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28 **Introduction**

29 Meat flavor plays a major role in determining consumers' liking and acceptance of
30 the meat (Khan et al., 2015). Meat flavor is the complex combination of unique tastes
31 and aromas perceived in the mouth, tongue, and nasal cavity, arising from the
32 interaction of various volatile organic compounds (VOCs) and taste components
33 produced through thermal and non-thermal processes (Dashdorj et al., 2015; Kerth &
34 Miller, 2015; Xu et al., 2023). Raw meat is generally described as bloody-like aroma
35 with metallic and salty tastes; however, during the thermal or non-thermal processes
36 such as cooking, aging, curing, etc., a strong meaty flavor develops along with roasted
37 and fatty aroma and umami taste, depending on the type of chemical reaction
38 (Kosowska et al., 2017; Xu et al., 2024). In particular, the formation of meat flavor is
39 largely influenced by cooking methods, such as grilling, boiling, frying, roasting, etc.
40 (Lee et al., 2021; Suleman et al., 2020). Among them, high-temperature heating can
41 contribute to the meat flavor owing to the Maillard reaction which occurs at high
42 temperatures (Yoo et al., 2020). Maillard reaction is a non-enzymatic reaction between
43 the amino group from amino acids, peptides, or proteins and the carbonyl group from
44 reducing sugars to produce Maillard reaction products (MRPs) which are responsible
45 for meat color and flavor (Chiang et al., 2019; Liu et al., 2023; Ma et al., 2020).

46 A Maillard reaction model system is effective in understanding the mechanism of
47 Maillard reaction and investigating the characteristics of MRPs in a simple way (Xu et
48 al., 2013; Zou et al., 2019). This model system includes a mixture of amino acids or
49 peptides which provide amino groups and reducing sugars which contain carbonyl
50 groups (Xiao et al., 2015). The precursors determine the sensory characteristics of
51 MRPs. A simple model system consisting of a pure amino acid and a reducing sugar
52 would yield a limited composition of VOCs (Xia et al., 2021). Adding protein

53 hydrolysates or lipids in a model, on the other hand, can enrich the flavor of MRPs. In
54 contrast to plant or yeast proteins which can partially simulate the natural meat flavor,
55 animal proteins and fats act as excellent precursors for producing rich and pure meaty
56 flavor with diverse kinds of VOCs owing to their abundant contents of amino acids
57 (Chai et al., 2018; Chiang et al., 2022; Xiao et al., 2015; Ye et al., 2022).

58 The purposes of using animal resources as the precursor of a model system are: (1) to
59 upcycle the animal by-products as value-added products for food sustainability; (2) to
60 enhance the sensory attributes or bioactivity of animal protein hydrolysates; (3) to
61 improve the meaty flavor of the MRPs, e.g. adding animal fat into the plant protein-
62 based model systems; (4) to understand the mechanism of animal peptides on the
63 participation of Maillard reaction and the formation pathways of the representative
64 VOCs (Chiang et al., 2019; Nie et al., 2017; Ye et al., 2022; Zou et al., 2019).

65 Nonetheless, the information about the generation of meaty flavor from animal-derived
66 flavor precursors via the Maillard reaction model system is still limited (Liu et al.,
67 2015).

68 This review comprises the comprehensive literature on the sensory characteristics of
69 MRPs that were prepared via the model system with animal resources and summarizes
70 the factors that influence the degree of reaction, composition of VOCs, and sensory
71 attributes. Information about the flavor precursors in meat products and their
72 contribution to meat flavor is also provided for a better understanding of the
73 experimental design of Maillard reaction model systems.

74

75 **Meat flavor formation through the Maillard reaction**

76 **Meat flavor precursors**

77 The flavor of raw meat can be described as salty, metallic, and bloody taste with little
78 aroma intensity (Hoa et al., 2012; Kosowska et al., 2017). However, when the flavor
79 precursors present in meat participate in the Maillard reaction, lipid oxidation, and the
80 interactions between the products from the Maillard reaction and lipid oxidation via
81 thermal processes, the cooked meat flavor with roasted and savory aromas and umami
82 taste develops (Resconi et al., 2013). Flavor precursors in meat are constituted of non-
83 volatile water-soluble components such as amino acids, peptides, reducing sugars, and
84 thiamine, and lipid components (Dashdorj et al., 2015; Song et al., 2012). Water-soluble
85 components contribute to the generation of typical meat flavor, while lipids are
86 responsible for species-specific meat flavor (Sun et al., 2014). The amount of each
87 flavor precursor is a critical factor in the development of the meat flavor, as the reaction
88 during the Maillard reaction and lipid oxidation occur differently depending on the
89 relative contents of flavor precursors.

90 Amino acids and peptides in the meat are largely responsible for the meat flavor. In
91 terms of the Maillard reaction, the participation of individual amino acids of alanine,
92 aspartic acid, phenylalanine, proline, serine, and tyrosine contributes to the floral aroma,
93 while glycine, lysine, threonine, and valine give a caramel odor, whereas the sulfur-
94 containing amino acids including cysteine and methionine produce a strong meaty
95 aroma, as each amino acid favors the formation of different VOCs (Aaslyng & Meinert,
96 2017; Wong et al., 2008). For instance, Li and Liu (2022a) added cysteine to heated
97 enzymatic pork trimmings hydrolysate and reported an increase in the sulfur-containing
98 VOCs such as 2-furfurylthiol which were absent in non-enzymatic samples. Further, the
99 participation of amino acid mixtures or peptides from the thermal or enzymatic
100 degradation of meat proteins in the Maillard reaction generates strong, complex, and
101 long-lasting sensory characteristics of MRPs (Zhang et al., 2020; Zou et al., 2019).

102 Therefore, meat flavor can be improved through adequate cooking methods or aging
103 processes which produce many amino acids and peptides (Kim et al., 2019; Suleman et
104 al., 2020). The low-molecular-weight peptides present in meat such as anserine,
105 carnosine, and glutathione can also be used as precursors for the development of meaty
106 flavor after thermal processes (Zhou et al., 2019). For peptides, the reaction mechanism
107 in the Maillard reaction and the sensory properties of the MRPs are greatly determined
108 by their amino acid composition, sequence, and molecular weight, which will be
109 discussed later.

110 In the case of reducing sugars, ribose is a representative carbonyl donor in meat
111 which exists mainly as inosine 5'-monophosphate with small proportions of ribose 5'-
112 phosphate and free ribose (Mottram & Nobrega, 2002). Other nucleotides such as
113 adenosine 5'-monophosphate and guanidine 5'-monophosphate also participate in the
114 Maillard reaction (Xu et al., 2018). Additionally, glucose and glucose 6'-phosphate in
115 meat were found as important flavor precursors for meaty flavor (Li & Liu, 2021).
116 However, the amount of reducing sugars in the meat is not high, and therefore the
117 addition of sugars can help increase the degree of Maillard reaction in meat. For
118 instance, Aliani and Farmer (2005) observed that the two- to fourfold increase in the
119 natural concentration of ribose in chicken meat significantly enhanced its roasted flavor.
120 Similarly, Li and Liu (2021) reported that a higher concentration of xylose in pork
121 hydrolysate promoted the formation of flavor compounds after heat treatment such as
122 furfural and 2-pentylfuran which were responsible for enhanced roasted and sweet
123 aromas.

124 Animal fat, as mentioned earlier, plays a vital role in the formation of characteristic
125 meat flavors, such as beef, pork, and chicken flavor (Ye et al., 2022). Animal fat
126 includes triglycerides and phospholipids, which the latter mainly contribute to the

127 sensory characteristics of cooked meat (Aaslyng & Meinert, 2017; Kosowska et al.,
128 2017; Mottram & Edwards, 1983). Oleic acid, palmitic acid, and stearic acid are
129 representative fatty acids that derive from the degradation of triglycerides; linoleic acid,
130 arachidonic acid, eicosatetraenoic acid, palmitoleic acid, and linolenic acid come from
131 the degradation of phospholipids (Fu et al., 2022). Free fatty acids that were released by
132 the degradation of triglycerides and phospholipids during cooking are oxidized to
133 produce hydroperoxides, which are subsequently converted into a variety of VOCs such
134 as aldehydes, ketones, alcohols, carboxylic acids, esters, etc. (Sun et al., 2022).
135 Therefore, the principle in species-specific meat flavor that arises from lipids is based
136 on the differences in fatty acid profiles and the resulting carbonyls (Arshad et al., 2018).
137 The polyunsaturated fatty acid composition is much higher in poultry compared to
138 ruminants, which differentiates the chicken meat flavor from beef or lamb flavor
139 (Jayasena et al., 2013). Furthermore, the intermuscular fat content and the degree of its
140 unsaturation are also responsible for the flavor of meat (Khan et al., 2015). The
141 moderate oxidation of lipids is beneficial for meat flavor; however, excessive lipid
142 oxidation may deteriorate the sensory quality due to the high aldehyde contents that
143 elicit off-flavor (Lee et al., 2024).

