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**TITLE PAGE**  
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| <b>ARTICLE INFORMATION</b>  | <b>Fill in information in each box below</b>  |
|---|---|
| <b>Article Type</b>   | Review article  |
| <b>Article Title</b>  | <b>Effective strategies for understanding meat flavor: A review</b>   |
| <b>Running Title (within 10 words)</b>  | <b>Understanding meat flavor</b>  |
| <b>Author</b>   | Min Kyung Park, Yun-Sang Choi   |
| <b>Affiliation</b>  | Food Processing Research Group, Korea Food Research Institute, Wanju 55365, Republic of Korea   |
| <b>Special remarks – if authors have additional information to inform the editorial office</b>  |   |
| <b>ORCID (All authors must have ORCID) <a href="https://orcid.org">https://orcid.org</a></b>  | Yun-Sang Choi ( <a href="https://orcid.org/0000-0001-8060-6237">https://orcid.org/0000-0001-8060-6237</a> )<br>Min Kyung Park ( <a href="https://orcid.org/0000-0002-3619-9491">https://orcid.org/0000-0002-3619-9491</a> )   |
| <b>Conflicts of interest</b><br>List any present or potential conflicts of interest for all authors.<br>(This field may be published.)  | The authors declare no potential conflict of interest.  |
| <b>Acknowledgements</b><br>State funding sources (grants, funding sources, equipment, and supplies). Include name and number of grant if available.<br>(This field may be published.) | This research was supported by the Main Research Program [E0211200-04] of the Korea Food Research Institute (KFRI), funded by the Ministry of Science and ICT (Republic of Korea). This research was also partially supported by the High Value-Added Food Technology Development Program [RS-2024-00398457] of the Korea Institute of Planning and Evaluation for Technology in Food, Agriculture, and Forestry (IPET), funded by Ministry of Agriculture, Food and Rural Affairs (Republic of Korea). This work was supported by the National Research Foundation of Korea (NRF) grant funded by the Korean government (MSIT) (NRF Project RS-2024-00338753). |
| <b>Author contributions</b><br>(This field may be published.)   | Conceptualization: Park MK, Choi YS.<br>Data curation: Park MK, Choi YS.<br>Validation: Park MK, Choi YS.<br>Investigation: Choi YS.<br>Writing - original draft: Park MK, Choi YS.<br>Writing - review & editing: Park MK, Choi YS.  |
| <b>Ethics approval (IRB/IACUC)</b><br>(This field may be published.)  | This article does not require IRB/IACUC approval because there are no human and animal participants.  |

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**CORRESPONDING AUTHOR CONTACT INFORMATION**

| <b>For the <u>corresponding</u> author (responsible for correspondence, proofreading, and reprints)</b> | <b>Fill in information in each box below</b>   |
|---|--|
| First name, middle initial, last name   | Yun-Sang Choi  |
| Email address – this is where your proofs will be sent  | <a href="mailto:kcys0517@kfri.re.kr">kcys0517@kfri.re.kr</a>                         |
| Secondary Email address   |  |
| Postal address  | Research Group of Food Processing, Korea Food Research Institute, Wanju 55365, Korea |

|                     |                |
|---------------------|----------------|
| Cell phone number   |                |
| Office phone number | 82-63-219-9387 |
| Fax number          | 82-63-219-9076 |

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## 9           **Effective strategies for understanding meat flavor: A review**

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### 12    **Abstract**

13       This study provides an effective strategy for understanding meat flavor. Understanding the  
14 taste of meat is essential for improving meat quality, and the taste should be analyzed based on  
15 complex chemical research to identify various factors that impact the composition, formation,  
16 and development of meat. To address flavor chemistry in meat, the discussion focuses on the  
17 major compounds responsible for the characteristic flavors of different meats, such as lipids,  
18 proteins, and Maillard reaction products (MRPs). Meat flavor is largely based on heat-induced  
19 chemical reactions that convert flavor precursors, such as sugars, proteins, and lipids, into  
20 volatile compounds. The flavor of meat is influenced by animal species, sex, age, feed, and  
21 processing, and in this respect, flavor is one of the representative quality indicators of meat.  
22 Research on meat flavor uses omics technology to study the molecular mechanisms that affect  
23 meat quality, including flavor, tenderness, and fat composition. Therefore, this study provides  
24 a comprehensive understanding of the complex processes governing meat flavor and provides  
25 avenues for further research and industrial applications to advance the meat industry.

26

27    **Keywords:** meat flavor; flavor chemistry; flavor factor; flavor analysis; omics

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29

## 30 **Introduction**

31 Meat flavor is a multidimensional sensory attribute that substantially influences consumer  
32 preference and the overall perception of meat quality (de Araújo et al., 2022). It is shaped by a  
33 complex interplay between various volatile and non-volatile compounds formed during meat  
34 processing, cooking, and storage (Vilar et al., 2022). Key contributors to meat flavor include  
35 Maillard reaction products (MRPs), lipid oxidation products, and an array of amino acids,  
36 peptides, and nucleotides (Ranmalingam et al., 2019; Sun et al., 2022). These compounds  
37 interact to create distinct aromas, tastes, and overall flavor characteristics that distinguish  
38 different types of meat and determine their acceptability to consumers (Dashdorj et al., 2015).

39 The Maillard reaction, which occurs between reducing sugars and amino acids during cooking,  
40 is particularly important for the development of characteristic browned flavors in cooked meat  
41 (Li et al., 2021). The products of this generate a myriad of volatile compounds, such as  
42 aldehydes, ketones, and pyrazines, which contribute to desirable roasted and savory notes  
43 (Mottram, 1998). In addition, lipid oxidation, which involves the breakdown of fats, results in  
44 the formation of compounds such as aldehydes, hydrocarbons, and alcohols, which add to the  
45 complexity of meat flavor (Fu et al., 2022).

46 Different cooking and aging methods, as well as meat processing techniques, can markedly  
47 affect meat flavor (Khan et al., 2015). Marination, curing, cooking, and smoking can also  
48 produce compounds that chemically impart a distinctive flavor (Smith & Acton, 2000). Even  
49 from the same carcass, meat cuts can substantially impact the formation of flavor compounds  
50 in meat (Wood, 2020), and this is influenced by the protein, fat, and moisture content of the  
51 meat, which in turn affects the flavor profile (Thu, 2006; Van et al., 2012).

