presence of extended-chain BCFAs in the milk and meat of both sheep and goats, particularly due to their potential health benefits (Ripoll, Alcalde, Argüello, Córdoba, & Panea, 2020). However, the jury is still out on exactly which metabolites are responsible for the difference in taste between goats and sheep.

Current methods for detecting flavour compounds include electronic nose technology (e-nose), electronic tongue, gas chromatography mass spectrometry (GC–MS), gas chromatography ion migration spectrometry (GC-IMS), and two-dimensional gas chromatography time-of-flight mass spectrometry (GC × GC-TOF-MS). The e-nose is popular due to its minimal need for pretreatment and its non-destructive impact on raw materials (Wei, Dan, Zhao, & Wang, 2023). The e-nose has been shown effectively and quickly differentiate between breeds and processing methods of various meats including duck (Li, Al-Dalali, Wang, Xu, & Zhou, 2022), fish (Yu et al., 2023), pork (Cheng et al., 2022), mutton (Kang et al., 2013), etc. However, it cannot specifically measure the chemical substances and concentrations involved.

Metabolomics is a rapidly developing field that analyzes small molecules to provide a comprehensive profile of biological systems or other complex materials. It enables precise, rapid analysis of small-molecule metabolites across different biological samples, reflecting dynamic metabolic changes. Key techniques of metabolomics including liquid chromatography-mass spectrometry (LC-MS), gas chromatography–mass spectrometry (GC–MS), nuclear magnetic resonance (NMR), and lipidomics (Azad & Shulaev, 2019). In our previous study, lipidomics was used to explore the effects of different radiation doses on the lipid composition and molecular nutrition of marble beef, identifying 9 lipid biomarkers and 122 different lipids (Zhang et al., 2023). Additionally, 13 aroma compounds were identified in the roasted mutton using UPLC-ESI-MS/MS and Orbitrap exploris GC techniques (Liu et al., 2022). Using a combination of flash GC e-nose and GC-O-MS during traditional charcoal roasting, 37 odorants were detected in roasted mutton (Liu et al., 2022).

Here, the objective of this study was to investigate the impact of key compounds on the flavour profiles of goats and sheep meat. Given the distinct taste differences between these two species of meat, understanding the underlying mechanisms is essential for improving meat quality and consumer acceptance. To achieve this, e-nose was utilized for the rapid and non-invasive detection of flavour substances in goats and sheep meat. Furthermore, HS-SPME-GC–MS was employed to perform both common and differential analysis of volatile flavour compounds, allowing for a deeper comparison of these two meats. Meanwhile, lipidomics was applied to analyze and classify the core lipids, shedding light on their role in flavour development. Finally, KEGG (Kyoto Encyclopedia of Genes and Genomes) pathway analysis was used to explore the relationship between volatile metabolites and lipids in goats and sheep meat. This study is crucial for understanding how volatile and lipid compounds contribute to the distinctive flavours of goats and sheep meat. By evaluating the flavour changes and identifying correlations between metabolites, we aim to explain the mechanisms behind the differences in flavour formation between the two meats. This findings could provide valuable insights for the meat industry, potentially guiding breeding, feeding, and processing practices to enhance meat flavour and quality.

2. Materials and methods

2.1. Ethics statement

The study was ratified by the Use Committee of Northwest A&F University (Yangling, China) and the Institutional Animal Care and Use Committee (IACUC). All procedures were conducted in accordance with the animal research guidelines established by Northwest A&F University. The goats and sheep used in the study were raised and slaughtered in compliance with the ethical standards set forth by the IACUC of Northwest A&F University (Yangling, China).

2.2. Animals and sample collection

Tan sheep were collected from Yanchi County, the Ningxia Hui Autonomous Region. Shanbei cashmere goats were obtained from Yulin City, Shaanxi Province. The nutritional composition of the experimental diet adhered to the agricultural industry standard of the People's Republic of China (NY/T816–2004). Six goats and six sheep, each aged eight months, were selected for the study.They were transported to the local abattoir, where they were allowed to rest for 24 h without food, but with ad libitum access to water. The abattoir facilities met the requirements set by the China Council on Animal Care. All goats and sheep were slaughtered following the standard abattoir procedures. The procedure was carried out under the supervision of official veterinarians by personnel who have received professional training. The animals were first stunned using carbon dioxide, and their right legs were suspended. After slaughter, the heads, tails, legs, and viscera were removed from the animals. Longissimus dorsi muscle samples (about 1 kg) were collected and transported to the laboratory at 0–4 °C for further analysis.

2.3. Electronic nose detection

The distinct flavour profiles of goats and sheep were determined by electronic nose (AIRSENSE, PEN3). For each sample, 3 g meat was placed in a 50 mL sample bottle and allowed to equilibrate at room temperature for 2 h before testing. Done it manually and repeated it at least 6 times for each sample. The parameters for the electronic nose were as follows: sample preparation time 5 s, cleaning time 300 s, detection time 60 s, automatic zero time 5 s, internal flow and sample flow 300 mL/min. The sensor signal values between 45 to 50 s during the detection phase were selected for data analysis.

2.4. Volatile metabolites extraction and HS-SPME-GC–MS analysis process

2.4.1. Mutton sample extraction

Raw mutton of 3 g was weighed in a 20 mL headspace little bottle, 2 μL internal standard solution (50 μg/mL n-Pentadecane-d^{32}) was added, and immediately sealed for metabolomic analysis by HS-SPME-GC–MS.

2.4.2. HS-SPME-GC–MS analysis

The analysis used an Agilent 8890 gas chromatography system

equipped with a 7697 A headspace sampler, which was coupled to an Agilent 5977B mass selective detector (Agilent, USA). The headroom conditions were as follows: The balance time of the sample bottle was 20 min, the temperature of headspace strip heating box was 80 °C, the aging station temperature of fiber head was 240 °C, the aging time of fiber head was 10 min, the adsorption time of sample was 10 min, the desorption time of sample was 2 min, the GC cycle time was 32 min, and the volume of sample bottle was 20 mL. The meat samples were infused in split mode into the GC–MS system for analysis. The injection volume was 1 μL, samples were used in splitting mode (10:1). The samples were separated by VF-WAXms (25 m × 0.25 mm × 0.2 μm) capillary column with 99.999 % helium as carrier gas at a flow rate of 2 mL per minute. The inlet temperature was 180 °C. The gas chromatographic column temperature was set at 40 °C for 2 min, then increased to 100 °C at a rate of 5 °C per minute, and then increased to 230 °C at a rate of 15 °C per minute, and maintained for 5 min. After that, the column temperature was maintained at 230 °C for 2 min. Mass spectrometry was performed with electron impact (EI) ionization at 70 eV, with an ion source temperature of 280 °C, a quadrupole temperature of 150 °C, and a mass scan range of *m/z* 30–1000 at a rate of 3.2 scans per second. During the run-on process, in order to assess and analyze the stability of the analytical system, we prepared a quality control sample (Quality Control, QC) during the experiment.

2.4.3. Data preprocessing and annotation of HS-SPME-GC–MS

The original data obtained by GC/MS mass spectrometer was pre-conditioned by Mass Hunter workstation quantitative analysis software (verision v10.0.707.0), and the 3D data matrix in CSV format was derived. Remove false-positive peaks which were known, including column bleeding, noise, derivative reagent peaks, from the data matrix to remove redundancy and peak pooling. In the meantime, metabolite identification process was conducted by searching databases, and the main databases used were public databases such as NIST (version 2017) and MS-DIAL (version 2021). The data matrix obtained by searching database was pre-processed, which mainly included missing value recoding and normalization of the original data.