144 In addition to the proteins, carbohydrates, and lipids, thiamine also affects the meat
145 flavor (Sun et al., 2014). It presents a relatively high content in muscle, approximately
146 0.08-0.11 mg, 0.17-0.18 mg, 0.23 mg, and 0.81-0.88 mg in 100 g of beef, lamb,
147 chicken, and pork, respectively (Ramalingam et al., 2019). Thiamine can be easily
148 degraded during thermal processes (Sun et al., 2022), resulting in the formation of many
149 nitrogen- or sulfur-containing VOCs, such as furans, thiols, thiophenes, and sulfides,
150 which are the major contributor to meaty and roasted aroma (Khan et al., 2015). Wei et
151 al. (2016) reported that marinating Chinese chicken with salt, xylose, cysteine, and

152 thiamine significantly enhanced the production of sulfur-containing VOCs, such as
153 benzothiazole and 4-methyl-5-thiazoleethanol, which contributed to a stronger meat-like
154 flavor.

155

156 **Mechanisms of the Maillard reaction**

157 The mechanisms of the Maillard reaction from the early stage, starting from the
158 interaction between amino group and carbonyl group to the final stage of the production
159 of melanoidins and the formation of representative VOCs during the reaction are well-
160 documented previously (Diez-Simon et al., 2019; Sohail et al., 2022; Sun et al., 2022).

161 Maillard reaction can be divided into three stages (Figure 1; Wang et al., 2022). It
162 starts from the condensation between the amino group from an amino acid or a peptide
163 and the carbonyl group from a reducing sugar at thermal conditions (Chiang et al.,
164 2019). Then, the primary intermediates called Amadori rearrange products are produced
165 through Amadori rearrangement (Sun et al., 2022). These compounds participate in
166 further reactions in the intermediate stages including enolizations and condensations to
167 form a variety of intermediates depending on the reaction condition (Lotfy et al., 2021).
168 For example, at low pH conditions, Amadori rearrangement products undergo 1,2-
169 enolization, subsequently releasing the amino compounds and producing furans,
170 furfurals, hydroxymethylfurfural, etc. (Bassam et al., 2022). On the other hand, at high
171 pH, Amadori rearrangement products are degraded via 2,3-enolization and generate
172 reductones and various fission products like acetol, diacetyl, and puryvaldehyde (Kutzli
173 et al., 2021). Particularly, the abovementioned compounds after 2,3-enolization of
174 Amadori rearrangement products are highly reactive and interact with aldehydes and
175 aminoketones that arise from the Strecker degradation, the process of degradation of
176 amino acids in the presence of dicarbonyl compounds (Hoa et al., 2012). As a result,

177 numerous nitrogen-containing heterocyclic compounds responsible for savory flavor are
178 formed. The final stage includes the formation of the brown macromolecular pigment
179 melanoidin.

180 Additionally, the products from the Maillard reaction and lipid oxidation or thiamine
181 degradation can interact directly or indirectly, affecting the overall VOC composition
182 through the alteration of various nitrogen- and sulfur-containing heterocyclic compound
183 contents that are responsible for meaty and roasted flavor (Liu et al., 2023).

184

185 **Flavor characteristics of VOCs**

186 During the Maillard reaction, many VOCs are formed through the fragmentation and
187 degradation of flavor precursors (amino acids and reducing sugars) and their
188 interactions (Figure 1). Among them, it is generally recognized that oxygen-, nitrogen-,
189 and sulfur-containing heterocyclic compounds are major contributors to the meaty
190 flavor of MRPs. Table 1 summarizes the list of VOCs that are frequently identified in
191 the animal resources-based model systems.

192 Oxygen-containing heterocyclic compounds include furans, furanones, and furfural.
193 A major pathway for the formation of oxygen-containing heterocyclic compounds is
194 sugar degradation (Wei et al., 2020). Amadori rearrange products are also the precursors
195 of oxygen-containing heterocyclic compounds through 1,2-enolization and cyclization
196 steps (Zheng et al., 2023). Specifically, acidic condition favors the formation of furans
197 (Xu et al., 2011). Furfural, a representative VOC in the Maillard reaction, has a strong
198 caramel and sweet flavor (Lotfy et al., 2021). 2-Pentylfuran is another compound that is
199 frequently found in the animal resources-based model system and elicits a meaty and
200 beany flavor (Song et al., 2017). Owing to their strong flavors, oxygen-containing
201 heterocyclic compounds greatly influence the flavor of MRPs.

202 The formation of sulfur-containing heterocyclic compounds such as thiols and
203 thiophenes during the Maillard reaction is mainly attributed to the reaction of H₂S that
204 is released from sulfur-containing amino acids such as cysteine and methionine. These
205 compounds are mainly responsible for the typical meaty and roasted flavor (Lee et al.,
206 2021). However, excessive concentrations of sulfur-containing heterocyclic compounds
207 may negatively affect the sensory attributes due to the strong sulfurous and burnt odors
208 (Xu et al., 2011). Major compounds found in the model system are 2-methyl-3-
209 furanthiol, 2-furfurylthiol, and 2-methyl-3-(methylthio)furan (Huang et al., 2023; Zou et
210 al., 2019).

211 Pyrazines, pyridines, and pyrroles are classified as nitrogen-containing heterocyclic
212 compounds. These compounds are responsible for meaty, roasted, nutty, and savory
213 flavors (Lee et al., 2021). In contrast to furans, high pH condition favors the formation
214 of nitrogen-containing heterocyclic compounds (de Sousa Fontes et al., 2024).
215 Additionally, a high heating temperature is necessary for the interaction between amines
216 and α -dicarbonyls through the Strecker degradation to produce nitrogen-containing
217 heterocyclic compounds (Liu et al., 2015).

218 In addition, aldehydes may account for a large portion depending on the type and
219 composition of precursors within the model (Wei et al., 2020). Aldehydes are derived
220 from lipid oxidation during thermal treatment or Strecker degradation (Liu et al., 2023;
221 Zheng et al., 2022). These VOCs elicit species-specific fatty odors (Shen et al., 2021).
222 Therefore, aldehydes are regarded as important VOCs in the formation of meat flavor.
223 Other kinds of VOCs e.g. acids, alcohols, esters, and ketones, have high odor
224 thresholds. However, these compounds have a complementary role in the overall flavor
225 of MRPs and can be utilized as precursors for further reactions (Ye et al., 2022).

226

227 **Maillard reaction model system consisting of animal resources**

228 A list of Maillard reaction model systems with animal resources in the previous
229 literature is presented in Table 2. Most studies applied aquatic products, beef, chicken,
230 and pork protein extracts or hydrolysates into the model system. In particular,
231 enzymatic hydrolysates from animal by-products such as bones and fish heads are
232 widely used for the model systems, as a direct application of these hydrolysates into the
233 food industry is limited due to their bitter tastes and undesirable off-odors. The
234 conversion of animal by-product hydrolysates into flavorful compounds through the
235 Maillard reaction has been reported in many studies (Chiang et al, 2019; Sun et al.,
236 2014; Zhang et al., 2020).

237 The resultant MRPs possessed a variety of VOCs, including representative VOCs
238 responsible for meat flavor such as 2-furfurylthiol, 2-methyl-3-furanthiol, furfural, 2-
239 pentylfuran, 2,5-dimethylpyrazine, and hexanal (Table 1). Depending on the content of
240 sulfur-containing amino acids in the animal protein hydrolysates used, there might be a
241 need for additional amino acid input into the model system to better develop a complex
242 and long-lasting meat flavor (de Sousa Fontes et al., 2024).

243

244 **Aquatic products**

245 A lot of by-products from aquatic products such as fish heads, bones, and skins are
246 discarded in the industry (Gan et al., 2022). Instead of processing these by-products into
247 animal feed ingredients or fertilizers that have a low market value, upcycling them into
248 value-added food ingredients through enzymatic hydrolysis is regarded as an effective
249 strategy (Li & Liu, 2021). However, a strong bitter taste, unpleasant fishy odor, and off-
250 flavor of fish hydrolysates are limiting factors for their application as flavorings (Dong
251 et al., 2019; Gao et al., 2020; Li, Wang et al., 2021). To address this issue, the

252 utilization of aquatic products protein hydrolysates in the Maillard reaction has been
253 widely conducted.

