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Histochemical characterisation of high-value beef muscles from different breeds, and its relation to tenderness.

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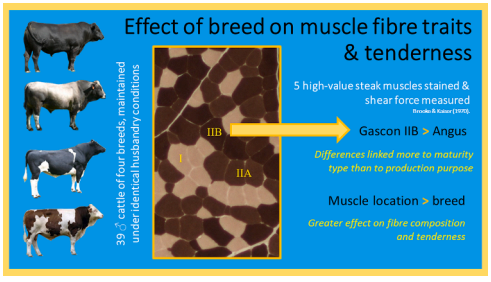
HIGHLIGHTS

- Angus and Gascon cattle differ in the histochemical characteristics of muscle fibers
- Differences in fiber composition are linked more to maturity than production type
- Muscle location has greater effects on fiber composition and tenderness, than breed
- Beef tenderness is related to muscle fiber composition

GRAPHICAL ABSTRACT



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ABSTRACT

The aim of the present study was to characterise and compare the muscle fibre traits of five muscles: *longissimus lumborum* (LL), *semitendinosus* (ST), *biceps femoris* (BF), *semimembranosus* (SM) and *psoas major* (PM) collected from four cattle breeds (Aberdeen Angus, AA; Gascon, GS; Holstein, HO; Fleckvieh, FL) differing in maturity type (early- and late-maturing) and production purpose (beef and dairy), but maintained under identical husbandry conditions. The relationships between histochemical characteristics and instrumental meat tenderness (Warner-Bratzler shear force) were evaluated. The most significant differences in muscle fibre traits were seen in the hindquarter muscles of Aberdeen Angus and Gascon cattle, with muscle location also having a large effect on tenderness. Under the identical husbandry practises used, the differences in muscle fibre composition were seemingly linked more so to muscle location and maturity type of the breed, rather than the production purpose of the breed. Based on their effects on high-value muscles in beef breeds, continuous evaluation of muscle fibre traits together with their association with various meat quality traits is required, as breeds progress genetically. However, various intrinsic and extrinsic factors, such as husbandry practises, need to be controlled so that accurate conclusions may be drawn from such investigations.

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1. Introduction

To produce high-quality meat, it is necessary to evaluate both intrinsic and extrinsic factors affecting its processing and eating quality (Christensen et al., 2011). Huge genetic variability, based on the diverse origin and subsequent crossbreeding of cattle for various purposes, has resulted in the establishment of numerous domesticated cattle breeds (Felius et al., 2011). The meat quality traits of various cattle breeds have been evaluated in many studies; however, due to substantial genetic progress made within commercial cattle breeds in production traits over time due to selective breeding, it is also necessary to re-examine the meat quality and composition traits of these breeds (Clarke et al., 2009).

Muscle fibre type and composition have been identified as important intrinsic factors influencing meat quality, as demonstrated in numerous animal species (Kim et al., 2016; Lee et al., 2010; Lefaucheur, 2010). Muscle fibres differ in their contractile and metabolic properties, as well as their morphological traits, such as the total number of fibres and cross-sectional area (CSA). Although several histochemical methods for classifying of muscle fibres exist, most of the available studies involving both fibre type composition and meat quality are based on the convenient myosin ATPase reaction, which allows for the subdivision of muscle fibres into three basic types – I, IIA, IIB (Brooke and Kaiser, 1970; Kim et al., 2016; Lefaucheur, 2010). However, recent studies (Gagaoua et al., 2016; Oury et al., 2010) also focus on immunohistochemical methods, where muscle fibre types can be classified from the detection of myosin heavy chain isoforms (MyHC I, IIa, IIx and IIb). There are marked differences in the fibre type composition of different muscle tissues, which influences meat quality, both within and between animals, depending on factors such as muscle location and function, animal age, weight, or breed (Choi and Kim, 2009; Lee et al., 2010; Lefaucheur, 2010). Therefore, it is important to control as many extrinsic and intrinsic factors as possible, in order to accurately compare the histochemical characteristics of various muscles in relation to their meat quality traits.

