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ARTICLE INFORMATION	Fill in information in each box below
Article Type	Research article
Article Title	Comparison of muscle fiber and meat quality characteristics of beef strip loin, tenderloin, and round cuts among Jeju black cattle, Hanwoo, and their crossbreeds
Running Title (within 10 words)	Meat quality and muscle fiber characteristics of Korean native cattle
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List any present or potential conflict s of interest for all authors. (This field may be published.)	The authors declare no potential conflict of interest.
Acknowledgements State funding sources (grants, funding sources, equipment, and supplies). Include name and number of grant if available. (This field may be published.)	This research work was carried out with the support of the "Cooperative Research Program for Agriculture Science and Technology Development (Project No. PJ01620103)," Rural Development Administration, Korea.
Author contributions (This field may be published.)	Conceptualization: Cho SH, Kim GD. Data curation: Song DH, Hoa VB, Kim YS, Kim HW, Bae IS, Kim DK, Seong PN, Cheong H, Du L, Im C Formal analysis: Park J, Song S. Methodology: Park J, Cho SH, Song DH, Kim GD. Writing - original draft: Park JY, Cho SH, Song S, Kim GD. Writing - review & editing: Cho SH, Song DH, Kim YS, Kim HW, Kim DK, Sung PN, Hoa VB, Bae IS, Im C, Song S, Cheng H, Park J, Du L, Kim GD.
Ethics approval (IRB/IACUC) (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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12

13 Abstract

14 This study assessed and compared meat quality and fiber characteristics of longissimus lumborum (LL), psoas major (PM), and semimembranosus (SM) muscles among 15 Hanwoo (HW), Jeju black (BL), and their crossbred (BH) cattle. Twelve carcasses from each 16 17 breed (36 in total) were used in this study. BL and BH had higher moisture and crude ash 18 contents and lower crude fat and protein contents than HW, regardless of the muscle type. BL 19 had higher redness, cooking loss, and shear force values than did the other breeds for all muscle types. The muscle fiber size (cross-sectional area) of BL and BH was larger than that 20 21 of HW for all muscle types. Type IIX was the dominant muscle fiber type in both BL and 22 BH, regardless of muscle type; however, HW had the highest composition of type I compared to the other types (IIA, IIAX, and IIX) in PM. Higher total fiber density was observed in the 23 24 LL and PM muscles of HW than in those of BL and BH. Meat quality and muscle fiber 25 characteristics of BL and BH were distinct from those of HW.

26 Keywords: Jeju black cattle, Hanwoo, meat quality, muscle fiber characteristics.

27 Introduction

Hanwoo (HW), a representative cattle beef in Republic of Korea, is known for its 28 29 high marbling and palatability. The name 'Hanwoo' consists of Han (meaning Korea) and 30 Woo (meaning cattle) and refers to Korean cattle. The coat color of HW is generally brown. 31 However, HW comprises four different breeds: Chickso (brindle with black and brown coat 32 color), Heukwoo (coat color is black but occasionally mixed brown on the face and back), 33 and Jeju-black (BL) (whole coat color is black) (Lee et al., 2014). In the National Report on the State of Animal Genetic Resources from the Republic of Korea (2004), cattle in the 34 Republic of Korea comprised 67% brown cattle, 37% Holstein, and the rest included 35 36 Chickso, Heukwoo, and BL. BL has been a natural monument 546 in the Republic of Korea after being formally registered with the FAO in this report. The population of BL was 1,087 37 in 2023, and the concerned body of Jeju Island has planned to increase this population to 38 39 2,000 by 2030. Overall, the BL breed still faces the threat of extinction, probably owing to the lack of consumer knowledge and need for this breed. 40 Studies on BL are scanty. Dadi et al. (2014) analyzed cattle genes distributed in East 41 42 Asia and reported specific mitochondrial DNA sequences of BL, brown HW, and brindle 43 HW. Alam et al. (2021) reported lower genetic heterozygosity in BL than in brown HW and 44 Holstein in the Republic of Korea. Han et al. (2011) reported that the melanocartine-1 45 receptor alleles ED, E+, and e are found in BL and that these traits are directly related to the coat color phenotype of HW, BL, and their crossbreeds. Although BL exhibits lower average 46

47 daily gain, live weight, and carcass weight, a higher feed efficiency has been observed than

48 that in Charolles and the crossbreeds of BL and Charolles raised for 18 months (Oh et al.,

49 2008). Lee et al. (2007) observed that pure BL shows a low average daily gain until 16

50 months, which increases during the period of 17–24 months, when compared with the those

51 of other breeds. In the same study, although the carcass weight of pure BL was low, no 52 significant difference in the carcass yield was observed. Moon et al. (2012) have compared 53 same-quality grade brown HW, BL, and imported Australian beef and found no significant 54 differences in the proximate composition; however, higher redness and lower melting point were observed for BL than for the other two breeds. Additionally, the fatty acid composition 55 56 of BL show low levels of saturated and high levels of unsaturated fatty acids (Hoa et al., 57 2024; Moon, 2012; Lee et al., 2019; Song and Hwang, 2023; Tuell et al., 2022). 58 BL is a traditional bovine cattle breed raised on Jeju Island in the Republic of Korea, and is served at national events such as the birthday of the King or memorial dates of the 59 60 Royal Family (Lee et al., 2019). Although some studies have focused on the characteristics of 61 BL, these were restricted to only genetics; additionally, meat quality has been evaluated only in loins. Therefore, this study aimed to evaluate the meat quality and fiber characteristics of 62 longissimus lumborum, psoas major, and semimembranosus muscles from BL, brown HW, 63 64 and their crossbreeds.

