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Comparative review of muscle fiber characteristics between porcine skeletal muscles

Abstract

Meat derived from skeletal muscles of animals is a highly nutritious type of food, and different meat types differ in nutritional, sensory, and quality properties. This study was conducted to compare the results of previous studies on the muscle fiber characteristics of major porcine skeletal muscles to the end of providing basic data for understanding differences in physicochemical and nutritional properties between different porcine muscle types (or meat cuts). Specifically, the muscle fiber characteristics between 19 major porcine skeletal muscles were compared. The muscle fibers that constitute porcine skeletal muscle can be classified into several types based on their contractile and metabolic characteristics. In addition, the muscle fiber characteristics, including size, composition, and density, of each muscle type were investigated and a technology based on these muscle fiber characteristics for improving meat quality or preventing quality deterioration was briefly discussed. This comparative review revealed that differences in muscle fiber characteristics are primarily responsible for the differences in quality between pork cuts (muscle types) and also suggested that data on muscle fiber characteristics can be used to develop optimal meat storage and packaging technologies for each meat cut (or muscle type).

Keywords: Muscle fiber characteristics; Skeletal muscle; Muscle fiber type; Pig

INTRODUCTION

Muscle food (meat), derived from skeletal muscles, which constitute the body of livestock, is an example of nutritionally excellent food. Different meat types not only differ in terms of nutritional characteristics [1,2] but also in terms of sensory and quality properties [3-5]. Reportedly, these nutritional characteristics as well as sensory and quality properties are very closely related to the meat constituents, histochemical characteristics, and muscle cell (fiber) characteristics [4,6,7]. Different meat types have considerably different nutritional and physicochemical properties depending on the species, breed, and muscle type. Further, the contribution of muscle fiber characteristics to these differences is relatively high [3,4]. Previous studies have also provided substantial evidence that meat quality changes during aging or refrigeration and quality deterioration accompanying freeze–thaw processes are associated with the composition of the muscle fibers constituting meat [8-10].

Among the various factors responsible for the differences in nutritional and physicochemical properties observed between different meat types, the characteristics of the muscle fibers comprising the meat has been identified as the most fundamental factor in this regard [4]. This correlation is well established [4,7]; thus, muscle fiber characteristics not only offer the possibility to predict the physicochemical characteristics of specific muscle types but also allow the prediction of the quality of aged and frozen–thawed meat [8-11]. However, given that the bodies of livestock comprise several muscle types, it is challenging to identify and compare the muscle fiber characteristics of the different muscle types simultaneously. For this reason, most studies conducted in recent decades have been focused on the muscle fiber characteristics of specific muscles [3,4,7,12].

Therefore, in this study, we aimed to enhance understanding regarding the differences in physicochemical properties between different muscle types (or meat cuts) via comparative review of the results of previous studies. Further, in this study, we suggest several strategies for improving the aging or storage quality of meat based on differences in the relationship between muscle fiber characteristics and meat physicochemical properties. Further, we focused on porcine skeletal muscles, which relatively, has been considerably investigated.

MUSCLE FIBER CHARACTERISTICS

Muscle fiber structure and components

Morphologically, the muscle fibers (myocytes) that make up skeletal muscles, which are also multinucleated cells, have long cylindrical shapes with diameter approximately10–100 μm and length in the order of hundreds to thousands of micrometers [13]. Further, the outer membrane of muscle fibers, composed of hundreds of myofibrils, is surrounded by sarcolemma (endomysium) [14], and their constituent organelles include nuclei, the sarcoplasmic reticulum, which stores Ca and functions in Ca secretion and retrieval, and mitochondria, which are mainly involved in energy metabolism. They also contain motor endplates and transverse canaliculi, which are responsible for transmitting motor stimuli, capillary vessels, which transport energy sources and oxygen, and adipose cells, which are often distributed within the muscle fibers [13,14].

Additionally, myofibrils are composed of two filament types: actin filaments (or thin filaments), which are mainly composed of actin, troponin complex (I, C, and T), and tropomyosin and myosin filaments (or thick filaments), which are mainly composed of myosin

[15]. The kinetic energy of the muscle fiber is generated by the contraction-relaxation mechanism (twitch), which occurs through the combined and separate action of the two (actin and myosin) filament types. The contraction-relaxation speed of the muscle fiber, the energy source required during contraction-relaxation, and the activity of myosin ATPase, which hydrolyzes energy (ATP) varies depending on the muscle fiber type [13-15].

Muscle fiber types and their characteristics

Muscle fibers are classified into several types according to their metabolic and contractile properties [12]. The energy source required for the contraction-relaxation mechanism is mainly derived from oxidative or glycolytic energy generation systems. Specifically, muscle fibers that predominantly use energy sources that require oxygen within mitochondria are called oxidative muscle fibers, whereas those that primarily use energy generated via glycolysis are called glycolytic muscle fibers [12,16]. They can also be classified according to their contractile properties as slow-twitch or fast-twitch. Unlike slow twitch muscle fibers, fast twitch muscle fibers can quickly and strongly generate kinetic energy; however, they easily become fatigued [12,16,17].

