

When the glue comes unstuck

ERIC DRANSFIELD

Station de la Recherches sur la Viande,
INRA de Theix,
St. Genès Champanelle,
63122 France

Texture of whole meats is important for consumer acceptability and modelling is providing insights into its origin and control in the industry. Texture has been modelled both 'empirically' and 'mechanistically'. Mathematical equations have analysed the relationships between changes in toughness with storage time, temperature, sarcomere length and pH. Equations have also been used to calculate rigor development and calpain activity in meat. Parameters derived from these equations enable better texture prediction and control.

A new mechanistic model is examined based on the fibrous composite nature of meat in which individual fibres are viewed as being held together by a matrix or 'glue'. With an intact matrix, as proposed in muscle soon after death, the tough structure exists because any stress built up in one fibre is taken up by the surrounding tissue and the structure resists total failure although individual fibres may break. With a weakened matrix, which may occur in aged meat, the fibres react more independently. Without linking support to other fibres, any break in one fibre places more stress on the remaining fibres which then break. The result is a rapid failure of the fibres and the whole structure breaks more easily and the meat is tender.

INTRODUCTION

The mechanical properties of muscle and meat are important because they control the behaviour of food material during production, further handling and determine their quality. To understand the basis of the mechanical properties, precise manipulation of raw material would be desirable but with muscle, unlike with fabricated materials, controlling the precise make-up of the muscle is beyond the scope of meat research workers and industry may be ethically undesirable. Thus the control and precise modification are often lacking but we are fortunate in being able to draw on a large amount of structural information, essential for understanding the origins of meat texture.

Toughness of meat is usually measured by shear, tensile or compression tests done unidirectionally although meat is anisotropic and mechanical testing could be done bidirectionally which has been achieved with myocardium (Smaill and Hunter, 1990).

Tenderness assessed by people is largely dependent on reducing the size of the meat by mastication. The number of chews taken to masticate the sample, prior to swallowing it, is more related to mechanical toughness than the force generated in chewing. The average person makes about 30 chews of roast beef before swallowing it (Harrier *et al.*, 1972) and interestingly, slightly more chews, on average, were required for roast beef when tasted cold than when tasted hot suggesting a tougher texture when cold. With this number of chews, half the particles would be over 1mm in length (Lillford, 1991). The swallowed particles are therefore extremely large in comparison with the size of the basic structural unit, the sarcomere, being the equivalent to one complete break for every 400 to 500 units. Also, there is little difference in light microscopic structure in the bolus formed after chewing tough and tender meats (Weidemann *et al.*, 1967). Because of the rarity in the number of breaks and the similar structure of the bolus, the structural origin of texture may be difficult to identify.

MODELS OF MEAT TEXTURE

In an attempt to understand the nature of the mechanical properties and texture of meat, various structural models have been proposed.

Following early sensory research, models centred on a 2 component system: the muscle fibre and the connective tissue. This gave rise to the idea of a background toughness due to the connective tissue component which was regarded as essentially inert. It changed principally with cooking temperature and therefore readily explained

categorisation of meat into different cooking classes. The relative contribution of these 2 components has been debated for over 2 decades despite some early work (Harries *et al.*, 1972) which showed that the use of a multicomponent profile, including separate reference to muscle fibres and connective tissue, was too elaborate and texture could be effectively assessed with only 2 scales: tenderness and juiciness. Later a complex concept combining the amount of connective tissue, its strength and a measure of fibre binding (Dransfield *et al.*, 1984) was developed. This structural interaction could explain why only part of the variability in sensory « amount and hardness of connective tissue » is attributable to the amount of collagen determined chemically and only 12% of its variability was accounted for by the contents of heat soluble collagen, total collagen and elastin (Cross *et al.*, 1973). In the 1980's, the tensile and adhesive properties and their changes during rigor were shown to be correlated well with pH and its rate of fall. The change in the tensile strength with storage time correlated well with changes in extracellular space. A 3rd factor was therefore proposed (Currie and Wolf, 1980) for meat tenderness which was that intrafibre water could be potentially important. Water may act as a plasticiser both within the myofibril and between fibres and water movement would change the mechanical properties. However this component has received little attention.

With the excellent work on rapid chilling in the 1970's and the recognition that muscles shortening had a large influence on texture, it was natural to construct models based on structural components of the sarcomere. Several models based on the sarcomere structure were proposed: the weakness of the I-band led to the proposal that the overall strength may be due to the frequency of finding or not a clear I-band region (Voyle, 1969). When no I-band is present, the A band would form a continuum which could be expected to be tough. The overlap of actin and myosin was also considered and modelled as a bridge span (Marsh and Carse, 1974). The longer the span between the Z-line and the A-band, the weaker was the meat, analogous to the weakening of a bridge when the span length increases. Locker *et al.*, (1977) considered the gap (titin) filaments as essential components of meat tenderness. Interactions between sarcomere length and collagen were later proposed in which the collagen orientation changed with sarcomere length (Rowe, 1974; Dransfield and Rhodes, 1976; Purslow, 1994).

However, none of these models have been shown to account for the interaction between muscle shortening and the extent of ageing.

An alternative model involving these interactions was the composite model in which interactions were viewed as a composite of muscle fibres and a flexible matrix component (Dransfield, 1986). Although we can learn much about mechanical properties from synthetic composite materials they remain relatively unsophisticated when compared to biological composites. Because of their diversity, attempts have been made to classify biocomposites such as bone. Five broad classes have been identified depending on the degree of importance of the matrix but no classification exists for extensible composites such as could be the case for muscle and meat.



FIGURE 1. Observations of the periodic fracture in meat

The figure on the left (from Dransfield *et al.*, 1986) shows the periodic fracturing (averaging 17µm between cracks) of aged raw meat fibres after extension. One fracture (top) is seen to have been opened out by the extension and the membrane is seen spanning the gap. In the centre (from Paul, 1965) and shows extensive and regular cracking of rabbit biceps femoris cooked at 24 hours. The distance between cracks averages 30µm. On the right (from Rejt, Kubicka and Pisula, 1978) is shown the regular cracking of muscle fibres of processed pork subjected to massage under vacuum. The distance between cracks averages 25µm.

This paper considers a further view of meat texture combining mechanical and structural approaches; considering fibres, matrix and their interactions as a basis for meat texture in order to improve our understanding and control of meat texture and aid development of new products.

