PRENATAL DEVELOPMENT OF MUSCLE FIBER TYPES
IN DOMESTIC ANIMALS*

C. ROBERT ASHMORE
University of California, Davis

P. B. ADDIS
University of Minnesota, St. Paul

INTRODUCTION

The area of study in muscle biology concerned with light (anaerobic) and dark (aerobic) muscle fibers has expanded considerably in recent years. For example, at the first Wisconsin symposium, "Physiology and Biochemistry of Muscle as a Food," held in 1965, no paper was presented which was primarily concerned with light and dark fibers. At the second symposium, four years later, one entire session, including five manuscripts, was devoted completely to the subject. Yet, in spite of this increased attention to, and increased information concerning muscle fiber types, several questions of extreme importance to animal scientists remain unanswered. They are: (1) How many different types of muscle fibers exist, and can a system of classification be applied which will accurately identify these types across species lines as well as under various physiological and developmental states? (2) What is the nature of the embryonic development of fibers, and at what time and place in myogenesis are the adult characteristics of muscle fibers determined? (3) What is the significance of this information to contemporary problems in meat science?

This report will (1) briefly review some of the early studies on light and dark fibers, (2) discuss the development of an improved system of fiber-type classification, (3) review recent research on pre- and postnatal development of muscle fibers, and (4) discuss and speculate upon the implications of these findings to meat science. We will report that (1) there are two fundamental fiber types in skeletal muscle, \( \alpha \) and \( \beta \), as demonstrated histochemically by staining for myofibrillar adenosine triphosphatase (ATPase) activity; (2) \( \beta \) fibers are red fibers, hence \( \beta \)-red (BR); (3) \( \alpha \) fibers are red (CR) at birth or hatching but have the capacity to transform to white (W) fibers giving rise to a third fiber type; (4) during prenatal or in ovo maturation, \( \beta \) fiber development precedes that of \( \alpha \) fibers, the latter forming by proliferation and fusion.


of myoblasts along the surface of the primary myotube, the β fiber; (5) it is hypothesized that genetic selection for leanness and musculature is accomplished by the deposition of additional α fibers in the bundle and the transformation of greater numbers of OR fibers to OW fibers in affected muscles.

PROPERTIES OF RED AND WHITE FIBERS

There is little doubt that muscle color varies closely with function. Notions to the contrary are dispelled by reading the account of the complex architecture and fiber distribution of pigeon pectoralis muscle summarized by George and Berger (1966). Dark muscles are, most often, tonic, contract slowly and usually perform postural functions. Light muscles contract quickly, with more strength than dark muscles, but fatigue more easily. Metabolic characteristics explain differences in rates of fatigue in the two fiber types. Red fibers contain myoglobin, generate ATP by oxidation of fat and carbohydrates, and are generally smaller in diameter which facilitates rapid exchange of substrates and toxic waste products. Due to such efficient metabolic mechanisms, they exhibit resistance to fatigue. White fibers depend primarily upon anaerobic glycolysis to produce ATP, contain little or no myoglobin and, therefore, tire quickly during strenuous activity as endogenous glycogen stores are depleted (Close, 1972).