Additionally, muscle is a complex tissue composed of several muscle fiber types with different metabolic and contractile characteristics. Thus, its physiological and kinetic characteristics are determined by the architecture and characteristics (such as size, composition, and density) of its constituent muscle fibers [3,13-15]. Previous studies have provided substantial evidence that the physicochemical properties of livestock muscles differ between muscles (or meat cuts) depending on the muscle fiber characteristics observed when the muscles are converted into meat following slaughter [4,7]. Specifically, muscle fiber types that rely on oxidative metabolism have relatively large number of mitochondria, hence a higher content of myoglobin, a protein that transports oxygen within the muscle. For this reason, muscles with a relatively high ratio of oxidative muscle fibers appear redder than their counterparts with a lower oxidative muscle fiber proportion. Conversely, in glycolytic metabolism-dependent muscle fiber types, glycogen remains for a certain period (up to 48 h postmortem, depending on the animal species and muscle type) after slaughter and is used in post-mortem metabolism. This process is accompanied by the accumulation of hydrogen ions in the muscles and a decline in pH. Therefore, muscles with a high proportion of glycolytic muscle fibers have a high post-mortem metabolic rate and a low ultimate pH, which result in meat with poor water-holding capacity, color, tenderness, and protein solubility [4,7].

Muscle fiber typing methods

To analyze muscle fiber characteristics, it is first necessary to classify the muscle fibers. A typical strategy in this regard is to use the metabolic and contractile characteristics of each muscle fiber type. One muscle fiber typing method that was published decades ago and remains currently in use is based on differences in myosin ATPase activity [18,19]. The key to successfully classifying muscle fibers based on this method is to biopsy livestock muscle or collect samples within approximately 1 h after slaughter (before myosin ATPase activity disappears) and freeze them to minimize the degradation. This classification method is based on the fact that myosin ATPase activity in each muscle fiber type shows a different level of lability to different pH ranges (acidic and alkaline) [18,19]. Thus, using this method, it takes less than 1 h to stain muscle fibers, and given that the staining procedure is relatively simple, this method is widely used. Furthermore, using this method, muscle fibers are classified into the slow, fast, and intermediate types (type I, IIB, and IIA, respectively) as previously demonstrated [7,18,19] (Fig. 1A).

Although the use of difference in myosin ATPase pH lability is simple and convenient, it has the disadvantage that it does not offer the possibility to classify fast-type muscle fibers in greater detail. In other words, several muscle fibers classified as fast type using this method still show different metabolic characteristics (oxidative vs. glycolytic), but cannot be distinguished further. Therefore, another strategy to distinguish muscle fibers is to make use of differences in the activities of enzymes involved in oxidative metabolism, of which succinic dehydrogenase (SDH) is a representative example [20]. There is further evidence to support the use of differences in both myosin ATPase and SDH activities as a more accurate and detailed strategy for classifying muscle fibers [12,21]. Thus, rather than classifying muscle fibers as fast or slow or as oxidative or glycolytic, it is possible to more accurately express the characteristics of each muscle fiber type by classifying them as slow-twitch/oxidative (SO), fast-twitch/oxidative (FO), and fast-twitch/glycolytic (FG) as previously reported [12,20] and shown in Fig. 1B.

Another strategy for classifying muscle fiber types is to analyze the distribution of myosin isoforms, specifically, myosin heavy chain and light chain isoforms (Fig. 1B). Thus, muscle fiber types can be divided into four or more types based on the distribution of myosin heavy chain isoforms or the combination of the distributions of myosin heavy-chain and light-chain isoforms [17,21]. Further, immunohistological methods using several commercially available antibodies offer the possibility to classify muscle fiber types into as many as seven or eight types [21]. In a previous study on pig skeletal muscles, muscle fibers were classified into six types and the effects of the physicochemical properties of the constituent muscle fibers on the characteristics of pork loin meat were reported [22]. In situ hybridization (ISH) is another strategy for typing muscle fibers [12]. Basically, ISH is primarily used to determine the location of specific nucleic acid sequences in chromosomes or tissues. Further, it involves the use of mRNA obtained from oligonucleotides and RNA probes followed by analysis using microscopy [23]. Notably, types I, IIA, IIX, and IIB porcine skeletal muscles have been previously distinguished using this method [12,24].

Taken together, muscle fibers are classified into several types depending on their contractile and metabolic characteristics, and given that each muscle type has distinct characteristics, the physicochemical properties of different meat cuts vary depending on the characteristics of their constituent muscle fiber types (composition, size, etc.). Further, there are several methods for typing muscle fibers, with each method having its own characteristics and depending on the purpose of a given study, different methods or multiple methods can be used in parallel.

COMPARISON OF THE MUSCLE FIBER CHARACTERISTICS OF DIFFERENT PORCINE SKELETAL MUSCLE TYPES

Muscle fiber characteristics generally include muscle fiber size (cross-sectional area, diameter, and perimeter), relative area or numerical composition, and density (number of muscle fibers distributed per unit area). Over the past 30 years, studies have been conducted to determine the muscle fiber characteristics of several animal species (cattle, pig, chicken, goat, duck, etc.), breeds (Yorkshire, Berkshire, Landrace, Duroc, Tamworth, cross breeds, etc.), sex, and muscle type. Table 1 summarizes representative results in this regard for porcine skeletal muscles [3,6,9,12,25-34].