254 The application of Antarctic krill hydrolysates into the model system was conducted
255 by Zhang et al. (2020). An Antarctic krill contains a high fluorine content of which
256 continuous consumption may provoke osteosclerosis, renal disease, or allergies.
257 However, the bitterness of the defluorinated Antarctic krill hydrolysates makes them
258 unacceptable to consumers. The Maillard reaction of Antarctic krill hydrolysates with
259 xylose successfully enhanced the sweet, roasted, shrimp meat aromas, owing to the
260 generation of pyrazines which were the main VOCs in the MRPs, along with aldehydes
261 and ketones. Dong et al. (2019) applied ultrasonic-assisted thermal treatment for the
262 production of mussel meat hydrolysates-based MRPs in an attempt to reduce the bitter
263 taste of the mussel. Heating for 90 min effectively suppressed the bitter taste and
264 increased the pleasant meat and fishy odor intensities of MRPs. In another study
265 conducted by Li, Wang et al. (2021), the grass carp bone hydrolysates-based MRPs
266 showed an increased ratio of umami-sweet taste amino acid to total amino acid, which
267 could lead to the flavor enhancement of the hydrolysates. Furthermore, after the
268 Maillard reaction, the kinds of aldehydes, alcohols, ketones, pyrazines, and other VOCs
269 increased, which may contribute to the masking effect of fishy off-odor. Meanwhile, the
270 flavor of protein hydrolysates from aquatic products can be improved by adding
271 cysteine and xylose into the Maillard reaction model system. Normah and Noorasma
272 (2018) investigated the effect of the addition of cysteine and xylose on the flavor of
273 mud clam hydrolysates and found that the additional cysteine and xylose significantly
274 strengthened the meaty flavor, umami and caramel taste due to the increased amount of
275 sulfur-containing heterocyclic compounds, furfural, and umami amino acids, and
276 decreased the fish off-odor and bitter taste intensity of the MRPs. Gao et al. (2020)

277 added fermented tilapia fish head hydrolysate into the cysteine-xylose model system
278 and optimized the reaction condition through response surface methodology based on
279 the production of 2-methyl-3-furanthiol and 2-furfurylthiol, which are two important
280 VOCs in exhibiting meaty flavor. The authors suggested that the flavor of fish
281 hydrolysates could be improved by the production of sulfur-containing heterocyclic
282 compounds via the Maillard reaction.

283

284 **Beef**

285 A few studies used beef hydrolysates derived from the hydrolysates in the model
286 system (Akbarabadi et al., 2020; Kang et al., 2019; Song et al., 2012). Zou et al. (2019)
287 revealed that specific peptides such as Cys-Gly-Val from beef hydrolysates acted as
288 effective precursors for key VOCs like 2-methyl-3-furanthiol and 4-butyl-2,5-
289 dimethylthiazole, significantly enhancing roasted and meaty flavors. However, a major
290 source of beef protein hydrolysates that has been universally used in the previous
291 literature is bovine bone, a high volume of meat by-product found in the industry
292 (Chiang et al., 2019; Song et al., 2016; Xu et al., 2018; Zheng et al., 2022). Bovine bone
293 marrow extract, or bone collagen, contains approximately 20-30% of protein content
294 (Song et al., 2016; Xu et al., 2019). Owing to their abundant protein content, the
295 utilization of bovine bone hydrolysates in the Maillard reaction can contribute to the
296 production of value-added products.

297 Xu et al. (2019) compared the sensory attributes of two MRPs that contained
298 hydrolyzed or unhydrolyzed bovine bone marrow extracts. The results revealed that 35
299 VOCs were found in the former, whereas only 22 VOCs were identified in the latter.
300 Furthermore, the overall content of the VOCs and the intensity of meaty aroma were
301 much higher in the MRPs prepared with hydrolyzed bovine bone marrow extracts,

302 suggesting that moderate hydrolysis is essential for bovine bone marrow extract.
303 Similarly, Begum et al. (2020) investigated the effect of the Maillard reaction on the
304 flavor development of bovine bone marrow extracts and their hydrolysates. The authors
305 observed that the meaty, roasted, and caramel aromas and umami, kokumi, and mellow
306 tastes were significantly enhanced in MRPs when the bovine bone marrow extracts
307 were enzymatically hydrolyzed. On the other hand, the undesirable fishy and sulfurous
308 aromas and bitter taste were weakened.

309 In addition to muscle and bone protein hydrolysates, beef tallow is a great precursor
310 that significantly contributes to the formation of beefy flavor in MRPs. A different
311 percentage from 2 to 20% of enzymatically hydrolyzed beef tallow was added into the
312 model system containing bovine bone hydrolysates, hydrolyzed vegetable proteins, and
313 yeast extract and heated at 110°C for 100 min (Chai et al., 2018). The authors reported
314 that the intensities of meaty and beefy flavors were the strongest while that of off-flavor
315 was the weakest in the MRPs when containing 10% of beef tallow hydrolysates,
316 whereas additional tallow increased tallowy flavor but decreased beefy flavor. Zheng et
317 al. (2022) investigated the role of phospholipids on the flavor of the bovine bone protein
318 hydrolysate-based MRPs. The results showed that the furan, thiophene, thioethers, and
319 alcohol contents were significantly higher when the model system included
320 phospholipids, suggesting that phospholipids could influence the VOC composition and
321 the sensory characteristics of MRPs.

322

323 **Chicken**

324 Chicken meat is a widely available meat product. Chicken meat has a strong umami
325 taste due to the high content of umami amino acids and flavor nucleotides (Jayasena et
326 al., 2013). Owing to this advantage, chicken meat is also a great participant in the

327 improvement of the umami taste of MRPs. Zhang et al. (2019) prepared chicken peptide
328 hydrolysates on the model system and reported the enhancement of boiled chicken
329 flavor and umami taste, continuity, mouthfulness, and overall acceptance. Xiao et al.
330 (2015) compared the effect of the chicken base content on the flavor of MRPs.
331 Depending on the chicken base content, the intensity of caramel and meaty flavor,
332 continuity, and umami taste of MRPs differed significantly, whereas the MRPs without
333 chicken base exhibited the strongest off-flavors with the lowest sensory attributes
334 abovementioned. This result confirms that the addition of chicken meat can be
335 beneficial for meat flavor improvement.

336 Chicken bone proteins as well as chicken meat proteins have been frequently used for
337 the model system due to the low cost (Chen et al., 2021). Conversely, in Asia and
338 Australia, meat flavorings that were prepared through the Maillard reaction of chicken
339 bone hydrolysates are regarded as a non-conventional food (Wang et al., 2016).
340 Therefore, the processing of hydrolysates from chicken by-products would be promising
341 for the production of profitable and marketable meat flavorings (Sun et al., 2014). The
342 bitter taste of chicken bone hydrolysates could be reduced through the Maillard reaction
343 which alters the free amino acid composition, ultimately affecting the taste of the
344 products (Sun et al., 2014). Especially, the umami intensity of the chicken bone
345 hydrolysate-based MRPs showed an increase until 60 min of reaction and then a
346 decrease at 90 min.

347 Meanwhile, Chicken liver has a high cholesterol content and exhibits an unpleasant
348 smell. Few studies utilized chicken liver protein hydrolysates on the Maillard reaction
349 model systems (Chen et al., 2021; Xiong et al., 2020). Unfortunately, these studies
350 mainly focused on the bioactivity of the MRPs rather than their organoleptic attributes.

351 Future studies on the utilization of chicken liver protein as meat flavorings through the
352 Maillard reaction would broaden the market value of chicken liver.

353 In addition to protein sources, chicken fat has been extensively studied using model
354 systems due to its ability to amplify meat flavor (Wei et al., 2020; Xia et al., 2021).
355 Zhao et al. (2019) demonstrated that the interactions between the degradation products
356 of chicken fat and the intermediate products from the Maillard reaction generated
357 unique VOCs including 2-pentylthiophene and 2-pentylpyridine that enriched stewed
358 meat-like aromas. Similarly, Yang et al. (2015) showed that the inclusion of chicken fat
359 in a cysteine-glucose reaction system suppressed the formation of sulfur-containing
360 VOCs while promoting the formation of alkyl heterocyclic compounds and aliphatic
361 aldehydes and ketones which led to the enhancement of species-specific flavor.

362

363 **Pork**

364 In terms of pork, bone proteins, plasma proteins, and gelatins as well as meat have
365 been applied to the model system (Benjakul et al., 2005; Qi et al., 2024; Tan et al.,
366 2012; Tan et al., 2013). However, only limited literature focused on the sensory
367 attributes of porcine protein hydrolysates-based MRPs (Li & Liu, 2021; 2022a; 2022b).
368 A major finding was the evident savory, roasted, meaty, fruity, and sweet flavors of the
369 MRPs which contained yeast and/or lactic acid bacterium-fermented pork hydrolysates,
370 with a dominant content of 2-furfurylthiol. The glycation of pork plasma and muscle
371 hydrolysates through the Maillard reaction with glucosamine was shown to be effective
372 in reducing their bitterness and increasing the favorable sensory characteristics (Fu et
373 al., 2020).