65 Materials and methods

66 Sample preparation

A total of 36 steers (12 steers per breed) of HW (31.8 \pm 1.0 months of age, 620.3 \pm 67 6.5 kg carcass weight), BL (33.2 \pm 2.4 months of age, 583.3 \pm 17.9 kg carcass weight), and 68 69 crossbreds (BH; 31.3 ± 1.4 months of age, 720.1 ± 23.8 kg carcass weight), which were 70 raised under the same conditions and fattened on a cattle farm located in Jeju Island, were randomly selected and transported to the abattoir of the National Institute of Animal Science 71 72 (NIAS), Wanju, Republic of Korea. Feeding was conducted according to the Korean Feeding Standard for Hanwoo (NIAS, 2022). Livestock transport, preslaughter management, and 73 74 slaughter were conducted in accordance with the Livestock Products Sanitation Control Act. 75 Beef carcasses were chilled at 1 °C for 48 h after slaughter; then, three muscles (M. 76 longissimus lumborum, M. psoas major, and M. semimembranosus) were removed from the 77 left sides of the carcasses. For immunohistochemistry, muscle tissues $(1.5 \times 1.5 \times 2.0 \text{ cm})$ 78 were immediately frozen in 2-methylbutane chilled with liquid nitrogen and stored at -80 °C 79 until analysis. The remaining muscle samples were used for analyzing physicochemical 80 properties (proximate composition, pH, color, cooking loss, and shear force).

81

82 Physicochemical properties

Moisture, crude protein, and crude ash contents were analyzed according to the guidelines of the Association of Official Agricultural Chemists (AOAC, 2000), with some modifications. Briefly, moisture content was determined by drying 10 g sample for 24 h in a dry oven at 105 °C and expressed as the percentage of total weight by calculating the difference in weight before and after drying. To determine the crude protein content, 1.0 g sample was digested with sulfuric acid and distilled ammonia into boric acid following the

89 Kjeldahl method (AOAC, 2000). Borate ions were titrated with hydrochloric acid, and crude 90 protein content was calculated from the total nitrogen content. Crude ash contents were 91 calculated by measuring the weights of samples before and after burning the muscles at 200, 92 400, 600, and 800 °C for 2 h after pre-drying at 100 °C for 2 h; the ash content was expressed 93 as a percentage. Crude fat content was measured as described by Folch et al. (1957). Briefly, 94 approximately 5.0 g sample was homogenized in 30 mL extraction buffer 95 (chloroform:methanol at a 2:1 v/v ratio) and filtered through a Whatman No. 1 filter paper 96 (Merck, Darmstadt, Germany). The filtrate was mixed with 0.88% sodium chloride and 97 incubated at room temperature for 2 h. Once the upper layer was removed using an 98 evaporator, 10 mL of the lower layer was dried in pre-weighted aluminum dish to obtain 99 crude fat. Crude fat content was expressed as the percentage of the sample. The proximate 100 composition was obtained from triplicate measurements for each sample. 101 For measuring the pH, 3.0 g sample was homogenized with 27 mL deionized water, 102 and the pH was measured using a pH meter (S220; Mettler Toledo, Greifensee, Switzerland) 103 calibrated with standard buffer solutions (pH 4.01, 7.00, and 9.21). The pH values were 104 determined from three replicates of each sample. Meat color intensity on the sample surface was measured after exposure to air for 20 105 106 min at room temperature. A colorimeter (CR-400, Minolta Co., Tokyo, Japan) was set up 107 with a D65 light source, an 8° illumination angle, and an 8-mm measuring aperture after 108 calibration with a standard plate (Y, 93.5; x, 0.3132; y, 0.3198). Color values for lightness 109 (CIE L*), redness (CIE a *), and yellowness (CIE b *) were represented according to the 110 Commission Internationale de l'Eclairag System (CIE, 1978). Meat color intensity was 111 measured in five different regions of each sample. 112 Approximately 25 g sample was cooked in a water bath (WB-22; Daihan Scientific, Wonjoo, Republic of Korea) at 75 °C to measure cooking loss. Samples for which the internal 113

114	temperature reached 70 °C were cooled to room temperature, and their weights were
115	measured. The difference in weight before and after cooking was monitored. Cooking loss
116	was calculated as the percentage of initial weight from triplicate measurements.
117	Cooked samples were used for measuring the shear force. Three cores (1.0 cm
118	diameter) of each sample were obtained by cutting parallel to the orientation of muscle fiber.
119	Shear force (N/cm ²) was measured using a texture analyzer (TA1; AMETEK, Largo, FL,
120	USA) equipped with a Warner-Bratzler shear blade at 3.0 mm/s and 50 kgf of load cell.
121	
122	Muscle fiber characteristics
123	Immunohistochemistry was conducted to analyze muscle fiber characteristics
124	according to the method described by Song et al. (2020), with some modifications. Briefly,
125	cross-sections (10 μ m thickness) obtained from each frozen sample were blocked with 10%
126	normal goat serum (Cell Signalling Technology, Danvers, MA, USA) and incubated with
127	primary antibodies (BA-F8, SC-71, and 6H1; DSHB, Iowa City, IA, USA). The cross-
128	sections were then incubated with secondary antibodies (anti-IgG and anti-IgM) conjugated
129	with Alexa Fluor 405, 488, or 594 (Thermo Fisher Scientific, Waltham, MA, USA). Images
130	of three different regions of each section were captured using a microscope (EVOS M5000;
131	Thermo Fisher Scientific). Muscle fiber characteristics (cross-sectional area, μm^2 ; relative
132	fiber area, %; fiber density, number/mm ²) were evaluated using approximately 800 muscle
133	fibers of each section. Image Pro Plus (Media Cybernetics, Rockville, MD, USA) was used to
134	analyze each image.
135	

136 Statistical analysis

All data are presented as mean ± standard error (SE). Statistical analyses were
conducted using SAS software v.9.4 (SAS Institute, Cary, NC, USA). Differences in

physicochemical and muscle fiber characteristics within the same muscle among breeds were evaluated using a one-way analysis of variance (ANOVA), followed by Duncan's multiple range post-hoc test. Pearson's correlation coefficients between physicochemical properties and muscle fiber characteristics were analyzed to describe the relationship between muscle fiber characteristics and physicochemical properties, regardless of muscle type. Statistical significance was set at p<0.05.