2.5. Lipid extraction and lipidomics analysis process

2.5.1. Lipid extraction

For lipid extraction, specific extraction methods refer to the reported by Zhang et al. (Zhang, Zhang, et al., 2023). In short, 50 mg mutton was mixed with 400 μL MTBE and 80 μL methanol, and then ultrasonic extraction was performed for 30 min. The sample was centrifuged at high speed after standing for 30 min, dried 350 μL supernatant in a vacuum concentrator, and then the 100 μL complex solution was re-dissolved. After vortex mixing for 30 s, ultrasound was carried out in the ice bath at 40 kHz for 5 min. After high speed centrifugation (13,000 rmp, 4 °C) for 5 min, 80 μL supernatant was removed into a vial with an internal intubation for analysis.

2.5.2. Lipidomics analysis

For lipidomics analysis process, in order to investigate the reproducibility of the entire analysis procedure, quality control samples (QC) were created by combining equal volumes of metabolites from all samples. In the process of instrumental analysis, insert one QC sample into every eight samples. Lipids chromatographic separation was carried out using a Thermo UHPLC Vanquish Horizon system, which was equipped with an ACQUITY BEH C18 column (100 mm × 2.1 mm i.d., 1.7 μm; Waters, Milford, USA). After on-board, the original data of LC-MS was imported into a lipidomics processing software, LipidSearch (Thermo, CA), for peak identification, baseline filtering, retention time correction, integration, identification, peak alignment, and finally obtained a data matrix of retention time, lipid name, peak intensity, mass-charge ratio, etc. Chromatographic, mass spectrometry conditions and data preprocessing search methods refer to our previous published articles (Zhang, Zhang, et al., 2023).

2.6. Statistical analysis

Six organisms were prepared independently and repeated for metabolic analysis. GraphPad Prism 8 and Excel 2010 were used for statistical analysis, and the data were expressed as mean ± SE. For principal component analysis (PCA) and orthogonal partial least squares discriminant analysis (OPLS-DA), the R package "ropls" (Version 1.6.2) was utilized, and 7-cycle interactive verification was carried out to evaluate the stability of the model. Metabolites that were determined as significantly different were those with a VIP value greater than > 1 and a *p* value less than< 0.05. The VIP values were obtained from the Variable Importance in the Projection (VIP) generated by the OPLS-DA model, while the *p* values were generated by student's *t*-test. For differential lipids, student's t-test and differential multivariate analysis were conducted for differential lipids. Through KEGG database (http://www.genome.jp/kegg/) metabolism of enrichment and pathway analysis, the differences between the two groups of metabolites mapped to the respective biochemical pathways. Metabolites can be classified according to the pathways they participate in or the functions they perform. Enrichment analysis was employed to analyze whether a set of metabolites appears or not in a function node. The principle was to expand the scope of annotation analysis from a single metabolite to a collective set of metabolites. We employed the Python package "scipy.stats" (https://docs.scipy.org/doc/scipy/) for conducting enrichment analysis, with the aim of identifying the most pertinent biological pathways associated with the experimental treatments. The difference among all groups were significant when *represents $p < 0.05$, ** represents $p < 0.01$, and *** represents $p < 0.001$.

3. Results and discussion

3.1. The electronic nose distinguishes the flavour differences between goats and sheep meat

The volatile components of different mutton were determined macroscopically by e-nose. Six samples from each treatment were selected, and the response values from 10 sensors in the e-nose were recorded. Significant differences were observed in the sensor response values of W2S (aldol ketones), W1W (inorganic sulfides), W1S (methyl groups), W1C (aromatic benzene), W3C (ammonia), W5S (nitrogen oxides), W5C (short-chain alkane aromatic components), and W3S (long chain alkane) between goats and sheep meat (Fig. 1A and B). In sheep meat, the sensor response values for W5S, W1S, W1W and W2S were above 5 (Fig. 1C), indicating that nitrogen oxides, methyl groups, inorganic sulfides and aldol ketones are the primary and stable volatile compounds in sheep meat. Furthermore, the response values for W1W, W5S, W1S, and W2S in sheep meat were approximately 5, 3.5, 3, and 3 times higher, respectively, than those in goat meat. This suggests that nitrogen oxides, methyl groups, inorganic sulfides and aldol ketones are the key factors contributing to the flavour difference between goats and sheep meat.

Our identification results of the above key compounds in sheep meat are basically consistent with the results of electronic nose analysis of different sheep breeds by Xiang et al. (Xiang et al., 2023). Additionally, Li et al. conducted similar research on mutton samples from the Taihang and Huanghuai breeds and found that goats and sheep meat samples exhibited differences in volatile compound concentrations, particularly in nitrogen oxides, methyl groups, and aldol ketones(Li et al., 2022). Our study further corroborates these findings, highlighting the important role these substances play in the flavour difference between goats and sheep meat. However, while our results align with those of previous studies, we also observed that the sensor response values for W2W and W6S did not show significant differences between goats and sheep meat. This suggests that organic sulfides and hydrides are not the major