MATRIX - FIBRE MODEL

Several types of mechanical tests are used to determine the mechanical properties of muscle and meats in relation to sensory tenderness. Extensibility (both of single fibres and whole strips of muscle) has been known for many years to relate to tenderness (Wang *et al.*, 1956). Extensibility was more recently employed to follow the changes during rigor development and during the subsequent ageing period (Dransfield *et al.*, 1986). Using a constant extension with low stress (up to 1N/cm²) showed that raw meat was very extensible (nearly 30%) during the rigor phase and had minimum extensibility (< 2%) at rigor. The extensibility increased gradually during ageing at 15°C reaching about 5% after 2 days. More importantly, after full rigor, the overall length of the test sample increased by about 40%, in line with the reduction in shear force of cooked meat. Presumably the extension at low stress was limited to 40% by the tensioning of the connective tissue. The rate of lengthening in raw meat increased with increase in temperature as did ageing in cooked meat. Weakening, which related to ageing, can therefore be detected in raw muscle. Previous work (Locker and Wild, 1982) had suggested that the I-bands fail at about 2N/cm² but these extension tests could induce lengthening with as little as 0.07N/cm² suggesting alternative weaker structures were involved. Figure 1 (left) shows the resultant histology of the stretched muscle. Most fibres were cracked, usually at the region of the Z-line and extensive periodic fracturing had occurred within each fibre. The fractures were at about 17µm apart. Other sections showed an opening out of the fractures with the sarcolemma membrane seen spanning the gap. When the widths of the cracks and gaps were summed, the total gap accounted for about half of the lengthening of the whole muscle strip. This implies that there had been a large amount of slippage between fibres or fibre bundles during the extension.

Fragmentation caused by mild homogenisation increases with storage and is related to improvement in tenderness. There is also an increase in fragmentation during rigor development (Jeremiah and Martin, 1978) but this is probably caused by the change in stiffness due to the development of rigor. In pre-rigor muscles the fibres are very extensible and would deform rather than break during the homogenisation. Later when the muscles become stiffer, fragmentation and total fibre breakage can be induced. Recent work (Chiung-Ying *et al.*, 1996) has shown that in adjacent myofibrils 1.8% were fractured in control at 1 day compared to 7.2% in electrically stimulated muscle.

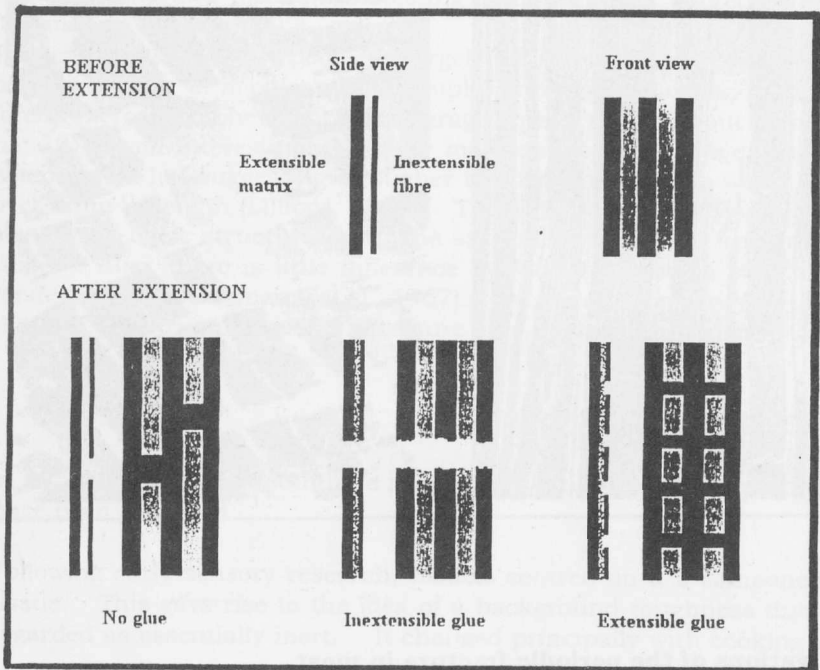


FIGURE 2 Modelling fracture

The figure shows the effect of gluing an inextensible material to an extensible backing. With no glue between the elements, when extended, the inextensible material breaks, leaving the extensible backing. Breaks will occur at the weakest parts of the inextensible material. When bonded with a stiff glue, both the material and the backing break when extended. With an extensible glue, the stiff material with break and then will break further with further extension. With several stiff elements, breaks will occur regularly in the different elements.

muscle. These increased to 12 and 14% respectively after 28 days. Unfortunately toughness was not measured but the half life for the changes was about 7 days which is similar to that expected rate for beef chilled ageing. In beef an increased amount of fragmentation was thought to increase tenderness (Cheng and Parrish, 1976; Hearn *et al.*, 1978) but cooking by microwave or conventionally increased fragmentation did not increase tenderness (Hutton *et al.*, 1981).

If Z-line weakening were the only or primary cause of loss of tensile strength, tensioning meat would cause an opening-out of the Z-line region and since each sarcomere is identical, an opening-out of Z-lines distributed randomly within the fibres. However, very regular cracking is observed within the fibre (Figure 1). This periodic cracking is similar to fibre fracture in man-made composites (Harris, 1980). In those stiff composites, the strength of the material depends on the fibre strength and fibre-matrix interactions. When extended along the direction of the fibres, a fibre will eventually fail first since they are the stiffest elements. At this point the load is transferred to the matrix and the ends of the broken fibre carry less than the mean fibre load. The load is transferred through the matrix back into the fibre and further extension may cause a further break in the same fibre. This process will continue until some critical length is reached which is too short to allow support of the full load and sections of the fibre shorter than this cannot be broken by stress transfer.

For good mechanical adhesion intimate contact should be obtained between both surfaces which may involve interlocking of the elements. This contact may be by electrostatic forces or by chemical bonding, which in muscle would include specific intermediate filaments or the cytoskeleton and connective tissue components.

Figure 2 shows a simple model which could account for the periodic cracking. This model considers a stiff element (fibre), such as a strip of aluminium foil, and an extensible material, such as foam rubber (matrix). When simply placed together and extended, the stiff element will break first at a point which is weakest in the foil. When two strips are used they will break probably at different locations because the weaknesses are randomly located. When the two elements are glued together by an inextensible glue and extended, both the elements will break together. When glued together with an extensible glue, the foil will break in several places at regular intervals due to stress transfer through the glue and the matrix. With two strips of foil, both will break in a similar fashion. This is similar to the fracture patterns seen in muscle (Figure 1).

In cooked beef (Dransfield *et al.*, 1995a) a similar regular fracturing occurred early after slaughter but at later times transverse fractures were seen to stop within and between the fibres. Both cohesive failure within the fibre and adhesive failure between structures (interfacial failure) had taken place (Figure 3). This suggests that the bonding materials had been weakened by storage of the meat.

Figure 1 shows the periodic fracturing, similar to that observed in raw and cooked beef, which has been obtained in rabbit and in massaged pork products.

With increasing chilled storage of rabbit muscle, increased separation between fibre bundles and between fibres occurred as the fibres shrunk. Oven cooking to an internal temperature of 80°C reduced the collagen to an amorphous state. Histological examination showed that, in cross section, the cooked fibres were shrunk from the 'endomysium' (which may have included membrane and collagenous components) and there were granules between the fibre and the endomysium. Extensive cross fibre cracking was seen which appeared to start in the I-band. Multiple cracking can be seen within each fibre (Figure 1, centre).