While the above patterns and differences are logical, some difficulty arises when attempts are made to correlate speed of contraction (twitch) with color. The early work of Paukul (1904) demonstrated that slow-twitch muscles were invariably red; however, not all red muscles were slow-twitch. It is now believed that the rate of hydrolysis of ATP limits the rate of contraction. Thus, separate actomyosins might be expected to exist in fast and slow fibers. Guth and Sameha (1969) obtained cytochemical evidence for the existence of different actomyosins between fast and slow fibers. They exposed tissue sections to acid and alkali prior to the ATPase reaction medium, and were clearly able to demonstrate differences between fibers; slow fibers lost activity during alkali preincubation, but activity persisted through acid treatment. The pattern was the reverse for fast fibers. They (Guth and Sameha, 1969) concluded that at least two distinct actomyosins exist, one for each type of fiber. Evidence obtained biochemically on purified myosin has shown that myosins from slow and fast muscle differ with respect to specific ATPase activity, acid and alkali stability, susceptibility to tryptic digestion, and in the number and molecular weights of light chain components (Saker et al., 1971; Sreret et al., 1966; Barany et al., 1965; Sameha et al., 1970a; Gergely et al., 1965). These findings are consistent with the hypothesis that muscle fibers can differ with regard to speed of contraction as well as in their capacity to resist fatigue, but importantly, these physiological characteristics are not necessarily correlated with each other and are therefore subject to separate control mechanisms.
Several systems for the classification of muscle fibers are currently in use. The finding of an "intermediate" fiber (Ogata, 1958), together with the inability of myologists to segregate all fibers into a simple dual system, fast-white and slow-red, has resulted in a proliferation of conventions (table 1). Stein and Padykula (1962) identified three fiber types "A", "B", and "C" based on the SDH stain. More recently, Samaha et al. (1970) demonstrated three fiber types based on myosin ATPase histochemical assay. The three types were designated α, β, and ω. However, the two systems were not compatible in a comparison of rat and cat fiber patterns (Yellin and Guth, 1970). The "B" fiber or "intermediate" fiber of both rat and cat contain alkali-labile ATPase (hence are β-fibers). However, the "A" or white fiber of the cat contains acid-labile ATPase (hence is α) whereas in the "A" fiber of the ATPase is intermediate in pH stability (hence is ω).

A study of postnatal development of fiber types in normal and dystrophic chicks lead to the development of a classification system which appeared to successfully combine the two systems (speed of contraction and metabolic profile) into a single system for chick muscle. Ashmore and Doerr (1971) studied the development of the pectoralis, sartorius and adductor muscles and found that the two basic fiber types (α and β), based on myosin ATPase activity, are initially red (hence OR and BR). The OR fiber has the capacity, by modulating metabolic enzymes, to transform to a white (cw) fiber. They further noted that in the sartorius, a muscle of mixed fiber types, the small BR fibers are located in the interior of the fiber bundles, intermediate diameter OR fibers are commonly adjacent to the BR fibers, and fibers in the extreme periphery of bundles are nearly always CW. Table 2 summarizes the properties of BR, OR and CW fibers.

The potential value of such a system of classification is greatly enhanced if it can be applied to many species. Such a study was conducted by Ashmore and Doerr (1971). Chick, mouse, bovine and porcine red and white muscles were studied. In mouse muscle, SDH activity of BR fibers as assayed cytochemically, was less than that of OR fibers, whereas in the other species SDH activity tended to be highest in BR fibers. However, when the ratio SDH/phosphorylase was calculated (a logical index of acerobiosis) BR fibers of all species exhibited the highest ratio. It was concluded that for the species studied, which include three species important to meat production, the BR, OR, CW system was compatible. It should be emphasized that the α fiber population most often exhibits a continuum of oxidative enzyme activity, reflecting the likelihood that α fibers, with respect to energy metabolism, are responsive to physiological demand. The identification of an α fiber as R or W therefore may be arbitrary. This is not generally a major problem, however, since the utility of muscle fiber classification most often lies in relative comparisons rather than in absolute ones.

More recently, Burke et al. (1971) have designated fibers as S (slowly contracting), FR (fast contracting, and fatigue resistant), and FF (fast contracting, fast fatigue). Their system is based on physiological features
TABLE 1. COMPARISON OF PREVIOUS FIBER TYPE CLASSIFICATION SYSTEMS TO THE ONE SUGGESTED BY ASHMORE AND DOERR, 1971