52 Recent advancements in analytical techniques, such as gas chromatography-mass  
53 spectrometry (GC-MS) and high-performance liquid chromatography (HPLC), have greatly  
54 enhanced our ability to identify and quantify flavoring compounds (Bubli et al., 2021; Wei et

55 al., 2023). These technologies allow the precise analysis of both volatile and non-volatile  
56 constituents of meat, providing detailed profiles of the flavor compounds present (Vilar et al.,  
57 2022). By understanding the composition and concentration of these compounds, researchers  
58 and industry professionals can improve meat quality and enhance consumer satisfaction.

59 Multi-omics approaches in meat flavor research integrate genomics, transcriptomics,  
60 proteomics, and metabolomics to comprehensively understand the molecular mechanisms  
61 underlying flavor formation. This holistic method enables the identification of key flavor-  
62 related genes, proteins, and metabolites, as well as their interactions and regulatory pathways.  
63 By providing insights into how factors like breed, diet, and processing influence flavor, multi-  
64 omics enhances precision in flavor optimization and supports targeted breeding and processing  
65 strategies.

66 The objective of this review was to effectively clarify meat flavor and contribute to the  
67 advancement of the meat industry based on a deeper understanding of meat flavor dynamics.  
68 Understanding the principles of various chemical reactions that contribute to meat flavor, along  
69 with the variables that differentiate meat flavors and molecular-level flavor component analysis  
70 techniques, can maximize the potential of meat's flavor profile. In particular, unlike existing  
71 reviews that primarily focus on flavor-inducing components and their formation mechanisms  
72 at the molecular level derived from processing technologies (Xu et al., 2023) or the nutritional  
73 composition of meat (Khan et al., 2015; Fu et al., 2022), this review expands to an interpretation  
74 using holistic information about organisms, such as genome, transcriptome, proteome,  
75 lipidome, and metabolome, that may influence flavor. This comprehensive approach could  
76 provide bridge molecular insights with systems-level understanding, paving the way for  
77 innovative strategies to enhance meat flavor in both research and industry applications.

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79

## 80 **2. Flavor chemistry in meat and meat products**

81 In general, raw meat has few flavor properties but a slightly smelly and blood-like taste (Van  
82 et al., 2012), however, it contains abundant flavor precursors, including sugars, proteins, and  
83 lipids, which contribute to its meaty flavor. The well-recognized flavor of meat is primarily  
84 attributed to volatile compounds generated upon heat treatment. During heat processing, the  
85 abundant precursors in meat undergo various chemical reactions, breaking down into smaller  
86 molecules (Landy et al., 1996) or undergoing oxidation processes (Kanner, 1994), transforming  
87 into volatile compounds with low molecular weights and flavor properties. These molecular  
88 changes include several multiple reactions derived from heat treatment: the Maillard reaction,  
89 Strecker degradation, lipid degradation, and thiamine and ribonucleotide degradation. **Figure**  
90 **1** illustrates the process of meat flavor formation, along with its precursors and the primary  
91 thermal reactions involved.

### 93 **2.1. Maillard reaction**

94 The Maillard reaction plays a crucial role in the formation of the unique flavor and color of  
95 meat. This nonenzymatic browning reaction occurs between reducing sugars and amino acids,  
96 producing various volatile flavor compounds that are essential to the sensory properties of  
97 cooked meat. Diverse volatile compounds, such as aldehydes, alcohols, ketones, furans, and  
98 their derivatives, including pyrrole, pyridine, pyrazine, thiophene, and sulfides, are generated  
99 during thermal processing (Chen et al., 2019; Sun et al., 2021; Yu et al., 2020). The Maillard  
100 reaction is not limited to simple sugars and amino acids and can also involve peptides. The  
101 involvement of food-derived peptides in the Maillard reaction produces MRPs that enhance  
102 meat flavor. Peptides with molecular weights ranging from 1000 to 5000 Da induce flavor-

103 enhancing effects through the Maillard reaction (Fu et al., 2020). These MRPs are crucial for  
104 generating the umami taste and contribute to the overall palatability of meat (Kang et al., 2019).

105 Notably, the colors, yields, and types of flavor compounds produced are determined by the  
106 specific conditions under which the Maillard reaction occurs, such as temperature, pH, and  
107 humidity (Ribeiro et al., 2024; Starowicz & Zieliński, 2019; Wei et al., 2019). The reaction  
108 proceeds through three stages: the formation of early glycation products, their degradation, and  
109 the generation of flavor compounds such as pyrazines and thiophenes, which contribute heavily  
110 to the characteristic meat flavor (Starowicz et al., 2019). The distinctive meat flavor produced  
111 by the Maillard reaction is influenced by the presence of specific precursors such as cysteine,  
112 ribose, and lysine, which produce sulfur- and nitrogen-containing compounds (Raza et al., 2020;  
113 Wang et al., 2012; Zhang et al., 2023; Zhu et al., 2018). Glutathione, a tripeptide containing  
114 glutamate, cysteine, and glycine, forms sulfur-containing volatile compounds by cleaving  
115 peptide bonds during thermal processing. It generates important precursors of meat flavors,  
116 such as pyroglutamic acid and cyclic dipeptides (Wang et al., 2012). The Maillard reaction is  
117 closely linked to lipid oxidation in cooked meat (Liu et al., 2024; Mottram & Elmore, 2005;  
118 Zamora & Hidalgo, 2011). The interaction between these two processes enhances the  
119 complexity of the meat flavor profile because volatile compounds derived from lipid oxidation  
120 react with Maillard reaction intermediates. This generates heterocyclic compounds containing  
121 nitrogen and sulfur, which are important for the formation of cooked meat aroma.

122 The Maillard reaction also influences the color of cooked meat. The final stage of the reaction  
123 leads to the formation of melanoidins, brown polymers that markedly influence the visual  
124 appeal of meat products (Murata, 2021). The dark brown color associated with these polymers  
125 is often perceived as an indicator of a more intense flavor, making it a desirable quality for  
126 many meat products. Higher temperatures generally accelerate the reaction, leading to more  
127 intense flavor formation and darker color in the meat (Bekhit et al., 2019; Kong & Singh, 2016).

128 In addition to flavor and color, the Maillard reaction also impacts meat texture (Starowicz et  
129 al., 2019; Sun et al., 2010). Cross-linking of proteins and other compounds during the reaction  
130 can influence meat tenderness, with high levels of MRPs contributing to a firmer texture  
131 (Renzone et al., 2022; Sulaiman et al., 2022).