Many recent studies confirm large variability in histochemical, chemical composition, instrumental and eating quality traits between major bovine muscles (Jeremiah et al., 2003b, 2003a; Torrescano et al., 2003). Of the various meat quality traits appraised during eating, tenderness plays a vital role in consumer acceptance and subsequently the repeated purchase of a product (Kerry and Ledward, 2009), and thus should always be considered in high-value muscles intended for fresh meat sale. Typically, higher amounts of type I and IIA fibres have been related to a darker fresh meat colour, due to their higher myoglobin content, but the relationship between fibre type composition and beef tenderness is still controversial (Joo et al., 2013; Lefaucheur, 2010; Listrat et al., 2016). For instance in bulls, a higher tenderness of the *longissimus thoracis* muscle is often associated with a decrease in the cross-sectional area of fibres and an increase in oxidative metabolism, whereas in the *vastus lateralis* and *semitendinosus* muscles, their higher glycolytic activity results in more tender meat (Chriki et al., 2013; Listrat et al., 2016). Furthermore, Picard et al. (2014) reported that in breeds characterized by a muscle metabolism that is more fast-glycolytic (French beef breeds), the most tender *longissimus thoracis* muscles were also the most oxidative.

However, few studies have compared the influence of muscle fibre parameters of various beef muscles of different breeds raised under identical husbandry conditions, and their relationship with tenderness. The aim of the present study was thus to evaluate the effects of breed on the histochemical characteristics of important beef muscles harvested from cattle raised under uniform conditions, and explore their relationship with meat tenderness (shear force).

2. Materials and methods

2.1. Animals, experimental design and data collection

All experimental procedures were conducted in accordance with the Council Directive 86/609/EEC, concerning the protection of animals used for experimental and other scientific purposes, and were approved by the Animal Care Committee of the Institute of Animal Science, Prague (IAS). A total of 39 purebred bulls of four breeds, differing in maturity type and production purpose, were used (early-maturing beef breed Aberdeen Angus, AA, n = 10; late-maturing beef breed Gascon, GS, n = 10; dairy breed Holstein, HO, n = 9; dual-purpose breed Fleckvieh, FL, n = 10). The bulls were maintained under identical husbandry and feeding conditions during a nine-month fattening experiment. Details regarding the experimental arrangements, chemical and nutritional compositions of the feeds used, as well as the growth performance, carcass composition and chemical and sensory profile of the *longissimus lumborum* (LL) muscle may be found within Bureš & Bartoň (2018).

At 651.5 ± 39.9 kg (approximately 17 months old), the animals were slaughtered, and muscle samples intended for fibre analysis were collected immediately from the right sides of the hot carcasses. Samples of the LL (between 9th and 11th ribs), *semitendinosus* (ST), *biceps femoris* (BF) and *semimembranosus* (SM) were taken from the central part of each muscle, while samples of the *psoas major* (PM) were taken from the cranial end of the muscle. The samples were immediately frozen, through immersion into isopentane cooled by liquid nitrogen, and kept at −80 °C until further analysis. For the determination of histological properties, serial transverse muscle sections (10 μm thick) were cut from the frozen muscle blocks (0.5 × 0.5 × 1.0 cm) in a cryostat CM1850 (Leica Microsystems GmbH, Nussloch, Germany) at −20 °C, and mounted onto glass slides. To differentiate between the muscle fibre types I, IIA and IIB, serial muscle sections were stained, after acid (pH 4.3) and alkaline (pH 10.3) pre-incubation, using the methodology detailed by Brooke & Kaiser (1970). This method was chosen as it has been widely used for the evaluation of relationships between muscle fibre characteristics and meat quality traits (Song et al., 2020).

