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ABSTRACT

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Yhteenveto: Longissimus dorsi lihaksen oksidatiivinen ja glykolyyttinen kapasiteetti ja niiden yhteys lihan laatuun verrattaessa eri sikarotuja ja risteytyksiä
Diss.

The oxidative and glycolytic capacities as well as the calcium release and uptake of sarcoplasmic reticulum and mitochondria of *longissimus dorsi* (LD) from seven pig breeds or crosses, i.e. Landrace, Yorkshire, Hampshire, Hampshire x (Yorkshire x Landrace), Duroc x (Yorkshire x Landrace), Landrace x (Yorkshire x Landrace), and Yorkshire x (Yorkshire x Landrace), were studied. These muscle properties were compared to meat quality. No studies concerning oxidative capacity or calcium metabolism of Finnish Landrace and Yorkshire pigs have been published before.

To determine the oxidative capacity of the LD muscle, the activities of citrate synthase and 3-hydroxyacyl-CoA-dehydrogenase as well as the mitochondrial volume density were measured. To elucidate the glycolytic capacity of the LD muscle, lactate, glycogen, the glycolytic potential as well as activity of glycogen phosphorylase and lactate dehydrogenase (LDH) were measured. Also the content of LDH isoenzymes were determined.

The muscle quality of Landrace and Yorkshire was similar. The LDH activity was lower in the Hampshire cross LD and higher in the Duroc cross LD than in either Landrace or Yorkshire. There were no other differences between breeds. Lower lactate and higher glycogen levels were noted in the Hampshire cross LD as compared to the Duroc cross LD. In Duroc cross and Hampshire muscle, the proportion of LDH-1 was higher and LDH-5 lower than in most other breeds. Higher glycolytic potential, but lower ultimate pH and LDH activity were noted in the Hampshire breed. In Hampshire and its cross, the ultimate pH was lower than in other breeds or crosses. The activities of 3-hydroxyacyl-CoA-dehydrogenase and citrate synthase were higher in Hampshire than in the other breeds. Calcium uptake of sarcoplasmic reticulum and mitochondria as well as mitochondrial calcium release were lower in crosses than in purebred pigs.

The redder the meat color (measured instrumentally), the higher the oxidative capacity and the glycolytic potential was. There was no correlation between the glycolytic potential and the sensory quality of meat. The LD of Hampshire was the most oxidative. High muscle oxidative capacity seemed to improve meat flavor and juiciness.

This study concerned only the pig LD, so the results can not be generalised to the whole pig. The muscle properties of Hampshire and Duroc crosses were quite similar to those of Landrace and Yorkshire in most of properties studied, but not in the LDH isoenzyme distribution. There was a great interindividual heterogeneity, in properties studied, in every breed and cross.

Key words: Calcium; glycolytic capacity; *longissimus dorsi;* meat quality; oxidative capacity; pig.

T. Suuronen, Paavonkuja 31, FIN-41400 Lievestuore, Finland.

CONTENTS

Abbreviations

ADP	adenosine diphosphate
AMP	adenosine monophosphate
αR	alpha red
ATP	adenosine triphosphate
a* value	redness of meat
βR	beta red
b* value	yellowness of meat
cAMP	cyclic 3,5-adenosine monophosphate
Carm15	calcium release of mitochondrial fraction, samples taken 15 min after stunning
Carm45	calcium release of mitochondrial fraction, samples taken 45 min after stunning
Carsr15	calcium release of sarcoplasmic reticular fraction, samples taken 15 min after stunning
Carsr45	calcium release of sarcoplasmic reticular fraction, samples taken 45 min after stunning
Caum15	calcium uptake of mitochondrial fraction, samples taken 15 min after stunning
Caum45	calcium uptake of mitochondrial fraction, samples taken 45 min after stunning
Causr15	calcium uptake of sarcoplasmic reticular fraction, samples taken 15 min after stunning
Causr45	calcium uptake of sarcoplasmic reticular fraction, samples taken 45 min after stunning
CP	creatine phosphate
CS	citrate synthase
CSSP	specific activity of citrate synthase
DFD	dark, firm and dry meat
DYL	Duroc x (Yorkshire x Landrace)
EM	electron microscopy
glyc	glycogen
glycpot	glycolytic potential
H	Hampshire
HADH	3-hydroxyacyl-CoA-dehydrogenase
H/M	ratio of heart type and muscle type subunits of lactate dehydrogenase
HN	halothane-negative
HP	halothane-positive
HYL	Hampshire x (Yorkshire x Landrace)
L	Finnish Landrace