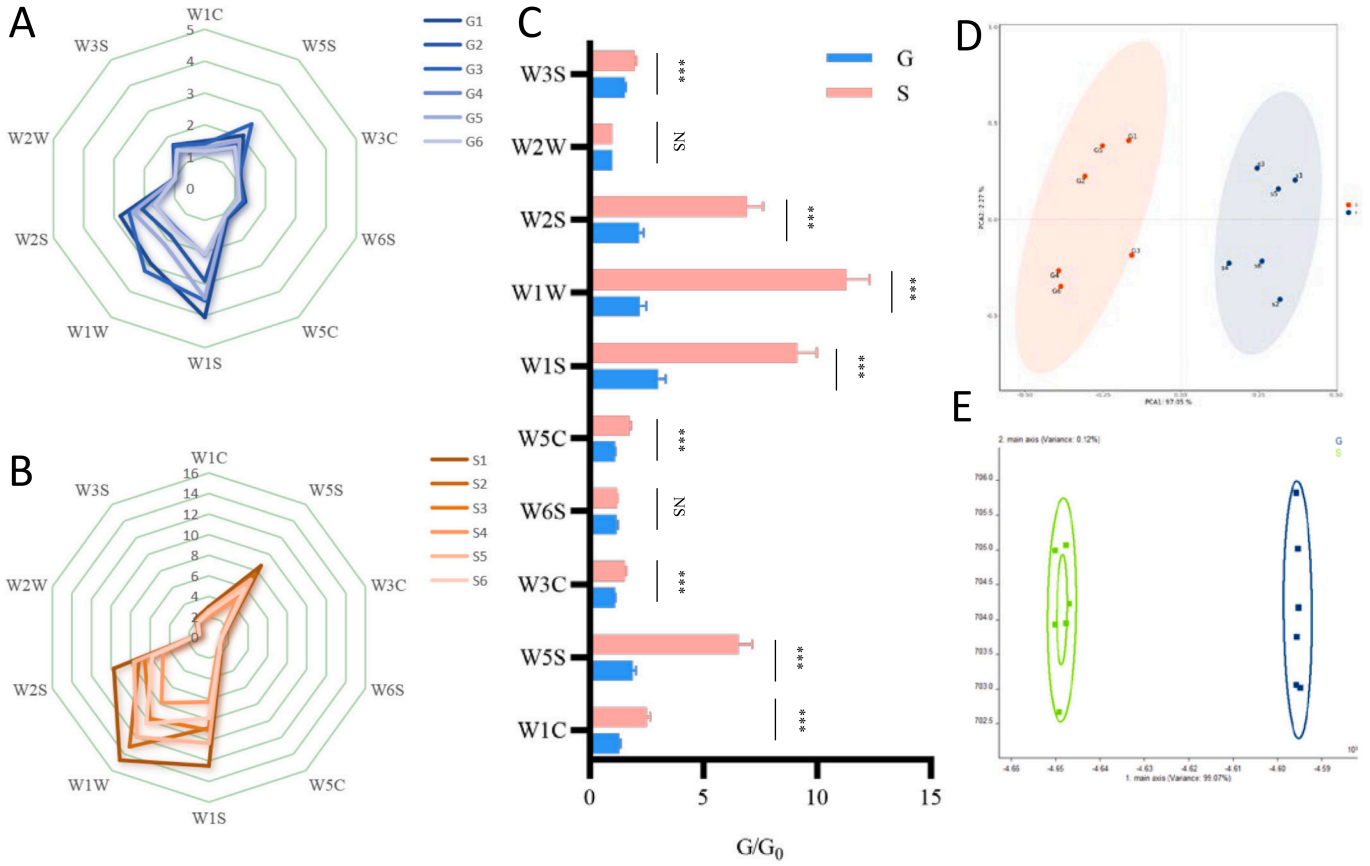

Fig. 1. Electronic nose rapid detection the flavour between goats and sheep meat. (A) and (B). Radar map of electronic nose for goats and sheep meat, respectively. (C). Response value of electronic nose sensor to goats and sheep flavour, *** represents $p < 0.001$. (D). PCA of electronic nose data for goats and sheep meat. (E). LDA of electronic nose data for goats and sheep meat.

contributors to the flavour differences between the two meats. This observation is in line with the results of Xiang et al. (2023) and Liu, Hui, Fang, et al. (2022), who also reported minimal differences in certain volatile components across different sheep breeds and mutton samples.

The response models for goats and sheep meat were established using PCA and Linear Discriminant Analysis (LDA) methods. The contribution rate of PC1 and PC2 is 97.05 % and 2.27 % respectively, cumulatively accounting for 99.32 % of the total variance, indicating that those two principal components could capture most of the information from the data. The PCA revealed clear separation between the goats and sheep meat along PC1 and PC2, with no overlap, indicating significant differences in their volatile compositions (Fig. 1D). Further analysis was conducted using the LDA method. In the LDA, the contribution rates of the first two linear discriminants, LD1 and LD2, were 99.07 % and 0.12 %, respectively, resulting in a total contribution of 99.19 % (Fig. 1E). The two groups showed no overlap, and the distribution of the samples in the LDA plot exhibited a clear trend of separation, effectively distinguishing sheep meat from goat meat. The large distance between A/D and B/C on LD1 indicates that the abundance of volatile substances increases with the increase of LD1. Electronic nose analysis of the volatile components in goats and sheep meat showed that PCA and LDA are both effective in distinguishing the two types of meat. Although the types of flavour compounds present in both goats and sheep meat are generally similar, there are differences in the content of certain compounds, including benzene, nitrogen oxides, ammonia, short-chain alkanes, methyl compounds, inorganic sulfides, aldehydes, and long-chain alkanes.

3.2. Differences of volatile metabolites in goats and sheep

3.2.1. Annotation of volatile metabolites in goats and sheep

This study aims to reveal the key compounds responsible for the flavour differences between goats and sheep meat by headspace solid phase micro-extraction (HS-SPME) and gas chromatography–mass spectrometry (GC–MS). PCA and partial least squares discriminant analysis (PLS-DA) were used to assess the similarity and differences between the samples. The PCA results showed that the first two principal components explained 12.90 % and 30.30 % of the total variance (Fig. 2A), indicating significant differences in the metabolite profiles between the two species of meat. PLS-DA further confirmed the clear distinction between goats (G) and sheep (S) meat samples (Fig. 2B), suggesting that volatile metabolites play an important role in the flavour differences between the two meats.

The raw data of HS-SPME GC–MS before preprocessing contained 88 volatile metabolites for identification. However, after preprocessing, the dataset was reduced to 63 quantitatively identified metabolites. Those 63 volatile metabolites were compared with HMDB (Human Metabolome Database, www.hmdb.ca) and KEGG (http://www.genome.jp/kegg/) databases to obtain metabolite annotation information. The KEGG compound classification categorizes metabolites based on their biological functions, with main categories including compounds with Biological effects, Endocrine Disrupting Compounds, Lipids and Bioactive Peptides, Pesticides, Phytochemical compounds. A comparison of the identified metabolites with the KEGG compound database revealed that 14 metabolites were successfully annotated and classified (Fig. 2C), with lipids accounting for 50.00 %. Additionally, 25 metabolites were annotated using the HMDB 4.0 database, and statistical analysis was