<table>
<thead>
<tr>
<th>OW&lt;sup&gt;a&lt;/sup&gt;</th>
<th>OR</th>
<th>BR</th>
</tr>
</thead>
<tbody>
<tr>
<td>White&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Red</td>
<td>Intermediate</td>
</tr>
<tr>
<td>White&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Intermediate</td>
<td>Red</td>
</tr>
<tr>
<td>White&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Intermediate</td>
<td>Red</td>
</tr>
<tr>
<td>IIF&lt;sup&gt;e&lt;/sup&gt;</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>II&lt;sup&gt;f&lt;/sup&gt;</td>
<td>II</td>
<td>I</td>
</tr>
<tr>
<td>A&lt;sup&gt;g&lt;/sup&gt;</td>
<td>C</td>
<td>B</td>
</tr>
</tbody>
</table>

<sup>a</sup> Ashmore and Doerr, 1971.
<sup>b</sup> Padykula and Gauthier, 1967, as applied to mice, rats, and guinea pigs.
<sup>c</sup> Ibid, as applied to domestic animals and man.
<sup>d</sup> George and Berger, 1966, as applied to avian muscle.
<sup>e</sup> Engle, 1962, as determined by the SDH histochemical assay.
<sup>f</sup> Ibid, as determined by the ATPase histochemical assay.
<sup>g</sup> Stein and Padykula, 1962.

TABLE 2. COMPARISON OF CHARACTERISTICS AMONG BR, OR AND OW FIBERS

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>BR&lt;sup&gt;a&lt;/sup&gt;</th>
<th>OR</th>
<th>OW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter</td>
<td>narrow</td>
<td>narrow-intermediate</td>
<td>broad</td>
</tr>
<tr>
<td>Color</td>
<td>red</td>
<td>red</td>
<td>white</td>
</tr>
<tr>
<td>Blood supply</td>
<td>high</td>
<td>intermediate</td>
<td>low</td>
</tr>
<tr>
<td>Myoglobin</td>
<td>high</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>Glycogen</td>
<td>low</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Phosphorylase</td>
<td>low</td>
<td>intermediate</td>
<td>high</td>
</tr>
<tr>
<td>Succinate dehydrogenase (SDH)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>high</td>
<td>intermediate</td>
<td>low</td>
</tr>
<tr>
<td>SDH/Phosphorylase&lt;sup&gt;b&lt;/sup&gt;</td>
<td>high</td>
<td>intermediate</td>
<td>low</td>
</tr>
<tr>
<td>Myofibrillar ATPase &lt;br&gt; pH 4.00</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>pH 10.40</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Contraction speed</td>
<td>slow</td>
<td>fast</td>
<td>fast</td>
</tr>
</tbody>
</table>

<sup>a</sup> Classification system suggested by Ashmore and Doerr, 1971.
<sup>b</sup> In the mouse and certain other species of laboratory animals, SDH activity as demonstrated cytochemically, of OR exceeds that of BR fiber. However, if the ratio SDH/Phosphorylase (an index of aerobiosis) is calculated and the same comparisons made, BR is classified as more aerobic than the OR.
of muscle fibers, but the cytochemical features, described by them, are
the same as those described by us for BR, CR, and CW fibers, respectively.

Barnard et al. (1971) have used the terms slow-twitch intermediate,
fast-twitch red, and fast-twitch white to identify fibers on the basis of
a contractile characteristic and on a metabolic characteristic. However,
their system of classification, developed from studies on mice and guinea
pigs, cannot be applied to most other species, since in the latter,
"intermediate" fibers (based on SDH activity) are fast fibers, not slow
fibers (Ashmore and Doerr, 1971a, b). Further, identification of a
contractile characteristic on the basis of a histochemical assay
(myofibrillar ATPase activity) is hazardous since it has been shown that
"slow" fibers in an early developmental state demonstrate an intense
histochemical reaction for myofibrillar ATPase activity (Ashmore et al.,
1972) and could therefore be erroneously classified as "fast" fibers.
Guth and Samaha (1972) have demonstrated a lack of correlation between
histochemical and biochemical assays for myofibrillar ATPase activity in
neonatal rat muscle.

DEVELOPMENT OF MUSCLE FIBER TYPES

Postnatal maturation of muscle fibers is concerned with the development
of preprogrammed potentials for growth, contraction, and energy generation.
Each of these is a multifaceted trait and optimal expression depends upon
correct environmental interactions with genetically determined potential.