145

146 **Results**

The proximate composition and meat quality traits of BL, brown HW, and BH are 147 148 shown in Figs. 1–3. All characteristics, except the pH, were significantly different in M. 149 longissimus lumborum. BL had relatively high moisture content and low crude fat and protein contents (p < 0.05; Fig. 1A-C). BH showed intermediate traits, in which the moisture content 150 151 was higher than that of HW, and a moderate level of crude fat content between those of HW 152 and BL (p < 0.05). The crude ash content of BH was higher than that of HW (p < 0.05; Fig. 1D), but no significant difference was observed when compared with that of BL (p>0.05). 153 154 HW showed higher lightness, redness, and yellowness than did BH (p < 0.05; Fig. 1F-H,). BL 155 showed lower lightness than did HW and higher redness and yellowness than did BH 156 (p < 0.05). The cooking loss in BL was significantly lower than in HW and higher than in BH (p < 0.05; Fig. 1I). The shear force was highest for BL, followed by that for BH and HW 157 158 (*p*<0.05; Fig. 1J). 159 Most traits, except crude protein content and lightness, showed significant 160 differences in M. psoas major among breeds. BL had higher moisture and crude ash contents 161 and a lower crude fat content than those of HW (p<0.05; Fig. 2A, B, D). The proximate

162 composition of the *psoas major* muscle of BH was similar to that of BL, but the crude ash

163 content was relatively higher in BL (p<0.05; Fig. 2A, B, D). The pH value for BH was 164 significantly lower than the values for HW and BL (p<0.05; Fig. 2E). BL showed greater 165 redness than did HW and BH; yellowness was significantly different between BL and HW 166 (p<0.05; Fig. 2G, H). Cooking loss in BH was significantly lower than that in BL and HW 167 (p<0.05; Fig. 2I). The highest and lowest shear force values were observed in BL and HW, 168 respectively (p<0.05; Fig. 2J).

169 Significant differences in all meat quality traits, except the pH, were observed in M. 170 semimembranosus (p<0.05) among different breeds. The results of proximate composition showed significantly high moisture and crude ash contents in BH, and crude fat and crude 171 172 protein content in HW (p<0.05; Fig. 3A-D). The color of M. semimembranosus was similar 173 to that of M. longissimus lumborum; HW showed higher lightness and lower redness and 174 yellowness than did BL and BH (p<0.05; Fig. 3F-H). BH showed lower cooking loss than did 175 BL and HW (p<0.05; Fig. 3I), and the values for BL and HW were not significantly different 176 (p>0.05). Significantly higher shear force was observed for BL than for HW (p<0.05; Fig.

177 3J), and no significant difference was observed in BH (p>0.05).

178 Representative immunofluorescent images of BL, HW, and BH for the analysis of 179 muscle fiber characteristics are shown in Fig. 4. The cross-sectional area, relative area ratio, 180 and density of muscle fibers were analyzed using those images; the results are shown in Fig. 181 5. Regarding the cross-sectional area of M. *longissimus lumborum*, the area was significantly higher in BL than in the other breeds, regardless of the muscle fiber type (p < 0.05; Fig. 4A). 182 Specifically, muscle fiber types IIA and IIAX were not significantly different between BL 183 184 and BH (p>0.05); however, fiber types I and IIX and mean cross-sectional area were 185 significantly higher in BL than in BH (p < 0.05). Type IIX fibers appeared to be largest in BL 186 and BH, whereas type IIAX was largest in HW (p < 0.05). No significant differences were 187 observed for type IIX (p>0.05; Fig. 5A); BL had a higher area ratio of type I, and a lower

area ratio of type IIA and IIAX than the other breeds (p<0.05; Fig. 5B). Regardless of breed, the area ratio of IIX was highest and that of IIAX was lowest (p<0.05). No significant difference was observed in type I among the breeds (p>0.05; Fig. 5C). Relatively high fiber density was noticed for the other and total fiber types for M. *longissimus lumborum* in HW, whereas the density of type IIA fiber and total density in BL was lower than those in BH (p<0.05).

194 The fiber characteristics of M. psoas major of the three different breeds are shown in 195 Fig. 5D-F. The cross-sectional area of BH was largest among all types, except for type IIAX and the mean area (p < 0.05). BL had significantly larger areas of types IIA, IIAX, and IIX 196 197 than did HW (p < 0.05). Within breeds, BL and BH had the largest areas of type IIX, whereas 198 type IIAX was largest in HW (p < 0.05). Regarding the relative area ratio, the highest ratio 199 over 50% for type I was found in HW, and the area ratio of IIA was significantly high in HW 200 (p < 0.05). No significant difference in type IIAX among the breeds (p > 0.05) was observed, 201 but BL and HW showed a significantly high area ratio of type IIX (p < 0.05). HW had the 202 highest area ratio of type I, followed by that of IIA, IIX, and IIAX; BL and BH showed the 203 highest area ratio of IIX, followed by that of I, IIA, and IIAX (p < 0.05). The highest densities 204 of type I and IIA, and the highest total density was noticed in HW; type IIX in BL was 205 significantly higher than that in the other breeds (p < 0.05). No significant difference was 206 noticed for type IIAX among the different breeds (p>0.05). Within the breeds, the density of type I was highest across all breeds, followed by that of IIX, IIA, and IIAX in BL and BH, 207 208 and IIA, IIX, and IIAX in HW (p < 0.05).