Images of the muscle samples were obtained using an optical microscope (Nikon Eclipse E200, Nikon, Tokyo, Japan) and evaluated using the image analysis software NIS-Elements AR 3.2. (Nikon Instruments Europe B.V., Amsterdam, Netherlands). Fields for analysing the muscle fibre composition were randomly selected from three serial sections of each sample, and an average of 200 fibres were analysed in each section. For each muscle fibre type, the fibre cross-sectional area (CSA; μm), fibre type proportion, and relative area of fibres (ratio of individual fibre type/area of fibres) were determined. Eight samples from each muscle (4 × 1 × 1 cm), adjacent to those samples taken for histological evaluation, were collected and used for Warner-Bratzler shear force (WBSF) measurement at 48 h after slaughter. As the method and temperature of heating affects the WBSF, through the changes in the biochemical parameters of muscle and connective tissue (Li et al., 2010; Modzelewska-Kapituła et al., 2012), samples of raw meat were evaluated to exclude this effect of cooking. The muscle samples were sheared across the fibres, using an Instron Universal Texture Analyzer 3365 (Canton, MA, USA) fitted with a Warner-Bratzler blade, at a crosshead speed of 100 mm/min. The peak force (N/cm^2) measured was then calculated as an average of the eight measures per muscle.

2.2. Statistical analysis

Statistical analysis was performed using the statistical package SAS (Version 9.4, SAS Institute Inc., Cary, NC, USA). Data were tested for normality using the Shapiro-Wilk test, and for homogeneity of variance with Levene's test. Data were subsequently analyzed using mixed models with repeated measures, following the REML method of the MIXED procedure in SAS. The model for the data presented in Figure 1 included the fixed effect of *muscle* and the random effect of *animal*. The

model for the parameters displayed in Tables 1 and 2 included the fixed effects of *breed* and *muscle fibre parameter* (Table 1) or *muscle* (Table 2), and their interaction, and the random effect of *animal*. Least squares means (LSM) of the simple effect of slices (by *muscle fibre parameter* in Table 1 and by *muscle* in Table 2) were determined, and multiple comparisons were performed using Tukey's test and adjusted P-values. A significance level of 5 % was used throughout. Association between shear force and histological parameters (muscle fibre type proportion) were illustrated by means of Principal Component Analysis (PCA), using the PRINCOMP procedure in SAS.

3. Results

No differences were seen between breeds for the muscle fibre parameters measured within the LL and PM muscles (Table 1). The ST muscles of AA cattle had higher proportions of type I fibres ($P = 0.002$) and a higher relative area of type I fibres ($P = 0.004$) than FL and GS cattle, but a lower relative area of type IIB fibres in the ST than GS cattle ($P = 0.008$; Table 1). The BF muscle of AA cattle had type IIA fibres with larger cross-sectional areas ($P = 0.016$) than FL cattle, and a higher proportional distribution of type I fibres ($P = 0.041$; Table 1) than GS cattle. Relative to the total area of fibres analysed, AA cattle had a lower relative area of type IIB fibres than GS cattle ($P = 0.007$; Table 1). AA cattle also had type IIA fibres with larger cross-sectional areas in the SM muscle compared with FL cattle ($P = 0.029$; Table 1), and when compared with GS cattle, the SM of AA cattle had a higher relative area of type IIA fibres ($P = 0.009$) but a lower relative area of type IIB fibres ($P = 0.002$; Table 1). No further differences were seen between muscles for histological parameters.

However, when the shear force is considered, differences were not seen between muscle samples from AA cattle compared with those from FL and GS cattle (Table 2). The LL muscle from GS cattle had lower shear force values than FL cattle ($P = 0.035$), while the PM muscle from FL cattle had lower shear force values than HO cattle ($P = 0.032$; Table 2). No further differences were seen between muscles for shear force values between the breeds. The muscle fibre cross sectional areas, fibre type proportions and Warner-Bratzler shear force values are summarized for the main effect of muscle within Figure 1, regardless of breed, for informative purposes.