LACT	lactic acid
LD	*longissimus dorsi,* the loin muscle
LDH	lactate dehydrogenase
LDH-1	lactate dehydrogenase isoenzyme 1, "heart isoenzyme"
LDH-2	lactate dehydrogenase isoenzyme 2
LDH-3	lactate dehydrogenase isoenzyme 3
LDH-4	lactate dehydrogenase isoenzyme 4
LDH-5	lactate dehydrogenase isoenzyme 5, "muscle isoenzyme"
LYL	Landrace x (Yorkshire X Landrace)
L* value	lightness of meat
M15	mitochondrial fraction samples taken 15 min after stunning
M45	mitochondrial fraction samples taken 45 min after stunning
MH	malignant hyperthermia
MIT	mitochondria
n	number of samples
NMR	nuclear magnetic resonance
nn	reactor to halothane test, homozygous halothane-positive
nN	nonreactor to halothane test, heterozygous carrier of halothane gene
NN	nonreactor to halothane test, homozygous halothane-negative
n.s.	statistically non significant
PFK	phosphofructokinase
pH_1	pH value measured 45 min after stunning
pH_{24}	pH value measured 24 hours after stunning
PHOS	glycogen phosphorylase
pH_u	ultimate pH, measured at 24 h postmortem
PSE	pale, soft and exudative meat
r_g	correlation cofficient
SD	standard deviation
SM	*semimembranosus*
SR	sarcoplasmic reticulum
SR15	SR fraction, samples taken 15 min after stunning
SR45	SR fraction, samples taken 45 min after stunning
Y	Finnish Yorkshire
YYL	Yorkshire x (Yorkshire x Landrace)

1 INTRODUCTION

Pork is an important source of nutrients in Finland. Pork consumption was 31 kg/capita in 1993 or approximately half of the meat consumption in Finland (Agrifacts 1994). Selective breeding of pigs has changed the population of pigs in Finland significantly. Modern pigs grow faster, produce leaner meat, farrow more effectively and are more economical than pigs of the past. The hygienic quality of meat has improved. However, consumers now demand more flavor from pork. Thus, more interest has been directed to the eating quality of meat. Lean meat is considered healthy, but more intramuscular fat would improve flavor.

The traditional pig breeds in Finland are Landrace and Yorkshire. Most meat pigs are crosses of Landrace and Yorkshire. In 1990, Hampshire pigs and Duroc sperm were brought to Finland from Sweden. These have been crossbred with Landrace, Yorkshire or their crosses. The purpose of the Hampshire and Duroc imports was to improve meat sensory quality by increasing intramuscular fat.

Already in 1678, Stefano Lorenzini observed that animal muscles could be subdivided into red and white, on the basis of color differences (Ciaccio 1898, cited by Dubowitz 1965). Red muscles primarily consist of red oxidative muscle fibers, while white muscles are mostly white glycolytic fibers. Red muscle fibers contain more lipids than white ones.