The muscle fiber characteristics of M. *semimembranosus* are shown in Fig. 5G-I. Unlike that in other muscles, a significant difference in cross-sectional area was observed only for type IIX fiber (p<0.05). Within the breeds, muscle fiber type IIX was largest in BL and BH, and the cross-sectional area of type IIAX was higher than that of type IIA in HW

213	(p < 0.05). The relative area ratio of M. <i>semimembranosus</i> was significantly higher for types I
214	and IIA in HW and BL than in BH and that for IIX was higher in BH than in the other breeds
215	(p <0.05). A comparison of muscle fiber types within the same breed revealed high-to-low
216	ratios in the order of type IIX, IIA, I, and IIAX, regardless of breed (p <0.05). Significant
217	differences in fiber density were noticed for types IIA, IIX, and total density; the density was
218	highest in HW (p <0.05). However, no significant differences were observed in type IIA and
219	total density compared with those in BL (p >0.05). Among the types within the same breed,
220	all breeds showed the same order of trend: types IIA, IIX, I, IIAX ($p < 0.05$).
221	The correlation coefficients between the muscle fiber characteristics and
222	physicochemical properties are shown in Table 1. The cross-sectional area of each fiber was
223	not significantly correlated with moisture and crude protein contents (p >0.05), while that of
224	type IIX showed negative and positive correlations with crude fat and crude ash contents,
225	respectively (p <0.05). Redness showed a correlation with the cross-sectional area, except in
226	type IIAX fiber (p <0.05), while lightness and yellowness exhibited no significant correlations
227	(p>0.05). The cross-sectional area of type IIX showed a significant correlation with cooking
228	loss ($p < 0.05$). Shear force exhibited a positive correlation with each muscle fiber type
229	(p <0.05). Relative fiber area of type I exhibited negative correlations with moisture, crude
230	protein, and crude ash contents, and shear force, while it showed a positive correlation with
231	crude fat content ($p < 0.05$). The relative area of type IIA was positively correlated with crude
232	protein content, yellowness, cooking loss, and shear force ($p < 0.05$). Relative fiber area of
233	type IIAX exhibited a negative correlation with moisture contents; however, it was positively
234	correlated with crude fat content and lightness (p <0.05). The relative area of type IIX
235	exhibited positive correlations with moisture, crude ash, and shear force but a negative
236	correlation with crude fat content (p <0.05). Correlation of type I fiber density with
237	physicochemical properties corresponded to that of relative type I fiber area ($p < 0.05$).

Proximate composition showed significant correlations with types IIA, IIAX, and total fiber density (p<0.05). Redness, yellowness, and cooking loss showed positive correlations with types IIX and IIA (p<0.05). Shear force showed a negative correlation with all muscle fiber density, including total fiber density (p<0.05). Among the physicochemical properties, only the pH did not show any significant correlation with muscle fiber characteristics (p>0.05).

243

244 **Discussion**

245 In the present study, BL and BH had relatively high moisture contents and relatively low crude fat and protein contents in the three different muscles. In contrast, HW had a 246 relatively low moisture content and relatively high crude fat and protein contents. BH had a 247 relatively high crude ash content, regardless of the muscle type. The quality grade of beef is 248 249 highly dependent on the intramuscular fat contents owing to the preference for grilling beef 250 as thin slices in the Republic of Korea; the general intramuscular fat content of HW is 6.60-251 23.85%. In the present study, the quality grade of HW seemed to be 1, and that of BH and BL between 1–2 (Jo et al., 2012; Gajaweera et al., 2020; Lee et al., 2015). The intramuscular fat 252 253 content affects eating quality, particularly tenderness and flavor (Gotoh et al., 2018; Wheeler 254 et al., 1994). The factors affecting the intramuscular fat contents of meat vary; nevertheless, 255 consumer demands can be met by increasing the intramuscular fat content through breeding or feeding systems, and likewise, HW was originally used for farming to meet such demands 256 257 (Avilés et al., 2015; Miller & Cross, 1987; Lee et al., 2014; Park et al., 2018). The pH 258 significantly affects muscle fiber characteristics, meat color, and water-holding capacity 259 (Ertbjerg & Puolanne, 2017; Hopkins et al., 2014; Ryu & Kim, 2006; Weglarz, 2010); 260 however, it did not significantly affect other meat quality traits in the present study. The 261 results of meat color showed higher lightness, redness, and yellowness in the M. longissimus

262 thoracis and M. semimembranosus of HW than in those of others. Wulf and Wise (1999) 263 reported that color positively correlates with lean maturity and marbling score; and another 264 study has reported significantly low redness of M. longissimus thracis with low intramuscular 265 fat in HW (Kim & Lee, 2003). However, a contrasting result for M. psoas major indicated 266 that intramuscular fat did not affect meat color in the present study. Jo et al. (2012) and Cho 267 et al. (2010) reported the lowest redness in quality grade 1 in HW, which increased following 268 an increase in the intramuscular fat content. Furthermore, Lee et al. (2012) have reported a 269 significant difference in redness in the intramuscular fat, ranging between 13.12–18.69 %, as analyzed from the HW marbling score. M. psoas major used in the present study had higher 270 271 intramuscular fat and lower moisture contents. These findings indicate that intramuscular fat 272 affects meat color, and the extent depends on the fat content. In all the three muscles, cooking 273 loss was higher in BH than in the other breeds, which is in line the results of a previous study 274 that analyzed proximate composition by doneness, wherein the degree of change in crude fat 275 and moisture contents was higher than that of crude protein and ash contents (Smith et al., 276 2011). Regardless of the muscle types, BL showed the highest and HW showed the lowest 277 shear force values, which is in agreement with the findings of Wheeler et al. (1994), who 278 reported that an increase in intramuscular fat content results in a reduction in the shear force 279 value. However, shear force does not affect all traits of meat, and additional analyses, such as 280 texture profile analysis or sensory evaluation, are necessary (Caine et al., 2003). 281 The aforementioned meat quality traits are dependent on individual trait and muscle fiber 282 characteristics. The trends such as large cross-sectional area of glycolytic muscle fibers, small 283 oxidative fibers, and intermediate fibers are intermediate have been reported previously 284 (Maltin et al., 1998; Spindler et al., 1980; Xie et al., 2012). Regarding significant differences 285 in the cross-sectional area, those of HW were smaller than those of the other breeds. No significant difference was found in the cross-sectional area of M. semimembranosus between 286