Muscle contraction consumes considerable quantities of ATP and muscle
fibers, therefore, require rather efficient mechanisms for generation of
high energy intermediates. In terms of metabolic pathways, some fibers
demonstrate a distinct dependence upon either the aerobic pathways (Kreb's
cycle enzymes and electron transport enzymes of mitochondria) or the
anaerobic pathway (enzymes associated with the breakdown of glycogen to
glucose-6-phosphate and then to lactic acid). Other fibers exhibit a
substantial capacity to generate ATP by both pathways, using the aerobic
pathway when sufficient oxygen is available and the anaerobic pathway when
the requirement for ATP exceeds the capacity of oxygen and aerobic metabolism
to meet the demand.

The development of aerobic metabolic capacity precedes the development
of anaerobic capacity so that initially all fibers could be described as
being "red". The β fiber population never develops any substantial capacity
for anaerobic metabolism and so remains red throughout its lifespan. In
support of this type of metabolism, β fibers remain relatively small in
diameter and are supplied with a liberal number of capillaries. The α
fiber population begins to exhibit an increasing capacity for anaerobic
metabolism approximately near birth. In a proportion of the α fiber
population, this increase is decidedly more rapid and is accompanied by a
rapid increase in fiber growth and a dilution of mitochondrial density.
Indeed, not only the specific activity of mitochondrial enzymes changes
but the pattern of mitochondrial enzymes as well as the morphology of the
organelles are altered during the transformation of GR to GW fibers. The regulatory signals and mechanisms which induce this transformation are not known, but it seems possible that it occurs in α fibers in which functional activity occurs at a level below that which is required to maintain a high aerobic capacity.

The developmental acquisition of specific characteristics by different muscle fibers is a matter of some importance to meat scientists since it is clear that the characteristics of meat are simply reflections of the sum of the characteristics of each of the muscle fibers of which meat is composed. We have recently discussed some of the possible effects on meat quantity and quality that might be expected to result from variation of the proportionality of muscle fiber types (Ashmore et al., 1972). Let us turn to some of our recent observations obtained in studies of fetal muscle.

Some earlier studies (see Cassens et al., 1969, for review) had shown fetal muscle fibers to be initially indistinguishable from each other, and that the development of specific fiber types occurred at different ages in different species. This is especially apparent with regard to energy metabolism since, as discussed above, all fibers are initially red, with subsequent development of GW fibers from GR fibers occurring in most species just before or just after birth. However, distinct α and β fiber populations can be observed during the early stages of myogenesis well before any substantial amount of muscular activity.

In the experiment to be reviewed (Ashmore et al., 1972), muscle of fetal lambs was examined at various times during gestation, which, for the sheep is 147 days. Muscle biopsies were placed in ice-cold saline for 1 min, then quick-frozen in dry-ice/acetone and sections (10 μ) were prepared and reacted for myosin ATPase (pH 10.0), succinic dehydrogenase (SDH), phosphorylase, and glycogen. The results obtained on the semitendinosus muscle will be presented.

At 50 days gestation the muscles are characterized by widely scattered fibers approximately uniform in cross-sectional area. All fibers react for myosin ATPase but are negative for both phosphorylase and SDH. Morphologically, all fibers exhibit one or more large vacuoles in the center of the fiber. Most often the entire central area of the fiber is devoid of myofibrillar staining material. These fibers are called presumptive β fibers.

At 55 days, more presumptive β fibers exist than at 50.

At 60 days of development, the presumptive β fibers are slightly increased in average cross-sectional area. In addition, a second population of fibers has begun to appear. They are smaller than the presumptive β fibers were at 50 days. In many cases direct contact occurs between the two types. The smaller fibers also exhibit myosin ATPase activity but at this age cannot be clearly differentiated cytchemically from the larger fibers by this reaction alone (figure 1).
At 70 days, the number of small fibers around the presumptive \( \beta \) fibers has roughly doubled. The difference in staining of myosin ATPase activity now is quite clear--permitting us to describe the large fibers as \( \beta \), the small fibers are \( \alpha \) (figure 2).