Muscle fiber size

Muscle fiber size is primarily evaluated via cross-sectional area measurements. A comparison of the muscle fiber sizes of 19 different porcine skeletal muscles is shown in Fig. 2. Among the skeletal muscles, M. *diaphragm* (DI) and M. *vastus* (VA) showed relatively small sizes regardless of the muscle fiber type, whereas M. *gluteus superficialis* (GS), M. *gracilis* (GR), M. *infra spinam* (IS), M. *semitendinosus* (ST), and M. *longissimus thoracis* (LT) showed larger sizes. Notably, M. *longissimus lumborum* (LL), LT, and M. *longissimus thoracis et lumborum* (LTL) were identified under the same muscle type. Further, the LTL is a very long muscle attached from the thoracic to the lumbar vertebrae. Thus, when sampling the LTL muscle, the thoracic (LT) region (ribeye cut) and the lumbar (LL) region (strip loin cut) are classified separately [35-37]. As shown in Fig. 2, LT is composed of larger muscle fibers than LL. This variation within a single muscle has also been previously reported [38]. A comparison of muscle fiber types showed a larger size for FG (types IIX, IIB, IIX/IIB, and IIBw) than for SO (type I) and FO (types IIA, IIA/IIX, and IIBr) muscle fiber types in most muscles. Generally, it has been reported that muscle fibers classified as Types I and IIA are smaller than those classified as Type IIX or IIB. However, IS, GR, and M. *infrahyoid* (IN) tend to have muscle fiber types with similar sizes and show muscle fiber size characteristics that are different from those of other muscles. This is because different muscle fiber sizes, depending on the muscle type, have different physiological characteristics, such as the ability to control movement at the location where each muscle is attached [3,39].

Muscle fiber composition

Generally, muscle fiber composition is evaluated base on area composition or number composition. However, when muscle fiber density, which represents the number of muscle fibers distributed per unit area, is also evaluated, the use of area composition is generally preferred [3,28,29]. In addition, given that area composition and numerical composition generally show similar trends, most often, the area composition alone is evaluated [3,28-30]. As shown in Fig. 2B, depending on the muscle type, muscle fiber area composition tended to be vastly different. Specifically, the proportion of SO muscle fibers in DI, IN, IS, M. *masseter* (MA), and M. *rectus abdominis* (RA) is approximately 30–55% and that of FO muscle fibers in DI, IN, and MS is greater than 30% [3,30]. Further, the proportion of FG muscle fibers in these muscles tended to be less than 10% FG. Conversely, GS and LTL (including LT and LL) were identified as muscles with a low proportion of oxidative metabolism-dependent muscle fibers (SO and FO) and a high proportion of glycolytic metabolism-dependent muscle fibers (FG) [3]. They all tended to possess SO or FO compositions of approximately 10% or below. In particular, the proportion of FG in GS and LL muscles was determined to be approximately 80%. GR, M. *rectus femoris* (RF), ST, M. *subcapularis* (SU), and M. *superficialis digital flexor* (SDF) muscles tended to possess similar ratios of muscle fiber types.

Muscle fiber density

DI showed a noticeable trend in muscle fiber density (Fig. 2C). The size of its constituent muscle fibers tended to be the smallest regardless of the muscle fiber type (Fig. 2A), and this served as the basis for predicting that it has the largest number of muscle fibers per unit area. Further, as shown in Fig. 2C, DI had the highest muscle fiber density [3]. We also observed that in DI, the densities of SO and FO tended to be much higher than that of FG. Furthermore, IN, RA, SU, and SDF showed muscle fiber density trends similar to that observed for DI. Conversely, the muscles in which the density of FG muscle fibers tended to be higher than those of SO or FO muscle fibers included LL, LT, LTL, M. *semimembranosus* (SM), and ST muscles [3,25,28,29,31]. Although these muscles showed different densities, they all have relatively high FG densities. Meanwhile, M. *biceps brachii* (BB) and RF muscles tended to have similar densities for each muscle fiber type.

Comparison of muscle fiber distribution between muscles

As mentioned above, muscle fibers can be classified according to their contractile and metabolic characteristics, which are representative muscle fiber characteristics [12]. To enhance understanding regarding differences in muscle fiber characteristics between muscles, the distribution of muscle fiber types for each muscle according to these two characteristics is summarized in Fig. 3. From this figure, it is evident that GS, LL, and LTL muscles tended to have more FG muscle fibers than other muscles. Conversely, MA, DI, IN, IS, and RA were identified as muscles with a higher proportion of SO muscle fibers. We noted that SU, SDF, and BF had similar proportions of slow-twitch and fast-twitch muscle fibers but contained relatively high proportions of oxidative metabolism-dependent muscle fibers than glycolytic metabolism-dependent muscle fibers. Another characteristic muscle is the LTL muscle. When it was categorized into the LT and LL muscles, similar ratios of slow-twitch and oxidative muscle fibers are observed; however, their fast-twitch to glycolytic muscle fiber ratio differed

(LL > LT). Therefore, as previously reported, this trend implies that in addition to differences in muscle fiber properties between muscles, variations in muscle fiber properties within the same muscle type also exist [38].

POST-HARVEST STRATEGIES FOR CONTROLLING MEAT QUALITY

Muscle fiber characteristics are reference traits that determine meat quality. They also provide basic information that can be applied to choose optimal storage or processing methods [4,40,41]. For example, when refrigerating or freezing pork, taking into consideration the histological and physicochemical characteristics of each meat part can improve meat quality or prevent quality deterioration [40,41]. In general, considerable effort is being made to identify excellent technologies for packaging and storing (aging) meat [35,42-45], and a deeper understanding of the muscle fiber characteristics of each muscle type or meat cut will make this process easier. Previous studies conducted from this perspective have shown that FG muscle fibers are more vulnerable to freezing than SO muscle fibers [40,41]. In addition, muscles with a higher SO ratio show less significant changes with age during storage. Thus, freezing should be avoided for muscles with a high proportion of FG muscle fibers, and muscles with a high proportion of SO muscle fibers do not need to be ripened for long durations [8]. In other words, regardless of the meat species, SM and ST muscles, which have a relatively higher proportion of FG muscle fibers than other muscle fiber types, show significant muscle tissue destruction and deterioration of meat quality due to freezing, so they should not be frozen unless long-term storage is necessary. On the other hand, PM (tenderloin), DI, SU, SDF, and RA muscles, where the ratio of SO muscle fibers is higher than that of FG muscle fibers, have relatively little change in meat quality even when frozen, so these muscles can be frozen if necessary.