287 BL and BH, and M. longissimus lumborum in BL and M. psoas major in BH had larger 288 cross-sectional areas than those of the other breeds. Although the carcass weight of BL was lowest, M. longissimus lumborum in BL and M. psoas major in BH exhibited largest cross-289 290 sectional area than those of other breeds, while the cross-sectional area of M. 291 semimembranosus was not significantly different between BL and BH. These results are in 292 accordance with previous findings showing a positive correlation with intramuscular fat and a 293 negative correlation with lightness of the cross-sectional area of types I and IIA (Wegner et 294 al., 2000). However, no significant correlation was observed in the present study. Similarly, a 295 previous study has reported that relatively small fiber size and increased number of oxidative 296 fibers promote metabolism, resulting in increased fat accumulation owing to energy 297 supplementation, thereby affecting meat quality (Schiffino & Reggiani, 1996). Although no 298 significant correlation was observed between crude fat content and oxidative fibers, type IIX 299 showed a negative correlation with crude fat content. Probably the increasing size resulted in 300 increased shear force (Joo et al., 2017), while the diameter did not (Hwang et al., 2010; 301 Ozawa et al., 2000).

Generally, the muscle fiber density of HW was higher, while the cross-sectional area 302 303 was similar to or lower than those of the other breeds in the present study. This implies that 304 the muscle fiber number in BL and BH is less than that in HW, and hyperplasia of HW or 305 hypertrophy of BL and BH can be considered, indicating that the characteristics of each cell from the three breeds are different (Picard & Gagaoua, 2020). While only a few studies have 306 307 compared muscle fiber characteristics of HW with those of other breeds, Kim et al. (2021) 308 have reported similar results, showing that HW consists of an increased number of muscle 309 fibers compared to that in Holstein raised for meat in the Republic of Korea; additionally, a 310 relatively low shear force has been observed. Xie et al. (2012) have reported different muscle 311 fiber characteristics among five different breeds raised in the same feeding system. Johnston

312 et al. (1975) and Splindler et al. (1980) have observed different muscle fiber characteristics 313 among breeds. Generally, the cross-sectional area of HW is smaller than that of the other 314 breeds, whereas the cross-sectional areas of BL and BH are larger than the area of HW. 315 Muscle fiber composition, representing muscle characteristics, is affected by breed, similar to that in other species (Picard & Gagaoua, 2020; Park et al., 2022). The present study 316 317 reported that each muscle has a different muscle-fiber composition. Unexpectedly, the 318 compositions of types I and IIX did not vary much from those of other muscles and were 319 found to be similar to those of M. psoas major of BL and BH. Some differences were observed between the muscles in terms of muscle fiber composition. HW showed results 320 321 similar to those of previous studies (Hwang et al., 2010; Kim et al., 2016). Type IIX fibers 322 are positively correlated with the shear force. A relatively low shear force value was observed for HW, which had a relatively low type IIX composition in the present study. A high number 323 324 of glycolytic fibers results in a reduction in the pH via accumulation of lactic acid during 325 glycolysis in the early postmortem period; however, this does not fully harmonize with the 326 results of the present study (Yu et al., 2019). The high content of oxidative fibers (types I and 327 IIA) results in an increase in redness owing to their metabolic traits (Jeong et al., 2009; Lefaucheur, 2010); however, the present study did not show similar results, which may be 328 329 due to the low fat content. Muscle fiber composition exhibited changes in proximate 330 composition in terms of fat accumulation, as previously described by Schiffino and Reggiani (1996). Moreover, a high ratio of type IIX fiber resulted in a high shear force, as also 331 332 previously described by Hwang et al. (2010). However, whether fat contents, type IIX 333 characteristics, or other factors cause this phenomenon should be clarified. 334

335

336 Conclusion

337 The meat quality traits and muscle fiber characteristics of three different muscles (M. 338 longissimus lumborum, M. psoas major, M. semimembranosus) from three different breeds (Jeju black, Hanwoo, and their cross-bred) were evaluated. Jeju black showed lower 339 340 intramuscular fat content and higher lightness, redness, yellowness, cooking loss, and shear 341 force then the other breeds. The cross-bred cattle had intermediate characteristics between 342 those of Jeju black and Hanwoo cattle. Hanwoo had smaller muscle fiber size and higher 343 muscle fiber density than did the other breeds. In conclusion, differences in physicochemical 344 and muscle fiber characteristics were confirmed, regardless of the type of muscle, among three breeds of Korean native cattle. 345 346 347 Acknowledgements 348 This research work was carried out with the support of the "Cooperative Research 349

