PRE- AND POST-NATAL GROWTH AND DEVELOPMENT OF SKELETAL MUSCLE IN RELATION TO LEAN MEAT QUANTITY AND QUALITY

D.M. Joubert

Department of Agricultural Technical Services, Pretoria

The animal scientist shares with his medical colleague a profound interest in skeletal or 'striated' muscle. But whereas in medicine this tissue is studied principally in relation to locomotion, tractility and repair, we see muscle primarily as the most valuable constituent of what is commonly known as meat. Meat, again, may be defined as the flesh of animals used as food although, as Lawrie (1966) points out, there is of course a conversion phase involved. The latter, in essence, embodies a series of biochemical and biophysical changes which are initiated in muscle at the death of the animal.

The object of this review is to gain perspective on the role of muscle growth in terms of meat quality. But quality alone cannot feed a people; the product concerned must also be available in sufficient quantity. The approach, hence, will be via the essential structural unit of muscle, viz. the fibre. However, since this discourse is intended also to provide background to subsequent papers, initially the elementary features of the tissue in question will also be considered.

Microanatomy

The musculature of our domestic animals consists of about 300 anatomically distinct units (Sisson & Grossman, 1963), though varying greatly both superficially and intrinsically in size and shape, in blood and nerve supply, in association with other tissues, and in their action. Yet, notwithstanding their differentiation, a basic structural pattern is common to all muscles: Surrounding the muscle as a whole is a sheath of connective tissue known as the epimysium. From the inner surface of the latter, septa of connective tissue penetrate the muscles thus creating fasciculi or 'bundles', the separating septa constituting the perimysium which contains the larger blood vessels and nerves. From the perimysium a fine connective tissue framework or endomysium passes further inwards to within the bundles, causing individual cells to cluster together. Finally a sheath — once considered structureless but now shown by electron microscopy to represent a double membrane (Robertson, 1957) — encloses the multi-nucleated cellular unit known as the muscle fibre. By definition an elongated cylindrical cell, the fibre is thus composed of its sheath or sarcolemma, the sarcoplasm of semifluid consistency in which myofibrils are embedded, and the nuclei themselves on the periphery.

The fibres are tightly packed within the bundles; the more so with increasing age (Joubert, 1956a). When freshly cut they are oval or spherical in cross-section, but they tend to become irregularly polyhedral if sectioned after fixation (Walls, 1960) due to shrinkage factors, a sub-

ject studied exhaustively in recent years (*vide* Naudé & Hegarty, 1970). These features are clearly discernible at a x20 magnification. When the magnification is increased to x200, it is possible to see that the fibres are crossed by parallel striations thus revealing the origin of the designation 'striated' muscle. At x2 000 magnification the myofibrils are visible, along with their dark A bands with a central clear H zone, alternated by light I bands with a dark Z line, which explains the striated effect. A x20 000 magnification reveals that the myofibril is itself composed of numerous parallel myofilaments, some thick and others thin, respectively consisting of molecules of the contractile proteins myosin and actin (*vide* Bourne, 1960; Huxley, 1960; Lawrie, 1966). It is in fact at this, the molecular level of myogenesis, that we find workers most active at present, with the inclusion of DNA analyses of individual fibre nuclei and tissue culture in their techniques (Message, 1968).

The fibre, therefore, is the common factor, whether the material derives from a 31 462 sperm whale (*Physeter catoden*) with a dorsal musculature weighing 2 692 kg, or a 11,83 g tiny musk shrew (*Crocidura hirta*) whose identical muscles do not exceed 0,1004 g (Joubert, 1971). It is significant, moreover, to bear in mind that the muscle fibre comprises between 80 and 90% of the muscle (*vide* Rowe & Goldspink, 1969); any change in the weight of a muscle during its growth must obviously be due very largely to a change in the bulk of the fibres. This hypothesis motivates in large measure our interest in the cellular unit.