CONCLUSIONS

Muscle foods (meat) are foods derived from the skeletal muscles of livestock, and determining the characteristics of their constituent muscle fibers is important for understanding differences in physicochemical properties between muscles or meat cuts. In this review, the differences between 19 major porcine skeletal muscles in terms of muscle fiber size, composition, and density were compared. We believe that our findings can be used as basic data to improve the quality of pork or to develop technologies for preventing meat quality deterioration during refrigeration, freeze–thawing, and packaging.

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FIGURE LEGENDS

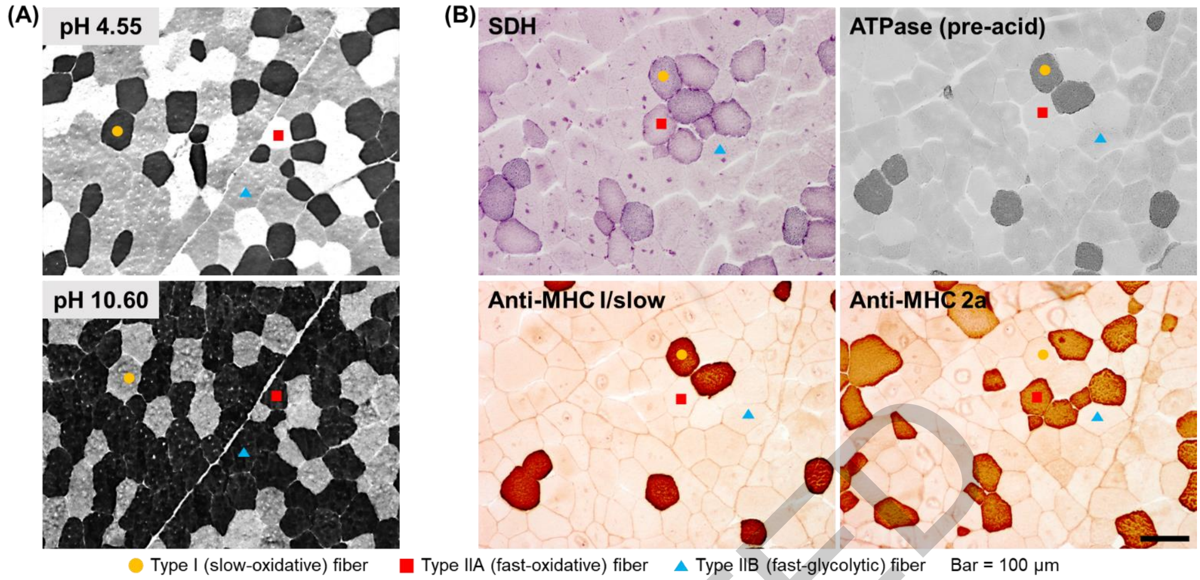

Fig. 1. Muscle fiber staining via histochemistry and muscle fiber type classification. (A) Muscle fiber typing based on differences in myosin ATPase lability in acidic and alkaline solutions. (B) Muscle fiber classification based on differences in succinic dehydrogenase (SDH) and myosin ATPase activity, and the distribution of myosin heavy chain (MHC) isoforms using anti-MHC I/slow and 2a. Muscle fiber types: I, slow-twitch and oxidative (slow-oxidative) fiber; IIA, fast-twitch and oxidative (fast-oxidative) fiber; IIB, fast-twitch and glycolytic (fast-glycolytic) fiber. Data were obtained from the Meat Science Laboratory, Seoul National University, Republic of Korea and presented after modification.