132

## 133 **2.2. Thermal degradation of carbohydrates**

134 Carbohydrate degradation plays a pivotal role in the formation of flavor compounds in meat.  
135 During the cooking process, carbohydrates, including pentoses and hexoses, are degraded  
136 through thermal reactions, such as the Maillard reaction, caramelization, and pyrolysis.  
137 Caramelization occurs at high temperatures (above melting temperatures of sugars) and  
138 converts sugars into compounds such as furfural and hydroxymethylfurfural, which are key  
139 contributors to flavor formation (Suleman et al., 2020). These intermediates can be further  
140 broken down into aromatic compounds, such as furans, which impart characteristic meat-like  
141 aromas. Chang et al. (2021) proposed a method for improving chicken flavor using a sugar-  
142 smoking technique. The authors primarily detected a notable increase in compounds such as  
143 furfural, 5-methyl-2-furancarboxaldehyde, 2-acetyl-5-methylfuran, and 1-(2-furanyl)-  
144 ethanone, known products of caramelization and the Maillard reaction. Pyrolysis also occurs  
145 upon exposure to high temperatures, leading to the production of various volatile compounds  
146 such as alcohols, aldehydes, and hydrocarbons. Sugars, particularly riboses from nucleotides,  
147 undergo degradation to form 5-methyl-4-hydroxyfuranone, a compound with a robust meat  
148 flavor (Begum et al., 2019). This process also releases hydrogen sulfide, which reacts with  
149 other flavor precursors to enhance the meat-like aroma (Shibamoto & Russell, 1976). The  
150 interaction between sugar degradation and the Maillard reaction, in which sugars react with  
151 amino acids, is another key pathway in the production of complex flavor compounds. This  
152 reaction generates volatile sulfur compounds such as thiophenes and thiazoles, which



153 contribute to the toasted and roasted flavors typical of cooked meat (Shibamoto et al., 1976).  
154 In summary, the combination of carbohydrate degradation, the Maillard reaction, and the  
155 breakdown of other precursors, such as amino acids, thiamine, and nucleotides, results in a  
156 diverse and complex flavor profile associated with meat.

157

### 158 **2.3. Strecker degradation of amino acids**

159 Strecker degradation is a chemical reaction that occurs when amino acids are degraded in the  
160 presence of dicarbonyl compounds produced during the Maillard reaction. This results in the  
161 formation of Strecker aldehydes, which are key contributors to the aroma of cooked meat (Chen  
162 et al., 2024). The interaction of Strecker degradation products with Maillard reaction  
163 intermediates leads to the formation of heterocyclic compounds, such as pyrazines, which  
164 further enhance the roasted flavor profile of cooked meat (Sohail et al., 2022). These  
165 interactions are crucial for generating the complex flavors associated with high-temperature  
166 cooking. Strecker degradation also produces sulfur-containing compounds, such as  
167 methanethiol and dimethyl disulfide, which are formed through the breakdown of methionine  
168 (Cerny, 2015; Schutte & Teranishi, 1974). Strecker degradation of sulfur-containing amino  
169 acids, such as cysteine and methionine, is particularly important in the formation of meaty and  
170 roasted flavors. These reactions produce volatile sulfur compounds that have a low odor  
171 threshold and strongly influence the aroma profile of cooked meat. Aldehydes generated from  
172 branched-chain amino acids, such as 2-methylbutanal and 3-methylbutanal, contribute to fruity  
173 and malty notes and add complexity to the flavor of meat (Wojtasik-Kalinowska et al., 2024).  
174 Strecker degradation is closely linked to lipid oxidation in meat. Lipid oxidation products can  
175 interact with Strecker intermediates, enhancing the development of flavor compounds such as  
176 aldehydes, which contribute to the overall sensory experience of cooked meat (Roldan et al.,  
177 2014; Utama et al., 2018).

178

#### 179 **2.4. Lipid oxidation and degradation**

180 In meat, fatty acids undergo oxidation, particularly at high temperatures, resulting in the  
181 formation of various volatile flavor compounds, such as aldehydes, ketones, and alcohols,  
182 which contribute to the overall flavor profile of cooked meat. During the heating process,  
183 phospholipids and triglycerides in meat undergo degradation, releasing short-chain fatty acids  
184 (Ren et al., 2024). These fatty acids are further oxidized to produce hydroperoxides, which can  
185 decompose into volatile compounds and enhance the aroma of cooked meat (Rasinska et al.,  
186 2019). The interaction between lipid oxidation products and MRPs is also essential for  
187 generating the complex flavor of cooked meat. Phospholipids play a pivotal role in these  
188 interactions, contributing to the formation of volatile compounds crucial for meat flavor (Cheng  
189 et al., 2024; Mottram & Edwards, 1983). Unsaturated fatty acids are particularly prone to  
190 oxidation, leading to the production of volatile compounds that can either enhance or degrade  
191 meat flavor depending on the degree of oxidation. Linoleic acid (C18:2n-6) and arachidonic  
192 acid (C20:4n-6) are easily oxidized, leading to the formation of volatile compounds, such as  
193 hexanal and 1-octen-3-ol, which are considered off-flavors in meat products (Yu et al., 2024).

194 To preserve meat quality, it is necessary to control lipid oxidation, which includes the use of  
195 antioxidants (Smet et al., 2008) and the maintenance of low temperatures (Soyer et al., 2010)  
196 during storage and cooking. Among the methods to inhibit lipid oxidation, freezing is effective  
197 in delaying irreversible biochemical reaction in meat, such as phospholipid oxidation and the  
198 generation of toxic compounds including malondialdehyde and cholesterol oxidation products  
199 (Soyer et al., 2010). These strategies help preserve meat flavor and extend its shelf life.

200

#### 201 **2.5. Thiamine and ribonucleotide degradation**

202 Thiamine (vitamin B1) is a bicyclic structure containing sulfur and nitrogen atoms, producing  
203 sulfur or nitrogen-containing heterocyclic compounds, such as furans, pyrimidines, thiols,  
204 thiazoles, sulfides, and disulfides (Brehm et al., 2019; Grosch, 2001; Dwivedi & Arnold, 1973).  
205 One important product is 4-methyl-5-(2-hydroxyethyl)thiazole, which is further degraded into  
206 various types of thiazoles. Specifically, it forms compounds such as **2-methyl-3-furanthiol**  
207 and **bis(2-methyl-3-furyl) disulfide**, both of which are associated with strong meat flavors  
208 (Tang et al., 2013). Additionally, **2-acetylthiophene (toasty)** and **2-formyl-5-**  
209 **methylthiophene** (meaty) contribute to the flavor complexity of cooked meat (Feng et al.,  
210 2018). These volatile compounds derived from thiamine degradation were selected as  
211 representative compounds of the characteristic aroma of pork, which is rich in thiamine  
212 precursors (Han et al., 2021).