Embryo and Foetus

Skeletal muscles arise in the embryo from the mesodermic somites, i.e. from the third (and central) germinal layer of the embryo. Muscle develops from the somites initially as a mass of closely-spaced, undifferentiated fusiform cells. However, as development proceeds two cell types become distinguishable, the one being primitive connective tissue and the other myoblasts. Multiplication, at first, is by mitotic division whereby the nuclear material is divided equally between mother and daughter cells. Later they elongate, become multinucleated and divide amitotically; simultaneously they increase in girth. Roughly at this stage the myofibrils can first be identified, themselves increasing in number by longitudinal fission as shown by Heidenhaim in 1913. A fibre is produced by the fibrils forming a hollow tube — hence the myotube stage — followed by the gradual filling of its interior. The nuclei become spaced out in a regular fashion, migrate to the margins of the fibre and eventually settle immediately

below the sarcoplasmic membrane. The now very numerous myofibrils come to occupy the central part of the muscle fibre. Thereafter multiplication of the myofibrils appears to continue for a long time as gestation proceeds (Boyd, 1960).

Whereas the embryological development has been unravelled in minute detail, it comes as a surprise to the student of muscle physiology to learn how vaguely foetal and perinatal growth was treated until comparatively recently. Most text books still condense the subject to a phrase composed from the exposé given in *Diseases of Muscle* by Adams, Denny-Brown & Pearson (1962), more or less as follows: 'Generally after the second half of intrauterine life, muscles increase in size not by augmenting the number of their constituent fibres (hyperplasia), but by increasing the size of the latter (hypertrophy) (*vide inter alia* Lawrie, 1966). This statement is clearly based principally on the work, in chronological order, of McCullum (1898), Bardeen (1900), Lewis (1910), Schafer (1912), Tello (1922) and Cuajunco (1942). These authors derived their results in the main from human post-mortem and biopsy material and it was not until the. 1950's that the subject came to be studied in a domestic mammal, in this instance the foetal sheep (Joubert, 1955; 1956b). The results corroborated earlier observations in as much that muscle fibre diameter increased but slightly (approximately 19,5 %) during the first two-thirds of pre-natal life, whereas the subsequent increase was substantial. In terms of a linear regression the increase amounted to 113,2 % from 108 days to full term. Measurement of fibres from muscles situated in different regions of the body moreover indicated differential growth patterns, rather similar to those expounded by Hammond (1932) for the animal body *in toto*.

It is generally assumed, furthermore, that the post-natal increase in size and weight of muscles is brought about essentially by an increase in the size of the constituent fibres, with the fibre number remaining constant. Previously this was deduced from a fairly consistent decrease in the coefficient of variation of fibre diameter with advancing age rather than from actual fibre counts within muscles (McMeekan, 1940–41; Joubert, 1956a). However the latter method has recently led Rowe & Goldspink (1969) to state that "... the total fibre number in all muscles was found to remain constant throughout the animal's life." Whilst their study on mice in effect corroborated Staun's (1963) conclusion following counts of pig muscle samples, it apparently contradicts their own earlier report (Goldspink, 1962) on an increase in the number of fibres in rodent muscles during the first few weeks after birth. However, they included only fully differentiated fibres in the latter counts.

Post-natal Phase

A comprehensive study of both his own material (Joubert, 1956a) as well as of the relevant literature available to that date (Joubert, 1956d), led the author to conclude that eight factors at least are implicated in the pattern and degree of post-natal muscle fibre growth. Measurement of the diameter of fibres in statistically adequate numbers, first of all, revealed interspecific differences: At birth, for example, rabbits and sheep have rather similar sized fibres(11μ), while those of the pig ($5\,\mu$) and bovine ($14\,\mu$) are respectively thinner and thicker. At maturity the pig has the largest fibres ($91\,\mu$), followed by the rabbit ($78\,\mu$), the bovine ($73\,\mu$) and the sheep 50μ). It is important to note that no relation exists between muscle fibre size and body size at either age, and also that the size of muscle fibres at maturity can largely be accounted for by the degree of post-natal development in body weight of the species concerned. In fact, to quote almost absurd extremes once again: although the weight of the sperm whale is $2^1/2$ million times that of the tiny musk shrew − 31 462 kg *vs* 11,83 g − its mean muscle fibre diameter is less than three times that of the latter species − 55 *vs* 19 μ (Joubert, 1971).