The association between shear force and the histological parameters of the five muscles for the four cattle breeds is demonstrated within Figure 2. The combination of principal component 1 (PC1) and PC2 explained 85.61 % of the total variance experienced, of which PC1 explained 49.72 % and PC2 explained 35.89 %. While the individual muscles show some grouping, the breeds showed no separation (Figure 2). The more tender muscles, the LL and PM, are concentrated mainly to the left of the vertical axis, while the more tough muscles, the ST and BF, are predominantly located towards the right side of the axis.

4. Discussion

Muscle fibre characteristics of cattle have been investigated in many studies within a diverse range of muscles and breeds (Chriki et al., 2013; Hwang, Kim, Jeong, Hur, & Joo, 2010; Kirchofer, Calkins, & Gwartney, 2002; Ozawa et al., 2000; Wegner et al., 2000; Xie, Meng, Cui, & Ren, 2012). However, there are only a few accessible studies assessing these parameters in cattle reared under identical husbandry conditions, none of which include Fleckvieh and Gascon breeds. Breed is an important factor which can influence the characteristics and composition of muscle tissue, and hence the fresh and processed quality of its meat products (Christensen et al., 2011). While the breeds used in the present study are of different origin and purpose, it seems that when the breeds are reared under identical conditions, the differences in their muscle fibre properties are not as pronounced as expected. In the present study, the most significant differences in fibre parameters were found between the beef breeds AA and GS, in all three muscles from the hindquarter (ST, BF, and SM). The reason for these differences could be attributed to the differences in maturity type of these two breeds, as the AA is an early-maturing British breed, and the GS is a late-maturing French breed. This result corresponds with those of Gagaoua et al. (2016), who observed a lower proportion of IIx+IIb MyHC in the *longissimus thoracis* muscle of HO and AA cattle, compared to the French breeds: Limousine and Blond d'Aquitaine. Differences in the intramuscular fat (IMF) content may also contribute to the breed differences in fibre parameters, as the IMF content is positively correlated with the red fibre content of muscles (Hwang et al., 2010; S. T. Joo et al., 2013). Although, in the previous study of Bureš & Bartoň (2018), the IMF content was measured only in the LL muscle, and was almost twice as high in the AA and HO meat samples than in the muscles from the FL and GS breeds. Thus, there may also be differences in the IMF content of the hindquarter muscles in these breeds, which could in turn influence the proportion of so-called red muscle fibres.

The muscles evaluated in the present study are of high-value in beef carcasses, and differences in their appearance and eating quality traits are well-described (Jeremiah et al., 2003a, 2003b). The distinct meat quality traits of these primal and sub-primal cuts are a result of their diverse muscle fibre compositions, which is essentially determined by the physiological function of the muscle itself (Kim et al., 2016). Differences between the fibre type composition of diverse muscles were observed in many studies (Hwang et al., 2010; Joo et al., 2017; Kim et al., 2016), and in the present study. Throughout these studies, the WBSF was lowest in the PM muscle (i.e. most tender), and higher in the muscles from the hindquarter (i.e. less tender). In the present study, the WBSF was evaluated on fresh (uncooked) meat 48 h *post-mortem*, after the reaching maximum *rigor mortis*, to exclude the effect of cooking method and ageing on the meat tenderness. Interestingly, breed differences in WBSF were only found for the LL and PM muscle, whereas no breed differences were observed for muscle fibre composition for these muscles in the present study. However, various other intrinsic and extrinsic factors may affect tenderness, including the pH, sarcomere length, the amount of connective tissue, the intramuscular fat content, proteolytic enzyme activity, or rate of meat tenderisation (Cawthorn et al., 2018; Christensen et al., 2011). Comparing the results from other studies is thus complicated, in addition to the different staining techniques used, the varied sampling times, and their intra-muscle location differences (Lebedová et al., 2020; Picard and Gagaoua, 2020; Realini et al., 2013; Song et al., 2020). The effect of location is particularly important within the ST and SM muscles, where a large intra-muscle variability in fibre type composition can be observed between the inner and outer areas of these muscles, as well as between the distal and proximal locations (Picard and Gagaoua, 2020; Realini et al., 2013). Nonetheless, differences in muscle fibre type composition between diverse cattle breeds, without significant differences in WBSF, were also found by Wegner et al. (2000) and Xie et al. (2012). Thus, it is likely that muscle fibre properties are weak indicators of beef tenderness, and that a greater impact is probably realized by connective tissue or IMF content, which should be considered in future studies.