350 Program for Agriculture Science and Technology Development (Project No. PJ01620103),"

351 Rural Development Administration, Korea.

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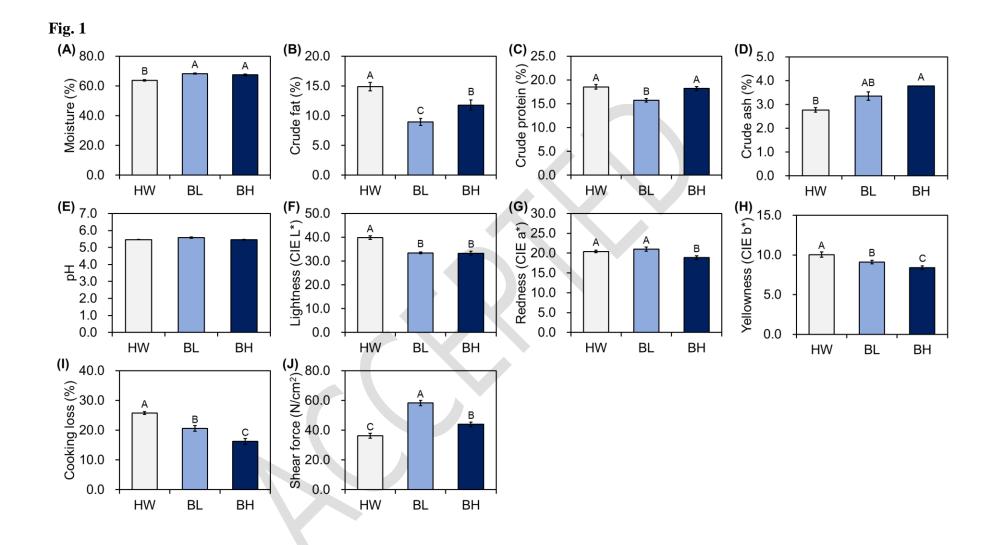
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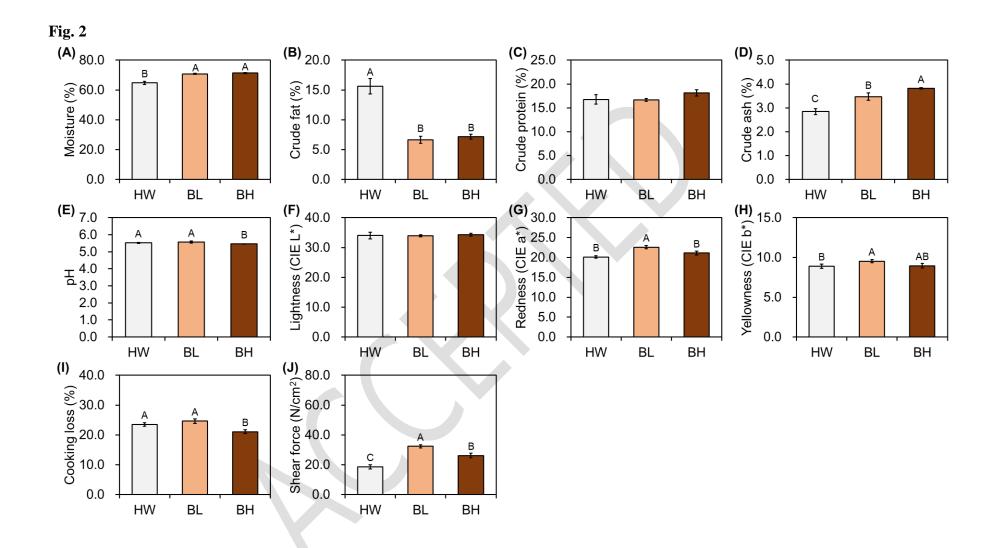
- 481 **Figure Legends**
- 482 Fig. 1. Comparison of proximate composition (A-D) and meat quality characteristics (E-
- 483 J) of M. longissimus lumborum among Hanwoo (HW), Jeju black (BL), and their cross-
- 484 **bred (BH) cattle.** Data represent mean ± standard error (bar). Significant differences
- 485 (p < 0.05) among the breeds are represented with different letters (A-C).
- 486 Fig. 2. Comparison of proximate composition (A-D) and meat quality characteristics (E-
- 487 J) of M. psoas major among Hanwoo (HW), Jeju black (BL), and their cross-bred (BH)
- 488 **cattle.** Data represent mean \pm standard error. Significant differences (p < 0.05) among the
- 489 breeds are represented with different letters (A-C).
- 490 Fig. 3. Comparison of proximate composition (A-D) and meat quality characteristics (E-
- 491 J) of M. semimembranosus between Hanwoo (HW), Jeju black (BL), and their cross-
- 492 **bred (BH) cattle.** represent mean \pm standard error. Significant differences (p < 0.05) among
- 493 the breeds are represented with different letters (A-C).
- 494 Fig. 4. Immunohistochemical analysis of cross-sections of M. longissimus lumborum, M.
- 495 psoas major, and M. semimembranosus of Hanwoo (HW), Jeju black (BL), and their
- 496 **cross-bred** (**BH**) **cattle.** Bar, 300 μm.
- 497 Fig. 5. Comparison of cross-sectional area (A, D, and G), relative fiber area (B, E, and
- 498 H), and fiber density (C, F, and I) of M. longissimus lumborum (A, B, and C), M. psoas
- 499 major (D, E, and F) and M. semimembranosus (G, H, and I) among Hanwoo (HW), Jeju
- 500 black (BL), and their cross-bred (BH) cattle. Data represent mean ± standard error.
- 501 Significant differences (p < 0.05) among the breeds (X, Y, and Z) within the same muscle fiber
- 502 type and between muscle fiber types (a-c) within the same muscle and breed are represented
- 503 with different lettersfig