Secondly, breed appears to play a rôle, particularly where distinct differences in size and type are involved. Thus statistically significant differences in mean muscle fibre size were found between purebred Shorthorn (44μ) and Friesian ($50\,\mu$) steers, but not between their crosses with either Hereford or Aberdeen Angus (46-$49\,\mu$).

Thirdly, muscle fibre diameter was shown to increase with age, for example in sheep on an unrestricted diet, from between 9 and 11μ at birth, to between 45 and 49μ at 290 days. But it was particularly evident that muscle growth is a function of physiological maturity, i.e. weight, rather than chronological age. It was demonstrated that in a group of lambs slaughtered at an identical age, the heavier individuals had the larger fibres, closely proportional to differences in total weight of muscle in the carcass. Weight therefore constitutes the fourth factor.

Fifthly, sex differences could be accounted for very nearly by the anticipated differences in respect of muscle weight. At later ages the deposition of intra-muscular fat tends however to distort the relationships. On the other hand studies on the muscle fibre sizes of lambs at birth (Joubert, 1956c) produced evidence in support of the theory that at comparable weights, males actually possess slightly thinner individual and therefore a greater number of fibres than females. This observation must of course be linked with the acknowledged tendency for the muscles of male animals to be larger than corresponding muscles in females. Since this is not entirely a reflection of differences in overall size, it would seem that the growth of some muscles is preferentially stimulated by sex hormones (Kochakian & Tillotson, 1957).

Nutrition is the sixth factor that influences the size and growth rate of muscle fibres at all ages. In mature animals on a supermaintenance diet there is, however, an inherent maximum diameter which apparently cannot be exceeded by increased nutrition, though the muscle mass may continue to enlarge due to fat deposition both

within and between the fasciculi (Joubert, 1965a). At nutritional levels below the optimum, fibre enlargement due to increased intra-cellular fat should, moreover, not be overlooked (Helander, 1959). A submaintenance diet contrarily causes the fibres to shrink (Joubert & De Wet, 1962); indeed acute starvation may eventually cause muscle fibres to become detached from their tendon junctions, with the sarcolemma less intimately attached to the underlying substance (Speidel, 1938).

The seventh factor concerns the individual muscle. Despite a wide range in respect of fibre sizes within any muscle, the average diameter for different muscles may vary significantly with increasing age. This depends on the position of the specific muscle in the carcase relative to either early or late maturing regions. Thus whilst at maturity fibres of M. longissimus dorsi are smaller than those of M.gastrocnemius, the former muscle exhibits greater post-natal growth in view of its later maturing situation in the body (Joubert, 1956a). It has also been demonstrated that in cases of hypertrophy of the musculature, as for example in the Doppelender phenomenon, this occurs selectively for individual muscles, being most pronounced in those which are the latest to develop (Pomeroy & Williams, 1962). Latterly, Butterfield & Berg (1966) have proposed terminology which classifies muscles in terms of their allometric growth coefficients. If pursued, this might provide a sound basis for differentiation also in respect of muscular histogenesis.

The eight and last factor is exercise. Although it is widely accepted that the diameter of muscle fibres increase in response to exercise (vide Walls, 1960), the process is overtly complicated. On the one hand it can be generalised that increased exercise enhances vasularisation which results in hypertrophy of muscle. On the other hand, in reviewing the subject Steinhaus (1933) points out that whereas exercises of speed, strength and effort induce hypertrophy, those of endurance leave the body muscles unchanged. Yet other workers in this field draw attention to the seemingly contradictory effects of rate of movement, slow reptiles for example have larger fibres than the swift avian species (Schafer, 1912). Also specific muscles vary in function within the body, being either relatively relaxed or fairly continuously stressed (Hammond, 1932). It would appear therefore that a satisfactory explanation is not yet forthcoming.