At 100 days, nearly all of the \( \beta \) fibers are completely filled with myofibrils. The number of \( \alpha \) fibers has again doubled. Large, early formed \( \alpha \) fibers have been displaced outward toward the periphery of the bundle by the small newly formed \( \alpha \) fibers (figure 3).

At 125 days, bundles and fibers are more tightly packed. Growth in size of both types of fibers has occurred to a substantially greater degree than has growth in numbers of fibers. It is clearly seen that the largest and smallest fibers are the \( \alpha \) type. \( \beta \) fibers are of uniform size (figure 4). Phosphorylase activity is uniformly high and low in \( \alpha \) and \( \beta \) fibers, respectively, at 125 days.

Some small \( \alpha \) fibers are still being formed at 130 days. At 140 days, however, this process has stopped and further growth occurs only by enlargement of existing fibers.

At 140 days, the SDH staining pattern is most intense in the \( \beta \) fibers and those \( \alpha \) fibers in the center of the bundle.

Therefore, these findings suggest that the differentiation of \( \alpha \) and \( \beta \) fibers (those destined to be fast and slow in mature muscles) would not seem to be related to the quantity of muscle contraction. The \( \beta \) fibers, referred to as primary myotubes in a recent electron microscope study of embryonic chick muscle (Kikuchi, 1971) serve as a structural framework upon which myoblast proliferation and fusion continue with the subsequent generation of secondary myotubes. These secondary generations of myotubes are those destined to be the \( \alpha \) fiber population. The \( \alpha \) fibers are progressively formed, released, and displaced outward. Thus, the first \( \alpha \) fibers formed in fetal lamb muscle are those which commonly reside on the periphery of fiber bundles in mature muscle. The \( \beta \) fiber population is completed in a relatively short period of time, precedes the formation of the \( \alpha \) fiber population, and serves some kind of role in the organization of muscle fiber bundles and therefore the muscle as a whole. The observation that \( \beta \) fibers serve as "nuclei" for the development of \( \alpha \) fibers explains the internal location of red fibers (BR) in adult fiber bundles.

Further studies on embryonic chick muscle have confirmed the findings obtained on lamb muscle (Addis and Ashmore, 1972). Embryos were examined daily from 7 days to hatching (21 days). At least 10 embryos were studied each day. Several embryo muscles were studied, including those of the pectoral, cervical, and femoral regions. The methods used for chick biopsy preparation were essentially the same as those used for lamb tissue except that the samples were not chilled in saline solution prior to freezing. Due to the small size and fragility of chick embryo muscle tissue, the muscles were not removed from the embryo, but instead, the entire femoral region was mounted. This permitted sectioning through the
Figure 1. Section from semitendinosus of 60 day fetal lamb. Myofibrillar ATPase.

Figure 2. Section from semitendinosus of 70 day fetal lamb. Myofibrillar ATPase.
Figure 3. Section from semitendinosus of 100 day fetal lamb. Myofibrillar ATPase.

Figure 4. Section from semitendinosus of 125 day fetal lamb. Myofibrillar ATPase.
entire femur and, consequently, the histochemically staining of several muscles simultaneously. Sections (10 and 16) were prepared and stained with hematoxylin and eosin and for myofibrillar ATPase (pH 10 and pH 4.1).

Although some myofibrillar ATPase activity is present as early as 7 days, organizational patterns and myotubes are discernable only after about 12-14 days in ovo incubation.

The development of embryonic chick muscle is, in general, similar to that noted in lamb muscle. The pattern is clearly biphasic in nature with \( \beta \) fibers forming during the initial stages of myoblast fusion followed by proliferation of \( \alpha \) fibers from the surface of the primary myotube during the latter stages of in ovo development (figures 5-7).