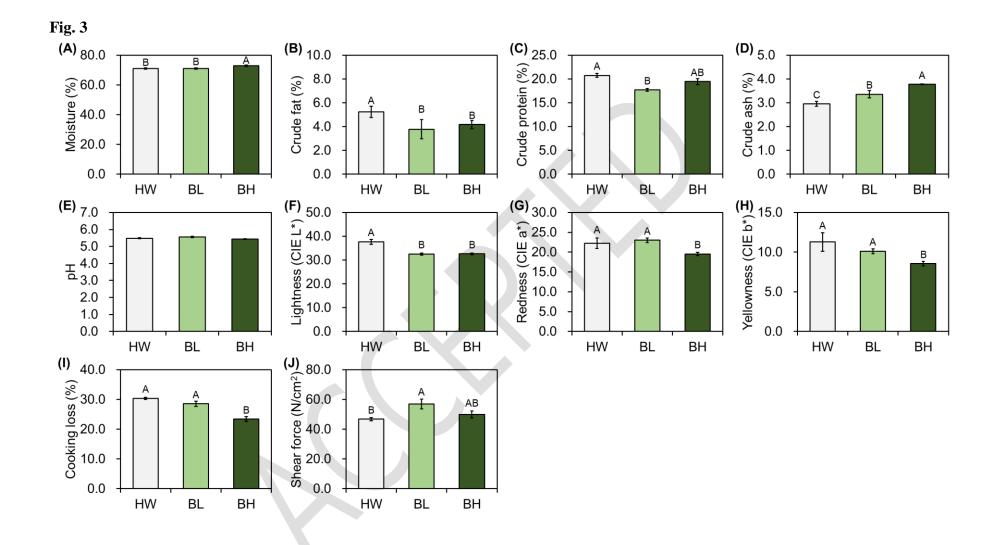
Cross-sectional area]	Relative	fiber area	l	Fiber density				
Ι	IIA	IIAX	IIX	Mean	Ι	IIA	IIAX	IIX	Ι	IIA	IIAX	IIX	Total
0.06	0.00	0.01	0.16	0.09	-0.39***	0.02	-0.41***	0.46***	-0.30**	-0.17	-0.41***	0.13	-0.21*
0.15	0.12	0.10	-0.01	0.08	-0.32***	0.36***	0.06	0.09	-0.23**	-0.01	0.00	0.08	-0.12
-0.15	-0.07	-0.06	-0.22*	-0.17	0.49***	-0.11	0.33***	-0.49***	0.39***	0.21*	0.36	-0.10	0.28**
0.02	0.11	0.07	0.26**	0.16	-0.29**	-0.15	-0.05	0.38***	-0.24**	-0.28**	-0.10	-0.09	-0.24**
0.01	-0.03	-0.04	-0.05	-0.03	0.15	-0.10	-0.06	-0.06	0.10	0.03	0.02	0.04	0.08
0.05	0.01	0.06	-0.11	-0.03	-0.15	0.19	0.23**	-0.01	-0.11	0.02	0.05	0.13	-0.03
-0.21*	-0.20*	-0.15	-0.19*	-0.21	-0.09	0.01	-0.03	0.09	0.01	0.10	0.04	0.27**	0.10
-0.06	-0.05	-0.05	-0.16	-0.10	-0.13	0.20*	0.05	0.00	-0.08	0.08	0.01	0.19*	0.02
0.00	-0.17	-0.11	-0.23**	-0.15	-0.15	0.33***	-0.05	-0.04	-0.04	0.21*	0.01	0.18	0.08
0.74*	0.65*	0.56*	0.69***	0.73	-0.52***	0.36***	-0.10	0.34***	-0.69***	-0.55***	-0.50***	-0.46***	·-0.70***
	0.15 -0.15 0.02 0.01 0.05 -0.21* -0.06 0.00	I IIA 0.06 0.00 0.15 0.12 -0.15 -0.07 0.02 0.11 0.01 -0.03 0.05 0.01 -0.21* -0.20* -0.06 -0.05 0.00 -0.17	I IIA IIAX 0.06 0.00 0.01 0.15 0.12 0.10 -0.15 -0.07 -0.06 0.02 0.11 0.07 0.01 -0.03 -0.04 0.05 0.01 0.06 -0.21* -0.20* -0.15 -0.06 -0.05 -0.05 0.00 -0.17 -0.11	I IIA IIAX IIX 0.06 0.00 0.01 0.16 0.15 0.12 0.10 -0.01 -0.15 -0.07 -0.06 -0.22* 0.02 0.11 0.07 0.26** 0.01 -0.03 -0.04 -0.05 0.05 0.01 0.06 -0.11 -0.21* -0.20* -0.15 -0.19* -0.06 -0.05 -0.05 -0.16 0.00 -0.17 -0.11 -0.23**	I IIA IIAX IIX Mean 0.06 0.00 0.01 0.16 0.09 0.15 0.12 0.10 -0.01 0.08 -0.15 -0.07 -0.06 -0.22* -0.17 0.02 0.11 0.07 0.26** 0.16 0.01 -0.03 -0.04 -0.05 -0.03 0.05 0.01 0.06 -0.11 -0.03 -0.21* -0.20* -0.15 -0.19* -0.21 -0.06 -0.05 -0.05 -0.16 -0.10 0.00 -0.17 -0.11 -0.23** -0.15	I IIA IIAX IIX Mean I 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.15 0.12 0.10 -0.01 0.08 -0.32*** -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** 0.02 0.11 0.07 0.26** 0.16 -0.29** 0.01 -0.03 -0.04 -0.05 -0.03 0.15 0.05 0.01 0.06 -0.11 -0.03 -0.15 -0.21* -0.20* -0.15 -0.19* -0.21 -0.09 -0.06 -0.05 -0.05 -0.16 -0.10 -0.13 0.00 -0.17 -0.11 -0.23** -0.15 -0.15	I IIA IIAX IIX Mean I IIA 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 0.05 0.01 0.06 -0.11 -0.03 -0.15 0.19 -0.21* -0.20* -0.15 -0.19* -0.21 -0.09 0.01 -0.06 -0.05 -0.16 -0.10 -0.13 0.20* 0.00 -0.17 -0.11 -0.23** -0.15 -0.15 0.33***	I IIA IIAX IIX Mean I IIA IIAX 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 -0.41*** 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.33*** 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 -0.05 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 -0.06 0.05 0.01 0.06 -0.11 -0.03 -0.15 -0.19 -0.23** -0.21* -0.20* -0.15 -0.19* -0.21 -0.09 0.01 -0.03 -0.06 -0.05 -0.16 -0.10 -0.13 0.20* 0.05 0.00 -0.17 -0.11 -0.23** -0.15 -0.15 0.33*** -0.05	I IIA IIAX IIX Mean I IIA IIAX IIX 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 -0.41*** 0.46*** 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 0.09 -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.33*** -0.49*** 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 -0.05 0.38*** 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 -0.06 -0.06 0.05 0.01 0.06 -0.11 -0.03 -0.15 -0.10 -0.06 -0.06 0.05 0.01 0.06 -0.11 -0.03 -0.15 0.19 0.23** -0.01 -0.21* -0.20* -0.15 -0.19* -0.21 -0.09 0.01 -0.03 0.09 -0.06	I IIA IIAX IIX Mean I IIA IIAX IIX I 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 -0.41*** 0.46*** -0.30** 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 0.09 -0.23** -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.33*** -0.49*** 0.39*** 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 -0.05 0.38*** -0.24** 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 -0.06 -0.10 0.05 0.01 0.06 -0.11 -0.03 -0.15 0.19 0.23** -0.01 -0.11 -0.21* -0.20* -0.15 -0.03 0.15 -0.10 -0.13 0.20* 0.01 -0.11 -0.06 -0.05 -0.16	I IIA IIAX IIX Mean I IIA IIAX IIX I IIA 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 -0.41*** 0.46*** -0.30** -0.17 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 0.09 -0.23** -0.01 -0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 0.09 -0.23** -0.01 -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.33*** -0.49*** 0.39*** 0.21* 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 -0.05 0.38*** -0.24** -0.28** 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 -0.06 -0.06 0.10 0.03 0.05 0.01 0.06 -0.11 -0.23 -0.21	I IIA IIAX IIX Mean I IIA IIAX IIX I IIA IIAX 0.06 0.00 0.01 0.16 0.09 -0.39*** 0.02 -0.41*** 0.46*** -0.30** -0.17 -0.41*** 0.15 0.12 0.10 -0.01 0.08 -0.32*** 0.36*** 0.06 0.09 -0.23** -0.01 0.00 -0.15 -0.07 -0.06 -0.22* -0.17 0.49*** -0.11 0.33*** -0.49*** 0.39*** 0.21* 0.36 0.02 0.11 0.07 0.26** 0.16 -0.29** -0.15 -0.05 0.38*** -0.24** -0.28** -0.10 0.01 -0.03 -0.04 -0.05 -0.03 0.15 -0.10 -0.06 0.10 0.03 0.02 0.05 0.01 0.06 -0.11 -0.03 -0.15 0.19 0.23** -0.01 0.01 0.03 0.02 <	I IIA IIA