374 Some researchers added lard to the model system to identify the role of lard in the
375 formation of pork flavor in the MRPs. Song et al. (2017) found that aldehydes were the

376 main compounds in the lard, such as hexanal, (Z)-2-decenal, and (E,E)-2,4-decadienal.
377 Lard, especially enzymatically hydrolyzed lard, showed a considerable effect on the
378 increase in the meaty and porky aroma intensity. The increase in the lipid oxidation-
379 derived VOCs such as alcohols, alkylfurans, and acids was observed by the addition of
380 lard, on the other hand, it showed a suppression effect of the formation of sulfur-
381 containing heterocyclic compounds. In a similar study conducted by Xu et al. (2011),
382 the presence of lard in a cysteine-xylose model system had an effect on suppressing the
383 formation of sulfur-containing VOCs while increasing the production of lipid oxidation-
384 derived VOCs, which may have a benefit on balancing sulfurous and fatty and roasted
385 characteristics, highlighting the key role of lard in modulating flavor profiles in the
386 Maillard reaction systems.

387

388 **Factors affecting the flavor of MRPs**

389 The development of meat flavor through the Maillard reaction is greatly influenced
390 by various parameters: source and concentration of the reactants, degree of lipid
391 oxidation, heating temperature and time, initial pH, buffer type and concentration, etc.
392 (Chiang et al., 2019; Shen et al., 2021; Zeng et al., 2017). It is essential to modulate the
393 abovementioned parameters and select the suitable reaction condition to strengthen the
394 desirable organoleptic attributes of MRPs while limiting the formation of off-flavor and
395 toxic compounds (Figure 2).

396

397 **Source of an amino group**

398 In a simple model system consisting of one or two kinds of pure amino acids and a
399 reducing sugar, the type of amino acid determines the flavor characteristics of the MRPs
400 (Aaslyng & Meinert, 2017; Wong et al., 2008). On the other hand, when the model

401 system contains animal protein hydrolysates or their resulting peptides, the mechanism
402 of the Maillard reaction is greatly influenced by the degree of hydrolysis, molecular
403 weight, and amino acid composition and sequence of the peptides (Normah &
404 Noorasma, 2018).

405 When MRPs are prepared with animal protein sources, enzymatic hydrolysis of
406 protein is necessary to provide amino acids and peptides that are the main participants
407 in the Maillard reaction. If the degree of hydrolysis of the sample is low, it would lead
408 to a weak meat flavor of MRPs. On the other hand, MRPs containing animal protein
409 hydrolysates with an excessive degree of hydrolysis may exhibit a strong burnt and
410 sulfurous aroma which can hamper the perception of meaty flavor. Zhang et al. (2019)
411 found that MRPs containing chicken protein hydrolysates prepared for 2-3 h of
412 hydrolysis procedures showed the strongest boiled chicken flavor, mouthfulness, and
413 overall acceptance. Xu et al. (2019) reported that the bovine bone marrow hydrolysate
414 with a 10% degree of hydrolysis was the most effective in enhancing the meaty and
415 roasted flavor and suppressing the formation of burnt aroma in MRPs.

416 Enzymatic hydrolysis of protein produces peptides with varying molecular weights.
417 Many researchers observed that low-molecular-weight peptides at approximately 1-5
418 kDa or smaller are the main precursors for the production of meaty aroma, which is
419 attributed to a large number of free amino groups with high reactivity toward reducing
420 sugars (Nie et al., 2017). Kang et al. (2019) observed that MRPs containing beef
421 hydrolysates with < 1000 Da showed higher intensity of meaty aroma, umami, and
422 kokumi taste, whereas MRPs with beef hydrolysates > 5000 Da did not show any
423 improvement in the meat flavor.

424 After hydrolyzing animal proteins, the resultant hydrolysates contain various kinds of
425 amino acids and peptides. The reactivity of each amino acid may vary when they are

426 present in the peptides (Xu et al., 2013). For example, cysteine releases H₂S more easily
427 when present as a free amino acid rather than as a peptide form (Zou et al., 2019). The
428 authors also identified that within peptides, Cys-Gly-Val showed a better contribution to
429 the meaty aroma, followed by glutathione, compared to Leu-Cys. It was revealed that
430 the position of cysteine, leucine, isoleucine, or phenylalanine at the N- or C-terminus
431 affects the reactivity of the peptides toward the Maillard reaction, which the former
432 favors the reaction whereas the latter shows less reactivity (Kang et al., 2019).
433 Meanwhile, leucine, isoleucine, valine, and phenylalanine in the peptide can participate
434 in the Strecker degradation although these amino acids are bound to the peptide (Liu et
435 al., 2015).

436 Finally, the different amino acid sequence of the peptide affects the formation of
437 VOCs in MRPs. Zhou et al. (2019) observed that pyrazines and pyridines were
438 generated in the model system consisting of carnosine, whereas sulfur-containing
439 heterocyclic compounds instead of nitrogen-containing heterocyclic compounds were
440 the main VOCs in the model systems which possessed glutathione or chicken protein-
441 derived dipeptide Cys-Gly due to the presence of cysteine in the peptide sources. Xu et
442 al. (2013) compared the resultant VOCs from the Maillard reaction of three beef protein
443 peptides, Asp-Trp-Glu-Phe-Pro-Asp-Pro-Lys, Gly-Val-Thr-Val-Phe-Glu-Asp-Leu-Lys,
444 and Glu-Thr-Asp-Asn-Leu-Asp-Ser-Val-Pro-Arg, and found that the formation of 2-
445 furfurylthiol was facilitated only when the first peptide was put into the model system.

446

447 **Type of reducing sugar**

448 The content of reducing sugar in the meat hydrolysates is a trace level (Li & Liu,
449 2021). Without reducing sugars added, the model system containing animal protein
450 hydrolysates would not exhibit strong meaty flavors (Chai et al., 2018). Therefore, the

451 addition of reducing sugar is essential for provoking a desirable flavor. However, the
452 rate of reaction differs significantly depending on the type of reducing sugar, due to the
453 different chemical structure that determines its reactivity (Chiang et al., 2019; Liu et al.,
454 2014; Zheng et al., 2022). It is well-documented that pentoses have a higher reaction
455 rate than hexoses (Gao et al., 2020; Xu et al., 2013; Zou et al., 2019). In the study
456 conducted by de Souza Cunha et al. (2023), the chicken bone hydrolysate-based MRPs
457 with xylose showed a higher browning intensity and higher proportions of aldehydes
458 such as decanal, octanal, pentanal, phenylacetaldehyde, (E)-2-octenal, (E,E)-2,4-
459 decadienal compared to those with glucose. Among aldopentoses, ribose was found to
460 be more reactive with shrimp hydrolysates during Maillard reaction compared to xylose
461 and arabinose, partially due to the higher proportion of acyclic carbonyls with less
462 stable ring form of ribose (Laroque et al., 2008). Meanwhile, the nature of reducing
463 sugar also affects its reactivity. Mottram and Nobrega (2002) compared the reactivity of
464 three forms of ribose and found that ribose 5'-monophosphate was the most reactive,
465 followed by free ribose, and inosine 5'-monophosphate was the least reactive in the
466 model system.

467 Compared to amino acids, the effect of reducing sugar on the sensory attributes of
468 MRPs is less significant (Chiang et al., 2019; de Souza Cunha et al, 2023; Zheng et al.,
469 2022). However, as the type of reducing sugar can largely influence the rate of the
470 reaction and formation of VOCs, it is still important to consider which sugar should be
471 used in the model system studies.

472

473 **Lipid oxidation**

474 The addition of animal lipids into a model system results in a differentiated flavor
475 characteristic of MRPs. In many cases, the heating condition for the Maillard reaction

476 model system would not be intense enough to cause lipid oxidation, and therefore a
477 fresh, non-oxidized lipid exists mainly as insoluble triglycerides, partially contributing
478 to the overall meat flavor (Song et al., 2017; Ye et al., 2022). Therefore, a moderate
479 degree of lipid oxidation is a prerequisite for animal fats to influence the overall flavor
480 of MRPs. Nonetheless, excessive lipid oxidation should be avoided as it produces high
481 content of lipid oxidation-derived VOCs, especially aldehydes such as hexanal, octanal,
482 and nonanal which give an unpleasant odor at high concentrations (Ma et al., 2020;
483 Song et al., 2012).

484 It was found that the choice of pre-oxidation method of animal lipid exhibited a
485 significant effect on the sensory characteristics of MRPs. Recently, the combination of
486 enzymatic hydrolysis and mild thermal treatment (below 100°C) proved its
487 effectiveness in enhancing the overall flavor of meat. Ye et al. (2022) found that the
488 addition of moderately-oxidized beef tallow through enzymatic hydrolysis combined
489 with mild thermal oxidation (90°C for 3 h) enhanced the meaty, umami, fatty, and
490 overall taste of the MRPs.