213 Nucleotide degradation, particularly of inosine monophosphate (IMP), is a key contributor to  
214 meat flavor, imparting characteristic umami and brothy flavors to meats such as pork and  
215 chicken (Yang et al., 2020; Zhang et al., 2018). The process through which the nucleotide  
216 adenosine monophosphate is broken down into IMP and hypoxanthine is responsible for  
217 changes in flavor during meat maturation, changing from a savory to a slightly bitter flavor  
218 with increasing hypoxanthine levels (Ichimura et al., 2017). The increase of hypoxanthine  
219 content (under 7.0  $\mu\text{mol/g}$  in sample) has been reported to positively influence the taste of cured  
220 meat (Ichimura et al., 2016). The Maillard reaction, which involves ribose and amino acids  
221 from nucleotide degradation, also plays a role in producing sulfur-containing flavor compounds  
222 that contribute to the meaty aroma. The addition of IMP to beef at ten times its natural  
223 concentration increased the production of thiols and disulfides containing furan groups, which  
224 are key compounds that contribute to the aroma of meat (Ichimura et al., 2017).

225

### 226 **3. Factors influencing the flavor of meat**

227 Meat flavor, a representative indicator of meat quality, is affected by animal species, sex, age,  
228 feed, and processing. The effects of these factors on meat flavor are described in Table 1. Animal  
229 species possess unique flavors owing to differences in their carcass composition, including protein,  
230 fat, and moisture. Meat flavor can be influenced by factors such as total fat, intramuscular fat, and  
231 fatty acid composition. Fat levels impact the fatty acid profile of meat, as greater fat accumulation  
232 tends to increase the amounts of saturated and monounsaturated fatty acids more rapidly, thereby  
233 reducing the relative proportions of polyunsaturated fatty acids and the polyunsaturated/saturated  
234 ratio (DeSmet et al., 2004). Ba et al. (2013) concluded that the breed (e.g., Hanwoo versus Angus)  
235 could considerably impact the physicochemical quality, sensory characteristics, and content of  
236 volatile flavor compounds in meat.

237 Additionally, the impact of animal sex on meat flavor has been well documented. Gorraiz et al.  
238 (2006) reported that Pirenaica and Friesian bulls and heifers demonstrated notable differences in  
239 volatile compounds, odors, and flavors. After cooking, bull beef had a bloody flavor that was  
240 linked to a high 2-propanone content, along with a more pronounced liver-like odor and flavor,  
241 whereas heifer beef exhibited a robust characteristic flavor. The differences in juiciness and flavor  
242 intensity between male and female lambs could be attributed to variations in intramuscular fat,  
243 which plays a major role in the development of aroma and flavor in meat (Brennand & Lindsay,  
244 1992).

245 The age of an animal can markedly impact flavor, resulting in a distinctive aroma or poor quality  
246 as it ages (Fry et al., 1958). Khan et al. (2015) reported that age impacts collagen solubility in the  
247 muscle and increases flavor intensity, with older animals possessing higher levels of straight-chain  
248 fatty acids. Foraker et al. (2020) found that animal age affects flavor and also influences overall  
249 taste in meat quality.

250 Animal feed is a notable cost factor in livestock production, and the type of feed plays a crucial  
251 role in determining carcass conformation and the physicochemical and organoleptic characteristics  
252 of meat, such as proximate composition, fatty acid profile, tenderness, and color (Andersen et al.,  
253 2005; Dinh et al., 2021; Wood et al., 2008). Feed systems affect carcass composition and fattening,  
254 which can affect meat flavor (Watkins et al., 2013). Young et al. (1997) reported that feed type  
255 affected the fatty acid composition of meat. Additionally, the authors detected the presence of  
256 volatile compounds such as terpenes and diterpenoids in pasture-raised lambs. Grain-finished  
257 animals also possess high concentrations of short-branched-chain fatty acids, which are associated  
258 with the "mutton" aroma of cooked sheep meat (Young et al., 2003). According to Melton (1990),  
259 high-energy grain diets produced more acceptable or more intense flavors in red meat than low-  
260 energy forage or grass diets, and that flavor changes were greater in beef than in pork as  
261 unsaturation in the diet increased.

262 The meat processing process can also impart a unique flavor, and various technologies have  
263 been developed to enhance this flavor. Curing, aging, cooking, and smoking are used to impart or  
264 enhance meat flavor. Wang et al. (2012) showed that decreasing the level of curing salt increased  
265 the formation of flavor-active volatiles in dry-cured turkey ham. Jia et al. (2024) reported that the  
266 addition of salt and nitrates/nitrites for meat curing was associated with the color and flavor of  
267 cured meat. Dou et al. (2022) reported that aging can improve meat flavor by increasing the amount  
268 of flavor compounds through enzymatic action, thereby enhancing the amount of volatile  
269 compounds. Liu et al. (2024) detected the presence of 62 volatile flavor compounds during the  
270 dry-aging period, and the contents of Strecker aldehydes (2-methyl-butanal and 3-methyl-butanal),  
271 acids, heterocyclic compounds, and ethyl acetate increased with increasing dry-aging time. Zhu et  
272 al. (2019) reported that cooking enhances the flavor of meat owing to its effects on the amounts of  
273 free amino acids, carnosine, pyrazine, and hexanol. Guo et al. (2021) found that wood-smoked

274 bacon had stronger smoke and fat aromas than liquid-smoked bacon, and aldehydes were the most  
275 abundant compound groups. Begić et al. (2022) detected a positive correlation between the  
276 contents of phenols and hydrocarbons, alcohols, ketones, esters and lactones, terpenes, aromatic  
277 hydrocarbons, and acids in dry-smoked goat meat using principal component analysis. Therefore,  
278 the meat processing process can increase the amount of volatile compounds to impart a unique  
279 flavor to meat, and the mechanism for producing flavor components can also change depending  
280 on the processing process method.