The conversion of muscle to meat is a very complicated series of events. It is influenced by events before, at and after slaughter. The metabolic capacity of muscle is important as well as the handling of pigs and carcasses. After exsanguination, oxygen supply to fibers and waste product transportation stop. Muscle fibers continue to produce energy by glycogenolysis with lactic acid as the product. Lactic acid then

accumulates in muscle fibers, decreasing muscle pH. The oxidative capacity and capillary content of muscle are important antemortem. If muscles are able to produce energy by oxidizing fuels and if the clearance of waste products is efficient, lactate will not begin to accumulate in muscle prior to slaughter. A muscle's oxidative capacity can be measured by determining activities of citric acid cycle or lipolytic enzymes as well as the amount of mitochondria present. The glycolytic capacity of muscle tells about the muscle's ability to produce lactic acid. It can be measured by determining the activity of lactate-forming enzyme, lactate dehydrogenase, or glycolytic potential, which is the sum of the main compounds likely to produce lactic acid postmortem. Muscle oxidative and glycolytic capacities are found to vary between muscles and pig breeds (Essén-Gustavsson & Fjelkner-Modig 1985, Fernandez *et al.* 1992, Karlsson *et al.* 1993).

Selective breeding may have generated some drawbacks. Stress-susceptible pigs have lower meat quality (e.g. higher drip loss and paler meat) and higher death rates during transportation than normal pigs. The incidence of PSE-meat (pale, soft and exudative) is still a problem, although the halothane gene has been removed from most of the Finnish pig population. So further research on the causes of PSE is important. In many cases, halothane-positive pigs, which are susceptible to malignant hyperthermia, are more muscular than halothane-negative ones. It has been postulated that selection for higher growth rates has led to animals whose muscles no longer function properly. The number of large, glycolytic muscle fibers have increased (Swatland & Cassens 1974). After birth the number of fibers does not increase, thus muscle growth takes place by hypertrophy. Therefore, large white glycolytic fibers have been favored at the cost of smaller oxidative red fibers (Ashmore *et al.* 1972, Swatland 1976). If the ability to use oxygen in energy production and, if the transportation of waste products is reduced in muscle fibers, the accumulation of lactate may start before slaughter as a result of stress (Kivikari & Puolanne 1989, Henckel *et al.* 1992).

Longissimus dorsi (LD) muscle, the pork loin, is a white muscle and consists mainly of non-oxidative fibers (Ruusunen 1994). It is one of the most valuable muscles of the carcass. Breeders have focused on improving the size of this muscle. It is a large muscle from which samples can be easily taken, hence it is the most studied muscle of pig.

This study is part of a larger project in which properties of production as well as meat and muscle quality of Hampshire and Duroc crosses have been compared to those of Finnish Landrace and Yorkshire. This study focuses on the oxidative and glycolytic properties of pig muscle fibers as well as calcium metabolism of sarcoplasmic reticulum and mitochondria and their connection to certain meat quality parameters

(Fig.1). No studies concerning oxidative capacity or calcium metabolism of Finnish Landrace and Yorkshire pigs have been published before. Muscle fiber type distribution was determined by Marita Ruusunen (1994), while sensory analysis, meat color, drip loss and water content were analyzed by Mikko Pajari (1994).