491 Additionally, oxidized animal fat has an inhibitory effect on the formation of sulfur-
492 containing heterocyclic compounds during the Maillard reaction (Xia et al., 2021). In
493 general, sulfur-containing heterocyclic compounds are highly associated with meaty and
494 roasted flavor; however, at high concentrations, these compounds have strong sulfurous
495 odors with unpleasant aromas (Xu et al., 2011). Following oxidation, the degradation
496 products of lipids react with amino acids and attenuate the release of H₂S, subsequently
497 suppressing the formation of sulfur-containing heterocyclic compounds (Wang et al.,
498 2022; Zhao et al., 2019). This, in turn, mitigates the strong sulfurous odors from sulfur-
499 containing heterocyclic compounds and strengthens the evident meaty aroma (Yang et
500 al., 2015). The improvement of the desirable flavor of MRPs with the addition of

501 moderately-oxidized animal fats is highly attributed to the formation of sulfur-free
502 oxygen-containing heterocyclic compounds which present caramel, sweet, fruity, and
503 nutty aromas (Ye et al., 2022).

504

505 **Heating condition**

506 Ketones, which mainly derive from sugar degradation, can be formed at temperatures
507 below 80°C (Liu et al., 2015; Sun et al., 2022). On the other hand, the formation of
508 important VOCs including nitrogen-, oxygen-, and sulfur-containing heterocyclic
509 compounds favors high temperatures above 100°C (Sohail et al., 2022). As the rate of
510 Maillard reaction increases with the increase in heating temperature, a high-temperature
511 heating (100-120°C) of the model system has been widely used to generate a strong,
512 pleasant roasted, and meaty flavor. However, the Maillard reaction at an excessively
513 high temperature (> 150°C) may give rise to burnt and off-flavors with hazardous
514 compounds including acrylamide, polyaromatic hydrocarbons, heterocyclic amines,
515 benzenes, formaldehyde, etc. (Augustine & Bent, 2022; Bassam et al., 2022).

516 Chai et al. (2018) reported that MRPs from the bovine bone hydrolysates-based
517 model system prepared at 90°C had low intensities of meaty, beefy, and tallowy flavor,
518 but these flavor intensities then increased gradually as the temperature rose and peaked
519 at 110°C. However, when the heating temperature exceeded 120°C, the burnt and off-
520 flavor of the MRPs became noticeable. Similar results were reported in the chicken
521 protein-based Maillard reaction model system (Liu et al., 2015). A low-temperature
522 heating was beneficial for broth-like flavor with strong umami and kokumi tastes,
523 whereas a higher temperature heating led to a dominant nutty/roasted aroma of MRPs.
524 In a study conducted by Gao et al. (2020), the tilapia fish head hydrolysate-based MRPs
525 contained more 2-furfurylthiol as the heating temperature increased from 150 to 190°C.

526 Heating time is another factor that determines the VOC composition of MRPs. A
527 balance between the production of desirable VOCs that elicit meaty and roasted flavors
528 and the limitation of burnt odor, off-flavor, and bitterness can be achieved by carefully
529 controlling the heating time of model systems. The taste of MRPs changes as the
530 composition of amino acids and carbohydrates changes by the thermal degradation of
531 animal peptides, caramelization, and the interaction between amino acids and reducing
532 sugars, along with the effect of newly produced polymers by Maillard reaction (Dong et
533 al., 2019; Sun et al., 2014). Commonly adopted heating time for animal resources-based
534 model systems ranges from 60-120 min, or up to 180 min (Sun et al., 2010; Xin et al.,
535 2022; Ye et al., 2022). Few studies conducted a very short (-30 min) or long period
536 (300-600 min) of the thermal process for model systems (Chiang et al., 2019;
537 Karnjanapratum et al., 2016; Su et al., 2016; Zhao et al., 2019).

538

539 **Solvent pH**

540 When preparing an aqueous model system, either distilled water or buffer can be
541 used. The rate of the Maillard reaction and subsequent formation of VOCs vary
542 depending on the pH of the model system (Mottram & Nobrega, 2002). Specifically, the
543 amino group of the amino acids becomes more protonated when the solvent is acidic,
544 which decreases the interaction with carbonyl groups (de Sousa Fontes et al., 2024).
545 Subsequently, an acidic pH condition favors the formation of furans and thiols, while
546 suppressing the formation of pyrazines. On the other hand, higher pH catalyzes the
547 reaction by promoting the formation of Schiff base, leading to the increased formation
548 of VOCs, especially pyrazines and Strecker's aldehydes (Lotfy et al., 2021).

549 In the case of using buffer solutions, the pH of the model systems ranged from 5.5 to
550 7.5 in most studies. In the study conducted by Chai et al. (2018), MRPs which contained

551 bovine bone hydrolysates and were prepared at pH 6.5 and 7.0 showed dominant meaty,
552 beefy, tallowy odors and low degree of off-flavor. Li, Wang et al. (2021) applied
553 response surface methodology to optimize the pH, heating temperature, and heating
554 time for preparing grass carp bone protein hydrolysate-based MRPs, and found that the
555 highest degree of graft would be obtained at initial pH of 7.07 when heated at 118.33°C
556 for 1.75 h. de Sousa Fontes et al. (2024) compared two goat protein hydrolysates-based
557 model systems with different pH adjustment, and observed that more acidic condition
558 (pH 4) led to strengthened meaty aroma, whereas less acidic condition (pH 6) increased
559 sweet, fatty, and goat aroma. On the other hand, a strong alkaline model system was
560 adopted in some studies, e.g. pH 8.26 for flatfish byproduct hydrolysates; pH 8.5 for
561 Antarctic krill hydrolysates; and pH 12 for crocodile meat protein sources (Choe et al.,
562 2016; Li, Hu et al., 2021; Zhang et al., 2020).

563

564 **Conclusion**

565 The Maillard reaction model system is an effective tool for understanding the
566 mechanism of the reaction and developing the meat flavor or flavor additives from a
567 mixture of amino acids and reducing sugars. Although animal resources are less
568 highlighted than plant proteins as reactants in the model system, these precursors have
569 great potential in terms of both academic research and industrial application due to their
570 great contribution to meat flavor enhancement with animal by-products. Considerations
571 should be made when animal resources are applied to the model system, such as the
572 source of amino groups, type of reducing sugars, degree of lipid oxidation, and heating
573 and solvent conditions. For now, these model systems face challenges in simulating
574 meat flavor as the formation pathways of meat flavor in real meat are much more
575 complex to elucidate. Future studies with a more complex combination of flavor

576 precursors from animal resources in more diverse reaction conditions may broaden our
577 understanding of the formation of meat flavor and provide an insight into the upcycling
578 of animal by-products into high market-value products.

579

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888

889 **Tables and Figures**

890 Table 1. Representative volatile organic compounds found in the Maillard reaction

891 model system with the use of animal resources

No.	Compound	Odor characteristics	References
<i>Acids</i>			
1	Acetic acid	Sour, pungent	1, 3, 14, 15, 20, 21, 24, 26, 27, 31
2	Benzoic acid		14, 20, 26, 27
3	Butanoic acid	Cheesy	1, 14, 24, 26
4	Decanoic acid		3, 14, 16, 21, 25, 26
5	Hexanoic acid	Fatty, pungent, sweet	1, 3, 7, 8, 13, 19, 21, 22, 25, 26
6	Heptanoic acid	Cheesy, fatty, sour, rancid	1, 4, 7, 13, 22, 25, 26
7	Nonanoic acid	Cheesy, diary, waxy	1, 3, 6, 7, 13, 14, 16, 17, 22, 25, 26
8	Octanoic acid	Cheesy, fatty, greasy, oily, pungent, rancid	1, 4, 6, 7, 8, 13, 14, 15, 16, 21, 22, 25, 26
9	Pentanoic acid	Acidic, sweaty, rancid	3, 6, 7, 25, 26
10	Propionic acid	Beany	24, 26, 27
11	3-Methylbutanoic acid		13, 24, 27
<i>Alcohols</i>			
12	Benzyl alcohol		9, 11, 13, 14
13	1-Heptanol	Fruity, nutty, waxy	2, 7, 9, 13, 14, 15, 17, 19, 20, 22, 25, 26