The influence of vacuum massage on changes of physical and chemical properties have been studied with a view to improving their texture (Rejt *et al.*, 1978). When selected muscles of ham and pork shoulder were cooked at 72°C for 90 min. and subjected to massage they had less cooking loss and smaller dimensional changes than did non-massaged hams. Massaged muscles showed a definite change in structure, particularly in the surface layers and an increased water holding capacity. Histological examination showed that massaging increased the intercellular spaces. Particularly at the surface of the meat, there was disruption of the muscle cells and fragmentation (Figure 1, right). Regular fibre fracturing at about 25µm was readily observed. Changes in the myofibrillar structure was thought to be one of the major contributors to the improved tenderness of massaged meat.

Although fracture patterns in fish have not been reported, a similar observation of release of intrafiber material to that which occurs in beef and rabbit has been observed. In fish muscle, it was proposed (Hatae *et al.*, 1990) that, during heating, the sarcoplasmic protein is released or squeezed from the muscle fibre and is coagulated in the interstitial spaces. When chewed, these coagulated proteins might impede the sliding of adjacent fibres past one another. It seems likely then that when there is more coagulated protein in the interstitial spaces, tougher meat would result. In conclusion, this protein on the periphery of the fibres is analogous to the model of fibre/matrix adhesion. In fish, this adhesion, together with differences in fibre diameter (see below), appear to account for differences in texture among fish species (Hatae *et al.*, 1990).

STRUCTURAL ASPECTS OF MATRIX - FIBRE INTERACTION

In looking for possible sites and structures which are represented as adhesion, we are fortunate in being able to draw on a very large amount of structural information provided by basic biological research on muscle organisation.

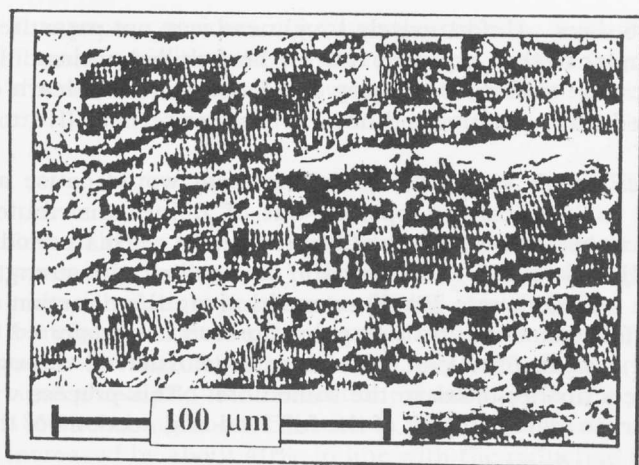


FIGURE 3
Appearance of cracking in aged beef

In cooked aged beef *pectoralis profundus* extended in the direction of the fibres, cracks can be seen within the fibres. In each of the fibres cracks can be seen passing longitudinally and across the fibres. Cracks rarely pass through to the adjacent fibres. Modified from Dransfield *et al.*, 1995b).

Fortunately, muscles are also structurally very regular and Figure 4 shows diagrammatically their hierarchical organisation. From the epimysium which surrounds the whole muscle extends the perimysium surrounding muscle bundles through to the endomysium surrounding the muscle fibre. The sarcolemma of single frog fibre is a somewhat slack system of helical fibres with an angle calculated to be 55° at rest length (Fields and Faber, 1977). This is also the angle permitting maximum volume of the muscle fibre which would limit the length changes to 70% to 40% of rest length and the sarcolemma has properties for a parallel elastic component. When lengthened the collagen fibres of the endo- and peri-mysium realign more with the direction of the muscle fibres (cargo model).

Collagen may be attached to the cell surface via collagen adhesion proteins on the surface of the plasma membrane and is found in a location where vinculin and talin are located internally. This connection may be an area where mechanical information from the extracellular matrix can be transmitted to the cytoskeleton of the cell. Such an arrangement of extracellular matrix to the cytoskeleton would be undoubtedly important for physiology (Bisschop *et al.*, 1982) and forms an extensive matrix throughout the hierarchical structure and therefore could be important in the texture of meat. Further connections are seen within the fibre. This cytoskeleton is a somewhat inappropriate but now accepted, term used to describe the structural fibrillar framework of the eucaryotic cell. The framework comprises: microtubules, actin filaments and intermediate filaments. The proteins, desmin, vinculin, talin, spectrin and others may present a transmembrane link. The myofibrils are organised into groups by the sarcoplasmic reticulum. The Z- and m-lines are linked transversely together and to the cell membrane by r-cords (the costameres).

When tested mechanically, whole muscle and meat are not notch sensitive (Offer *et al.*, 1989) which means that energy cannot be transported from any region in the structure to a fracture region (Gordon, 1978) and shows that all the structures are not equally mechanically connected to one another. When a fracture goes around a structure this implies that the 'glue' around the structure is weaker than the structure itself. When a transverse slice of cooked meat is pulled apart in a direction perpendicular to the direction of muscle fibres, cavities first open up between the muscle bundles. Histological investigation shows that the site of the breaks is between the perimysium and endomysium (Purslow, 1985; Tornberg *et al.*, 1994) and the last structure to break is the perimysium (Purslow, 1985).

There are no structures which could directly induce a regular fracturing along the fibre. The sarcomeres are identical and all the I bands are equally strong. No regular collagen or extracellular structures have been identified which would strengthen only parts of the fibre in regularity.