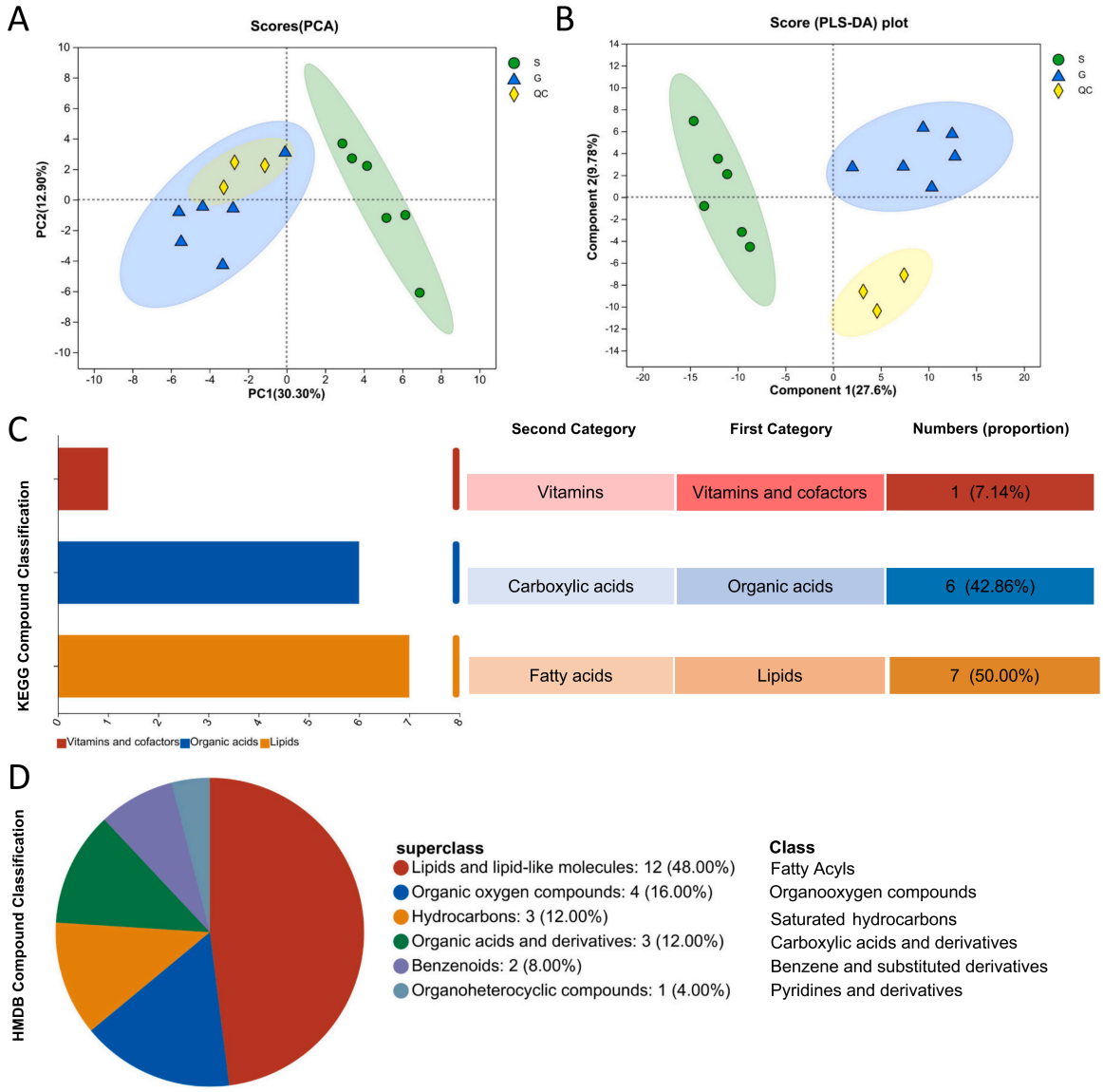

Fig. 2. Annotation of volatile metabolites in goats and sheep. (A) and (B). The distance of each coordinate point in PCA and PLS-DA score plots represents the degree of aggregation and dispersion between samples. The closer the distance, the higher the similarity between the samples. (C). The classification of KEGG Compound is based on the biological function level in which metabolites participate, and the color of the bars indicates that they belong to the primary classification category of compounds. (D). The name of the selected HMDB level (Superclass, Class, or Subclass) and the percentage of metabolites are displayed, in order from highest to lowest, according to the number of metabolites.

performed, as shown in Fig. 2D, where lipids and lipid-like molecules constituted 48.00 %.

3.2.2. *Different volatile metabolites in goats and sheep*

The volcano plot identified 18 differential volatile metabolites with $p < 0.05$ and VIP > 1 (based on the OPLS-DA), including 17 upregulated and 1 downregulated metabolites, found in both goats and sheep (Fig. 3A, Table S1). To visually highlight the significance and expression trends of those metabolites, cluster heat maps and VIP histograms were used to compare the expression patterns, p values, and VIP values between the two groups. Based on the OPLS-DA model, 18 differential volatile metabolites with VIP>1 were selected (Fig. 3B). Among these, three metabolites—octanoic acid (VIP: 2.0497), 1,14-tetradecanediol (VIP: 2.0085), and 13-octadecenal (Z) (VIP: 2.1594) showed VIP >2 and $p < 0.05$, further highlighting their significance (Fig. 3B).

The 18 volatile distinct metabolites were classified, including 6 acids, 4 esters, 3 alcohols, 2 aldehydes, 2 alkanes, and 1 to ketones. These compounds play a crucial role in the flavour profile of goats and sheep meat. Vladana Grabež et al. used non-targeted methods to identify 75 volatile compounds in sheep and mutton including lean meat and adipose tissue. Their findings also highlighted aldehydes (19), alcohols (11), and alkanes (15) as key contributors to flavourflavor (Grabež et al., 2019), which aligns with our results, confirming the importance of acids, esters, alcohols, and aldehydes in shaping mutton flavour. Previous research identified aldehydes (strecker and lipid-derived), pyrazines, ketones, sulphides and alcohols as the primary flavour compounds in boiled goat meat (Madruga, Elmore, Oruna-Concha, Balagiannis, & Mottram, 2010). These results emphasize the crucial role of alcohols in both raw and cooked mutton flavour. Our study corroborates this, showing that alcohols, especially in the form of alcohols like hexanol and octanol, are significant contributors to the flavour profile of goats and sheep meat.

In addition, Zhang et al. indicated that linolenic acid and linoleic acid are key factors in flavour differences of lambs with varying intramuscular fat (IMF) content (Zhang, Yuan, Li, & Yue, 2022). Similarly, our study found that fatty acids such as octanoic acid and nonanoic acid