Meat Quality

Studies of the muscle fibre as a microscopically discernible entity date back to Malpighi of Bologne (1628–1694) and the Hollander Antonius van Leeuwenhoek (1632–1723). For close on two centuries, however, little was added to their early observations until the appearance of Bowman's treatise on muscle in the now classic Cyclopaedia of Anatomy and Physiology (1839–1847). Subsequently muscle histology was studied essentially by German scientists. In the medical field Kölliker (1850) was the undisputed leader, while Adametz in 1888 first

linked basic microscopic anatomy with problems of animal production. But more than four decades were to pass before the subject came to its own with a firm basis for continued research. This was provided in Sir John Hammond's (1932) monumental Growth and Development of Mutton Qualities in the Sheep which, following 18 years of research, went to press exactly 40 years ago. However, Hammond did not fail to acknowledge the study by Waters (1909) in which the effect of nutritional plane on muscle fibre diameter in steers was described.

Although the primary object of Hammond's investigation was to determine the conditions which affect the rate of growth in live weight — in one breed of sheep (Suffolk), under set conditions of soil and locality (Cambridge, England) — he followed his study through to its logical conclusion: the factors, namely, associated with edibility. Attention at the time was focussed particularly on tenderness and flavour, the former related to the fascicular architecture of muscle and the latter in the main to the degree of marbling and outcome of relatively simple organoleptic trials.

The expansion of knowledge during the subsequent four decades is evident from the successive reviews of Hirzel (1939), Pàlsson (1955), Joubert (1956e), Yeates (1965) and Lawrie (1966). The field, indeed, has now expanded to include such a wide range of factors that quality can no longer be approached unilaterally. Hence the factors involved are grouped into pre- and post-slaughter influences, followed by pre- and post-cooking effects. The title of this review obliges me however to return to one factor alone, i.e. tenderness, and then primarily in relation to the micro-structure of muscle.

It has been pointed out that muscle fibre size is related to age. This was confirmed by Hiner, Anderson & Fellers (1955) who reported an increase in mean diameter of from 40 to 50 μ at 10 weeks for most muscle groups in cattle carcasses, to 60 to 70 μ in the same muscles of nine year old animals. It was shown moreover that at all ages the fibre diameters in M. psoas (fillet) were less than those of other, generally considered 'tougher' muscles. In another report Hiner and his colleagues (1953) had already demonstrated a highly significant correlation between fibre diameter and tenderness (resistance to shear).

One is tempted therefore to generalise that the smaller the muscle fibres, whether due to youth or the particular muscle, the greater should be the tenderness. This, however is not necessarily the case. In the preamble it was pointed out that undernutrition causes shrinkage of the extant muscle fibres. But Yeates (1964) showed that when this occurs the meat in fact becomes tougher due to connective tissue concentration; a correlation therefore between fibre diameter and tenderness at that stage brings to light exactly the opposite relationship. Furthermore Yeates demonstrated that there is no permanent impairment of the eating quality of the muscle due to undernutrition. Following reinflation of individual muscle

fibres due to improved nutrition, tenderness of the meat was restored.

While it is often believed that prolonged exercise would make muscle 'stringy' and tough, this was disproved many years ago by the work of Mitchell & Hamilton (1933). These authors, in a well-conducted experiment, demonstrated with the aid of both a tasting panel and mechanical tests that the steaks from exercised cattle were, if anything, slightly more tender than those of penned animals. The muscular work in fact tended to reduce the relative collagen content of muscle. Bull & Rusk (1942) have since substantiated this finding.