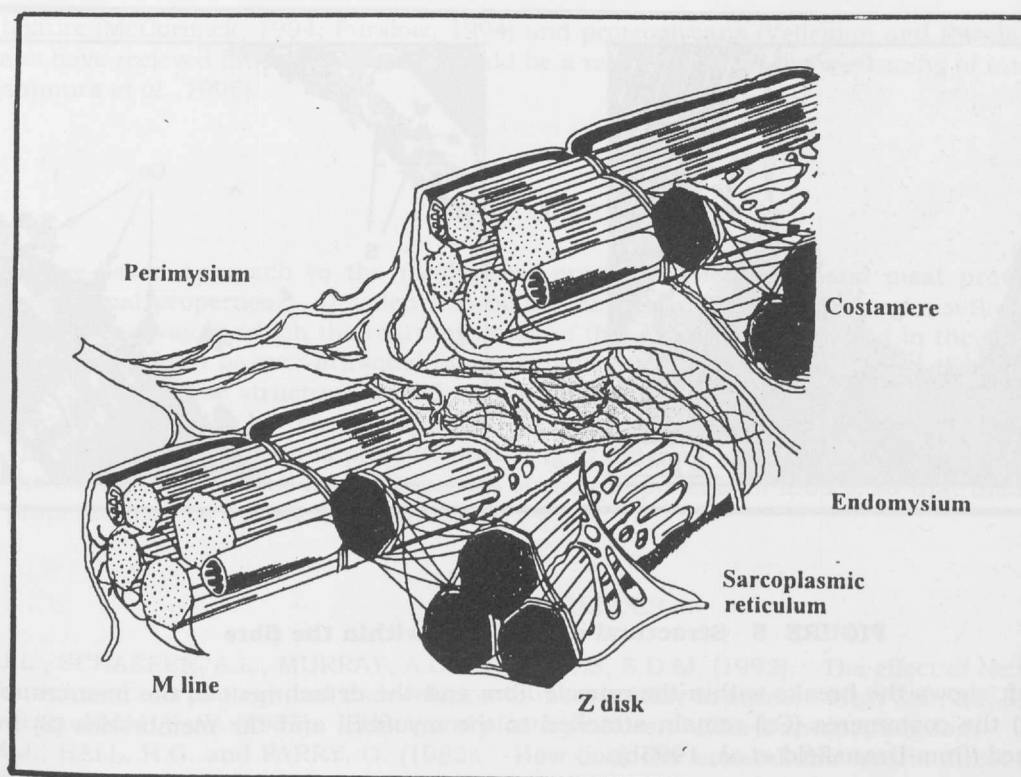


FIGURE 4 Diagrammatic representation of structural elements in muscle (after Lazarides, 1980)
The hierarchical organisation of fibres separated by the endomysial connective tissue which is branched to the perimysial connective tissue.

The importance of muscle fibres in any consideration of tenderness is obvious - they constitute more than 75% of the total volume and are related to mastication. Using undamaged fibres up to 15mm in length, the extensibility was determined by manual extension to break (Wang, 1956). Fibre extensibility was usually less than 50% for raw fibres and up to 150% for fibres from cooked meat. Storage up to 4 weeks reduced the extensibility of raw fibres and reduced by about half the extensibility of cooked fibres. The more extensible were the fibres the less tender was the cooked meat by panel tests).

Fibre diameter influences the volume fraction which plays an important role in the overall strength of composites and the water distribution within meat can be affected by difference in osmotic pressure across the cell membrane which can cause swelling or shrinkage of the fibre (Tornberg *et al.*, 1993). The fibre diameter is correlated with toughness, larger fibre diameters leading to tougher meat in pork (Tornberg *et al.*, 1994) and the number of fibres/unit area in a transverse cut of muscle decreased as the percentage lean increased. Adhesion, breaking strength across the direction of fibres was lower with more fibres and may be due to the increased probability of having a weak perimysial-endomysial junction (Tornberg *et al.*, 1994). Gault (1985), however, suggested that a decrease in the number of load bearing elements (fibres) increases tenderness which is similar to that observed in fish muscle (see below). Others have shown increased fibre diameters (more 'white' fibres) increased shear force (Aalhus *et al.*, 1992) in pork. But in beef, fibre diameter correlated with shear force up to 3 days and not at later times (Crouse *et al.*, 1991). This would be consistent with a reduced fibre strength in a matrix during storage. Fibre diameters in 8 to 14 month-old steers ranging from 30µm in tenderloin (PM) to 53µm in foreshank. The greatest change in fibre diameter was during rapid growth of the animal. Diameters increased with age in cows the diameter were 47µm and 72µm respectively. For all muscles, shear force was positively correlated with fibre diameter ($r=0.83$ curvilinear, Hiner, *et al.*, 1954). However, the fibre diameter is closely related to animal age (Tuma *et al.*, 1962) in beef, increasing fibre diameter with increasing age and when the effect of age was removed, there was no significant relationship between fibre diameter and tenderness. In a more recent study, fibre size did not explain tenderness in beef (Koochmaraie *et al.*, 1988).

The clearest relations of tenderness and fibre diameter have been shown for different fish species. In fish, firmness of cooked flesh increases with decrease in fibre cross-sectional area across species (Hurling *et al.*, 1996), that is, species with finer fibres had firmer meat. Also, dark muscles (with smaller fibre diameters) had firmer texture. Higher collagen contents gave less tender raw meat but were not related to texture of cooked fish (Hatae *et al.*, 1990). The texture was compared to that of glass fibres; the smaller their diameter, the higher the strength due to the « scaling effect ». A model of fibre diameter was proposed in which the fibre diameter and the proportion of the cross-section taken up by the fibres. As the proportion increased, the firmness decreased. In fibrous analogues,

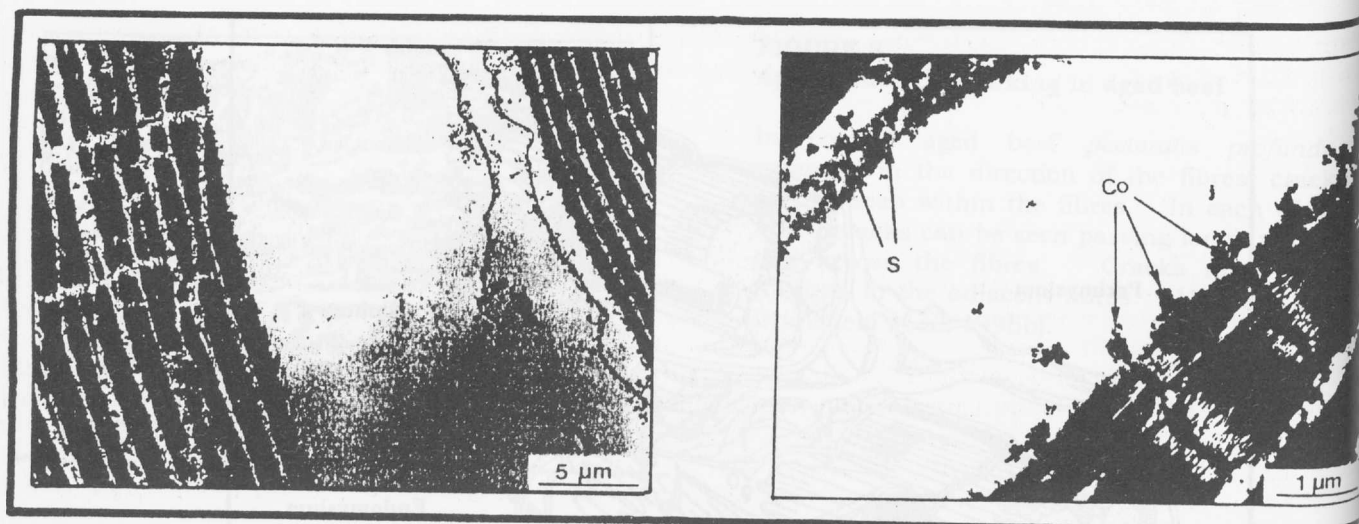


FIGURE 5 Structural degradation within the fibre

The figure on the left shows the breaks within the muscle fibre and the detachment of the membrane. At high magnification (right) the costameres (Co) remain attached to the myofibril and the membranes (S) from adjacent fibres remain attached (from Dransfield *et al.*, 1995b)

Chen and Clayton (1995) have recently reported that extruded analogues, with similar textural properties to fillets, had similar fibre diameters to those of 'natural fillets'.