14	1-Hexanol	Fermented, green, oily	2, 4, 7, 8, 9, 11, 13, 14, 15, 19, 25
15	1-Octanol	Citrus, green, fatty, fruity, mushroom, pungent, waxy	2, 3, 4, 7, 9, 11, 13, 14, 15, 19, 20, 21, 22, 23, 24, 25, 26, 27, 29
16	1-Octen-3-ol	Earthy, meaty, mushroom, oily	2, 3, 4, 8, 9, 11, 13, 15, 17, 19, 20, 22, 25, 26, 29
17	1-Pentanol	Baked, oily, pungent	2, 4, 7, 8, 11, 13, 14, 15, 19, 20, 25
18	1-Penten-3-ol		9, 13, 15
19	2-Ethyl-1-hexanol	Citrus, oily, sweet	4, 9, 13, 15, 17
20	2-Furanmethanol	Burnt	1, 2, 13, 24
<i>Aldehydes</i>			
21	Benzaldehyde	Almond, nutty, oily	1, 2, 4, 5, 6, 8, 9, 10, 11, 13, 14, 15, 16, 17, 21, 23, 24, 26, 27, 29
22	Benzeneacetaldehyde	Fermented, flowery, fruity, sweet	3, 4, 6, 8, 10, 26, 27
23	Decanal	Citrus, pungent, soapy, tallowy, waxy	2, 3, 4, 13, 16, 17, 19, 20, 29
24	Heptanal	Fatty, fresh, fruity, green, oily	2, 3, 4, 7, 8, 9, 11, 13, 14, 15, 17, 19, 20, 22, 23, 25, 27, 30
25	Hexadecanal		4, 13, 16

26	Hexanal	Grass, green	2, 4, 6, 8, 9, 13, 14, 15, 17, 19, 20, 21, 22, 23, 26, 27, 29
27	Methional	Earthy, potato	4, 8, 26, 31
28	Nonanal	Citrus, fatty, green, nutty, soapy, waxy	2, 3, 4, 7, 8, 9, 11, 13, 14, 16, 17, 19, 20, 22, 23, 25, 26, 29
29	Octanal	Citrus, fatty, fruity, pungent, sour	2, 3, 4, 7, 11, 13, 14, 15, 16, 19, 20, 22, 23, 24, 25, 26
30	Pentanal	Baked, fermented	2, 4, 8, 9, 15, 17, 19, 20
31	Tetradecanal	Creamy, greasy	4, 16, 17
32	Undecanal	Fatty, pungent, waxy	4, 13, 16, 17, 23
33	2-Dodecenal	Fatty, pungent	19, 20, 26
34	2-Methylbutanal	Cocoa, coffee, nutty	4, 8, 9, 15, 24
35	2-Methylpropanal	Chocolate, fresh, malty, pungent	4, 6, 9, 10
36	2-Octenal		8, 15, 21
37	3-Methylbutanal	Chocolate, fatty, greasy, malty	4, 6, 9, 10, 15, 17, 19, 21, 23, 31
38	(E)-2-Decenal	Earthy, fatty, greasy, waxy	2, 3, 4, 11, 13, 17, 19, 22, 25
39	(E)-2-Heptenal	Fatty	2, 15, 19, 20, 22, 25
40	(E)-2-Hexenal		2, 13, 20, 25

41	(E)-2-Nonenal	Cucumber, fatty, greasy, green, tallowy	2, 3, 4, 11, 19, 20, 23, 25
42	(E)-2-Octenal	Greasy, green, herbal	2, 3, 4, 6, 19, 20, 22, 23, 25
43	(E)-2-Undecenal	Fresh, fruity	3, 4, 25
44	(E,E)-2,4-Decadienal	Chicken, fatty, fried, greasy	2, 3, 4, 9, 11, 12, 13, 20, 22, 25
45	(E,E)-2,4-Heptadienal		9, 20, 22, 25
46	(E,E)-2,4-Hexadienal	Fatty, green	9, 18, 19, 25
47	(E,E)-2,4-Nonadienal	Fatty, waxy	2, 3, 9, 11, 12, 13, 20, 22, 25
<i>Ester</i>			
48	Ethyl acetate	Fruity	6, 15, 27
<i>Furans</i>			
49	Furfural	Almond, baked, caramel, sweet	1, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 19, 21, 23, 28, 29, 30
50	2-Acetylfuran	Almond, balsamic, nutty, sweet	4, 14, 15, 19, 21, 24, 28, 30
51	2-Butylfuran	Spicy, sweet, winey	6, 8, 10, 12, 23, 25, 27
52	2-Ethylfuran	Burnt, earthy, malty, sweet	6, 8, 9
53	2-Furanmethanol	Caramel, roasted	10, 19, 26
54	2-Heptylfuran		7, 8, 22, 29
55	2-Hexylfuran		2, 4, 7, 8, 11, 25, 29

56	2-Methylfuran	Chocolate, ethereal	1, 4, 7, 9, 11, 14, 21
57	2-Octylfuran		6, 7, 8, 22, 25, 26
58	2-Pentylfuran	Buttery, earthy, fatty, green bean, meaty	2, 3, 4, 6, 7, 8, 9, 11, 13, 14, 15, 19, 20, 21, 22, 23, 25, 26, 27, 29
59	3-Phenylfuran		1, 4, 5, 6
<i>Hydrocarbons</i>			
60	Dodecane		3, 4, 5, 6, 20
61	Tetradecane		3, 4, 5, 6, 9, 17, 20, 29
62	Toluene	Paint	5, 20, 24, 30
<i>Ketones</i>			
63	Acetophenone	Almond, hawthorn	13, 24, 26
64	1-Octen-3-one	Earthy, herbal, mushroom	6, 15, 20
65	2-Butanone	Camphor, ether, fruity, sweet	4, 10, 14, 15, 24
66	2-Decanone	Floral, greasy	3, 4, 22, 25, 27
67	2-Heptanone	Fatty, fruity, soapy, sweet	3, 4, 7, 8, 9, 14, 17, 19, 25, 26, 27, 29
68	2-Nonanone	Fruity, herbal, musty, soapy, sweet	3, 4, 11, 13, 14, 16, 19, 22, 23, 26, 27
69	2-Octanone	Earthy, fruity, herbal	2, 3, 4, 6, 7, 13, 14, 17, 21, 26
70	2-Pentanone	Fruity, sweet	14, 23, 24
71	2-Undecanone	Fatty, fruity, oily	4, 11, 13, 25, 27

72	2,3-Octanedione	Asparagus, coriander	2, 4, 27
73	2,3-Pentanedione	Almond, buttery, fruity, toasted	4, 14, 23, 24
74	3-Octanone	Cheesy, fresh, mushroom, musty, sweet	4, 6, 27
75	5-Methyl-2-hexanone	Sweet	1, 23, 29
<hr/>			
<i>Phenol</i>			
76	Phenol		13, 14, 15
<hr/>			
<i>Pyrazines</i>			
77	Pyrazine	Nutty	10, 21, 27, 30
78	Methylpyrazine	Nutty, roasted	2, 9, 10, 24
79	Tetramethylpyrazine	Chocolate, meaty, roasted	3, 10, 26
80	Trimethylpyrazine	Baked, nutty, roasted	1, 3, 10, 14, 24
81	2-Ethyl-5-methylpyrazine	Popcorn	1, 2, 10, 26
82	2-Ethyl-6-methylpyrazine		1, 3, 26
83	2-Methylpyrazine	Chocolate, meaty, nutty, roasted	1, 4, 14, 19, 26, 27, 30
84	2,3-Dimethylpyrazine	Popcorn, roasted	10, 14, 24, 27
85	2,5-Dimethylpyrazine	Chocolate, cocoa, creamy, meaty, nutty, popcorn, roasted	1, 4, 5, 10, 12, 14, 19, 24, 26, 27
86	2,6-Dimethylpyrazine	Chocolate, meaty, nutty, roasted	1, 2, 9, 14, 15, 24, 26, 27

87	3-Ethyl-2,5-dimethylpyrazine	Nutty, roasted	1, 9, 10, 16, 24, 26, 27
88	3,5-Diethyl-2-methylpyrazine	Baked	1, 16, 24
<i>Pyridine</i>			
89	Pyridine	Burnt, roasted	10, 12, 13, 30
<i>Pyrroles</i>			
90	Pyrrole	Nutty, pungent	14, 15, 26
91	1-Furfurylpyrrole	Caramel, coffee, nutty, toasted	1, 4, 14, 26
92	2-Acetylpyrrole	Nutty	1, 19, 21, 24, 28
<i>Thiazoles</i>			
93	Thiazole	Fishy, meaty, nutty	4, 11, 21, 28, 30
94	2-Acethylthiazole	Meaty, nutty, roasted, toasted	4, 10, 21
95	4-Methylthiazole	Green, nutty, vegetable	4, 9, 21
<i>Thioethers</i>			
96	Bis(2-methyl-3-furyl)disulfide	Meaty, roasted, sulfurous	4, 6, 21, 31
97	Dimethyl disulfide	Onion, sulfurous	1, 5, 6, 7, 14, 29, 31
98	Dimethyl trisulfide	Alliaceous, sulfurous	1, 5, 6, 14, 31
<i>Thiols</i>			
99	2-Furfurylthiol	Burnt, chocolate, coffee, meaty, roasted, toasted	4, 6, 7, 11, 16, 17, 23, 26, 28, 29, 30, 31

100	2-Methyl-3-furanthiol	Coffee, meaty, sulfurous	4, 6, 7, 11, 16, 17, 21, 23, 24, 26, 28, 29, 30, 31
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Thiophenes

101	2-Ethylthiophene	Meaty, styrene	19, 23, 28
102	2-Hexylthiophene	Green, meaty	11, 28, 29
103	2-Methylthiophene	Onion, sulfurous	19, 21, 23, 24, 28, 31
104	2-Pentylthiophene	Fatty, fruity, green, meaty, sweet	19, 28, 29
105	2- Thiophenecarboxaldehyde	Sulfurous	6, 19, 23
106	2,5-Dimethylthiophene	Nutty, sulfurous	6, 19, 28
107	3-Methylthiophene	Greasy, sulfurous, winy	4, 6, 7, 11, 19, 31
108	3- Thiophenecarboxaldehyde	Meaty, roasted, sulfurous	6, 10, 11, 23, 26
109	5-Methyl-2- thiophenecarboxaldehyde	Meaty, roasted, sulfurous	10, 19, 24, 28, 31

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899 al. (2022); 27. Zhang et al. (2020); 28. Zhao et al. (2019); 29. Zheng et al. (2022); 30.
900 Zhou et al. (2019); 31. Zou et al. (2019).

