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**Structural Variations in the Muscle Fiber in Relation  
to Tenderness of Meat: A Review<sup>1</sup>**

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Approximately 40% of bovine live body weight is skeletal muscle, of which 75% is muscle fibers. Any variation as to quantity of the muscle components can ultimately affect tenderness of meat. Therefore a thorough appreciation of the important tissues composing muscle must be realized before any consideration of fiber variation can be made.

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With the advent of technological advancements in electron and light microscopy and new methods of tissue preparation, the structure of the skeletal muscle fiber has drawn considerable interest. A brief review of the literature relative to the striated muscle fiber will be given before considering variations.

Although Bardeen (1903) showed that muscle fibers vary in degree of branching, Walls (1960) described the muscle fiber as a cylindrical, elongated syncytium that generally does not branch. The muscle fiber is surrounded by a sheath, the sarcolemma, that is very similar to the plasma membrane and internal membranes of other cells. The sarcolemma is not a perfectly smooth cylindrical membrane, but is marked by several small vesicles and caveolae (Porter and Palade, 1957). Beneath the sarcolemma, a fluid matrix, the sarcoplasm, is made of various soluble proteins such as myogen and myoglobin. The sarcoplasm serves a function similar to that of typical cellular cytoplasm and contains the various cellular inclusions and organelles. An organelle, the myofibril, has received considerable attention due to its contractile properties. The myofibril is an elongated striated structure comprised of two different types of myofilaments. A coarse filament is approximately 100 Å in diameter and 1.5 $\mu$  in length. A fine filament is approximately 50 Å in diameter and 2 $\mu$  in length (Huxley and Hanson, 1960). The thick filament, comprised of the protein myosin, is called the A band. The thin filament, comprised of the protein actin, is referred to as the I band. Between adjoining I bands there is another band, the Z disc. The distance from one Z disc to another comprises the contractile unit (sarcomere) of the myofibril.

*Inherent variation*—Walls (1960) reported that there is considerable variation in fiber diameter, with a range of 10 to 100 $\mu$  commonly being accepted. Fiber size differs in vertebrate classes with fish having the thickest fibers and birds the thinnest (Mayeda, 1890, *vide* Joubert, 1956a). The fibers of one muscle may be generally thicker than those of another muscle in the same animal (Hammond and Appleton, 1932). In addition, the fiber diameters vary considerably within the same muscle. Other factors such as species, size, age, breed, sex, and level of nutrition also have been found to influence this variation.

Joubert (1956a) reported that muscle diameter had no clear relationship to body size, however, an increase in fiber diameter was closely associated with relative increase in body weight.

Joubert (1956a) studied the effect of breed on fiber diameter in cattle and found that British Friesian, whether crossbred or purebred, had significantly larger fiber diameters than Dairy Shorthorn. This breed significance was not shown to be independent of body weight. Other workers (Adametz, 1888; Hammond and Appleton, 1932; Strateciuc, 1933; Mehner, 1938; and Glebina, 1952) have supported the findings that interbreed differences do exist; however, in most cases the difference is proportional to differences in body size.

A review of early studies caused Joubert (1956a) to conclude that males generally have thicker fibers than females. However, when size was considered, he found that there was a slight tendency for females to have thicker fibers than males. Adametz (1888; see Joubert, 1956a) found that muscle fibers of bulls were appreciably larger than those of cows but that only slight differences existed between bulls and steers. Hammond and Appleton (1932) using sheep, Mehner (1938, *vide* Joubert, 1956a) with fowl, and Ishihara et al. (1953), in Japanese Black cattle, have confirmed these results.

Contradictory evidence was presented by Brady (1937) and Satorius and Child (1938), who found that cows had significantly thicker muscle fibers than steers. The true relationship, if any, that does indeed exist

still a matter of conjecture.