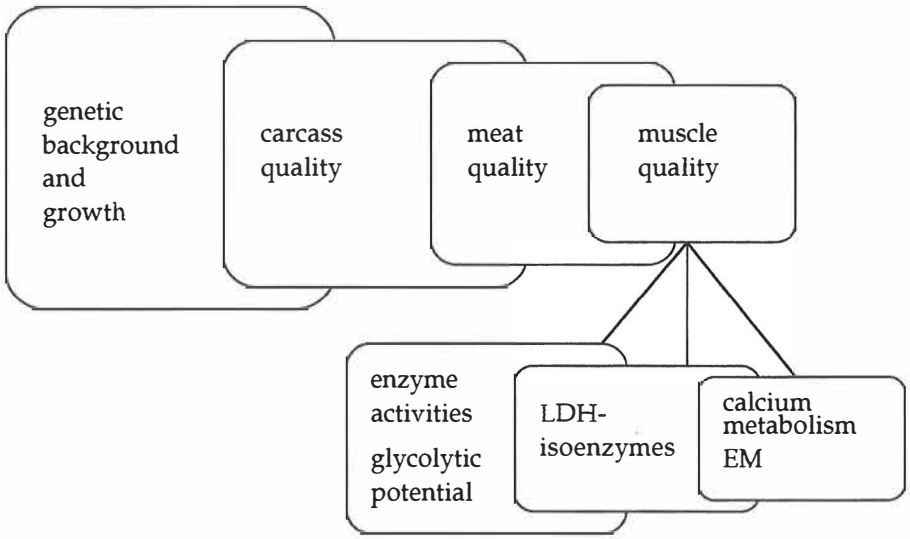

FIGURE 1 Experimental design of three-way cross study. This study is a part of a larger project in which the properties of Hampshire and Duroc crosses have been compared to those of Landrace and Yorkshire.

2 REVIEW OF THE LITERATURE

2.1 Biology of the pig

There are about 90 pig breeds in the world and over 200 geographically isolated populations which have their own characteristics and distribution (Pond & Houpt 1978). Pigs are white, black, red, grey, brown or of all combinations of these colors. They can be striated, smooth or curly coated or even hairless. The weight of adult males varies between 75 and 200 kg, and of females between 35 and 150 kg.

The pig belongs to the order Artiodactyla, even-toed ungulates, and the family Suidae. The foot has four digits, of which two are non-functional. The nose is a long mobile snout adapted for digging. The pig is an omnivore, but primarily acts as an herbivore. The litter size of the wild pig is 4-6, and that of the domestic pig, 8-12 or more. The sow farrows 112-120 days after mating. Some modern breeds may reach the puberty at 5-6 months of age. Pigs can live up to 25 years (Epstein & Richard 1984).

The pig is one of the oldest domestic animals. It was domesticated approximately 9000 years B.C. (Reed 1977). The domestic pig is progeny of the wild pig. With breeding, the small intestine has lengthened, while the growth rate and number of teats has increased. Pigs reach sexual maturity earlier and are more prolific. The number of ribs as well as thoracic and lumbar vertebrae has increased (Pond & Houpt 1978). Also, pig behavior has changed, but this change has been more quantitative than qualitative. Pigs are active social animals who establish dominance hierarchies (Rasmussen *et al.* 1962). This becomes important when strange pigs are mixed together during transportation to and holding at slaughterhouses.

The chromosome number of pigs is polymorphic. Domestic and Japanese wild pigs have 38 chromosomes, while the European wild pig has either 36 or 37 chromosomes (see ref. Pond & Houpt 1978). The domestic and European wild pig hybrid has 37 chromosomes with no evidence of reduced fertility.

Pigs have thick fat layer under the skin which is effective in preserving body heat. They are not able to sweat (Ingram 1965). This can be a problem in situations such as transportation (Honkavaara 1989), where environmental temperature is high and pigs are unable to move to a cooler place. There are differences in the growth rate of muscles, bones and fat during development. Bones and muscles develop first, and when their rate of growth decreases, fat deposition increases (Tess *et al.* 1986). Body fat content increases with age and body weight in pigs (Gu *et al.* 1992, Rajar & Zlender 1993). Castrated males are fatter than gilts or boars (Enfält *et al.* 1993b, Barton-Gade 1987) and gilts are fatter than boars (Edwards *et al.* 1992). Feeding has an effect on the quality of body fat (Morgan *et al.* 1992).

2.2 Pork production in Finland

Finnish pork production in 1993 was 169 million kilograms or about half of the total meat production (Agrifacts 1994). Traditional Finnish pig breeds are Landrace and Yorkshire. Forty percent of sows are Yorkshire, 40% are Landrace and 20% are Landrace x Yorkshire (Ojala *et al.* 1988). The majority of meat pigs are crosses of these breeds. In recent years, Hampshire pigs and Duroc sperm have been brought to Finland from Sweden. They have been crossbred with Yorkshire, Landrace or (Landrace x Yorkshire).

The average herd size in Finland is 30 sows. One-third of Finnish sows are artificially inseminated. Sows farrow for the first time at approximately one year of age. Piglets are weaned at the average age of 37 days. The average litter size of Landrace or Yorkshire pigs in Finland is over 12 (Ojala *et al.* 1988).