In the same vein one could mention the popular misconception that the muscles of males are bound to be tough and of unpleasant odour. The idea can no doubt be traced back to times when livestock were generally slaughtered at greater ages and large numbers of old culled bulls, boars and rams reached the market. The relationship between body size or weight and muscle fibre diameter previously discussed, therefore clearly enters into the picture. On the other hand we are well aware of current trends in which young uncastrated animals are now often marketed for slaughter. Yeates (1965) in reviewing the subject reminds the reader that Hammond (1932) showed entire males to have a slightly larger fibre diameter than castrates. On the basis that cross-sectional area is a function of the square of diameter, he argues that the difference in diameter of the fibres should be sufficient to account for the greater overall muscle thickness in bulls. As this might conceivably cause a connective tissue 'dilution', Yeates suggests that this characteristic should be advantageous rather than the reverse, tending to enhance both tenderness and succulence. Contrarily it should be noted that Joubert & Dreyer (1965) could not establish statistically significant differences in the mean fibre diameter of young bulls and steers slaughtered at identical weights. Reports on the organoleptic qualities of the prepared wing-rib cuts revealed that no difference in either tenderness or flavour were detectable by the members of a tasting panel.

Conclusion

While the mean fibre diameter within a given muscle or at a given age certainly influences the tenderness of the meat concerned, its rôle is clearly integrated with those of many other factors which become involved successively as one proceeds from pre-natal to post-natal life, and ultimately from the carcass to the prepared portion of meat on the plate. Yeates (1965) suggests that muscle fibre *per se* is at no stage important, but rather its association with connective tissue concentration. He argues that at any age of the animal the proportion of connective tissue is reduced by muscle fibre inflation;hence anything which favours increase in muscle fibre diameter without any corresponding increment in connective tissue should be desirable. This ties up with the concept of a high plane of nutrition favouring fibre inflation, thereby reducing the proportion of connective tissue and hence increasing tenderness.

It is inevitable, however, that one should finally return to the fasciculi. The basis is to be found in the straight-forward statement by Walls (1960): "The size of the fasciculi composing a muscle determines its texture." This explains why in the visual judging of carcases the socalled 'grain' of the meat is considered to be indicative of either the coarseness or fineness of the muscle bundles, the latter determined by stroking the thumb across the cut surface of the muscles, usually at the position of quartering. Hammond (1960) himself made bold with the following generalization: "Since the muscle fibres are arranged in bundles, this growth of muscle fibres means increase in the size of muscle bundles and so increase in the coarseness of the grain of the meat ... For this reason the meat of young animals is finer grained and less stringy than the meat of older animals. For this reason too some muscles ... are more tender and are preferred to others ... of the same carcase. Small species and breeds of animals have smaller muscle bundles and finer grained meat than larger ones and so are usually preferred for meat purposes. A large breed, however, killed at an early age has fine grained meat."

It is possible, therefore, to explain the world-wide trend for consumers to go for the fillet (*M. psoas*) wherever particularly tender meat is desired, irrespective of its source; why South African sheep farmers firmly believe that the relatively small conventional Merino has the tastiest mutton of all breeds, even at comparatively old age; and why cattle farmers insist that the diminutive Jersey x Afrikaner cross-bred heifer or young cow produces the most palatable beef obtainable anywhere. But Yeates (1965) reminds us that there appears to be no critical experimental evidence to support the view that coarse grain is associated with toughness and fine grain with tenderness. In fact emaciated muscle tends to be fine and smooth grained, probably because of the small muscle fibre diameter. Thus, he concludes, at the present state of knowledge it would seem best to remain openminded as to the relationship between texture and quality. Moreover Naudé & Joseph (1970) recently drew attention once again to the lie of fibre bundles and topography of major sheets of intra-muscular connective tissue, which in rare instances only is of simple design. They in fact recommended sampling systems which would ensure that fasciculi will be perpendicular to the main parallel faces of beef steak cuts.