Joubert (1956a) reported the effect of age on fiber diameter. McMeekan (1940-41), Thompson (1942), and Meara (1947) studied the effect of age on fiber diameter. Similar work was done by Hiner et al. (1953), Tuma et al. (1962), Carpenter et al. (1962) and Henrickson et al. (1963). There is general agreement that fiber diameter increases from birth to maturity and that it increases in size rapidly while the animal is quite young and tends to level off as the animal approaches maturity.

Yeates (1964) studied starvation changes and subsequent recovery of adult beef muscle. The experiment revealed that, with starvation of the adult animal, the shrinkage in cross-sectional areas of the muscles, after allowing for the loss of some intramuscular fat, was associated with the reduction in diameter of the individual fibers. In consequence of repair, recovery both of whole muscle dimensions and muscle fiber diameter appeared to be complete.

*Post-mortem variations*—Other causes of structural variation in the muscle fibers are the conditions to which they are subjected after the animal is slaughtered.

Muscle contraction referred to as rigor mortis has received much attention by investigators. Rigor mortis is defined as the physical and chemical changes that take place after death of the animal. This discussion will be limited to the physical effects of rigor on the muscle fiber. The main observed physical change is from a highly extensible elastic condition of muscle of freshly killed animals to the inextensible and rigid condition of the muscle fiber in full rigor. This is a result of the actin filaments becoming bound to the myosin filaments, thus greatly decreasing fiber extensibility. This actomyosin complex remains locked in a contracted state until rigor resolves (Marsh, 1954). Along with this change in extensibility, there is a gradual shortening of the sarcomere as rigor approaches and the muscle is left in a semicontracted state (Locker, 1960). Similar results, with an increase in fiber diameter and a decrease in sarcomere length, were obtained at the Oklahoma Station. Another well known physical effect of rigor on the muscle fiber is the presence of rigor kinks found in localized areas along some fibers. In an attempt to objectively determine the amount of kinkiness in different muscles, and as a result of different treatments, we devised a method of expressing the amount of kinkiness on a percentage basis. This method consisted of subjectively assigning a value to the condition of the muscle fiber, similar to the subjective appraisal of carcass grade, and then relating this measurement with other known estimates of contraction.

The effect of temperature on the condition of the muscle fiber has been shown to have considerable influence. Locker and Hagyard (1963) showed that shortening of the muscle fiber occurs when exposed to very cold temperatures. This phenomenon, called cold shortening, is currently believed to occur simultaneously with the formation of cross-linkages in rigor; a degree of internal strain or actual disorganization occurs and actually increases the resistance of the muscle to cleavage. Herring et al. (1965a) reported that slightly more shortening appeared, as indicated by sarcomere length, takes place in stretch-restrained muscle samples at 1 C. than at 5 C. It was postulated in this experiment that some cold shortening may have occurred at this temperature as well. Cook and Wright (1966), using samples of unfrozen and prerigor frozen ovine semitendinous muscle, incubated for 24 hr at six temperature levels between 0 and 40 C., found that variations in temperature caused muscle fibers to be in various states of contraction. The variations in sarcomere length of unfrozen and prerigor frozen muscle did not follow any specific course in relation to temperature, but a difference did exist.

Harrison et al. (1949) noted that the differences between sections of

raw and cooked muscle were slight; however, the cooked sections tended to have straighter fibers than the raw muscle sections.

Paul et al. (1944, *vide* Harrison et al., 1949) noted that the histological appearance of the muscle fibers varied with biological aging. Harrison et al. (1949) noted that freshly killed beef muscle showed poorly differentiated, straight to slightly wavy fibers. After 1 day of storage at 1.7 C. the fibers and cross striations were more and the longitudinal striations less distinct. Contracture nodes, kinks, and waves increased in the fibers with longer aging but tended to disappear after 4 to 9 days of storage. Disappearance of cross striae in small, infrequent areas of the fibers was noted on the second day of storage, and this disintegration tended to increase in frequency and extent as the storage time increased.