Figures 8 and 9 are comparable to figures 6 and 7, respectively, but the myofibrillar ATPase reaction was performed after preincubating the sections at pH 4.1 for 10 minutes. In this case the \( \beta \) fibers stain intensely whereas the activity in the \( \alpha \) fibers is inhibited. This is the preferred technique for identification of \( \beta \) fibers in fetal and embryonic muscle since immature \( \beta \) fibers also stain intensely after alkaline preincubation (figure 2 and 5). Indeed, in M. complexus of the chick, \( \beta \) fibers cannot be identified adequately by the alkaline preincubation technique until 1 week after hatching (Ashmore et al., 1972).

**SIGNIFICANCE TO MUSCLE AS A FOOD**

The reader is referred to several reviews concerning the relation of fiber type, morphology and postnatal development to ultimate properties of muscle as a food (Hegarty, 1971; Kauffman, 1971; Swatland, 1971; Topel, 1971; Van Sickle, 1971; Cassens and Cooper, 1970; Cassens et al., 1969).

The biphasic development of \( \alpha \) and \( \beta \) fibers observed in the fetal lamb and embryonic chick raises several questions of significance to meat animal development. For example, can an animal physiologically support only a limited number of red fibers (\( \beta_R \) and \( \alpha_R \))? If so, then any further increase in muscularity of meat animals which is achieved by increasing the total number of muscle fibers would result specifically in an increase in the number of \( \alpha_W \) fibers.

Just as the subject of light and dark muscle fibers has received much attention from researchers, the relationship of red: white fiber ratio to muscle quality has been thoroughly investigated. Nevertheless, considerable disagreement exists in the literature. We believe that consideration of the organization, development and biochemical properties of \( \beta_R, \alpha_R \) and \( \omega_W \) fibers as presented in the foregoing discussion, may provide an explanation for these discordant viewpoints.

Numerous studies have been published on the histology, histochemistry and biochemistry of light and dark muscles, areas of muscles, or fibers in relation to postmortem properties. It is logical to expect white muscles,
Figure 5. Section from leg muscle of 14 day chick embryo. Myofibrillar ATPase.

Figure 6. Section from leg muscle of 16 day chick embryo. Myofibrillar ATPase.
Figure 7. Section from leg muscle of 18 day chick embryo. Myofibrillar ATPase.
Figure 8. Section from leg muscle of 16 day chick embryo. Myofibrillar ATPase after acid preincubation. Staining pattern of α and β fibers is reversed from that seen after alkaline preincubation (see Figure 6).
Figure 9. Section from leg muscle of 18 day chick embryo.

Myofibrillar ATPase after acid preincubation

(see Figure 7).
areas or fibers to exhibit rapid pH decline compared to their red counterparts since upon exsanguination anoxic conditions are established more quickly in white muscle tissue. At the cessation of oxidative phosphorylation, as dictated by the "Pasteur Effect" (Van Eys, 1961), anaerobic glycolysis would commence. Beecher et al. (1965a) determined that the rate of pH decline in light area of the semitendinosus exceeded that of the dark area of the same muscle. Beecher et al. (1965b) determined light and dark fiber ratio in seven porcine muscles. Sudan Black B (a lipid stain) was utilized to differentiate fibers. Red muscles contained more red fibers, greater myoglobin concentrations and had longer sarcomeres than white muscles. Further studies (Beecher et al., 1969) noted that gluteus medius and longissimus dorsi muscles exhibited more rapid loss of ATP and more rapid pH decline than in the red rectus femoris muscle. Lactate dehydrogenase (LDH) activity of white muscle exceeded (P < .01) that of red muscle. LDH isoenzyme patterns corresponded to these data with more of an anaerobic distribution among white muscles. The results of the above studies were confirmed by Addis and Allen (1970). They noted that light muscles (l. dorsi, light b. femoris, light semitendinosus and g. medius) exhibited greater total LDH activity (per mg soluble protein) than dark muscles (dark b. femoris, semitendinosus and trapezius). LDH isoenzyme V, the muscle type, also segregated light muscles from dark muscles.