ACCEPTED

901 Table 2. A list of Maillard reaction model systems with the use of animal resources

Amino compound	Carbohydrate	Lipid	Reaction condition	References
<i>Amino compounds from a single source</i>				
Amino acid (Cys)	Glucose	Chicken fat	140°C for 2 h (pH 5.5)	Yang et al., 2015
Amino acid (Cys)	Xylose	Lard	120°C for 1 h (pH 5)	Xu et al., 2011
Amino acid (Cys)	Xylose	Mutton tallow	120°C for 40 min	Ma et al., 2020
Amino acid (Cys)	Xylose	Tallow	120°C for 90 min (pH 5.5)	Lee et al., 2024
Amino acid (Cys, Met)	Xylose	Tallow	120°C for 2 h (pH 7)	Ye et al., 2022
Gelatin (Beef)	Ribose	-	95°C for 15-60 min	Tan et al., 2012
Gelatin (Pork)	Ribose	-	95°C for 15-60 min	Tan et al., 2012
Hydrolysates (Shrimp)	Arabinose, fructose, glucose, ribose, xylose	-	55°C for 6-24 h (pH 6.5)	Laroque et al., 2008

Hydrolysates (Porcine plasma protein)	Fructose, galactose, glucose	-	95°C for 30-360 min	Liu et al., 2014
Hydrolysates (Chicken bone)	Galactose	-	100°C for 90 min	Nie et al., 2017
Hydrolysates (Fish skin gelatin)	Galactose	-	70°C for 36 h	Karnjanapratum et al., 2016
Hydrolysates (Glycosylated bovine bone collagen)	Galactose	-	95°C for 150 min (pH 9)	Qi et al., 2024
Hydrolysates (Glycosylated chicken bone collagen)	Galactose	-	95°C for 150 min (pH 9)	Qi et al., 2024
Hydrolysates (Glycosylated porcine bone collagen)	Galactose	-	95°C for 150 min (pH 9)	Qi et al., 2024
Hydrolysates (Porcine plasma protein)	Galactose	-	95°C for 30-360 min	Liu et al., 2016
Hydrolysates (Chicken liver)	Galactose, glucose, fructose, maltose, sucrose, xylose	-	90°C for 130 min (pH 8)	Xiong et al., 2020
Hydrolysates (Salmon frame)	Glucosamine	-	120°C for 60 min	Sharma et al., 2024

Hydrolysates (Chicken bone extract)	Glucose	-	100°C for 2 h (pH 6.5)	Chiang et al., 2022
Hydrolysates (Grass carp bone)	Glucose	-	120°C for 1 h (pH 6-8)	Li, Wang et al., 2021
Hydrolysates (Half-fin anchovy)	Glucose	-	120°C for 100 min (pH 9)	Song et al., 2018
Hydrolysates (Shrimp by-product)	Glucose	-	110°C for 10 h (pH 6.5)	Zha et al., 2015
Hydrolysates (Chicken bone)	Glucose, xylose	-	113°C for 10 min (pH 6.5)	de Souza Cunha et al., 2023
Hydrolysates (Mechanically deboned chicken residue)	Glucose, xylose	-	90-120°C for 1 h	Sun et al., 2010
Hydrolysates (Mussel)	Glucose, xylose	-	115°C for 2 h (pH 6)	Dong et al., 2019
Hydrolysates (Anchovy)	Ribose	-	110°C for 30 min (pH 7)	Su et al., 2016

Hydrolysates (Bovine bone)	Ribose	-	113°C for 10 min (pH 6.5)	Chiang et al., 2019
Hydrolysates (Bovine bone)	Ribose	-	113°C for 10 min (pH 6.5)	Chiang et al., 2020
Hydrolysates (Flatfish by-product)	Ribose	-	121°C for 38 min (pH 8.26)	Choe et al., 2016
Hydrolysates (Chicken)	Ribose, xylose	-	100°C for 3 h (pH 7.5)	Zeng et al., 2017
Hydrolysates (Antarctic krill)	Xylose	-	105°C for 50 min (pH 8.5)	Zhang et al., 2020
Hydrolysates (Beef tallow)	Xylose	-	100°C for 1 h	Cui et al., 2022
Hydrolysates (Bovine bone marrow)	Xylose	-	120°C for 70 min	Xu et al., 2018
Hydrolysates (Chicken liver)	Xylose	-	120°C for 90 min (pH 7)	Chen et al., 2021
Hydrolysates (Fish head)	Xylose	-	150-190°C for 1-2 h	Gao et al., 2020

Hydrolysates (Fermented pork)	Xylose	-	100°C for 60 min (pH 5.5)	Li and Liu, 2022b
Hydrolysates (Goat protein)	Xylose	-	121°C for 1 h (pH 4 or 6)	de Sousa Fontes et al., 2024
Hydrolysates (Mud clam)	Xylose	-	120°C for 2 h (pH 7.4)	Normah and Noorasma, 2018
Hydrolysates (Pork trimmings)	Xylose	-	90-100°C for 1 h (pH 5.5)	Li and Liu, 2021
Hydrolysates (<i>Takifugu obscurus</i>)	Xylose	-	120°C for 2 h (pH 7.4)	Wang et al., 2019
Hydrolysates (Tuna viscera)	Xylose	-	120°C for 1 h	Boonbumrung et al., 2023
Hydrolysates (Yeast fermented pork)	Xylose	-	100°C for 1 h (pH 5.5)	Li and Liu, 2022a

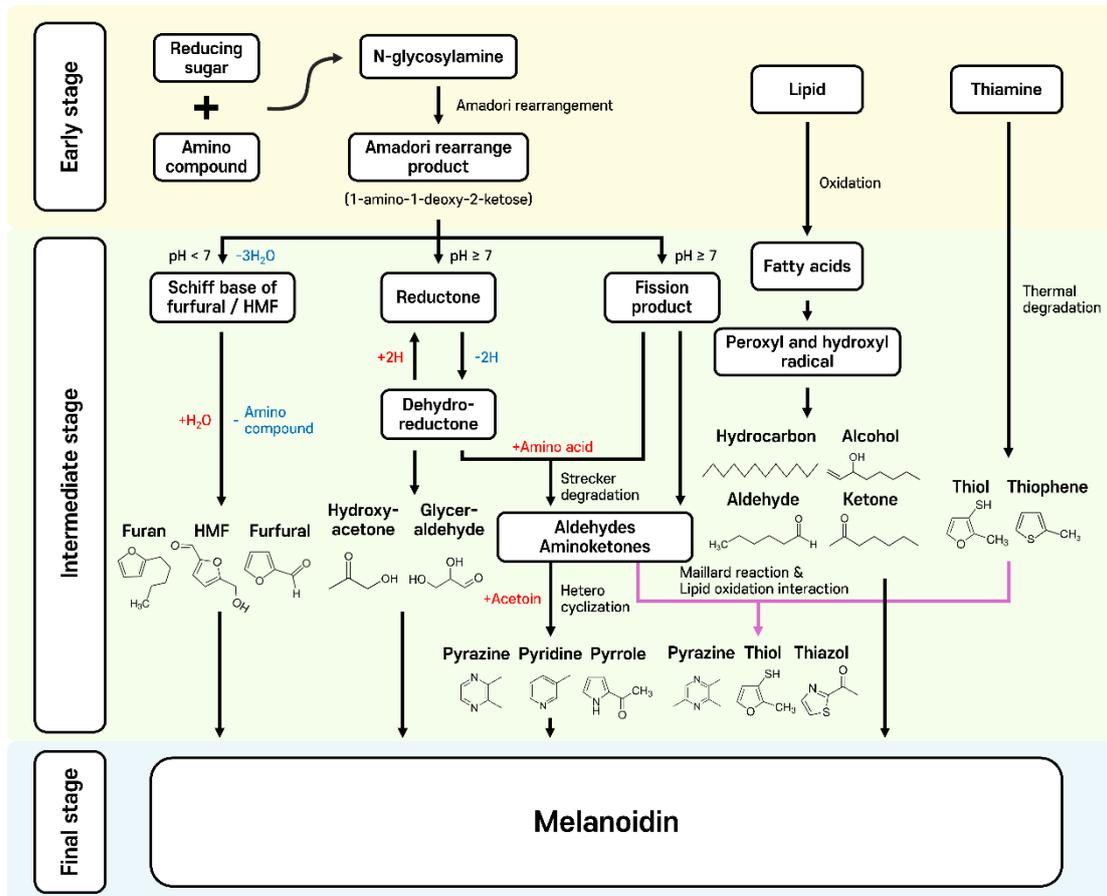
Meat (Beef)	Ribose	-	95°C for 20-100 min	Akbarabadi et al., 2020
Meat (Chicken)	Ribose	-	95°C for 1 h	Tan et al., 2013
Meat (Pork)	Ribose	-	95°C for 1 h	Tan et al., 2013
Meat (Crocodile)	Xylose	-	100°C for 192 min (pH 12)	Li, Hu et al., 2021
Peptides (Chicken)	Glucose	-	90-150°C for 30-240 min	Bai et al., 2017
Peptides (Glutathione)	Glucose	Chicken fat	140°C for 5 h (pH 6.5)	Zhao et al., 2019
Peptides (Chicken)	Ribose	-	180°C for 2 h (pH 6.3)	Zhou et al., 2019
Peptides (Smooth hound hydrolysates)	Sucrose	-	90°C for 120 min	Abdelhedi et al., 2017
Peptides (Beef hydrolysates)	Xylose	-	125°C for 2 h (pH 5.5)	Zou et al., 2019