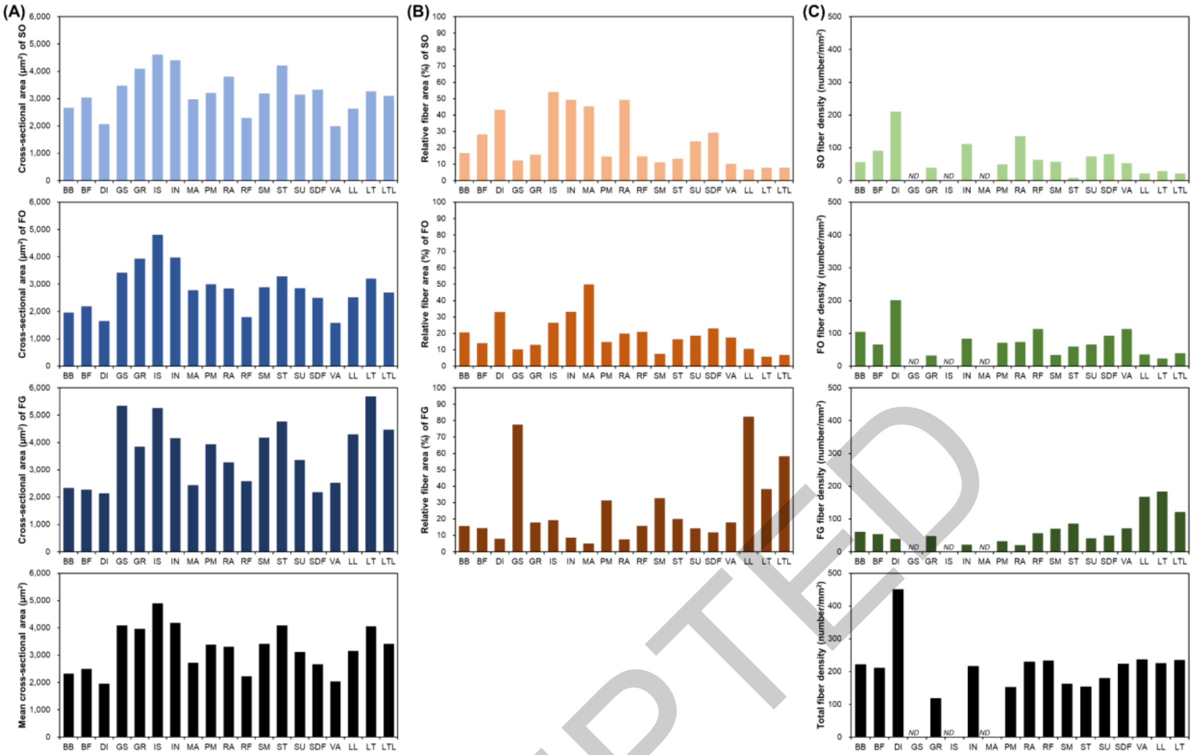

Fig. 2. Comparison of the muscle fiber characteristics of 19 porcine skeletal muscles reported in previous studies (summarized in Table 1). (A) Muscle fiber size (cross-sectional area). (B) Relative muscle fiber area. (C) Muscle fiber density. Muscle fiber types: SO, slow-twitch and oxidative; FO, fast-twitch and oxidative; FG, fast-twitch and glycolytic. *ND*, no data. Muscle name: BB, M. *biceps brachii*; BF, M. *biceps femoris*; DI, M. *diaphragm*; GS, M. *gluteus superficialis*; GR, M. *gracilis*; IS, M. *infra spinam*; IN, M. *infrahyoid*; MA, M. *masseter*; PM, M. *psoas major*; RA, M. *rectus abdominis*; RF, M. *rectus femoris*; SM, M. *semimembranosus*; ST, M. *semitendinosus*; SU, M. *subcapularis*; SDF, M. *superficialis digital flexor*; VA, M. *vastus*; LL, M. *longissimus lumborum*; LT, M. *longissimus thoracis*; LTL, M. *longissimus thoracis et lumborum*.