Table 1. Correlation coefficients between physicochemical properties and muscle fiber characteristics

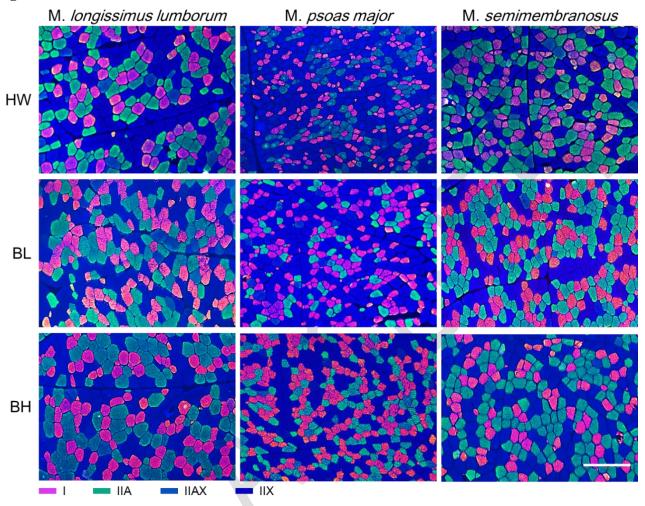
*, p<0.001. *, p<0.05; **, p<0.01;











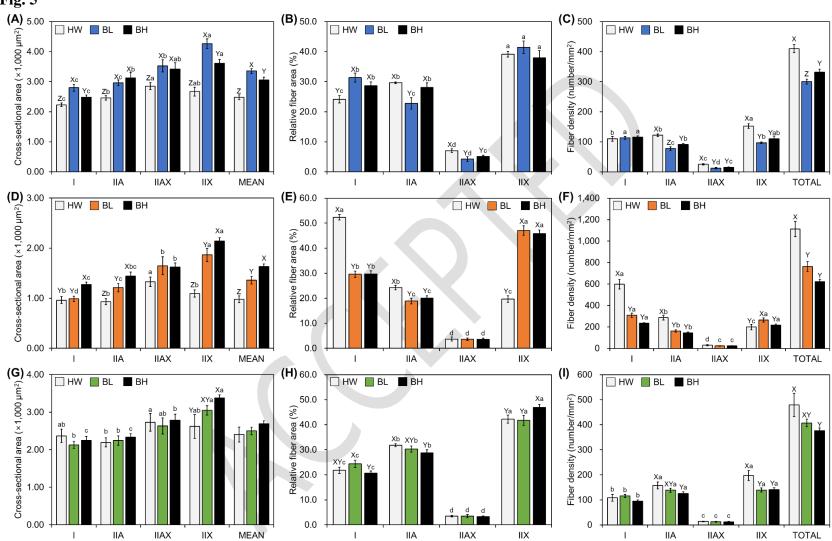


Fig. 5