Younger and Baigent (1965) studied the effect of precooking on freeze-dried lamb and noted that uncooked freeze-dried meat appeared to suffer much more fiber damage, in terms of fiber distortion and shrinkage, than the cooked, freeze-dried samples. When rehydrated, the samples revealed a similar pattern; the uncooked, freeze-dried material revealed considerable distortion of the fibers and many were smaller in diameter than normal. The cooked, freeze-dried samples very closely resembled fresh meat. The fibers were restored almost completely in size and shape, with no abnormal spaces between them.

Carcass position has a definite effect on sarcomere length and fiber diameter (Herring et al., 1965b). When the carcass is suspended vertically, certain muscles are in a stretched state, as indicated by sarcomere length, while some are in a shortened state. In general, the differences in sarcomere lengths were associated with differences in diameter. When the muscles shortened, there was a corresponding decrease in sarcomere length and an increase in fiber diameter.

Recent work at the Oklahoma Station with semitendinous and semimembranous muscles from five choice grade steers of similar age, weight, and genetic background, indicated that a positive relationship existed between muscle tension and sarcomere length, fiber diameter, and percent kinkiness. Both muscle types were removed from the carcass prior to slaughter (45 min), divided into four samples ( $6 \times 6 \times 21$  cm), and subjected to four degrees of tension (0, 1000, 2500, and 5000 g pull). The samples were held in this state for 48 hr post-mortem at 34 C. Histological and shear samples were then taken.

An analysis of variance showed that a highly significant difference ( $P < 0.01$ ) existed for sarcomere length for the different degrees of tension. Further analysis, using Duncan's new Multiple Range test, clearly indicated that, with succeeding increases in tension, a corresponding increase in sarcomere length occurred. All ranges were highly significant at the  $P < 0.01$  level, except the range 2500-5000 (significant at the  $P < 0.05$  level).

These findings are in general agreement with those of Herring et al. (1965a) who noted that sarcomere length of the semitendinous muscle decreased as a result of prerigor excision, but that the prerigor-excised, stretch-restrained, semitendinous muscles generally exhibited longer sarcomeres than the control samples.

A highly significant difference ( $P < 0.01$ ) in fiber diameter was found for the different degrees of tension. There was also a highly significant difference ( $P < 0.01$ ) between muscles, indicating that, with an increase in the amount of tension, there was a corresponding decrease in fiber diameter, to a point.

Variation in percent kinkiness was found to be highly significant ( $P < 0.01$ ) for the different degrees of tension and significant differences

at the ( $P < 0.05$  level) were noted between muscles and for a muscle by tension interaction. The semimembranous muscle and an average of both muscles were found to have highly significant ( $P < 0.01$ ) differences in percent kinkiness for ranges of 0-1000, 0-2500 and 0-5000 g pull.

Work at the Oklahoma Station on the effect of prerigor excision of three bovine muscles on fiber diameter and percent kinkiness show interesting relationships. Percent kinkiness was greater ( $P < 0.10$ ) for the prerigor-excised longissimus dorsi muscle than for postrigor-excised muscle. However, the opposite was true for the gluteus medius muscle in support of Locker's (1960) postulate that different internal strains among muscles exist in the vertically suspended carcass. This also is in agreement with our findings that the percent of kinkiness is, to a certain degree, a function of muscle tension.

We also found that the fiber diameter in pre-rigor, excised, semitendinous muscle was greater than that in postrigor-excised muscles, apparently because of muscle shortening.

Hiner et al. (1953) showed that a curvilinear relationship exists between fiber diameter and tenderness. He found that, up to a point, an increase in fiber diameter results in a increase in shear force. Tenderness in this context is considered as the resistance to shear. A positive correlation exists between the taste panel score for tenderness and a mechanical shear force. Tuma et al. (1962) also reported that with an increase in fiber diameter there was a corresponding increase in shear force among different age groups of cattle. However, when the effect of age was removed, little relationship existed. Carpenter et al. (1962) on the other hand found that with an increase in maximum fiber diameter there was a decrease in shear force of raw longissimus dorsi muscle. Opposite results were found for cooked longissimus dorsi muscle. They postulated that for a given size core there may be more small than large fibers per unit area; therefore more of the sarcolemma and endomysial connective tissue was present, resulting in a less tender product.