Daily weight gain of meat pigs is nearly 1000 g. In 1992, it averaged 1012 g in Landrace progeny test pigs and 997 g in Yorkshire progeny test pigs. At time of slaughter, pigs are about 6 months of age and weigh about 100 kg (Kuosmanen 1993a). Daily weight gains from Finnish Landrace and Yorkshire pigs compare well with values from many other European countries (Kuosmanen 1993b)

The aims of pig breeding have been to improve fertility and growth rate, as well as slaughter and utilization properties (Veijonen

1984). However, meat quality has been impaired. Because of intensive halothane testing in Finland, the incidence of halothane gene has decreased. Currently, all artificial insemination and farm boars as well as over 95% of sows in breeding farms were registered halothane-free in 1992 (Kuosmanen & Puonti 1993).

Pigs in Finland are, on average, very healthy. Many harmful diseases occurring abroad are unknown in Finland (Maijala 1969, Ojala *et al.* 1988).

2.3 Porcine muscles and muscle fibers

The skeletal muscular system of our common domestic animals, such as cattle, pigs and sheep, consists about 300 distinct muscles (Lawrie 1985). Muscle structure across species is basically similar, although they differ in shape, size and activity.

Porcine muscles can be divided to dark/red or light/white, depending upon their color (Beecher *et al.* 1965). For example, *trapezius*, *serratus ventralis*, *rectus femoris*, as well as part of *semitendinosus* and *biceps femoris* can be regarded as dark muscles (high in red fiber content) and *longissimus dorsi*, *gluteus medius*, as well as the other part of *semitendinosus* and *biceps femoris* can be regarded as light muscles (low in red fiber content). Dark muscles have a higher myoglobin concentration, lower degree of glycogen metabolism, and lower postmortem initial concentration of pyruvate than light muscles (Beecher *et al.* 1969). High activity of phosphorylase and lactate dehydrogenase as well as low activity of citrate synthase and 3-hydroxyacyl-CoA-dehydrogenase are typical for white muscle of higher animals (Bass *et al.* 1969). The opposite is typical for red muscles. Generally, post-rigor sarcomere length is longer in red than in white muscles (Beecher *et al.* 1965). Muscle contraction is under neural control. By changing innervation, fiber type can be changed (Ganong 1987). It has been suggested that diminished neural control may lead to an increase in glycolytic metabolism (Swatland & Cassens 1974).

Skeletal muscles are specialized for producing bodily movement. The principal duty of muscle fibers is to contract. Fibers are long (from 1 to hundreds of mm), cylindrical, and multinucleated. The diameter of fibers can vary approximately from 10 to 100 μm (Swenson 1990). In many muscles, individual fibers are shorter than the overall length of the muscle. Each muscle is enveloped in a layer of connective tissue, the epimysium. Muscle fibers are grouped into bundles, which are surrounded by a sheet of thinner connective tissue, the perimysium. Each fiber is covered by delicate connective tissue, the endomysium (Wheater *et*

al. 1987). Capillaries lie longitudinally in the endomysium between individual muscle fibers and cross anastomoses are common (Leeson & Leeson 1981).