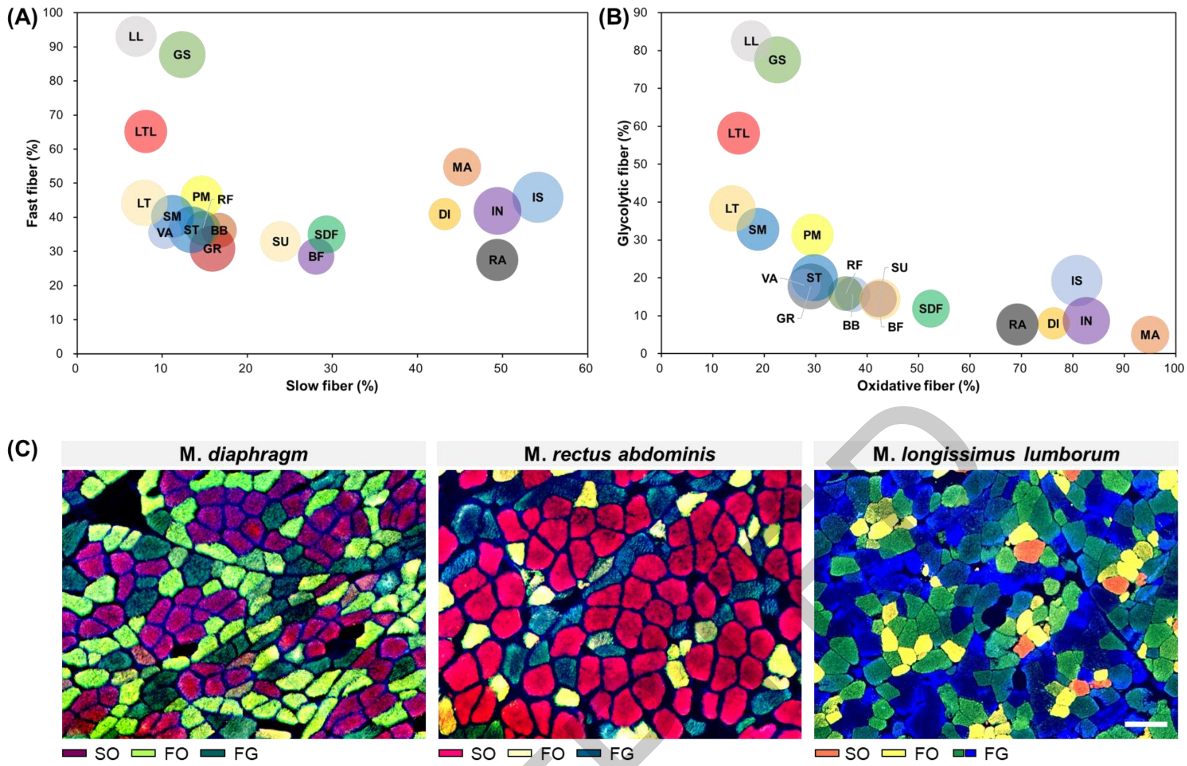

Fig. 3. Comparison of porcine skeletal muscles according to the proportions of different muscle fiber type (contractile, slow and fast; metabolic, oxidative and glycolytic) (A and B) and cross-sections of representative muscles with high ratios of slow-twitch and oxidative fibers (M. *diaphragm* and M. *rectus abdominis*) and fast-twitch and glycolytic fibers (M. *longissimus lumborum*) (C). The results shown in Table 1 and Fig. 2 were reconstructed to indicate A and B, and the abbreviated muscle names are as shown in Fig. 2. Images were obtained from the Meat Science Laboratory, Seoul National University, Republic of Korea and presented after modification. Muscle fiber types: SO, slow-twitch and oxidative; FO, fast-twitch and oxidative; FG, fast-twitch and glycolytic. Bar = 100 µm.

Table 1. Summary of results on muscle fiber characteristics of porcine skeletal muscle reported in previous studies

Breed1)	Sex	Age (day)	Weight (kg)2)	Muscles	Typing Method3)	Muscle fiber characteristics4) Type	CSA	Area %	Number %	Density	References
Yorkshire	Female	170	(L) 100	M. *longissimus thoracis et lumborum*	ISH	I	-	-	10.9	-	[12]
						I/IIA	-	-	0.1	-	
						IIA	-	-	6.7	-	
						IIA/IIX	-	-	0.3	-	
						IIB	-	-	62.3	-	
						IIX	-	-	17.5	-	
						IIX/IIB	-	-	2.2	-	
					mATPase	I	-	-	11.0	-	
						IIA	-	-	7.0	-	
						IIB	-	-	82.0	-	
				M. *rhomiboide*	ISH	I	-	-	68.0	-	
						I/IIA	-	-	-	-	
						IIA	-	-	12.0	-	
						IIA/IIX	-	-	-	-	
						IIB	-	-	-	-	
						IIX	-	-	20.0	-	
						IIX/IIB	-	-	-	-	
					mATPase	I	-	-	68.0	-	
						IIA	-	-	12.0	-	
						IIB	-	-	20.0	-	
LYD	Male Female	185	(L) 105	M. *longissimus thoracis*	mATPase	I	4,226	12.5	12.7	29.7	[25]
						IIA	4,204	9.4	9.9	22.9	
						IIB	4,624	78.1	77.4	183.4	
Yorkshire	Male	-	(L) 101	M. *longissimus thoracis et lumborum*	mATPase	I	2,376	6.8	9.6	-	[26]
						IIA	1,751	3.3	6.2	-	
						IIBr	2,483	7.5	10.0	-	
						IIBw	3,666	82.4	74.3	-	
					SDH	I	2,415	6.5	9.5	-	
						IIA	1,868	3.5	6.6	-	
						IIBr	2,616	7.5	10.0	-	
						IIBw	3,940	82.5	73.9	-	
Berkshire	Male Female	172.7	(C) 77.75	M. *longissimus thoracis et lumborum*	mATPase	I	-	7.5	10.7	-	[27]
						IIA	-	5.8	9.0	-	
						IIB	-	85.0	80.3	-	
Landrace			(C) 77.75			I	-	6.2	9.1	-	
						IIA	-	5.6	9.4	-	
						IIB	-	88.2	81.5	-	
LYD			(C) 81.85			I	-	5.4	8.1	-	
						IIA	-	7.1	12.4	-	
						IIB	-	87.5	79.4	-	
Yorkshire			(C) 75.4			I	-	6.8	8.9	-	
						IIA	-	6.4	10.6	-	
						IIB	-	86.8	80.5	-	
LYD	Male	-	(C) 78.5	M. *longissimus thoracis*	IHC	I	2,743	6.2	12.9	-	[9]
						IIA	3,052	3.4	6.1	-	
						IIA/IIX	4,765	0.4	0.6	-	
						IIB	6,114	68.1	63.1	-	
						IIX	6,869	17.6	14.6	-	
						IIX/IIB	8,251	4.4	3.1	-	