It has been previously concluded that muscle fibre composition affects *post-mortem* meat ageing, which is quicker in fast-twitch glycolytic muscles than in slow-twitch oxidative muscles, and thus a higher proportion of glycolytic fibres has a beneficial effect on meat tenderness (Joo et al., 2013; Lefaucheur, 2010; Listrat et al., 2016). On the other hand, there are studies which report negative associations between glycolytic fibres and meat tenderness, or a high variability of such results between individual muscles and breeds (Calkins et al., 1981; Chriki et al., 2013; Hwang et al., 2010; Listrat et al., 2016; Picard et al., 2014). It is apparent from Figures 1 and 2, that the effect of muscle location on the muscle fibre parameters and tenderness is larger than the effect of breed thereon. Furthermore, it can be observed that the relationship between muscle fibre properties and meat tenderness can be rather diverse, depending on the muscles themselves. For example, in the present study, the SM muscle was more glycolytic, and had smaller

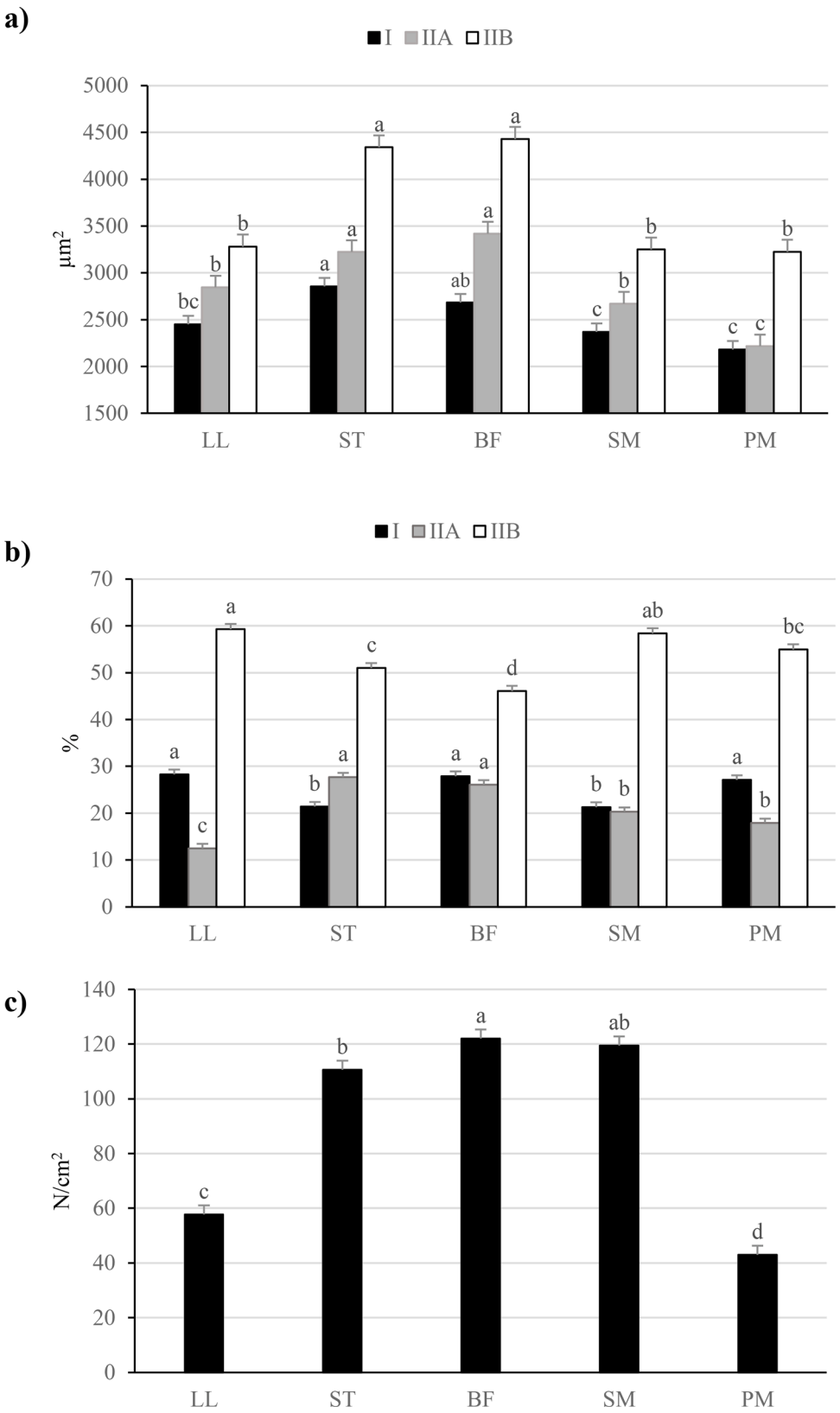

Figure 1. Muscle fibre cross sectional areas (a), fibre type proportions (b) and Warner-Bratzler shear force values (c) of *longissimus lumborum* (LL), *semitendinosus* (ST), *biceps femoris* (BF), *semimembranosus* (SM), and *psoas major* (PM) muscles from cattle, regardless of breed.
[a,b,c,d] Values with different superscripts differ at $P < 0.05$

Table 1
LSMeans for the cross-sectional area, fibre type proportion and relative area of type I, IIA and IIB muscle fibre types within five muscles, harvested from four breeds of cattle at slaughter.