The strength of the fibre may also be affected by sarcomere length. Investigations on cold shortening suggests that the transverse cytoskeleton is weakened or the myofibril is strengthened or both (Willems and Purslow, 1990) caused by a reduction in I-band length (Voyle, 1969) or stronger muscle myofibrillar components by overlap of actin and myosin (Marsh and Carse, 1974). In high pressure treated pre rigor meat, sarcomere lengths (1.8 µm) are about 10% shorter than in non-pressurised controls but the cooked meat is more tender (Elgasim and Kennell, 1982). Structure of raw muscle shows distorted endomysal and sarcolemmal sheaths, interfibrillar spaces, intermyofibrillar spaces and globular material of the surface of the fibres (probably disintegrated collagen coagulated sarcoplasmic protein). The Z-line was disintegrated and thought to be the origin of the tenderness.

The changes at the protein level responsible for muscle weakening during storage has long been studied. Earlier reports showed an increase in non-protein nitrogen and free amino acids. However, the majority of the increase occurred after tenderisation had occurred and could be due to their release from sarcoplasmic proteins (Fujimori and Deatherage, 1964), which are thought not to be involved in tenderness, or that only few cleavages are required to tenderise meat (Parrish *et al.*, 1969). An alternative possibility is that the proteins would form the glue and during ageing their progressive degradation would form weaker glues and weaken the whole structure. Many more recent studies have looked at structures and individual protein changes. One of the first events post mortem is the alteration in the membrane (Figure 5). The membrane is detached and the costameres appear to remain attached to the fibre. One of the proteins involved in this breakage is likely to be vinculin (Taylor *et al.*, 1995) although the rate of its disappearance (as in nebulin) is too fast to account for the changes in tenderness. Desmin (skelemin or 10nm filament protein) disappeared during storage at 15°C at about the same rate as tenderisation (Young *et al.*, 1980). The most recent detailed study (Chiung-Ying *et al.*, 1996), comparing normal and electrically stimulated meats showed that intact desmin and troponin-T decrease faster in stimulated meat than in controls. Unfortunately toughness was not reported but the rates of disappearance of desmin and troponin-T were similar to the expected rate for beef chilled ageing. Alterations in the Z-line components may therefore release titin and nebulin and cause the fracturing. Titin and nebulin were degraded more rapidly than desmin or troponin-T.

Few studies have shown effect on the extracellular components which could be important in binding the fibres in the composite. Two of the major extracellular matrix components are collagen and proteoglycans. These form the extracellular scaffold containing fibres (collagen) and ground substance (proteoglycans). These interact with other extracellular matrix molecules and cells. Several recent reviews have discussed the role of collagen and cross-

linking to texture (McCormick, 1994; Purslow, 1994) and proteoglycans (Velleman and Racela, 1994). Changes in proteoglycans have received little attention but could be a major factor in the weakening of intramuscular connective tissues (Nishimura *et al.*, 1996).

FUTURE DEVELOPMENTS

A microstructure-based approach to the mechanical properties of muscle and meat provides a framework for modelling mechanical properties. Detailed information is available about the organisation of muscle structure. What is needed is the way in which the rearrangement of this structure is reflected in the macroscopic mechanical responses. We should not be over-attracted by the unique structure of muscle when the simple concept of a glue may suffice. Studies on the structural modifications which influence texture will continue and will become easier as techniques and antibodies become widely used. Changes in materials which affect adhesion are less easy to determine and may involve numerous proteins operating at different sites in the muscle. Also important will be to determine the strengths and mechanical properties of the components of muscle so that their contributions to the composite properties can be modelled quantitatively.

REFERENCES

- AALHUS, J.L., SCHAEFER, A.L., MURRAY, A.C. and JONES, S.D.M. (1992). The effect of ractopamine on myofibre distribution and morphology and their relation to meat quality in swine. *Meat Sci.*, **31**, 397-409.
- ATKINS, A.G. and MAI, Y.-W. (1985). *Elastic and plastic fracture*. Ellis-Horwood, London.
- BISSEL, M.J., HALL, H.G. and PARRY, G. (1982). How does the extracellular matrix direct gene expression? *J. Theoretical Biology*, **99**, 31-68.
- BOUTON, P.E., CARROLL, F.D., HARRIS, P.V. and SHORTHORSE, W.R. (1973). Influence of pH and fibre contraction state upon factors affecting tenderness of bovine muscle. *J. Food Sci.*, **38**, 404-407.
- CHEN, X.J. and CLAYTON, J. (1995). Microstructural analysis of fish fillets and fabricated fish fillet analogues. TCA Institute Food Technology Annual Meeting, 1995, p. 285.
- CHENG, C.S. and PARRISH, F.C. (1976). Scanning electron microscopy of bovine muscle: effect of heating on ultrastructure. *J. Food Sci.*, **41**, 1449-1454.
- CHIUNG-YING, H., STROMER, M.H. and ROBSON, R.M. (1996). Effect of electrical stimulation on post-mortem titin, nebulin, desmin, and troponin-T degradation and ultrastructural changes in bovine longissimus muscle. *J. Anim. Sci.*, **74**, 1563-1575.
- CROSS, H.R., CARPENTER, Z.L. and SMITH, G.C. (1973). Effect of intramuscular collagen and elastin on bovine muscle tenderness. *J. Food Sci.*, **38**, 998-1003.
- CROUSE, J.D., KOOHMARAIE, M. and SIEDEMAN, S.D. (1991). The relationship of muscle fibre size to tenderness of beef. *Meat Sci.*, **30**, 295-302.
- CURRIE, R.W. and WOLFE, F.H. (1980). Rigor related changes in mechanical properties (tensile and adhesive) and extracellular space in beef muscle. *Meat Sci.*, **4**, 123-143.
- DRANSFIELD, E. (1986). Meat as a fibrous composite. Symposium 'Food Rheology'. The British Society of Rheology and the Institute of Food Research, Norwich, paper 12, UK.
- DRANSFIELD, E. and RHODES, D.N. (1976). Effect of post-rigor length on the texture of meat. *J. Sci. Food Agric.*, **27**, 483-486.
- DRANSFIELD, E., FRANCOMBE, M.A. and WHELEHAN, O.P. (1984). Relationships between sensory attributes in cooked meat. *J. Texture Studies*, **15**, 33-48.
- DRANSFIELD, E., LOCKYER, D.K. and PRABHAKARAN, P. (1986). Changes in the extensibility of raw beef muscle during storage. *Meat Sci.*, **16**, 127-142.
- DRANSFIELD, E., LACOURT, A. and LACOURT, P. (1995a). Fibre fracture of bovine *M. Pectoralis profundus* cooked pre- and post-rigor. *J. Texture Studies*, **26**, 71-87.
- DRANSFIELD, E., BRÜGGEMANN, ASTRUC, T. and LACOURT, A. (1995b). Structural weakening of muscle post-mortem. 2nd Dummerstorf Muscle-Workshop: *Muscle Growth and Meat Quality*. Rostock, Germany.
- ELGASIM, E.A. and KENNICK, W.H. (1982). Effect of high hydrostatic pressure on meat microstructure. *Food Microstructure*, **1**, 75-82.
- FIELDS, R.W. and FABER, J.J. (1970). Biophysical analysis of the mechanical properties of the sarcolemma. *Can. J. Physiol. Pharmacol.*, **48**, 394-404.
- FUJIMAKI, M. and DEATHERAGE, F.E. (1964). Chromatographic fractionation of sarcoplasmic proteins of beef skeletal muscle on ion-exchange cellulose. *J. Food Sci.*, **29**, 316-326.
- GAULT, N.F.S. (1985). The relationship between water holding capacity and cooked meat tenderness in some beef muscles as influenced by acidic conditions below ultimate pH. *Meat Sci.*, **15**, 15-30.
- GORDON, J.E. (1978). In: *Structures, or why things don't fall down*. Penguin, New York.
- GREASER M.L. (1991). An overview of the muscle cell cytoskeleton. *Proc. Reciprocal Meat Conf.* **44**, 1-5.