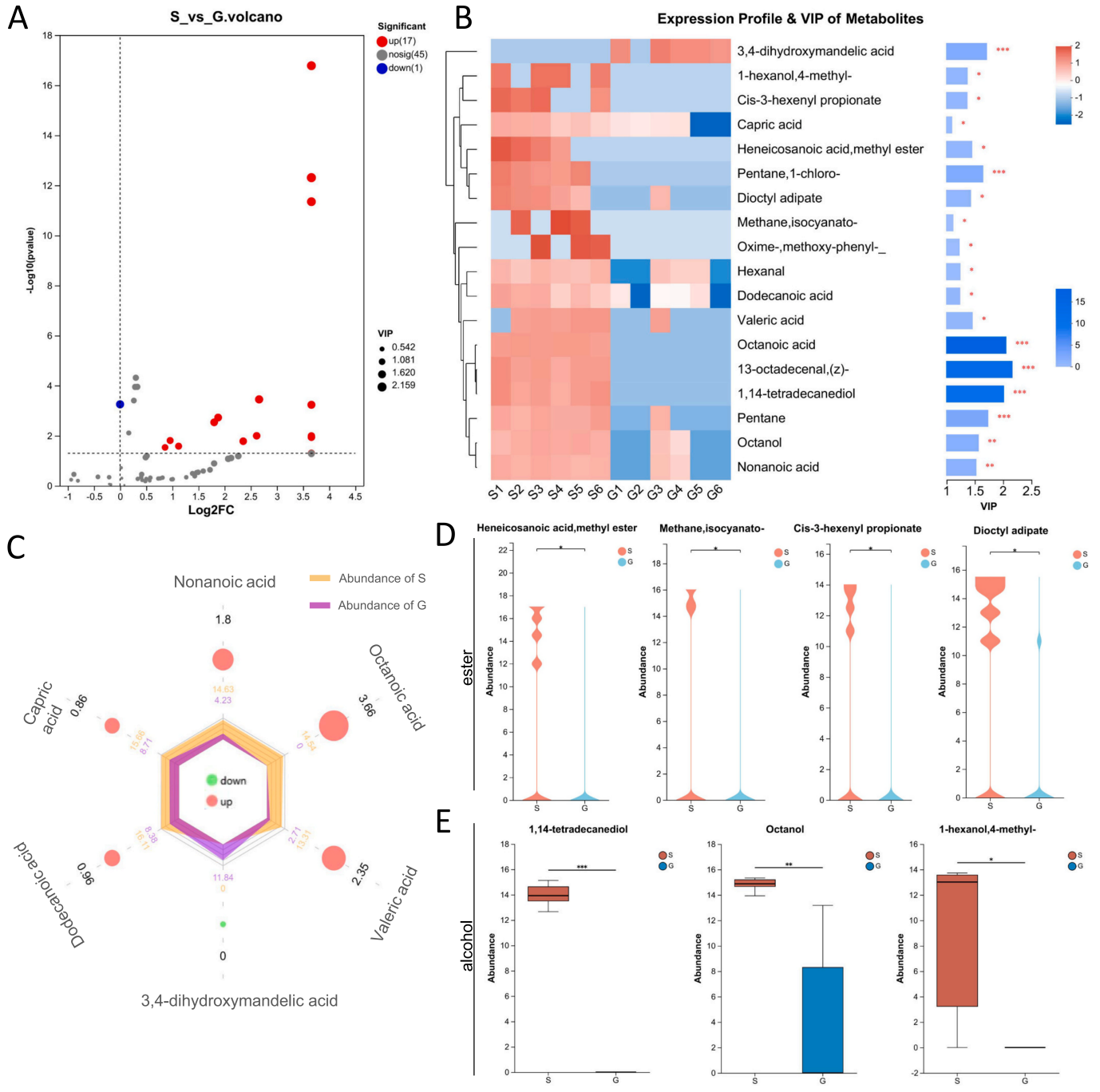

Fig. 3. Different volatile metabolites in goats and sheep. (A). Volcano plots presenting the differential volatile metabolites of goats and sheep. Each dot in the figure represents a specific metabolite, and the size of the dot indicates the VIP value. (B). VIP histogram of 18 volatile differential metabolites. The left is the metabolite cluster tree, and the right is the metabolite VIP bar. The smaller *P*-value is, the larger -log10(P-value) is, and the darker the color is. The right * represents $p < 0.05$, ** represents $p < 0.01$, and *** represents $p < 0.001$. (C). In the differential metabolite radar map, the numbers represent the log2(FC) value, the red and green circles represent the up-regulated and down-regulated genes respectively, and the size of the circles varies according to the size of the log2(FC) value, the yellow and purple data represent the average expression of genes in goats and sheep respectively, and the irregular shape in the figure represents the expression abundance of goats and sheep on each axis. (D). Violin diagram of different ester distributions in each group of samples. (E). Box plots of the distribution of different alcohols in each group of samples, with the lines in the middle of the box representing the median relative expression abundance of metabolites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

have significant effects on the flavour of sheep and goats meat. The main acids that affect the flavour of sheep and goats include 3,4-dihydroxymandelic acid, octanoic acid, valeric acid, nonanoic acid, dodecanoic acid and capric acid (Fig. 3C). These acids are responsible for the characteristic "mutton flavour", which further supports the notion that fatty acids are essential to the distinct flavour of sheep and goats meat. Kaffarnik et al. used GC–MS to identify 4-ethyloctanoic acid, 4-methylnonanoic acid and 4-methyloctanoic acid as key flavour compounds in goats and sheep meat (Kaffarnik, Preuß, & Vetter, 2014). Our findings are in agreement with these results, particularly highlighting octanoic acid and nonanoic acid as primary acids that influence mutton flavour. Furthermore, we identified several esters, such as heneicosanoic acid

methyl ester, cis-3-hexenyl propionate, and dioctyl adipatewhich also play a role in the overall flavour of goats and sheep meat. (Fig. 3D).

Short-chain branched-chain fatty acids (BCFAs) are another important group of compounds that contribute to the characteristic flavour of goats and sheep meat. Watkins et al. noted that BCFAs, particularly 4-ethyloctanoic acid, 4-methylnonanoic acid, and 4-methyloctanoic acid, are strongly associated with the "mutton flavour" (Watkins et al., 2021) (Watkins & Frank, 2019). These BCFAs increase in concentration as the animal ages, contributing to the development of mutton flavour over time. Our results support this, confirming that these compounds are