Muscle	Breed				SEM	*P* - value
	Angus	Gascon	Holstein	Fleckvieh		
Longissimus lumborum						
Cross-sectional area (μm^2)						
I	2560.4	2601.6	2301.3	2338.3	206.30	0.602
IIA	3293.2	2929.9	2578.0	2578.2	245.11	0.083
IIB	3294.1	3351.5	3204.1	3272.3	215.40	0.956
Fibre type proportion (%)						
I	28.8	26.7	28.6	29.0	2.09	0.828
IIA	12.7	12.4	9.0	15.8	2.17	0.159
IIB	58.5	60.9	62.4	55.2	2.93	0.302
Relative area of fibres (%)						
I	23.4	22.6	22.3	23.7	2.49	0.969
IIA	13.1	11.3	8.0	14.6	2.10	0.128
IIB	63.5	66.1	69.7	61.7	3.06	0.263
Semitendinosus						
Cross-sectional area (μm^2)						
I	2840.9	2806.4	2893.4	2875.6	211.02	0.990
IIA	3433.6	3047.9	3521.3	2889.6	273.62	0.255
IIB	4040.9	4520.5	4293.5	4508.0	283.37	0.517
Fibre type proportion (%)						
I	26.7[a]	18.4[b]	23.5[ab]	17.1[b]	2.15	0.002
IIA	25.5	27.3	28.4	29.4	2.07	0.527
IIB	47.8	54.3	48.1	53.5	2.35	0.076
Relative area of fibres (%)						
I	21.7[a]	13.8[b]	18.3[ab]	13.0[b]	2.06	0.004
IIA	24.0	21.4	26.5	22.9	1.88	0.240
IIB	54.3[b]	64.8[a]	55.2[ab]	64.1[ab]	2.84	0.008
Biceps femoris						
Cross-sectional area (μm^2)						
I	2898.3	2452.7	2905.8	2484.3	189.59	0.120
IIA	4054.8[a]	3036.5[ab]	3710.6[ab]	2882.9[b]	313.62	0.016
IIB	4702.4	4372.6	4211.9	4412.0	336.91	0.755
Fibre type proportion (%)						
I	32.6[a]	24.5[b]	28.9[ab]	25.6[ab]	2.32	0.041
IIA	25.3	26.5	24.6	27.9	1.90	0.581
IIB	42.1	49.0	46.5	46.5	2.01	0.090
Relative area of fibres (%)						
I	24.2	17.2	23.7	18.3	2.36	0.052
IIA	25.4	22.6	24.5	23.2	2.09	0.728
IIB	50.4[b]	60.2[a]	51.8[ab]	58.5[ab]	2.39	0.007
Semimembranosus						
Cross-sectional area (μm^2)						
I	2456.8	2533.3	2344.3	2143.9	172.52	0.343
IIA	3080.2[a]	2489.4[ab]	2884.9[ab]	2244.9[b]	228.48	0.029
IIB	3104.7	3858.7	3072.3	2986.9	277.91	0.072
Fibre type proportion (%)						
I	23.6	19.4	22.4	20.0	1.57	0.143
IIA	21.0	20.2	18.3	21.5	1.62	0.499
IIB	55.4	60.4	59.3	58.5	1.64	0.145
Relative area of fibres (%)						