Skeletal muscle consists of a mixture of fiber types having different contractile and metabolic properties. Muscle fibers can be classified using several factors, e.g. the content of mitochondria, glycogen or fat, or the activity of some enzymes. According to their myosin-ATPase activity, they can be classified to I, IIA and IIB fibers (Brooke & Kaiser 1970). Type I fibers, "red" fibers, are slowly contracting oxidative fibers which are small in diameter (Marinova & Stefanova 1993) with a large number of mitochondria and myoglobin. Type I fibers can maintain contraction longer than type IIB fibers. Type IIB fibers, "white" fibers, are fast contracting glycolytic fibers. They have less mitochondria and myoglobin, but extensive SR and more glycogen (Beecher *et al* 1969, Peachey *et al.* 1983). On the other hand, Essén & Henriksson (1974) did not find a difference in glycogen content between fast twitch and slow switch fibers of man. There are more capillaries around red than white pig muscle fibers (Van Den Hende *et al.* 1972). Type IIA fibers, "intermediate" fibers, are fast contracting, but their energy metabolism is between the two fiber types. Also, a fourth fiber type has been described, type IIC. They are rare and probably in the transition into either type I or II (Lutz *et al.* 1979). In 1929, Denny-Brown noted that red fibers from the cat have more fat than white ones (Dubowitz & Pearse 1960). It is also the same in pig (Beecher *et al.* 1965). It is typical, in the pig, that red fibers are grouped in clumps that are surrounded by white fibers (Van Den Hende *et al.* 1972, Lindholm *et al.* 1979, Seideman *et al.* 1984, Lefaucheur & Vigneron 1986). Red fibers are larger in diameter than the other fiber types in wild pigs (Solomon & West 1985).

During early prenatal development, muscle fibers are produced by hyperplasia. Muscle fibers originate from mesenchymal cells. These cells undergo proliferative and quantal mitosis to yield mononucleated myoblasts. Following quantal mitosis, they fuse with one another to become multinucleated myotubes. Myotubes develop to myofibers and further differentiate to red, white and intermediate fibers, which form muscles (Swatland 1984a). Red fibers usually exist at birth and then can transform to white or intermediate fibers. With aging, there is a rapid loss of oxidative fibers (Van Den Hende *et al.* 1972, Essén-Gustavsson *et al.* 1988a) and an increase of glycolytic fibers (Kiessling *et al. 1982*, Lefaucheur & Vigneron 1986) in the pig LD. Actin and myosin filaments may already be visible in mononucleated myoblasts (Seidemann *et al.* 1984). Neonatal pigs have an exceptionally high glycogen content in their muscles relative to other species (Shelley 1961).

Postnatal development and muscle growth occurs by hypertrophy of existing fibers (Swatland & Cassens 1974, Stickland *et al.* 1975, Seidemann *et al.* 1984). Both the diameter and length of the fiber increases. In rats, fiber length can increase either by the generation of new contractile units or by the fusion of myogenic cells with the existing fibers (Moss & LeBlond 1971). Muscle fiber diameter increases by increasing the number of myofibrils. When myofibrils reach a certain critical size, they split longitudinally (Peachey *et al.* 1983). It has been shown in pigs (Swatland 1984b) and hamsters (Howells & Goldspink 1974) that muscle fibers become increasingly anaerobic when their cross-sectional area increases, and the periphery of the fibers is more oxidative than the axis. The different metabolic characteristics of pig white and red muscles are established by about two weeks of age (Dalrymple *et al.* 1974). Pigs with a high fiber number grow faster than those with low fiber number (Miller *et al.* 1975, Dwyer *et al.* 1993), although opposite results have also found (Ruusunen 1994).

Longissimus dorsi muscle, the loin, whose anterior part is called *longissimus thoracis* and posterior part *longissimus lumborum* (Kauffman *et al.* 1990), is an economically important part of a pig carcass. In pig, 80-90% of LD muscle fibers are type IIB (Essén-Gustavsson *et al.* 1988b, Karlsson *et al.* 1993, Ruusunen 1994). *Longissimus dorsi* has tetanic activity requiring high resting level of ATP and a preference toward anaerobic metabolism (Beecher *et al.* 1969). Leaner pigs have fewer fibers per unit of the whole area of *longissimus dorsi* than obese pigs, but there is no difference in fiber type distribution (Seideman *et al.* 1989).

2.4 Energy metabolism of the skeletal muscle fiber

Muscle fibers need energy for biosynthesis, active transport and contraction. Fibers obtain free energy in a chemical form from the catabolism of nutrient molecules, particularly carbohydrates, fats, and to lesser extent, proteins. Adenosine triphosphate is the link between energy-yielding and energy-requiring reactions (Ganong 1987). When energy is needed, ATP is split to ADP and high-energy phosphate, P_i. Under catabolism of energy-rich fuels ATP is made from ADP and P_i. In normal muscle, the ATP content is much higher than that of ADP and AMP. Adenosine triphosphate and ADP exist largely as MgATP and MgADP complexes (Lehninger 1982, Stryer 1988).