Herring et al. (1965b) noted that, as fiber diameter increased, tenderness decreased whereas the opposite was true when fiber diameter decreased. It was also shown that a change in fiber diameter was related to a change in sarcomere length. In a previous experiment Herring et al. (1965a) found that stretching a muscle, rather than not stretching it, increased tenderness and resulted in smaller fiber diameters. It was assumed that a greater number of fibers, per unit area, were being severed in the stretched sample. This assumption is in agreement with that of Carpenter et al. (1962) in that the greater number of smaller fibers should theoretically make the muscle less tender. However, the stretched muscle was tenderer, indicating that the thickness of the sarcolemma and endomysial connective tissue was reduced in thickness when the fibers were stretched (Cassella, 1950).

This fact is applicable to our work with muscles subjected to four degrees of tension. An analysis of variance indicated a significant difference ( $P < 0.05$ ) in shear force. Further analysis indicated that shear force decreased up to 1000 and 2500 g pull for the semimembranous and semitendinous muscles, respectively.

Fiber diameter and shear force decreased as tension increased, indicating that the stretched samples with the smallest average diameters were tenderest.

The relation of fiber size, amount of fat, and amount of connective tissue per unit area undoubtedly all affect tenderness.

The degree of muscular contraction as it affects tenderness has received considerable interest in recent years. Locker (1960) first postulated that different muscles in the carcass go into different states of

contraction in rigor as a result of different internal strains imposed on the muscles of the vertically suspended carcass. In an experimental study of the effects of prerigor excision of several muscles, he concluded that muscles in a relaxed state, as indicated by fibrillar pattern, are tenderer than those partly contracted. To this effect Marsh and Leet (1966) studied the effects of cold shortening on tenderness. They noted that with a decrease in length of up to about 20% caused little or no toughening, but with 20 to 40% shortening the toughness increased several fold. Beyond 40% shortening the meat became increasingly tenderer, and at 60% shortening it was cleaved almost as easily as meat in which almost no shortening had occurred. They postulated that the 40-60% range may be a zone of progressive rupturing that causes a rapid decrease in internal strain in this phase, with consequent realignment of previously distorted cleavage planes.

Our work agrees with that of Herring et al. (1965a) and indicates that, with increasing amounts of strain on a muscle, sarcomere length increases to a point of physical limitation, and there is a subsequent increase in tenderness.

The percent kinkiness decreased with the application of tension to the muscle samples. The fibers of semimembranous muscle increased in percent kinkiness when the tension was greater than 1000-g pull. A gradual increase in shear force was also noted after the 2500-g-pull treatment for this muscle, indicating that some fiber breakage may have occurred when the amount of tension overcame the physical limits of the fiber. This may have resulted in partial contraction of some of the broken fibers which would account for the increase in shear. Theoretically this also would allow these broken fibers to be distorted to a greater degree. A similar response was noted by Herring et al. (1965a) when they tried to stretch the psoas major muscle; tearing and failure of the muscle to regain its initial length resulted.

In summary, the condition in which the muscle fiber is found is highly variable. Inherent differences of diameter and sarcomere length as a result of species, breed, sex, age, and level of nutrition exist. Differences occur after the slaughter of the animal as a result of contraction and distortion in rigor, due to temperature change, and as a result of different amounts of tension on the muscle.

These structural variations affect the ultimate tenderness of the muscle. It stands to reason then that some of the commonly associated differences in tenderness with age, sex etc. may be due to the structural condition of the muscle fiber.

Further work appears necessary to clarify the relationship of sex to muscle fiber size and fiber size to tenderness. A tool more sensitive than those now available may be necessary to satisfy these relationships.

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