I	19.5	15.0	18.3	16.2	1.50	0.068
IIA	21.5[a]	15,1[b]	18.5[ab]	18.2[ab]	1.51	0.009
IIB	59.0[b]	69.9[a]	63.2[ab]	65.6[ab]	1.87	0.002
Psoas major						
Cross-sectional area (μm^2)						
I	2022.2	2191.2	2234.1	2278.1	184.65	0.725
IIA	1926.1	2115.3	2495.6	2328.8	216.10	0.220
IIB	2832.9	3434.4	3419.1	3215.1	234.53	0.181
Fibre type proportion (%)						
I	27.7	23.6	27.2	30.0	2.48	0.261
IIA	18.9	19.2	18.1	15.5	2.05	0.511
IIB	53.4	57.2	54.7	54.5	2.29	0.627
Relative area of fibres (%)						
I	23.2	17.8	21.0	24.3	2.28	0.136
IIA	14.5	14.3	15.1	12.5	1.74	0.713
IIB	62.3	67.9	63.9	63.2	2.56	0.354

[a,b] Values with different superscripts within each row differ at $P < 0.05$SEM = standard error of the mean

CSAs, than the other muscles from the hindquarter (ST, BF), and the WBSF of the SM was higher than that of the LL and PM muscles. Hwang et al. (2010) evaluated the muscle fibres in the LL, SM and PM muscles of highly marbled Hanwoo cattle, and in accordance with the results of the present study, they observed a higher content of IIB fibres in the SM than the LL and PM muscles, and smaller CSAs of all fibre types in the SM, compared to the LL. Furthermore, the WBSF was the highest in the SM, and lowest in PM muscle, with the correlation between the proportion of

Table 2
LSMeans for the Warner-Bratzler shear force values (N/cm^2) of five muscles, harvested from four cattle breeds (all bulls), as measured on uncooked/raw muscle samples at 48h after slaughter.

Muscle	Breed				SEM	*P* - value
	Angus	Gascon	Holstein	Fleckvieh		
Longissimus lumborum	58.2[ab]	48.5[b]	59.4[ab]	64.9[a]	4.35	0.035
Semitendinosus	108.1	105.8	121.3	107.2	7.18	0.371
Biceps femoris	123.8	115.4	134.3	114.2	8.66	0.303
Semimembranosus	119.2	121.1	117.8	119.9	9.57	0.995
Psoas major	43.3[ab]	41.3[ab]	51.5[a]	35.8[b]	4.11	0.032

[a,b] Values with different superscripts within each row differ at $P < 0.05$SEM = standard error of the mean