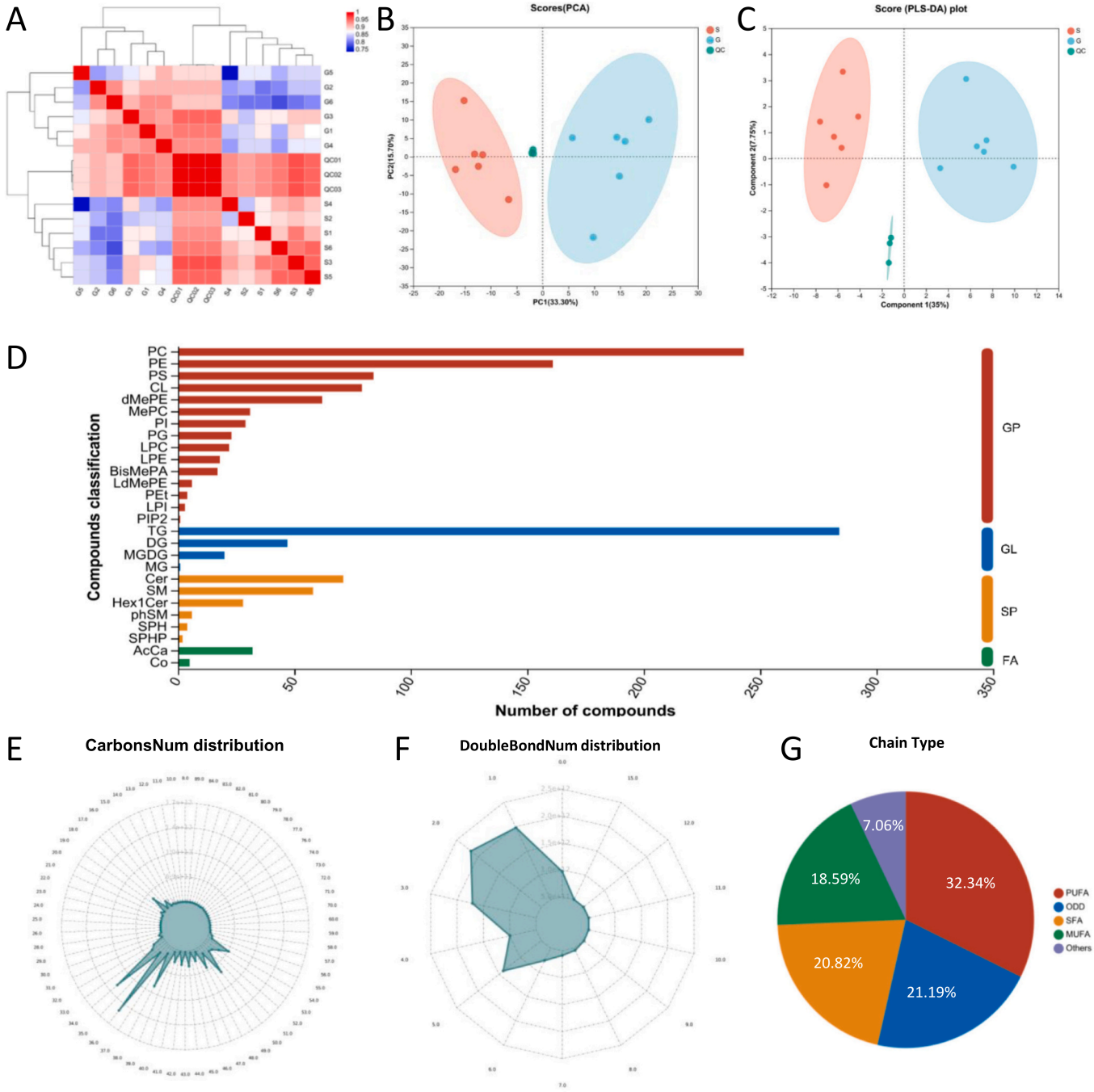

Fig. 4. Annotation of lipids in goats and sheep. (A). Each grid in the correlation heat map represents the correlation between goats (G) and sheep (S), different colors represent the relative size of the correlation coefficient between samples, and the length of the clustering branch represents the relative distance between samples, which is similar in the samples on the same branch. (B—C). PCA and PLS-DA score chart are often used to visually show the classification effect of the model. The greater the degree of separation between the two groups of samples in the chart, the more significant the classification effect. The confidence ellipse indicates that the "real samples" of this group are distributed in this region with 95 % confidence. Exceeding this area indicates that the sample may be abnormal. (D). The horizontal coordinate is the number of lipids identified for each subclass, and the vertical coordinate is the name of the subclass. Use the different color to label the category name to which each column belongs. (E). The grid lines represent the lipid content from low to high from the inside out, and the green shadows are made up of lines with the number of lengths of each carbon chain. (F). The grid lines represent the lipid content from low to high from the inside out, and the green shade consists of the content lines for each double-bond number classification. (G). Different colors on the pie chart show different types of content, including saturated fatty acyls (SFA), monounsaturated fatty acyls (MUFA), polyunsaturated fatty acyls (PUFA) and odd-numbered fatty acyls (ODD). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

major contributors to the characteristic aroma of sheep meat. Additionally, such as 1-hexanol, 4-methyl, Octanol and 1,14-tetradecanediol, these compounds were identified as important substances affecting the flavour of both goats and sheep as shown in Fig. 3E. These alcohols, along with the other compounds identified, forming a complex network of volatile compounds that influence the overall sensory profile of the meat.

3.3. Overview of the lipidomics results in goats and sheep

3.3.1. Annotation of lipids in goats and sheep

The lipidomic profiling of goats and sheep meat using the Thermo UHPLC Vanquish Horizon system with electrospray ionization (ESI) allowed for a detailed comparison of their lipid compositions in goats and sheep. In our results, Correlation heat map (Fig. 4A), PCA analysis (Fig. 4B), and PLS-DA analysis (Partial Least Squares-Discriminant Analysis) (Fig. 4C) showed the correlation between goats and sheep samples. The three results confirm each other, indicating differences in metabolite composition and abundance between goats and sheep samples. Our results, supported by correlation heatmaps (Fig. 4A), PCA (Fig. 4B), and PLS-DA (Fig. 4C), clearly demonstrate significant differences in metabolite composition and abundance between goats. These results suggest that lipidomics can be used as an effective tool to analyze meat quality, consistent with previous findings in the field. For example, Wang J et al. used lipidomic and metabolomic to detect the diverse in meat quality between concentrate-fed and pasture-fed sheep/goats, highlighting how diet influences lipid metabolism (Wang et al., 2021). Similarly, Zhang M et al. used lipidomics to analyze lipid transformation in Mongolian sheep during refrigerated aging after death (Zhang et al., 2023).

Before data preprocessing, a total of 777 lipid metabolites were initially identified in positive ion mode, with 583 metabolites detected in negative ion mode. After data pretreatment, 578 lipid metabolites were recognized under positive ions and 485 lipid metabolites under negative ions. KEGG pathway annotation of these metabolites identified 67 lipid species, which were further categorized using Lipidmaps into sphingolipids (SP, 179 metabolites), fatty acids (FA, 38 metabolites), glycerophospholipids (GP, 791 metabolites), and glycerolipids (GL, 352 metabolites) (Fig. 4D). This classification highlights the complexity of lipid metabolism in meat, with glycerophospholipids being the most abundant category.

Lipid metabolites can be classified into different categories according to different classification methods. The analysis of lipid chain length (Fig. 4E) revealed a diverse distribution of lipids, with the majority of identified lipids having carbon chain lengths of 36 (178 lipids), 38 (166 lipids), and 40 (131 lipids) carbons. This suggests that both goats and sheep meat have a substantial presence of mediumto longchain fatty acids, which are essential for various physiological processes. Meanwhile, the obtained lipids were classified according to quantitative lipid double bonds, both lipids 1 and 2 had lipidmore than 200 quantitative double bonds, as shown in Fig. 4F. Additionally, the classification of lipids based on their unsaturation (Fig. 4G) showed a rich composition of polyunsaturated fatty acids (PUFAs), which constituted 32.34 % of the total lipids. This finding is meaningful because PUFAs, particularly ω-3 fatty acids, are widely recognized for their health benefits, including anti-inflammatory effects and cardiovascular health. These results also align with previous studies emphasizing the importance of ω-3 PUFAs in human health. For instance, Zhang et al. highlighted that ω-3 PUFAs are critical for various biological functions and are considered essential for maintaining overall well-being (Zhang et al., 2018). The relatively high abundance of PUFAs in both goats and sheep meat suggests that these meats could offer potential health benefits, particularly in terms of their fatty acid profiles, which could be important for consumers seeking to improve their diet quality.

3.3.2. Differential lipids in goats and sheep

To investigate the effect of lipids on the flavour of goats and sheep meat, we analyzed the differential lipids using the OPLS-DA model. Lipids with $p < 0.05$ and VIP >1 were considered significantly different and are highlighted in the volcano diagram in Fig. 5A. A total of 314 differential lipids were identified, with 162 were detected in positive ion mode and 152 in negative ion mode. Among these, 182 lipids were up-regulated, and 132 were down-regulated. These Lipids were categorized into eight major classes based on the Lipid Metabolic Pathway Research Program (LIPID MAPS), including Glycerolipids (GL), Prenol Lipids (PR), Fatty Acyls (FA), Glycerophospholipids (GP), Sterol Lipids (ST), Sphingolipids (SP), Prenol Lipids (PK) and Saccharolipids (SL), which are further divided into 96 subclasses (Mi et al., 2018). 314 differential lipids of goats and sheep were classified into GP, SP, GL and FA according to the LIPID MAPS. There are 15 subclasses in the GP class, as shown in the Fig. 5C. The SP class contains 6 subclasses (Fig. 5D), the GL contains 3 subclasses (Fig. 5E), and the FA contains 2 subclasses (Fig. 5F).

We used heat maps to cluster the top 50 differential lipids and categorized them into four major groups: Glycerophospholipids (GP), Sphingolipids (SP), Glycerolipids (GL), and Fatty Acyls (FA) as shown in Fig. 5B. The results showed distinct clustering between goats and sheep, indicating that there are differences in various lipids between goats and sheep. Utilizing the OPLS-DA model, we assessed the expression patterns, p values, and VIP values of metabolites, with the results visualized through cluster heat maps and VIP bars. These analyses effectively highlighted the most significant and varying lipid expressions across the two groups. From the OPLS-DA model, the top 30 metabolites with a VIP > 1 metabolites were chosen as Fig. 5G and Table S2. Among those, the top five lipids with the highest VIP values, such as TG (4:0/17:1/18:1), TG (6:0/8:0/18:1), MePC (12:0/20:4), PC (18:2/18:2), and PC (16:1/21:0) are of particular interest because of their potential involvement in the flavour profile of mutton. Previous studies have shown that specific phosphatidylcholines, such as PC 18:1e, PC 18:2e, are the key markers for differentiating between grazing and concentrate-fed sheep and goats (Wang et al., 2021). This suggests that lipid species like PC may not only serve as markers of dietary influence but could also impact the overall flavour and texture of meat. Furthermore, the downregulation of triglycerides (TG) in the later stages of meat storage, particularly those involved in the formation of saturated fatty acids, as reported by Xu et al., could have implications for the aging process of mutton (Xu et al., 2023). These results indicate that PC and TG are important in the formation of mutton flavour. This aligns with our findings, where triglycerides were among the most significant lipids, suggesting their potential role in mutton flavour formation. The findings from this study support the hypothesis that lipids, particularly phosphatidylcholines (PC) and triglycerides (TG), play a vital role in defining the flavour profile of mutton. The identification of these lipids as key differentiators between goat and sheep mutton could further reinforces their importance in meat quality and flavour formation.