- HARRIES, J.M., RHODES, D.N. and CHRYSTALL, B.B. (1972). Meat Texture I. Subjective assessment of texture of cooked beef. *J. Texture Studies*, **3**, 101-114.
- HARRIS, B. (1980). In: The mechanical properties of biological materials. Eds: Vincent, J.F.V. and Curry, J.D. 73.
- HEARN, L.E., PENFIELD, M.P. and GOERTZ, G.E. (1978). Heating affects on bovine semitendinosus: shear muscle fibre measurements and scanning electron microscopy. *J. Food Sci.*, **43**, 13-16.
- HINER, R.L., HANKINS, O.G., SLOANE, H.S., FELLERS, C.R. and ANDERSON, E.E. (1954). Fibre diameter relation to tenderness of beef muscle. *Food Res.*, 364-376.
- HURLING, R. RODELL, J.B. and HUNT, H.D. (1996). Fibre diameter and fish texture. *J. Texture Studies*, 679-685.
- HUTTON, C.W., NEGGERS, Y.H. and LOVE, T.O. (1981). Scanning electron microscopy, proteolytic enzyme activity and acceptability of beef semitendinosus cooked by microwave and conventional heat. *J. Food Sci.*, **46**, 1314.
- JEREMIAH, L.E. and MARTIN, A.H. (1978). Histological and shear properties of bovine muscle and alterations during post-mortem ageing. *Meat Sci.*, **2**, 169-179.
- KOOHMARAIE, M., SEIDEMAN, S.C., SCHOLLMEYER, J.E., DUTSON, T.R. and BABIKER, A.S. (1988). Factors associated with the tenderness of three bovine muscles. *J. Food Sci.*, **53**, 407-410.
- LAZARIDES, E. (1980). Intermediate filaments as mechanical integrators of cellular space. *Nature*, **283**, 249-251.
- LILLFORD, P.J. (1991). Texture and acceptability of human foods. In: *Feeding and the texture of food*. Eds: Vincent, J.F.V. and Lillford, P.J. Soc. Exptl. Biol. Seminar Series 44, Cambridge University Press, Cambridge. pp. 231-243.
- LOCKER, R.H. and WILD, D.J.C. (1982). A machine for measuring yield point in raw meat. *J. Texture Studies*, **13**, 71-82.
- LOCKER, R.H., DAINES, G.J., CARSE, W.A. and LEET, N.G. (1977). Meat tenderness and the gap filaments. *Meat Sci.*, **1**, 87-104.
- MARSH, B.B. and CARSE, W.A. (1974). Meat tenderness and the sliding filament hypothesis. *J. Food Technology*, **9**, 129-139.
- MCCORMICK, R.J. (1994). The flexibility of the collagen compartment of muscle. *Meat Sci.*, **36**, 79-91.
- MORIOKA, K., KURASHIMA, K. and SHIMIZU, Y. (1992). Heat gelling properties of fish sarcoplasmic proteins. *Bull. Japanese Soc. Sci., Fish*, **58**, 767-772.
- NISHIMURA, T., HATTORI, A. and TAKAHASHI, K. (1996). Relationship between degradation of proteoglycans and weakening of the intramuscular connective tissue during post-mortem ageing of beef. *Meat Sci.*, **42**, 251-256.
- PARRISH, F.C., GOLL, D.E., NEWCOMB, W.J., De LUMEN, B.O., CHAUDRY, H.M. and KLINE, E.A. (1994). Molecular properties of post-mortem muscle. 7. Changes in non-protein nitrogen and free fatty acids of bovine muscle. *J. Food Sci.*, **34**, 196-202.
- PAUL, P. (1965). Storage- and heat-induced changes in the microscopic appearance of rabbit muscle. *J. Food Sci.*, **30**, 960-968.
- PURSLOW, P.P. (1994). The structural basis of meat toughness: What role does the collagenous component play? Proceedings 40th International Congress Meat Sci. Technol., The Hague, Netherlands. pp. 27-34.
- REJT, J., KUBICKA, H. and PISULA, A. (1978). Changes in physical and chemical properties and of histological structure of meat subjected to massage under vacuum. *Meat Sci.*, **2**, 145-153.
- ROWE, R.W.D. (1974). Collagen fibre arrangement in intramuscular connective tissue. Changes associated with muscle shortening and their possible relevance to raw meat toughness measurements. *J. Food Technology*, **9**, 501-508.
- SAMEJIMA, K., ISHIOROSHI, M. and TASUI, T. (1982). Heat-induced gelling properties of actomyosin: Effect of tropomyosin and troponin. *Agric. Biol. Chem.*, **46**, 535-540.
- SMALL, B. and HUNTER, P. (1990). Structure and function of the diastolic heart: Material properties of passive myocardium. In: *Myocardial Heart*. Hunter and McCulloch, Springer Verlag.
- TAYLOR, R.G., GEESINK, G.H., THOMPSON, V.F., KOOHMARAIE, M. and GOLL, D.E. (1995). Is Z-line degradation responsible for postmortem tenderization? *J. Anim. Sci.*, **73**, 1351-1367.
- TORNBERG, E., ANDERSON, A. and von SETH, G. (1993). Water distribution in raw pork muscle (*M. longissimus dorsi*) of different meat qualities. Proc. 39th International Congress Meat Sci. Technol., Calgary, Canada. pp. 201-209.
- TORNBERG, E., von SETH, G. and GÖRANSSON, A. 1994. Influence of ageing time, storage temperature and percentage lean on the eating quality of pork and its relationship to instrumental and structural parameters. *Science des Aliments*, **14**, 373-385.
- TUMA, H.J., VENABLE, J.H., WUTHIER, P.R. and HENRICKSON, R.L. (1962). Relationship of fibre diameter to tenderness and meatiness as influenced by bovine age. *J. Animal Sci.*, **21**, 33-36.
- WEIDEMANN, J.F., KAESSE, G. and CARRUTHERS, L.D. (1967). The histology of pre-rigor and post-rigor ox muscle before and after cooking and its relation to tenderness. *J. Food Sci.*, **32**, 7-13.
- VELLEMAN, S.G. and RACELA, J.R. (1994). Meat tenderness. Connective tissue influence on tenderness and potential role for proteoglycans. Meat Focus International, CAB International, Oxford, UK. pp. 512-516.
- VOYLE, C.A. (1969). Some observations on the histology of cold shortened muscle. *J. Food Technol.*, **4**, 275-281.