				M. *psoas major*		I	2,375	18.5	23.5	-	
						IIA	2,166	20.4	28.1	-	
						IIA/IIX	-	-	-	-	
						IIB	4,191	32.4	23.2	-	
						IIX	3,409	28.8	25.2	-	
						IIX/IIB	-	-	-	-	
				M. *semimembranosus*		I	3,055	6.3	12.0	-	
						IIA	3,011	4.7	8.6	-	
						IIA/IIX	6,631	2.9	2.6	-	
						IIB	6,997	79.3	65.4	-	
						IIX	3,634	7.2	11.4	-	
						IIX/IIB	4,520	2.3	2.9	-	
				M. *semitendinosus*		I	4,866	23.9	26.7	-	
						IIA	4,468	14.1	17.0	-	
						IIA/IIX	4,992	1.6	1.7	-	
						IIB	6,282	29.7	25.7	-	
						IIX	5,407	24.8	24.7	-	
						IIX/IIB	7,479	6.0	4.3	-	
Berkshire	-	-	(L) 110	M. *longissimus thoracis et lumborum*	mATPase	I	3,302	6.5	-	20.0	[28]
						IIA	2,801	9.4	-	34.0	
						IIB	4,398	84.1	-	194.0	
Duroc						I	3,025	6.1	-	20.0	
						IIA	3,014	9.1	-	30.0	
						IIB	5,133	84.9	-	170.0	
Landrace						I	2,933	6.5	-	22.0	
						IIA	2,781	7.6	-	27.0	
						IIB	4,987	86.0	-	177.0	
Yorkshire						I	3,031	6.9	-	23.0	
						IIA	2,698	8.3	-	31.0	
						IIB	5,050	84.8	-	173.0	
KNP and Landrace	Male Female	203	(C) 89.2	M. *longissimus thoracis et lumborum*	mATPase	I	3,877	9.1	12.1	-	[6]
						IIA	3,989	8.3	11.3	-	
						IIB	4,843	80.8	77.2	-	
Berkshire	Male	-	-	M. *longissimus thoracis et lumborum*	IHC SDH ISH	I	-	9.8	10.19	-	[24]
						IIA	-	4.0	3.61	-	
						IIB	-	54.8	55.70	-	
						IIX	-	29.8	29.96	-	
				M. *psoas major*		I	-	11.9	12.31	-	
						IIA	-	10.6	10.20	-	
						IIB	-	41.7	42.58	-	
						IIX	-	41.6	41.69	-	
Duroc				M. *longissimus thoracis et lumborum*		I	-	14.5	11.40	-	
						IIA	-	3.4	4.03	-	
						IIB	-	52.8	52.36	-	
						IIX	-	29.6	34.71	-	
				M. *psoas major*		I	-	14.7	8.54	-	
						IIA	-	15.0	8.67	-	
						IIB	-	39.5	50.62	-	
						IIX	-	39.8	33.01	-	
Tamworth				M. *longissimus thoracis et lumborum*		I	-	12.3	14.69	-	
						IIA	-	5.9	3.16	-	
						IIB	-	49.2	51.85	-	
						IIX	-	32.3	29.64	-	
				M. *psoas major*		I	-	12.1	14.62	-	
						IIA	-	7.6	14.76	-	

						IIB	-	38.2	40.13	-	
						IIX	-	41.5	39.36	-	
Yorkshire				M. *longissimus thoracis et lumborum*		I	-	12.1	12.87	-	
						IIA	-	3.7	6.13	-	
						IIB	-	51.3	49.68	-	
						IIX	-	35.6	31.44	-	
				M. *psoas major*		I	-	9.2	12.74	-	
						IIA	-	8.4	7.81	-	
						IIB	-	49.5	38.65	-	
						IIX	-	33.9	40.71	-	
KNP and Landrace	Male Female	190	(C) 79.85	M. *longissimus thoracis et lumborum*	IHC	I	4,797	8.6	-	21.6	[29]
						IIA	4,242	7.6	-	16.8	
						IIA/IIX	4,494	3.6	-	5.3	
						IIB	5,601	58.8	-	99.2	
						IIX	6,823	19.5	-	33.5	
						IIX/IIB	7,566	7.4	-	8.2	
Domestic pig	Male Female	165	(C) 81	M. *gluteus superficialis*	mATPase	I	2,880	6.8	-	-	[30]
						IIA	3,420	4.0	-	-	
						IIB	5,940	89.3	-	-	
				M. *infra spinam*		I	4,780	53.0	-	-	
						IIA	5,390	19.7	-	-	
						IIB	5,780	27.3	-	-	
				M. *longissimus thoracis et lumborum*		I	2,950	6.5	-	-	
						IIA	2,750	3.2	-	-	
						IIB	5,790	90.3	-	-	
				M. *masseter*		I	2,700	22.5	-	-	
						IIA	2,850	70.8	-	-	
						IIB	2,450	6.7	-	-	
				M. *semimembranosus*		I	3,050	6.6	-	-	
						IIA	3,480	3.6	-	-	
						IIB	6,210	89.8	-	-	
Wild pig				M. *gluteus superficialis*		I	4,070	17.9	-	-	
						IIA	3,430	16.4	-	-	
						IIB	4,760	65.8	-	-	
				M. *infra spinam*		I	4,450	55.3	-	-	
						IIA	4,230	33.5	-	-	
						IIB	4,740	11.3	-	-	
				M. *longissimus thoracis et lumborum*		I	3,400	13.0	-	-	
						IIA	2,900	17.3	-	-	
						IIB	3,740	69.7	-	-	
				M. *masseter*		I	3,240	68.0	-	-	
						IIA	2,700	28.7	-	-	
						IIB	2,410	3.3	-	-	
				M. *semimembranosus*		I	3,890	16.6	-	-	
						IIA	3,230	16.1	-	-	
						IIB	3,760	67.3	-	-	
Polish Large White	Female	176	(C) 78.8	M. *longissimus lumborum*	IHC	I	2,516	4.9	8.2	18.0	[31]
						IIA	2,485	9.5	15.0	33.0	
						IIB	4,658	85.6	76.9	167.0	
Puławska	Female	198	(C) 76.34			I	2,752	8.9	11.6	27.0	
						IIA	2,547	11.7	16.3	38.0	
						IIB	3,926	79.4	72.1	169.0	
YLD	-	-			mATPase	I	-	5.7	8.4	-	[32]