In his review of the problems of quality in meat Joubert (1956e) pointed out that the final factor involved and which often nullifies all others previously involved, centres around the purely human element, viz. the ability of the cook. Hence it appears appropriate to examine in conclusion the changes which occur at the terminal stage in respect also of the muscle fibre. From actual measurements (Joubert, 1956e) it was calculated that pressure cooking (6,8 kg for 35 min) resulting in a loss of 41% on sample weight, caused individual muscle

fibres to shrink to 74% of their original size. Subsequent roasting (20 min at 138°C) gave rise to a further 3% weight loss and an additional fibre shrinkage of 7%. While it is appreciated that these values will vary considerably depending upon the cut involved, it is significant to note that Doty & Pierce (1961) reported a change (denaturing) of muscle fibres during cooking (broiling to 68°C) so that their resistance to shear as well as extensibility was notably increased. It was furthermore observed that the surface of the fibres was sometimes slightly 'eroded', which probably indicates that the fluid cytoplasmic material is coagulated only near the cell periphery.

This then, broadly, reviews 'traditional' past knowledge. But we appear to be on the threshold of spectacular changes and advances. Staun (1968) recently proposed that muscle fibre measurements, especially the total number of fibres in the cross-section of the muscle, might become important in breeding for improved meat quantity and quality. And at the molecular level pertinent questions are posed as the mysteries of the nucleus during myogenesis and its DNA content are increasingly probed (Message, 1968). In the light of these developments it is not surprising to hear biologists ask whether a change in muscle could not be effected pre-natally with a view to altering its post-natal growth pattern. However it should be pointed out that hitherto no one has even ventured to study experimentally the influence, for example, of foetal nutritional planes on subsequent development of musculature. Indeed, notwithstanding apparently complete recovery of the body *in toto* from intra-uterine inanition on an adequate post-natal feeding regime, it seems reasonable to enquire whether the former treatment could not possibly extend the hyperplastic phase of muscle growth to well beyond birth?

The field clearly remains vast and complicated. Yet in time more sophisticated techniques will no doubt provide answers to these questions along with a host of others; and will also reveal the innermost secrets and true significance of the muscle fibre in relation to the meat we eat.

References

ADEMETZ, L., 1888. Landw. Jahrb. 17, 577.

ADAMS, R.D., DENNY-BROWN, D. & PEARSON, C.M., 1962. Diseases of Muscle: A study in Pathology, 2nd edn. London: Henry Kimpton.

BARDEEN, C.R., 1903. Anat. Anz. 23, 241.

BOURNE, G.H., 1960. The Structure and Function of Muscle, Vol. I, Structure. New York: Academic.

BOWMAN, W., 1839–47. Muscle. In Cyclopaedia of Anatomy and Physiology, Vol. III. London: Longmans.

BOYD, J.D., 1960. Development of Striated Muscle. Ch. 3 in BOURNE (1960).

BULL, S. & RUSK, H.P., 1942. Bull. Ill. agric. expt. sta. No. 488.

BUTTERFIELD, R.M. & BERG, R.T., 1966. Res. vet. Sci. 7, 326.

CUAJUNCO, F., 1942. Contr. Embryol. Carnegie Inst. 30, 127.

DOTY, D.M. & PIERCE, J.C., 1961. Tech. Bull. Agric. Market Serv. U.S.D.A. No. 1231.

FIELD, R.A., PEARSON, A.M., MAGEE, W.T. & MERKEL, R.A., 1970. J. Anim. Sci. 30, 717.

GOLDSPINK, G., 1962. Proc. R. Ir. Acad. 62B, 135.

HAMMOND, J., 1932. Growth and Development of Mutton Qualities in the Sheep. Edinburgh: Oliver & Boyd.

HAMMOND, J., 1960. Farm Animals, 3rd edn. London: Edward Arnold.

HEIDENHAM, M., 1913. Arch. mikr. Anat. 83, 427.

HELANDER, E., 1959. Acta morph. near-scand. 22, 230.

HINER, R.L., HANKINS, O.G., SLOANE, H.S. FELLERS, C.R. & ANDERSON, E.E., 1953. Fd. Res. 18, 364.

HINER, R.L., ANDERSON, E.E. & FELLERS, C.R., 1955. Fd. Technol., Lond. 9, 80.

HIRZEL, T., 1939. Onderstepoort J. vet. Sci. 12, 379.