- WANG, H., DOTY, D.M., BEARD, F.J., PIERCE, J.C. and HANKINS, O.G. (1956). Extensibility of single muscle fibres. *J. Animal Sci.*, **15**, 97-108.
- WILLEMS, M.E.T. and PURSLOW, P.P. (1996). Effect of postrigor sarcomere length on mechanical and structural characteristics of raw and heat-denatured single porcine muscle fibres. *J. Texture Studies*, **27**, 217-233.
- YOUNG, O., GRAAFHUIS, A.E. and DAVEY, C.L. (1980). Post-mortem changes in cytoskeletal proteins of muscle. *Meat Sci.*, **5**, 41-55.

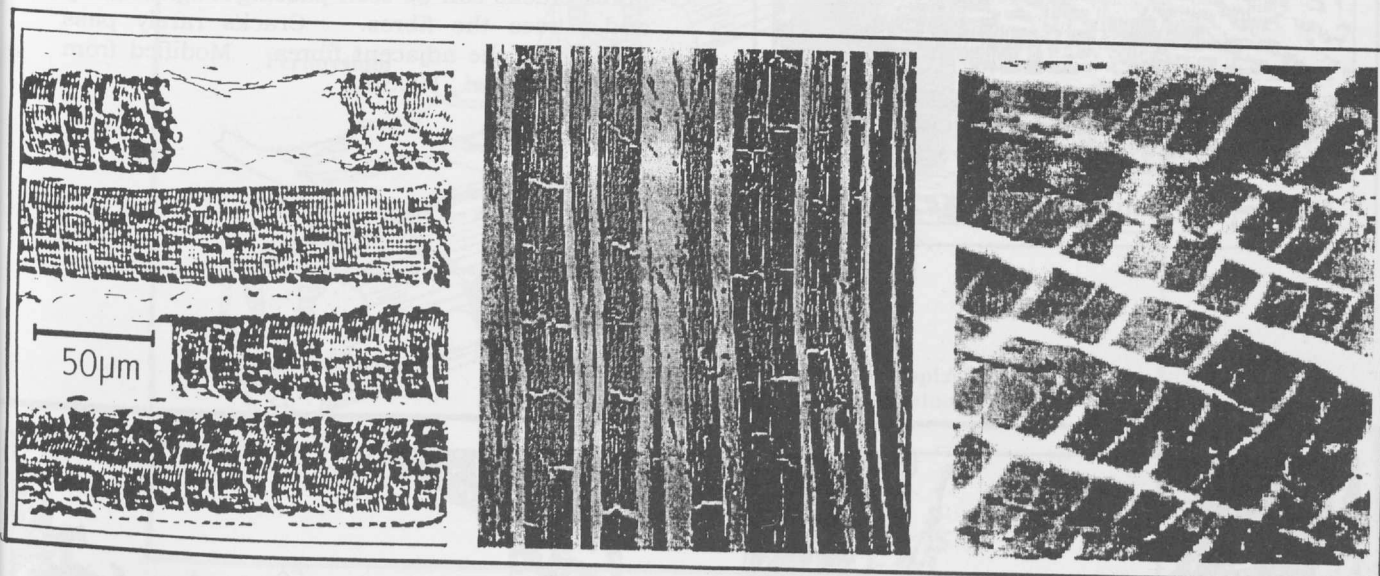


FIGURE 1. Observations of the periodic fracture in meat

The figure on the left (from Dransfield *et al.*, 1986) shows the periodic fracturing (averaging 17 μm between cracks) of aged raw meat fibres after extension. One fracture (top) is seen to have been opened out by the extension and the membrane is seen spanning the gap. In the centre (from Paul, 1965) and shows extensive and regular cracking of rabbit biceps femoris cooked at 24 hours. The distance between cracks averages 30 μm. On the right (from Rejt, Kubicka and Pisula, 1978) is shown the regular cracking of muscle fibres of processed pork subjected to massage under vacuum. The distance between cracks averages 25 μm.

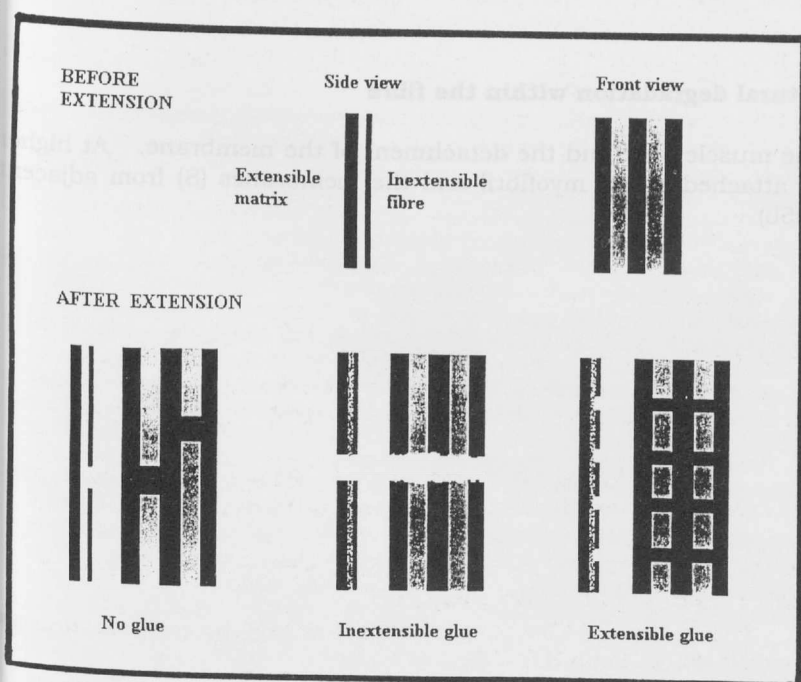


FIGURE 2 Modelling fracture

The figure shows the effect of gluing an inextensible material to an extensible backing. With no glue between the elements, when extended, the inextensible material breaks, leaving the extensible backing. Breaks will occur at the weakest parts of the inextensible material. When bonded with a stiff glue, both the material break when extended. With an extensible glue, the stiff material with break and then will break further with further extension. With several stiff elements, breaks will occur regularly in the different elements.