Peptides (Chicken)	Xylose	-	80-140°C for 30-120 min (pH 6.5)	Liu et al., 2015
Powder (Mussel)	Fructose, glucose, ribose, xylose	-	100-140°C for 60-150 min	Xin et al., 2022
Powder (Oyster)	Galactose, glucose, xylose	-	120°C for 30-150 min (pH 7.0-7.2)	Fu et al., 2023
Protein (Porcine plasma)	Fructose, galactose, glucose	-	100°C for 1-5 h	Benjakul et al., 2005
<i>Amino compounds from multiple sources</i>				
Amino acid (Cys) + Hydrolysates (Bovine bone marrow)	Glucose, xylose	-	110°C for 1 h	Xu et al., 2019
Amino acid (Cys) + Hydrolysates (HVP)	Glucose, xylose	Lard	105°C for 1 h (pH 6)	Song et al., 2017
Amino acid (Cys, Met) + Hydrolysates (Bovine bone + HVP)	Glucose, xylose	Tallow	110°C for 100 min (pH 5.5-8.0)	Chai et al., 2018

Amino acid (Cys, Glu, Met, Pro) + Hydrolysates (Beef + HVP)	Glucose, xylose	Tallow	120°C for 2 h (pH 6.5)	Song et al., 2012
Amino acid (Cys, Glu, Met, Pro) + Hydrolysates (Beef + HVP)	Glucose, xylose	Tallow	110°C for 2 h (pH 6.5)	Song et al., 2014
Amino acid (β -Ala, Cys, Gly) + Hydrolysates (Chicken breast)	Glucose, xylose	-	105°C for 1 h (pH 6.5)	Xiao et al., 2015
Amino acid (Cys) + Hydrolysates (Beef)	Xylose	-	125°C for 2 h (pH 5.5)	Kang et al., 2019
Amino acid (Cys) + Hydrolysates (Bovine bone)	Xylose	-	110°C for 90 min (pH 7)	Song et al., 2016
Amino acid (Cys) + Hydrolysates (Bovine bone)	Xylose	Tallow, phospholipid	115°C for 2 h (pH 6.5)	Zheng et al., 2022
Amino acid (Cys) + Hydrolysates (Bovine bone marrow)	Xylose	-	120°C for 1 h	Begum et al., 2020

Amino acid (Cys) + Hydrolysates (Chicken)	Xylose	-	100°C for 2 h (pH 6.5)	Zhang et al., 2019
Amino acid (Cys) + Hydrolysates (Chicken bone)	Xylose	-	105°C for 90 min (pH 7)	Wang et al., 2016
Amino acid (Cys) + Hydrolysates (Chicken bone extract)	Xylose	-	105°C for 30-90 min (pH 7)	Sun et al., 2014
Amino acid (Cys) + Hydrolysates (Flaxseed protein)	Xylose	Chicken fat	120°C for 2 h (pH 7.5)	Wei et al., 2020
Amino acid (Cys) + Hydrolysates (Peony seed meal protein)	Xylose	Chicken fat	120°C for 2 h (pH 7.5)	Xia et al., 2021
Amino acid (Cys) + Peptide (Beef)	Xylose	-	140°C for 90 min (pH 4.8)	Xu et al., 2013

902 HVP, hydrolysed vegetable protein.



903

904 Figure 1. Meat flavor formation pathway through the Maillard reaction, lipid oxidation,

905 thermal degradation of thiamine, and their interactions. HMF, hydroxymethylfurfural

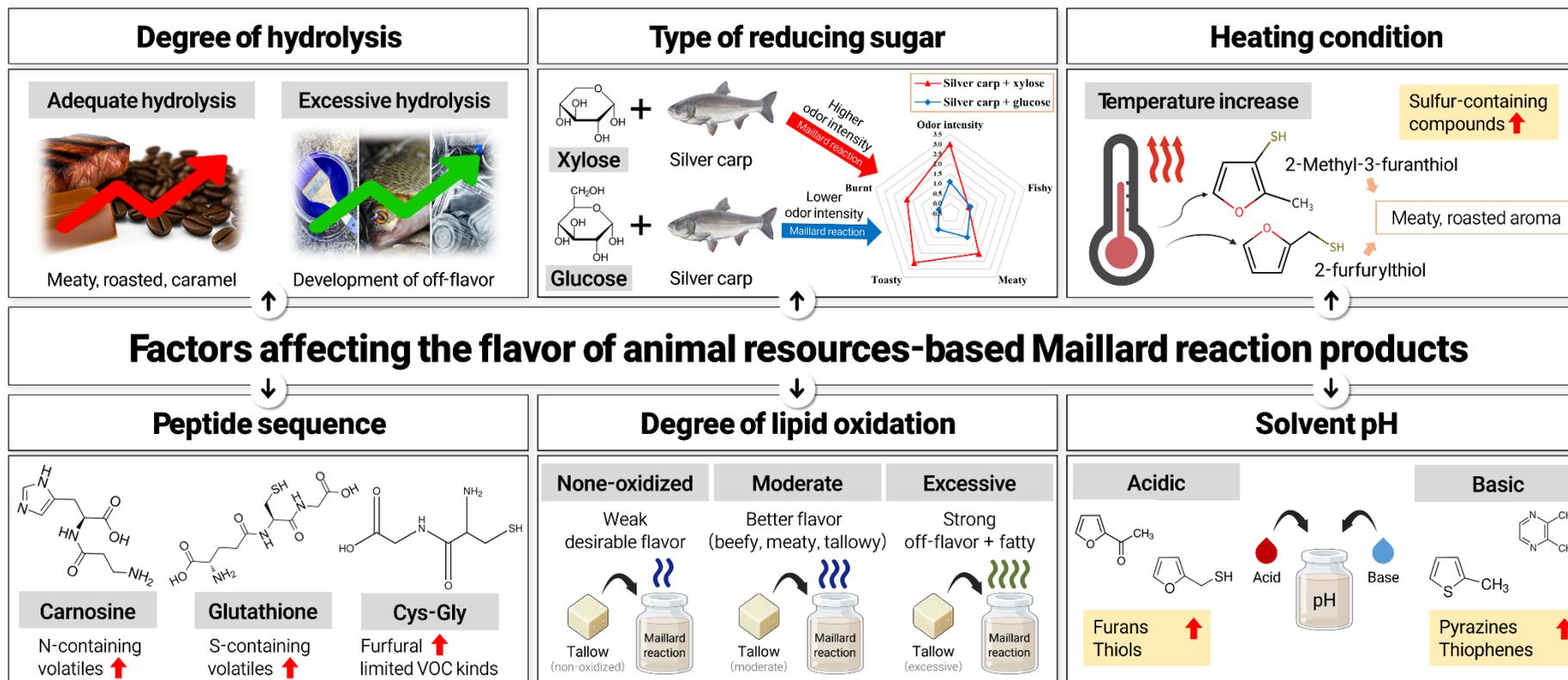


Figure 2. Overview of the influencing factors on the flavor of Maillard reaction products.