The question of greater importance than comparisons among muscles within the same breed are comparisons between breeds and strains known to differ in degree of stress-susceptibility. The first study to demonstrate an interaction among environmental treatment, light: dark fiber ratio and postmortem glycolytic rate was Howe et al. (1968). They utilized psychrometric chambers to rear animals under four different environmental treatments. Forty "stress-susceptible" Poland China barrows were used. Sudan black B was used to stain muscles. Environment during growth significantly affected the light:dark fiber ratio; a high ratio was found in the treatment which elicited the most rapid pH decline of the four treatments studied.

The first direct comparison of fiber distribution between stress-resistant and stress-susceptible breeds was conducted by Sair et al. (1970). Unexpectedly, their findings suggested that the stress-resistant breed displayed a higher ratio of light:dark fibers than the susceptible breed.

Cooper et al. (1969), using histochemical assays for ATPase, amylophosphorylase, and an oxidative enzyme system stain, further characterized differences in muscle from stress-resistant and stress-susceptible pigs. Their findings indicated that muscle from stress-susceptible animals contained more intermediate fibers. Under the system of classification used by us, these fibers would likely correspond to CR fibers. Muscles from the two breeds did not differ in the capillary/fiber ratio.

Dildey et al. (1970) grouped forty barrows (Hampshire-Yorkshire) according to (1) postmortem muscle color-structure, and (2) muscularity. Histological sections were taken from the l. dorsi and stained for sudan
black B. Statistical analysis of histochemical data revealed that PSE pigs exhibited a higher \((P < .01)\) light: dark fiber ratio than animals exhibiting normal muscle color-morphology.

From the foregoing discussion it is apparent that no clear consensus exists among researchers concerning the histochemical characteristics of muscle in relation to the degree of stress-susceptibility in the animal. These questions are of extreme importance in relation to the larger question of genetic aspects of hypermuscularity, stress-susceptibility and postmortem muscle quality. In light of the new laboratory procedures, fiber classification and nomenclature information, and the improvement in our understanding of fiber interrelationships reported earlier in this paper, it would be extremely interesting to reexamine some of the above mentioned research projects. For example, the work of Howe et al. (1968) was completed prior to research demonstrating the dynamic interrelationship between \(\alpha R\) and \(\alpha W\) fibers. Thus, it is possible that their results reflected the conversion of some \(\alpha R\) fibers into \(\alpha W\) fibers as elicited by the same growing environment which was detrimental to muscle properties. The importance of using myofibrillar ATPase and SDH histochemical assays on serial sections to determine the distributions of \(\beta R\), \(\alpha R\) and \(\alpha W\) fibers, now that such techniques are available, cannot be over-emphasized.

Studies on bovine hypermuscularity, although limited in number, suggest that an alteration has occurred in fiber distribution. Recent studies in our laboratory confirm the increase in the relative proportion of \(\alpha W\) fibers (figures 10 and 11) reported earlier for muscles of the "double muscled" bovine mutant (Ashmore and Robinson, 1969), but in addition provide evidence for an increase in the total number of fibers as well as a reduction in the percentage of the red fiber population (Holmes and Ashmore, 1972).

**SUMMARY**

The studies reported herein provide good evidence for the following: (1) the embryonic development of \(\alpha\) and \(\beta\) fibers occurs sequentially, and (2) a major determinant of muscle quantity and quality is the rate and time of \(\alpha\) fiber formation in the second phase of myogenesis. Finally, and perhaps most importantly, the observation of phasic development of \(\alpha\) and \(\beta\) fiber populations makes possible the design of new types of experiments not heretofore encouraged by the thought that all fetal muscle fibers were initially equivalent.
Figure 10. Section from semitendinosus of 4 month old normal calf. SDH reaction.

Figure 11. Section from semitendinosus of 4 month old "double muscled" calf. SDH reaction.
REFERENCES