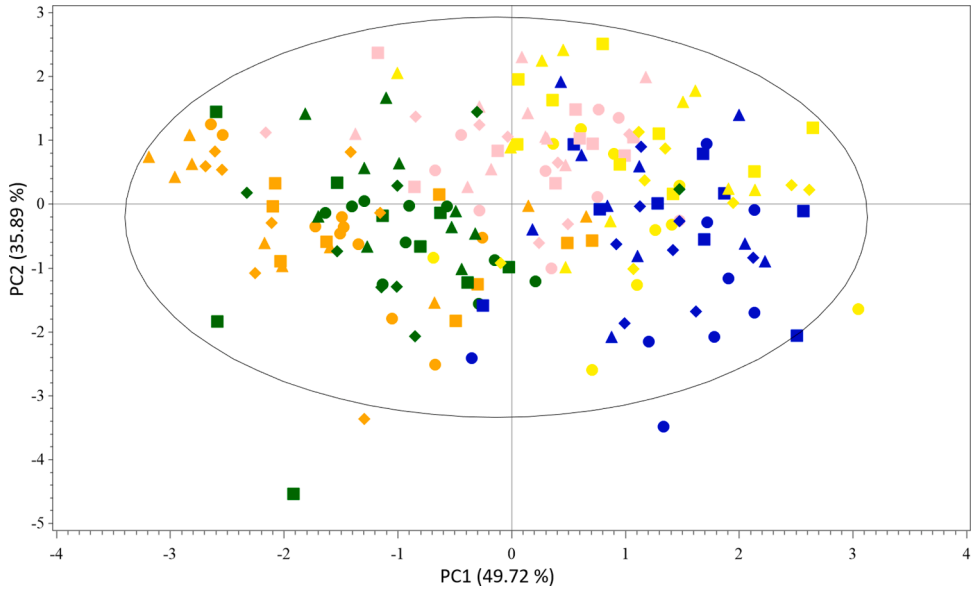

Figure 2. Principal Component Analysis (PCA) component scores 95% prediction ellipse, indicating the means of the associations between tenderness and histological parameters of four breeds (AA: dot; GS: triangle; HO: diamond; FL: square) for the *longissimus lumborum* (LL; orange), *semitendinosus* (ST; yellow), *biceps femoris* (BF; blue), *semimembranosus* (SM; pink), and *psoas major* (PM; green) muscles (four values were identified as outliers, but not removed).

IIB fibres and WBSF being positive (Hwang et al., 2010). Based on these observations, it can be said that although the tenderness of meat is affected by numerous factors, some relationship between the histochemical composition of muscle fibres and meat tenderness does exist. However, for its specification, it is necessary to precisely define the selected animal species, breeds, muscle type, location of sampling, and the analytical methods used to evaluate the muscle fibres.

5. Conclusion

This study presents the first results of histochemical classification of muscle fibres in Gascon and Fleckvieh cattle, to the best of the authors' knowledge, and shows that there are significant differences in the muscle fibre composition of Aberdeen Angus and Gascon cattle, in the high-value muscles of hindquarter. The differences in muscle fibre composition were primarily attributed to muscle location and maturity type of the breed, rather than the production purpose of the breed (meat versus dairy). Similarly, muscle location had a large effect on meat tenderness, more so than breed itself. While beef tenderness is influenced by a variety of complex factors, muscle fibre traits remains an indispensable factor influencing beef meat quality, and should be continuously examined as genetic progress is made in livestock. However, various intrinsic and extrinsic factors need to be controlled so that accurate conclusions may be drawn from such investigations.

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Declaration of Competing Interest

The authors have no conflict of interest to declare.

CRediT authorship contribution statement

Nicole Lebedová: Investigation, Visualization, Writing – original draft. **Daniel Bureš:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft. **Tersia Needham:** Validation, Writing – review & editing, Funding acquisition. **Jaroslav Čítek:** Conceptualization, Investigation, Resources. **Zuzana Dlubalová:** Formal analysis. **Roman Stupka:** Supervision. **Luděk Bartoň:** Conceptualization, Writing – review & editing, Project administration, Funding acquisition, Supervision.

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