281

## 282 **4. Techniques for identifying flavor compounds in meat**

### 283 **4.1. Extraction and analysis of odor-active volatile compounds in meat**

284 The components that contribute to the flavor and aroma of meat are highly dynamic and diverse,  
285 making it advisable to apply strategies and techniques tailored to the specific research objectives  
286 (Figure 2). Volatile compounds are organic chemicals that easily evaporate and release distinct  
287 odors, which are commonly found in plants, fruits, and essential oils. These compounds play  
288 crucial roles in determining the aroma and flavor profiles of foods, beverages, and perfumes  
289 (Chambers IV & Koppel, 2013; Guichard, 2002). They are highly reactive and unstable; therefore,  
290 various factors, such as temperature, extraction time, and interaction with the matrix, must be  
291 considered when extracting volatile compounds from food (Madruga et al., 2009; Wagner &  
292 Franco, 2012). Food flavor analysis is typically performed to separate individual volatile  
293 compounds from the food matrix based on their physicochemical properties while simultaneously  
294 gathering the entire set of volatile compounds. It can efficiently extract volatile compounds from  
295 foods using the chemical properties of solvents; however, it has high selectivity owing to the  
296 affinity between the compounds and the solvent. Recently, there has been an increasing preference  
297 for extraction methods that avoid the use of organic solvents or employ nonthermal techniques.

298 Steam distillation is a typical extraction process, in which steam is used to separate volatile  
299 compounds from a liquid matrix at low temperatures. Simultaneous distillation extraction  
300 combines steam and solvent extraction and is an important extraction method for isolating 3-  
301 methylindole and p-cresol, which are crucial to the 'pastoral' flavor characteristics of lamb  
302 (Schreurs et al., 2007). Solvent-assisted flavor evaporation is a gentle technique that operates at  
303 low temperatures and high vacuum, preserving sensitive compounds during extraction. It can be  
304 used for flavor extraction from milk, raw meat, and ham (Colahan-Sederstrom & Peterson, 2005;  
305 Liu et al., 2022); however, it is a time-consuming and laborious process. Solid-phase  
306 microextraction (SPME) involves exposing a fiber coated with an adsorbent to the sample or  
307 headspace to capture volatile compounds. This technique is preferred for flavor analysis owing to  
308 its simple extraction process, cost-effectiveness, solvent-free nature, and high sensitivity. SPME  
309 is an effective extraction method capable of identifying volatile compounds in various meat  
310 products, as demonstrated in a previous study that compared volatile compound extraction from  
311 beef and lamb fats (Watkins et al., 2012). Stir-bar sorptive extraction (SBSE) uses a coated stir bar  
312 to absorb volatile compounds from a sample in the absence of solvents. SBSE has an extraction  
313 phase that is 50–250 times larger than that of SPME (Ngamchuachit et al., 2020), resulting in  
314 enhanced extraction capabilities, and is used to extract volatile compounds from various meat  
315 products (Benet et al., 2015; Ngamchuachit et al., 2020).

316 Mass spectrometry (MS) is a typical analytical method for volatile flavor compound analysis  
317 owing to its ability to provide detailed chemical identification and quantification of individual  
318 compounds. Coupled with GC-MS, MS facilitates the precise separation and detection of complex  
319 volatile compound mixtures. Liquid chromatography-MS (LC-MS) is well suited for in-depth  
320 flavor analysis, enabling the identification of semi- or non-volatile compound profiles in foods. To  
321 identify key flavor compounds and elucidate the mechanism of flavor formation in foods, it is

322 important to identify the composition of volatile and non-volatile compounds. Kang et al. (2024)  
323 investigated key volatile and non-volatile metabolites and their metabolic pathways using GC-MS  
324 and LC-MS to determine the molecular regulatory mechanisms and support molecular breeding  
325 for yak meat flavor formation. In addition, Zhang et al. (2024) provided a rapid LC-MS/MS  
326 method to detect livestock species in meat products.

327 The electronic nose (E-nose) mimics human olfactory senses by using an array of sensors to  
328 detect volatile compounds based on patterns, although it cannot identify individual compounds. It  
329 is used for the rapid classification and comparison of aroma profiles, particularly for quality control  
330 and differentiation of products. Similarly, the electronic tongue (e-tongue) assesses flavor  
331 attributes, such as sweetness, bitterness, and umami, using sensors that detect taste-related  
332 chemicals in liquids. These electronic sensory devices can be used to determine the freshness of  
333 meat samples (Chotimah et al., 2024), provide indicators to distinguish their origin (Yuan et al.,  
334 2024), or yield information regarding unique flavor characteristics depending on the muscle type  
335 (Zhou et al., 2024).

336 Gas chromatography-olfactometry (GC-O) combines chemical analysis with sensory evaluation;  
337 human panelists sniff the GC effluent to identify odor-active compounds. GC-O is particularly  
338 useful for detecting specific compounds that contribute the most to the overall aroma or flavor of  
339 a product. Determination of odor-active compounds involves sensory and chemical techniques,  
340 including aroma extract dilution analysis (AEDA) and time-intensity methods. In AEDA, flavor  
341 extracts are diluted in a stepwise manner, and panelists evaluate each dilution for aroma, allowing  
342 identification of the most potent odor-active compounds based on their detection at higher dilutions.  
343 The time-intensity method records the perception of an aroma over time, providing insight into the  
344 duration and intensity of the impact of an odor-active compound. To quantify the contribution of  
345 these compounds, the odor activity value (OAV) is calculated by dividing the concentration of



346 each compound by its odor threshold (the concentration at which it can be perceived). Compounds  
347 with an OAV greater than one are considered to substantially contribute to the overall aroma. The  
348 identification of odor-active compounds in meat not only provides crucial indicators for the  
349 sensory perception of meat flavor but also provides essential information for recreating its aroma  
350 (Nie et al., 2024; Pu et al., 2020; Wang et al., 2022). These methods allow researchers to prioritize  
351 compounds not only by presence but also by their sensory relevance, combining chemical data  
352 with human perception to effectively identify the compounds that define a product's aroma profile.  
353 This approach ensures that both potency and perceptibility are considered in flavor analysis.

354

#### 355 **4.2. Omics technology**

356 Recent advances in high-throughput sequencing technologies, particularly genomics,  
357 transcriptomics, proteomics, and metabolomics, have enabled a comprehensive understanding of  
358 meat quality and taste at the molecular level (Table 2). These omics technologies are employed to  
359 explore the genetic, protein, and metabolic contributions to meat quality. Genomic studies have  
360 focused on identifying genes related to economically important traits such as tenderness, fat  
361 deposition, and meat color (Arikawa et al., 2024; Marín-Garzón et al., 2021). Advanced  
362 sequencing tools, such as long-read sequencing (Liu et al., 2024) and combination with artificial  
363 intelligence (Hamadani et al., 2022), have made it easier to investigate the role of these genes in  
364 improving meat quality. Long-read sequencing is a technology developed to overcome the  
365 limitations of NGS (Next-Generation Sequencing), which struggles with errors in genome  
366 assembly and difficulties in decoding repetitive regions due to its short read lengths. It leverages  
367 the advantages of TGS (Third-Generation Sequencing), including long read lengths, real-time base  
368 sequencing, and the ability to directly sequence DNA/RNA without PCR amplification. TGS  
369 offers significant advantages in livestock research by enabling the detection of rare genes,

370 structural variations, and transcriptional complexity, while facilitating superior breeding, genetic  
371 reproduction, and epigenetic analysis through its long reads, real-time sequencing, and reduced  
372 bioinformatics costs.