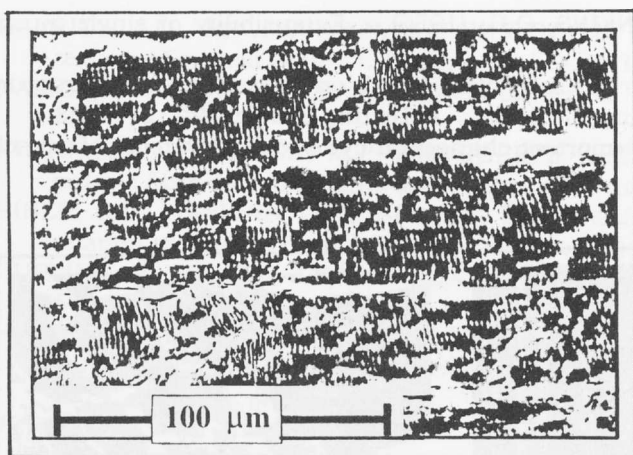


FIGURE 3
Appearance of cracking in aged beef

In cooked aged beef *pectoralis profundus* extended in the direction of the fibres, cracks can be seen within the fibres. In each of the fibres cracks can be seen passing longitudinally and across the fibres. Cracks rarely pass through to the adjacent fibres. Modified from Dransfield *et al.*, 1995b).

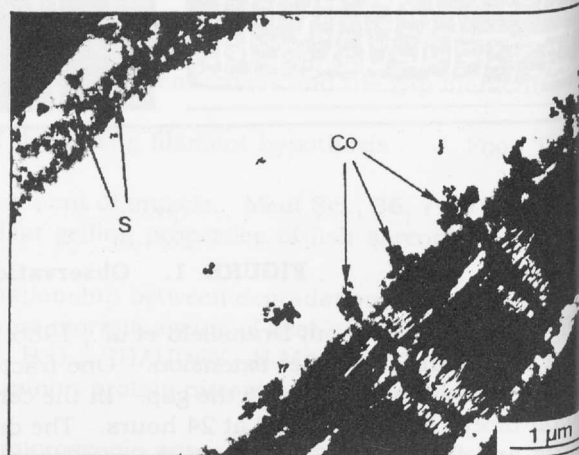
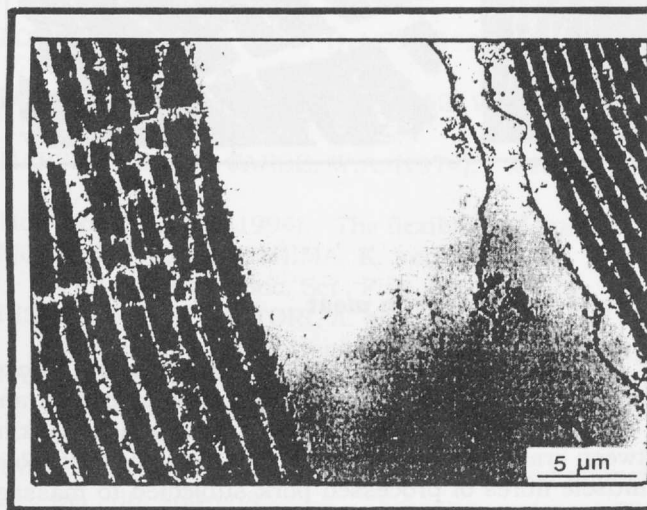


FIGURE 5 Structural degradation within the fibre

The figure on the left shows the breaks within the muscle fibre and the detachment of the membrane. At high magnification (right) the costameres (Co) remain attached to the myofibril and the membranes (S) from adjacent fibres remain attached (from Dransfield *et al.*, 1995b)

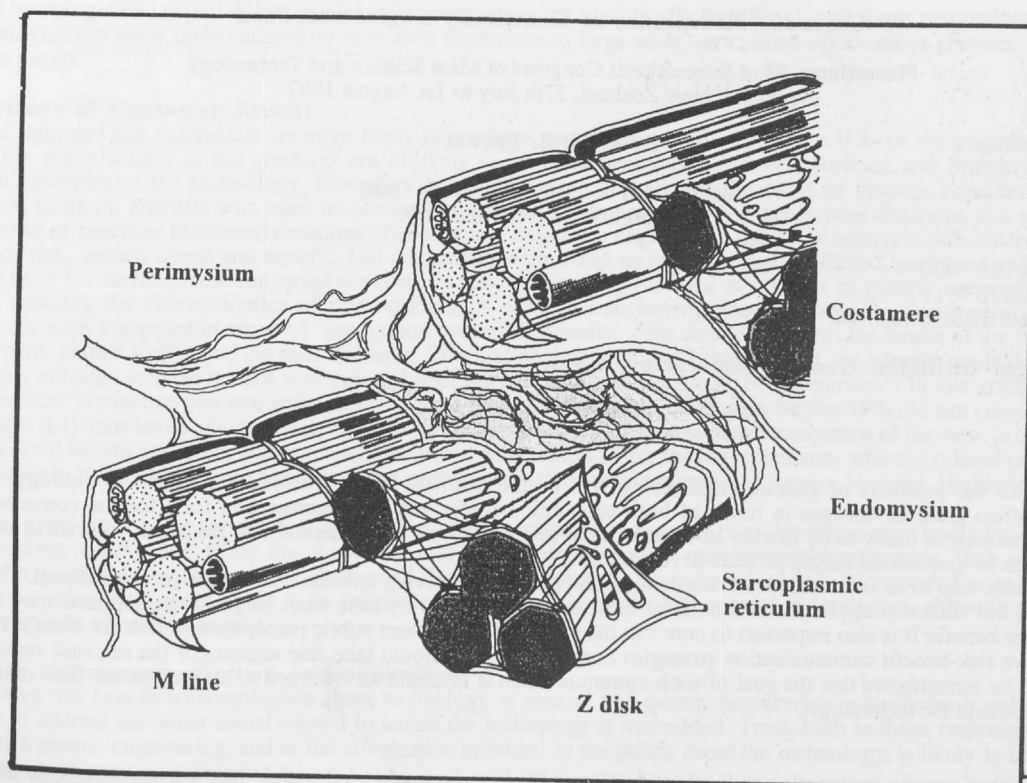


FIGURE 4 Diagrammatic representation of structural elements in muscle (after Lazarides, 1980)
The hierarchical organisation of fibres separated by the endomysial connective tissue which is branched to the perimysial connective tissue.