HUXLEY, H.E., 1960. In the Cell, Vol. 4. Eds. J. Brachet & A.E. Mirsky. New York: Academic.

JOUBERT, D.M., 1955. Nature, Lond. 175, 936.

JOUBERT, D.M., 1956a. J. agric. Sci., Camb. 47, 59.

JOUBERT, D.M., 1956b. J. agric. Sci., Camb. 47, 382.

JOUBERT, D.M., 1956c. J. agric. Sci., Camb. 47, 449.

JOUBERT, D.M., 1956d. Z. Tierzücht. ZüchtBiol. 67, 359.

JOUBERT, D.M., 1956e. Colon. Pl. Anim. Prod. 6, 79.

JOUBERT, D.M., 1971. On body size and cell size in the musculature of large and small mammals. Agroanimalia (In the press).

JOUBERT, D.M. & DE WET, P.J., 1962. Proc. S. Afr. Soc. Anim. Prod. 1, 91.

JOUBERT, D.M. & DREYER, J.H., 1965. Proc. S. Afr. Soc. Anim. Prod. 4, 151.

KOCHAKIAN, C.D. & TILLOTSON, C., 1957. J. Endocr. 60, 607.

KOLLIKER, A., 1850. Mikroskopische Anatomie, 2 Aufl. Leipzig: Engelmann.

LAWRIE, R.A., 1966. Meat Science. London: Pergamon.

LEWIS, W.H., 1910. Anat. Rec. 4, 183.

MacCALLUM, J.B., 1898. Bull. Johns Hopkins Hosp. 9, 208.

McMEEKAN, C.P., 1940–41. J. agric. Sci., Camb. 30, 276; 31, 1.

MESSAGE, M.A., 1968. Some Problems Associated with the Development of the Mammalian Skeletal Muscle Fibre. In Growth and Development of Mammals. Eds. G.A. Lodge & G.E. Lamming. London: Butterworths.

MITCHELL, H.H. & HAMILTON, T.S., 1933. J. agric. Res. 46, 917.

NAUDE, R.T. & HEGARTY, P.V.J., 1970. Proc. S. Afr. Soc. Anim. Prod. 9, 217.

NAUDE, R.T. & JOSEPH, R.L., 1970. Ir. J. agric. Res. 9, 311.

PÁLSSON, H., 1955. Conformation and Body Composition. Ch. 10 in Progress in the Physiology of Farm Animals. Vol. II. Ed. J. Hammond. London: Butterworths.

POMEROY, R.W. & WILLIAMS, D., 1962. Anim. Prod. 4, 302.

ROBERTSON, J.D., 1957. J. Physiol. 90, 276.

ROWE, R.W.D. & GOLDSPINK, G., 1969. J. Anat. 104, 519.

SCHAFER, E.A., 1912. In Quain's Anatomy, 11th edn. Eds. E.A. Schafer, J. Symington & T.H. Bryce, London: Longmans Green.

SISSON, S. & GROSSMAN, J.D., 1963. The anatomy of Domestic Animals 4th edn. London: Saunders.

SPEIDEL, C.C., 1938. Am. J. Anat. 62, 179.

STAUN, H., 1963. Acta Agric. scand. 13, 293.

STAUN, H., 1968. Muskelfibrenes diameter of antal samt deres betydning for kødfylde og kødkvalitet hos svin af Dansk Landrace. Copenhagen: Frederiksberg.

STEINHAUS, A.H., 1933. Physiol. Rev. 13, 103.

TELLO, J.F., 1922. A. Anat. EntwGesch. 64, 348.

WALLS, E.W., 1960. The microanatomy of Muscle. Ch. 2 in BOURNE (1960).

WATERS, H.J., 1909. Proc. 30th Ann. Meet. Soc. Prom. Agric. Portland, p. 70.

YEATES, N.T.M., 1964. J. agric. Sci. Camb., 62, 267.

YEATES, N.T.M., 1965. Modern Aspects of Animal Production. London: Butterworths.