373 Research on meat flavor using transcriptome analysis contributes to improving the taste and  
374 quality of meat by uncovering various gene expression patterns and metabolic pathways.  
375 Transcriptomics, which focuses on gene expression profiles, has revealed the influence of genes  
376 on fat accumulation, muscle development, and tenderness (Bongiorni et al., 2016; Wang et al.,  
377 2024). These data help us understand how feeding management and other factors affect meat  
378 quality at the genetic level. Studies using transcriptomic approaches to investigate the molecular  
379 basis of beef quality highlight the strengths of high-throughput transcriptomics as a more sensitive  
380 and accurate analytical method for comprehensively exploring the transcriptional landscape of  
381 biological systems (Wang et al., 2009).

382 Molecular-level research, including proteomics, lipidomics, and metabolomics, can integrate  
383 data obtained from various biological layers, advancing meat quality and flavor studies in a more  
384 precise and practical direction. Proteomics is a technology that analyzes protein expression,  
385 modifications (e.g., phosphorylation, glycosylation), and interactions to identify their functional  
386 roles, making it highly useful for meat quality analysis. Proteomics is used to investigate how  
387 proteins influence meat quality, particularly how they change during the pre- and post-slaughter  
388 phases (Kim et al., 2021; Lamri et al., 2023). Proteomics has also revealed the impact of various  
389 factors, such as animal breed, on protein expression profiles in meat (Di Luca et al., 2022).  
390 Lipidomics comprehensively analyzes lipid metabolites, including studies on fatty acid  
391 composition and lipid metabolic pathways. It is particularly important for evaluating fat  
392 accumulation and its impact on meat flavor and juiciness (Guo et al., 2022; Zhang et al., 2023).  
393 Lipid metabolism plays a pivotal role in determining the organoleptic properties of meat, including

394 its taste and texture (Ramalingam, Song, & Hwang, 2019). Finally, metabolomics aims to quantify  
395 and qualitatively analyze the end products of metabolism to interpret biochemical pathways.  
396 Metabolomics focuses on small molecules and metabolites involved in real-time changes in meat  
397 quality. Based on the metabolic approach, biochemical processes such as lipid oxidation and  
398 glycolysis contribute to the flavor and tenderness of meat (Jia et al., 2021; Tamura et al., 2022; Yu  
399 et al., 2024).

400 Multi-omics approaches integrate different omics platforms to provide deeper insights into the  
401 molecular mechanisms responsible for meat quality. This integration facilitates the identification  
402 of biomarkers related to taste, texture, and other sensory attributes. Multi-omics approaches have  
403 also been applied to study food fraud and the authenticity of meat products. Comprehensive  
404 strategies are particularly useful for detecting species-specific markers that can reveal the  
405 adulteration of meat products (Liu et al., 2024; Ma et al., 2024; Zhang et al., 2024). Proteomics  
406 and metabolomics can be to uncover regulatory connections between proteins and metabolites,  
407 while metabolomics and transcriptomics has primarily explored how fat deposition can be  
408 controlled and tenderness of meat is enhanced through the involvement of various genes and  
409 signaling pathways. According to research on beef quality (Ma et al., 2024), intramuscular fat is a  
410 key factor in determining beef quality. Through integrated omics approach, including  
411 metabolomics and transcriptomics, it was revealed that the composition of flavor compounds  
412 significantly differed based on the contents of intramuscular fat and identified major genes  
413 associated with this variation. In meat science, omics research involves improving the accuracy  
414 and efficiency of these technologies, which includes optimizing bioinformatic tools and expanding  
415 existing databases to better predict and control meat quality.

416

417

## 418 **Conclusion**

419 This review provides insights into effective strategies for understanding meat flavors. The  
420 strategic presentation of meat flavor, the most important factor affecting meat quality, could be a  
421 cornerstone in advancing the meat industry. Meat flavor is primarily developed through heat-  
422 induced chemical reactions that transform flavor precursors such as sugars, proteins, and lipids  
423 into volatile compounds. These reactions, including the Maillard reaction and lipid degradation,  
424 contribute to the complex flavor profile of cooked meat. Meat flavor is influenced by factors such  
425 as species, sex, age, feed, and processing, which affect its physicochemical, sensory, and volatile  
426 compound characteristics. Processing methods like curing, aging, cooking, and smoking enhance  
427 flavor by altering volatile compounds and flavor precursors. Volatile compounds, essential for  
428 aroma and flavor, are extracted using methods like steam distillation, SPME, and SBSE, with  
429 analysis often conducted via GC-MS or LC-MS for detailed profiling. Advanced techniques,  
430 including electronic noses and GC-O, integrate sensory and chemical data to identify key odor-  
431 active compounds and their contributions to food flavors. Omic technologies, including genomics,  
432 proteomics, and metabolomics, offer comprehensive insights into the molecular mechanisms that  
433 influence meat quality, such as flavor, tenderness, and fat composition. This review was aimed at  
434 overcoming this situation and providing insights into the development of the meat industry,  
435 thereby contributing to its development of the meat industry.