3.4. HS-SPME-GC–MS and comprehensive analysis of lipidomics

To better understand the relation between the lipidomics and metabolomics of goats and sheep, KEGG pathway analysis was performed on all identified lipids and volatile metabolites. The enrichment analysis of KEGG pathway refers to the abundance analysis of selected metabolic sets, with metabolite concentrations determined using the hypergeometric distribution algorithm. For HS-SPME-GC–MS, 18 different volatile metabolites were enriched in 14 KEGG pathways (Fig. 6A). Changes in metabolites concentrations with in each metabolic pathway were reflected by the Differential Abundance (DA) Score, the differential abundance scores of those KEGG pathways were also plotted. The results showed that an up-regulated pathway is marked with a score of 1, and a down-regulated pathway is marked with a score of −1. The absolute value of the DA score is represented by the length of

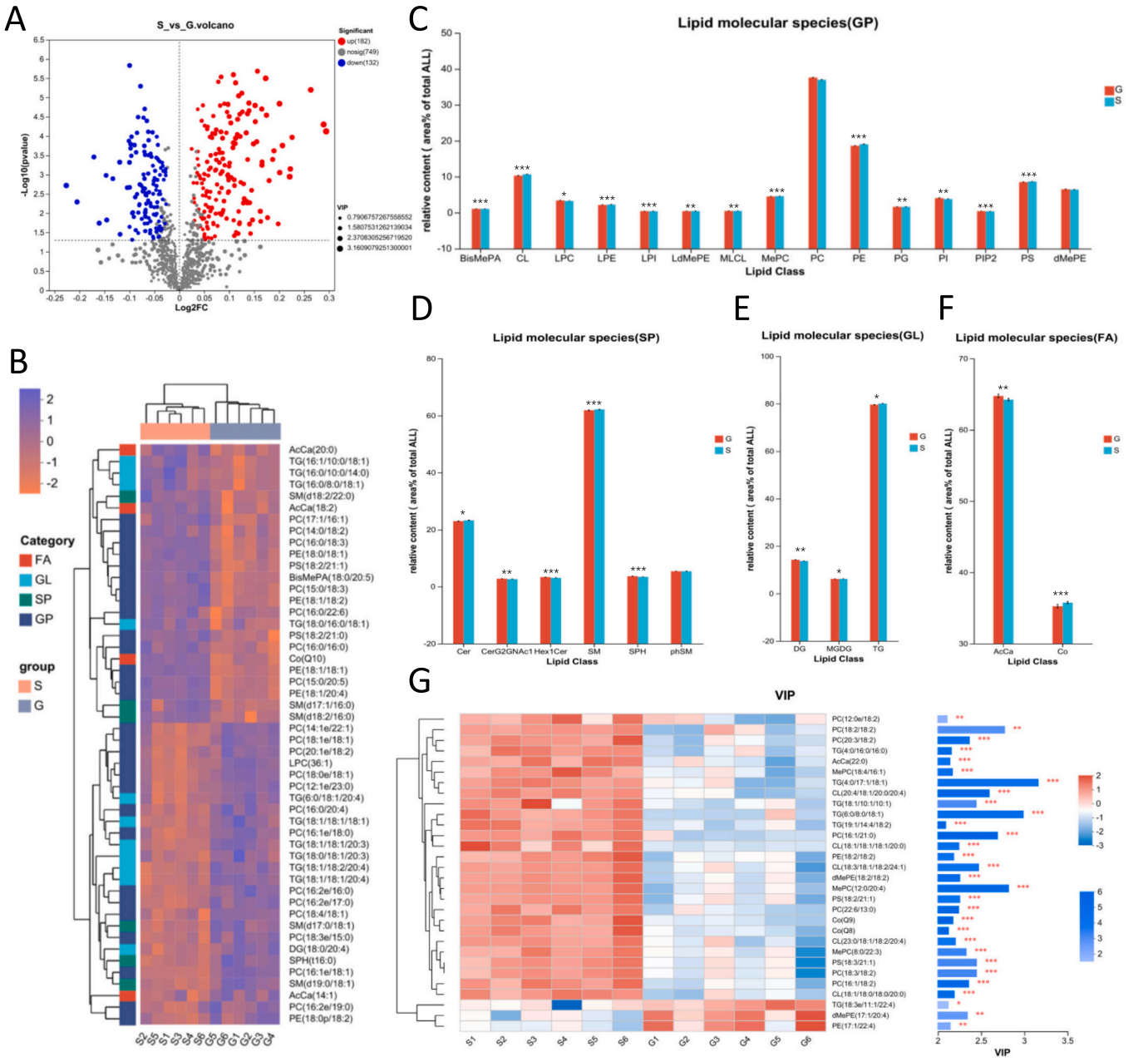

Fig. 5. Differential lipids in goats and sheep. (A). Volcano plots presenting the differential lipids of goats and sheep. Each dot in the figure represents a specific metabolite, and the size of the dot indicates the VIP value. As the number of points increases on both the left and right, the differences become more significant. (B). The heat map shows the clustering of different lipids. The tree diagram of metabolite clustering is on the left, and the tree diagram of sample clustering is on the top. (C—F). Lipid metabolites can be classified into different categories according to different classification methods, where GP is glycerophospholipids, FA is fatty acyls, SP is sphingolipids and GL is Glycerolipids. (G). The left is the lipid cluster tree, and the right is the lipid VIP bar. The smaller *P*-value is, the larger -log10(P-value) is, and the darker the color is. The right * represents $p < 0.05$, ** represents $p < 0.01$, and *** represents $p < 0.001$.

the line segment. All KEGG pathways were up-regulated, except for tyrosine metabolism (Fig. 6B). For lipidomics, 14 fat-related KEGG pathways were identified (Fig. 6C). These pathways included Linoleic acid metabolism, alpha-Linolenic acid metabolism, lipid metabolism, and Arachidonic acid metabolism, all of which were up-regulated. However, Glycerolipid metabolism process was down-regulated (Fig. 6D). The KEGG pathway enrichment analysis of differential lipid and volatile metabolite revealed that three KEGG pathways were co-enriched in both lipidomics and HS-SPME-GC–MS, including cholesterol metabolismand absorption, fat digestion and lipid and atherosclerosis (Fig. 6E). TG(18:1/20:4/20:4), TG(18:1/18:2/20:4), TG(18:1/18:1/20:4), DG(18:0/20:4), and dodecanoic acid take part in cholesterol metabolism and absorption, fat digestion and lipid and atherosclerosis, and the relevant information is shown in Fig. 6 and Figure S1 to S7. Dodecanoic acid is up-regulated in fat digestion and absorption, cholesterol metabolism and lipid and atherosclerosis simultaneously. TG (18:1/20:4/20:4), TG (18:1/18:2/20:4), TG (18:1/18:1/20:4), and DG (18:0/20:4) were down-regulated in fat digestion and absorption, cholesterol metabolism and lipid and atherosclerosis simultaneously (Fig. 6F). The combined lipidomics and metabolomics analysis using KEGG pathway enrichment highlights key biological pathways involved in lipid metabolism, fat digestion, and atherosclerosis. Above several lipid categories, including triglycerides (TG) and phosphatidylcholine (PC), as well as volatile metabolites such as dodecanoic acid, exhibit