			(C) 79.2	M. *longissimus thoracis et lumborum*		IIA	-	7.7	13.4	-	
						IIB	-	86.6	78.2	-	
LYD	Male	-	(C) 79.2	M. *biceps brachii*	IHC	I	2,669	16.7	-	56.5	[3]
						IIA	1,965	20.5	-	105.0	
						IIA/IIX	1,802	3.6	-	17.7	
						IIB	2,656	10.8	-	36.9	
						IIX	2,625	32.4	-	121.9	
						IIX/IIB	2,267	16.0	-	65.8	
				M. *biceps femoris*		I	3,040	28.1	-	92.0	
						IIA	2,192	14.1	-	65.9	
						IIA/IIX	1,286	1.0	-	7.6	
						IIB	2,905	32.1	-	114.0	
						IIX	2,898	17.6	-	65.9	
						IIX/IIB	2,019	7.1	-	29.1	
				M. *diaphragm*		I	2,062	43.2	-	210.7	
						IIA	1,654	33.0	-	200.7	
						IIA/IIX	-	-	-	-	
						IIB	2,609	5.7	-	23.2	
						IIX	1,960	10.1	-	51.8	
						IIX/IIB	1,859	8.1	-	43.5	
				M. *gracilis*		I	4,095	15.9	-	38.9	
						IIA	3,937	13.1	-	32.9	
						IIA/IIX	4,462	1.0	-	2.2	
						IIB	3,897	9.7	-	26.1	
						IIX	4,043	50.6	-	128.7	
						IIX/IIB	2,968	9.7	-	33.1	
				M. *infrahyoid*		I	4,404	49.4	-	111.8	
						IIA	3,981	33.2	-	83.5	
						IIA/IIX	-	-	-	-	
						IIB	-	-	-	-	
						IIX	4,042	9.4	-	23.6	
						IIX/IIB	4,284	8.0	-	19.5	
				M. *longissimus thoracis et lumborum*		I	1,937	4.2	-	21.9	
						IIA	1,107	11.2	-	102.5	
						IIA/IIX	-	-	-	-	
						IIB	1,719	42.2	-	242.8	
						IIX	1,802	26.4	-	152.0	
						IIX/IIB	2,010	15.9	-	79.0	
				M. *psoas major*		I	4,050	21.5	-	49.8	
						IIA	3,834	26.5	-	71.3	
						IIA/IIX	3,399	2.0	-	5.0	
						IIB	4,171	10.7	-	24.2	
						IIX	3,886	14.5	-	42.3	
						IIX/IIB	4,578	24.4	-	57.7	
				M. *rectus abdominis*		I	3,803	49.4	-	135.2	
						IIA	2,838	19.8	-	74.3	
						IIA/IIX	3,312	2.3	-	6.9	
						IIB	2,932	3.1	-	9.4	
						IIX	3,761	18.1	-	43.9	
						IIX/IIB	3,104	7.4	-	23.3	
				M. *rectus femoris*		I	2,302	14.8	-	63.6	
						IIA	1,791	21.0	-	113.2	
						IIA/IIX	1,971	0.9	-	4.7	
						IIB	2,921	32.7	-	112.3	

						IIX	2,518	11.2	-	44.8	
						IIX/IIB	2,902	18.6	-	65.7	
				M. *semimembranosus*		I	2,757	15.3	-	57.6	
						IIA	1,817	5.8	-	34.3	
						IIA/IIX	1,857	2.7	-	15.1	
						IIB	3,167	51.0	-	157.7	
						IIX	2,268	22.9	-	102.3	
						IIX/IIB	2,765	2.3	-	8.9	
				M. *semitendinosus*		I	3,551	3.0	-	8.3	
						IIA	2,096	18.5	-	59.7	
						IIA/IIX	-	-	-	-	
						IIB	2,736	32.0	-	116.5	
						IIX	3,259	26.8	-	82.9	
						IIX/IIB	3,246	19.7	-	59.2	
				M. *subcapularis*		I	3,150	23.9	-	73.8	
						IIA	2,850	18.6	-	66.0	
						IIA/IIX	2,847	1.3	-	4.8	
						IIB	3,569	16.7	-	46.7	
						IIX	3,519	27.7	-	77.4	
						IIX/IIB	3,523	11.7	-	34.8	
				M. *superficialis digital flexor*		I	3,329	29.3	-	80.8	
						IIA	2,492	23.1	-	93.6	
						IIA/IIX	2,489	2.0	-	8.0	
						IIB	2,355	18.3	-	72.0	
						IIX	1,705	13.3	-	58.7	
						IIX/IIB	2,190	14.0	-	60.2	
				M. *vastus*		I	1,995	10.3	-	52.9	
						IIA	1,577	17.5	-	113.2	
						IIA/IIX	1,795	2.9	-	17.6	
						IIB	2,747	25.4	-	101.3	
						IIX	2,835	21.3	-	86.4	
						IIX/IIB	2,750	22.6	-	81.0	
LYD	-	-	(C) 82.5	M. *longissimus thoracis*	IHC	I	2,977	6.4	10.3	-	[33]
						IIA	2,709	5.5	9.6	-	
						IIB	5,490	75.1	66.0	-	
						IIX	4,439	12.9	13.7	-	
LYD	-	-	(L) 132.9	M. *longissimus thoracis*	IHC	I	3,129	6.3	10.3	-	[34]
						IIA	2,853	5.3	9.4	-	
						IIB	5,682	75.3	66.4	-	
						IIX	4,895	13.0	13.9	-	

Data expressed as ranges in previous studies are presented as average values.

1)LYD, crossbred of (Landrace × Yorkshire) × Duroc; YLD, crossbred of (Yorkshire × Landrace) × Duroc; KNP, Korean native black pig.

2)L, live weight; C, carcass weight.

3)ISH, *In situ* hybridization; mATPase, myosin ATPase; SDH, succinic dehydrogenase; IHC, immunohistochemistry.

4)CSA, cross-sectional area (μm^2); Area%, relative fiber area (%); Number%, relative fiber number (%); Density, fiber density (number/mm^2).