436

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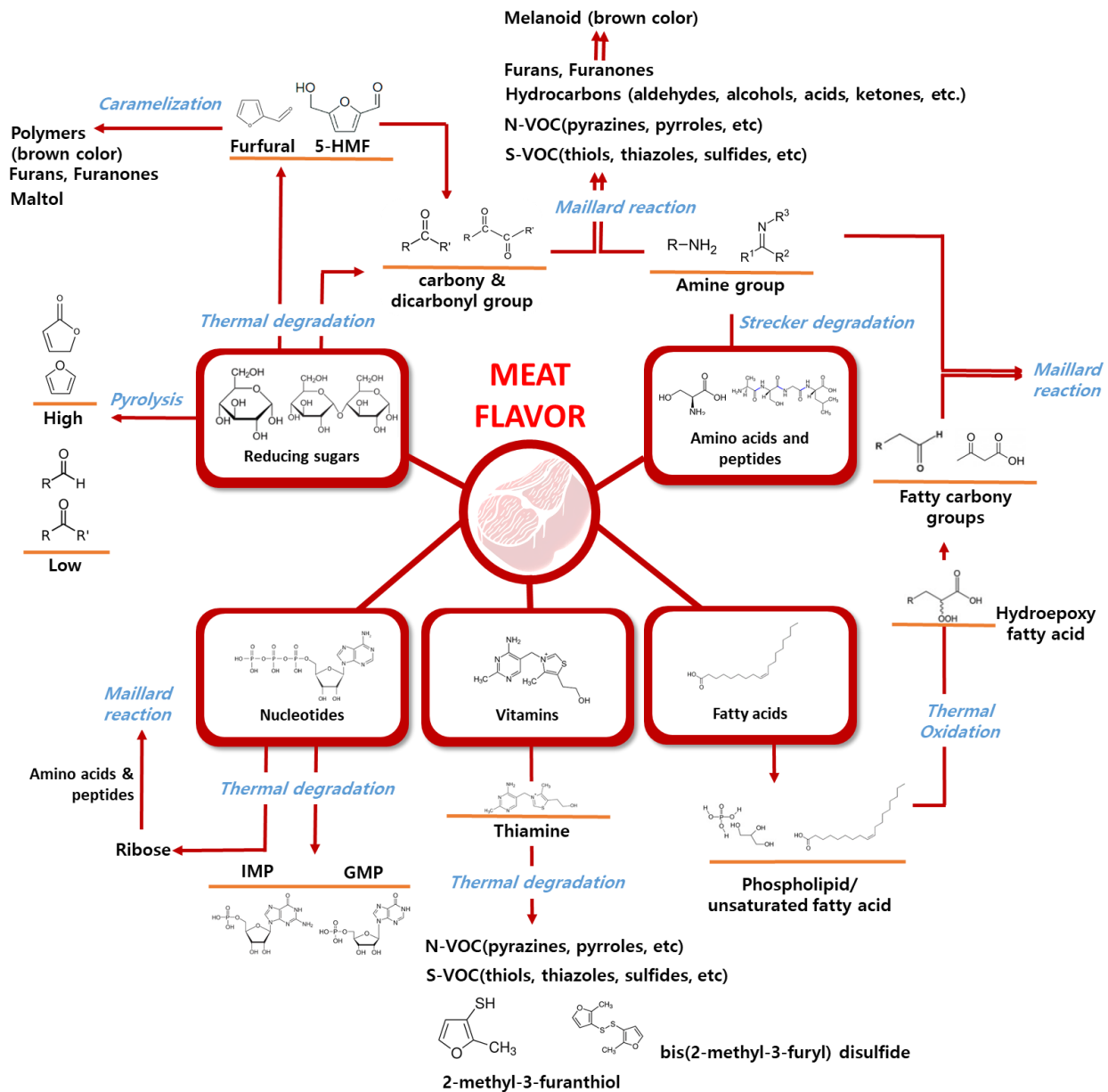
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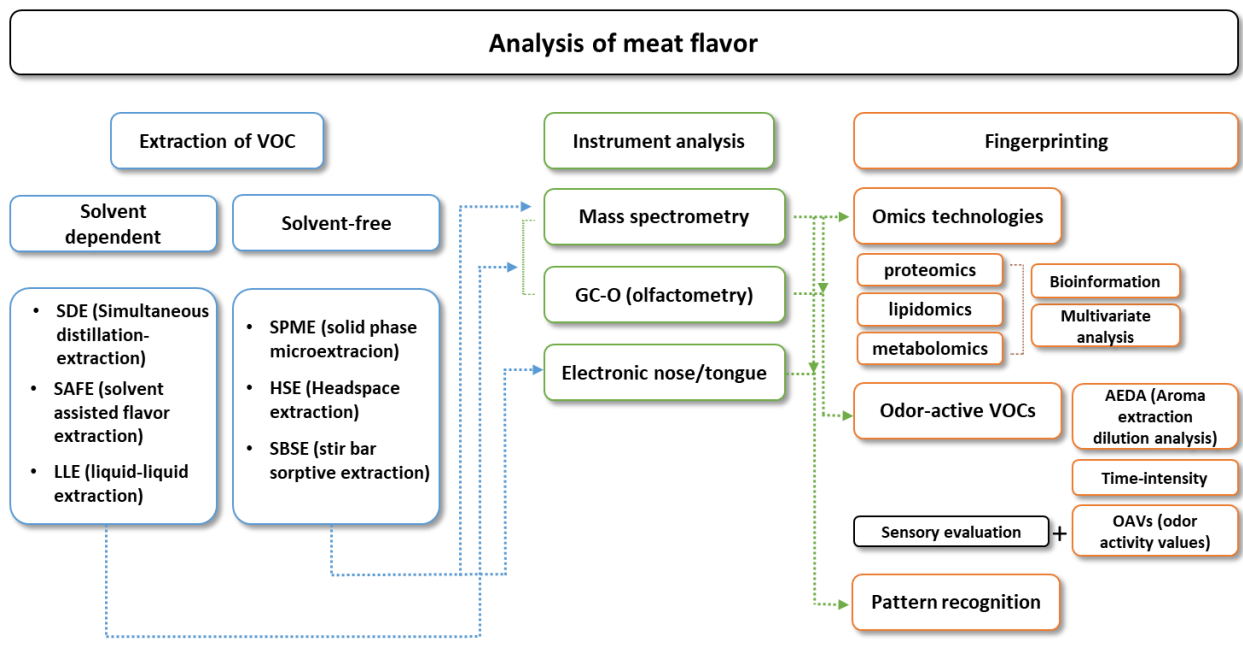


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755 **Fig. 1.** A simple overview of the formation of flavor compounds in meat.

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759 **Fig. 2.** Analytical methods for assessing meat flavor

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ACCEPT

**Table 1.** Analysis of factors influencing meat flavor

| Factors  | Influencing meat flavor   | References   |
|--|---|--|
| Animal species                                   | Animal species have a unique flavor due to differences in protein and fat content   | Dinh et al., 2021; Park et al. 2024.                           |
| Animal sex                                       | Differences in intracutaneous and subcutaneous fat between the sexes of animals may influence flavor-related compounds.   | Jayasena et al., 2014; Khan et al., 2015; Lorenze et al., 2013 |
| Animal age                                       | Animal age affects intramuscular collagen solubility and fatty acid composition, affecting flavor.  | Jaborek et al., 2020   |
| Animal feed                                      | Animal feed affects flavor by changing the fatty acid composition and meat composition.   | Wood et al., 2008  |
| Processing (curing, aging, cooking, and smoking) | Curing produces desirable flavors by chemical reactions of proteins and fats with salt and nitrite.   | Martin, 2001; Ramarathnam & Rubin, 1994                        |
|  | Aging enhances the flavor of meat by increasing the amount of flavor compounds via enzymatic action or by increasing the amount of volatile compounds derived from fatty acid degradation.        | Dou et al., 2022; Liu et al., 2024                             |
|  | Cooking enhances the flavor of meat by impacting the amount of free amino acids, carnosine, pyrazine, and hexanol. Cooking also induces the oxidation of lipids contained in meat to form flavor. | Khan et al., 2015; Lorenzen et al., 2005; Zhu et al. 2019      |
|  | Smoking affects the satisfactory flavor of meat owing to the influence of phenols, alcohols, methyl ketones, and esters   | Gue et al., 2021; Van et al., 2012                             |