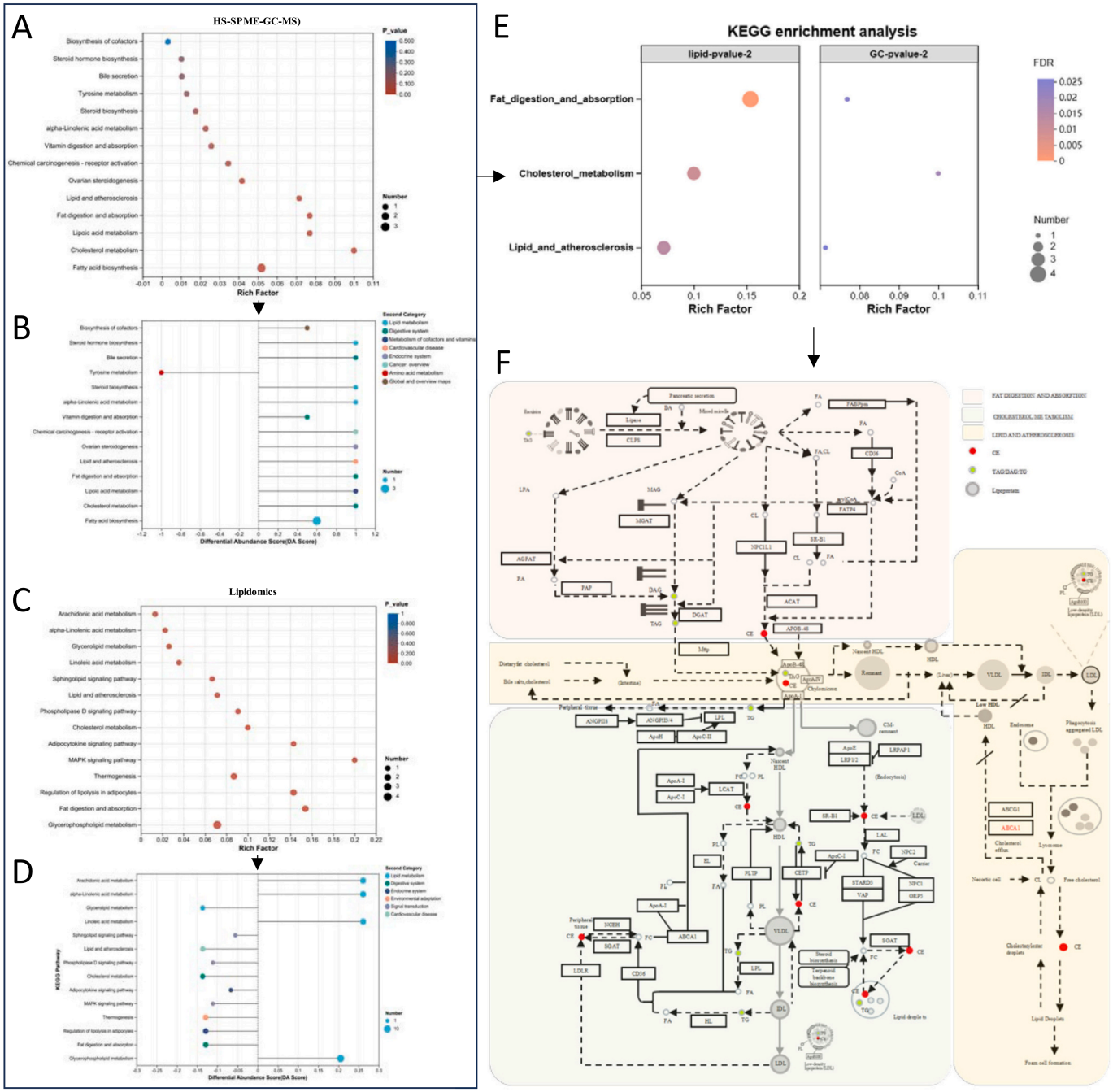

Fig. 6. KEGG pathway analysis of goats and sheep. (A) and (C). KEGG enrichment bubble diagram. Horizontal coordinate is enrichment rate and the ordinate is the KEGG pathway. The size of bubbles in the figure represents the enrichment of metabolic compound in this pathway, and the color of bubbles represents the *p* values of different enrichment significance. (B) and (D). DA Score reflects the overall change of all metabolites in the metabolic pathway. The Score of 1 indicates that the expression trend of all annotated differential metabolites in the pathway is up-regulated; −1 indicates that the expression trend of all annotated differential metabolites in the pathway is down-regulated; the length of the line segment indicates the absolute value of DA Score. (E). 3 KEGG pathways were found to be co-enriched by the lipidomics and HS-SPME-GC–MS. (F). Key KEGG pathways involved in goats and sheep with different lipids and volatile metabolites.

differential regulation across these pathways, providing valuable insights into the metabolic and lipidomic changes in goats and sheep.

4. Conclusion

This study identifies key volatile metabolites and lipids that contribute to the flavour differences between goats and sheep meat. The electronic nose successfully distinguished the two meats, revealing significant variations in volatile compounds. HS-SPME-GC–MS and lipidomics analysis identified 18 volatile metabolites and 314 lipids as key contributors to the flavour difference. Key compounds, including Triglycerides, Diacylglycerol and Dodecanoic acid were found to influence flavour by participating in important metabolic pathways such as fat digestion, cholesterol metabolism, and lipid metabolism. This research provides valuable insights into the metabolic and lipidomic mechanisms underlying mutton flavour, laying the foundation for future studies in flavour optimization for the meat industry.

CRediT authorship contribution statement

Ju Zhang: Writing – review & editing, Methodology, Conceptualization. **Shuang Pang:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Ge Yan:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Lulu Wang:** Investigation, Methodology, Writing – review & editing. **Yuan Xu:** Writing – review & editing, Methodology, Investigation. **Yuheng Bai:** Writing – review & editing, Methodology, Investigation. **Ran Li:** Writing – review & editing, Methodology. **Xihong Wang:** Methodology, Writing – review & editing. **Yu Jiang:** Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors assert that they have no personal or financial conflicts of interests that could have influenced the work presented in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2024.102042.

Data availability

No data was used for the research described in the article.

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Update

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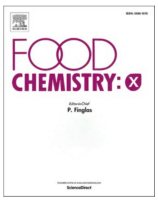

Corrigendum to "Integrated electronic nose and multi-omics reveal changes in flavour characterization of cashmere goats and tan sheep meat" [Food Chem. X 25 (2025) 102042]

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