**Table 2.** Analysis of recent studies to identify trends in meat flavor analysis methods

| Keywords           | Samples  | Extraction                             | Instrument                            | Analytical method  | References                                |
|--------------------|--|--|---------------------------------------|--|---|
| Flavor extraction  | Chicken, pork, duck, beef, mutton meat                   | HS-SPME                                | GC-MS                                 | Volatile profiling<br>Multivariate analysis (PCA, PLS_DA, OPLS-DA) | Yu et al., 2024                           |
|                    | Beef, raw ham, baked ham, pork sausage, and chicken meat | HS-SPME                                | GC-MS                                 | Volatile profiling<br>Multivariate analysis (PCA)                  | Acquaticci et al., 2024                   |
|                    | Dry-cured ham  | Headspace sorptive extraction, DHE     | GC-MS                                 | Volatile profiling,<br>Multivariate analysis (PCA)                 | Segura-Borrego, Callejón, & Morales, 2023 |
|                    | Grilled chicken  | DHE, SBSE                              | GC-O/MS                               | Volatile profiling,<br>olfactory detection                         | Ngamchuac hit et al., 2020                |
|                    | Dry-rendered beef fat                                    | SAFE                                   | GC-MS, GC-O                           | Odor-active compounds identifying                                  | Yang, Pei, Du, & Xie, 2023                |
|                    | Jinhua ham   | SAFE, SPME, Needle trap                | GC-TOF/MS                             | Odor-active compounds identifying                                  | Liu et al., 2022                          |
| Electronic sensor  | Vacuum-packaged Chicken meat                             | Headspace extraction                   | Electronic nose                       | discrimination of freshness  | Chotimah et al., 2024                     |
|                    | Yak Jerky  | Headspace extraction, aqueous solution | Electronic nose/tongue, GC-IMS        | Flavor profiling and discrimination model                          | Zhou et al., 2024                         |
|                    | Sauced Pork  | Headspace extraction, aqueous solution | Electronic nose/tongue, GC-MS, GC-IMS | Discrimination of different regions                                | Yuan et al., 2024                         |
| Omics technologies | Beef cattle  | -                                      | -                                     | Genomics   | Arikawa et al., 2024                      |
|                    | Pork meat  | -                                      | -                                     | Transcriptomics  | Wang et al., 2024                         |
|                    | Broiler chicken breast                                   | 2% SDS buffer                          | HPLC-MS/MS                            | Proteomics   | Yang et al., 2023                         |
|                    | Beef meat  | Acid hydrolysis, SE(cold acetone)      | LC-MS/MS                              | Proteomics   | Kim et al., 2021                          |
|                    | Chicken meat   | LLE (chloroform/methanol)              | UPLC-ESI-MS                           | Lipidomics   | Zhang et al., 2023                        |
|                    | Dry-cured mutton ham                                     | Solvent extraction                     | UPLC-MS/MS                            | Lipidomics   | Guo et al., 2022                          |
|                    | Meat exudate   | LLE (cold methanol/water)              | UHPLC-MS/MS                           | Metabolomics   | Yu et al., 2024                           |
|                    | Goat meat  | LLE (methanol/acetonitrile /water)     | UHPLC-Q-Orbitrap-MS                   | Metabolomics   | Jia et al., 2021                          |

|              |                           |   |                                     |                                    |                       |
|--------------|---------------------------|---|-------------------------------------|------------------------------------|-----------------------|
|              | Aged pork                 | LLE<br>(methanol/chloroform<br>/water)                    | GC-TOF/MS                           | Metabolomics                       | Tamura et al., 2022   |
|              | Roasted quail<br>meat     | SAFE, LLE<br>(chloroform/methanol<br>)                    | GC-O/MS,<br>HPLC-HRMS               | Lipidomics &<br>volatilomics       | Liu et al.,<br>2024   |
|              | Pork cuts                 | Headspace extraction,<br>LLE<br>(chloroform/methanol<br>) | GC×GC-<br>TOF/MS, LC-<br>MS/MS      | VOC, Lipidomics<br>& Transcriptome | Zhang et al.,<br>2024 |
|              | Xinjiang brown<br>beef    | Headspace extraction,<br>SE (methanol)                    | GC×GC-<br>TOF/MS, LC-MS             | Metabolomics &<br>Transcriptomics  | Ma et al.,<br>2024    |
| Sensory test | Chicken broth             | HS-SPME, SAFE   | GC-O/MS                             | AEDA                               | Nie et al.,<br>2024   |
|              | Beef flavoring            | SPME, DHS, LLE  | SGC×GC-O/MS,<br>Sensory test        | AEDA, OAV                          | Wang et al.,<br>2022  |
|              | Smoked cured<br>pork meat | SDE   | GC-MS, GC-<br>O/MS, Sensory<br>test | AEDA, OAV                          | Pu et al.,<br>2020    |

\* HS-SPME, headspace-solid phase microextraction; DHE, Dynamic headspace extraction; SBSE, stir bar sorptive extraction; SAFE, solvent-assisted flavor extraction; SE, solvent extraction; LLE, liquid-liquid extraction; SDE, simultaneous distillation and extraction; GC-MS, gas chromatography-mass spectrometry; GC-O, gas chromatography-olfactometry; GC-TOF/MS, gas chromatography-time of flight-mass spectrometry; GC-IMS, gas chromatography-ion mobility spectrometry; LC-MS, liquid chromatography-mass spectrometry; UPLC-ESI-MS, ultra-performance liquid chromatography-electrospray ionization-mass spectrometry; SGC×GC-O/MS, switchable two-dimensional gas chromatography-olfactometry-mass spectrometry; PCA, principal component analysis; PLS-DA, partial least squares-discriminant analysis; OPLS-DA, orthogonal partial least squares discriminant analysis; AEDA, aroma extract dilution analysis; OAV, odor activity values.