The three main sites of ATP utilization in muscle fibers are myosin ATPase, sarcoplasmic reticulum Ca-ATPase and Na/K-ATPase in plasmalemma (Lehninger 1982). The amount of ATP hydrolyzed during a

muscle contraction may vary depending on the muscle type. Fast-twitch muscle myosin ATPase activity is higher than that of slow-twitch muscle. The actomyosin reaction needs three times as much ATP as Ca-ATPase in the SR to function. The Na ion is moved out of the cell by Na/K-ATPase with one hundredth part of energy needed by Ca-ATPase to pump Ca into SR (Bechtel & Best 1985). Other ATP consumers are, for example, mitochondrial ATPase and phosphorylase b kinase - phosphorylase a phosphatase.

High-energy phosphate is transported between myofibrils and mitochondria, where ATP is localized, by phosphocreatine (Bessman & Geiger 1981). Phosphocreatine is a storage form of high-energy phosphate groups. It keeps ATP concentrations at constant levels. When ATP is used, ADP is formed. Through the action of creatine kinase, phosphocreatine quickly donates its phosphate group to ADP to restore the normal ATP level.

Muscle fiber ATP stores are large enough for only a few seconds of work. Then the fiber uses creatine phosphate stores for ATP resynthesis, which are adequate for only a few more seconds. The main energy stores in fibers are glycogen and lipids. Glycogen forms subcellular particles, "glycogen particles", which contain glycogen and the major enzymes to synthesize and break down glycogen (Bechtel & Best 1985). These enzymes are phosphorylase, phosphorylase kinase and glycogen synthase. Swatland (1975b) states that the high intracellular distribution of glycogen in porcine muscle is due to excessive glycogen synthesis rather than the absence of degradative enzymes. Glycogen is a branched polysaccharide of α-D-glucose units. Glucose is an important fuel of most cells. It can be quickly mobilized from glycogen stores when sudden demands for energy are made. The cell can prepare ATP from glycogen either aerobically or anaerobically. Typical pig muscles have lower glycogen stores than horse or ox muscles (Lawrie 1960). Lipids can be used only aerobically. Aerobic energy production is more efficient in ATP-production than anaerobic. Under normal conditions, all long term energy production occurs aerobically.

Glycolysis is the process by which the glucose molecule is enzymatically degraded in a sequence of 10 catabolic reactions to yield two molecules of pyruvate (Lehninger 1982, Stryer 1988). Pyruvate, the end product of glycolysis, follows different catabolic pathways depending on the metabolic condition of the cell. In aerobic conditions, pyruvate is oxidized to form acetyl-CoA. Then the acetyl group is completely oxidized to CO_2 and H_2O via the citric acid cycle in mitochondria. In anaerobic conditions, pyruvate is reduced to lactate by lactate dehydrogenase. This anaerobic conclusion to glycolysis is an important energy source during intensive physical activity and postmortem. Anaerobic glycolysis yields

two molecules of ATP for each molecule of glucose degraded, whereas complete glucose oxidation produces 38 ATP molecules (Stryer 1988). In figure 2, there is a view of glucose and glycogen conversion to CO_2 and H_2O or lactate. Glycolysis, both aerobic and anaerobic, take place in the sarcoplasm, the citric acid cycle occurs in the mitochondrial matrix (Dubowitz & Pearse 1960) while electron transport and oxidative phosphorylation happen the inner mitochondrial membrane.

The endogenous glycogen is the main energy source for muscular contraction in white muscles (Van Den Hende *et al.* 1972). Type IIB fibers have a low capacity for oxidative metabolism, so they rely mainly on glycogenolysis, creatine phosphate catabolism and ATP for energy production (Essén-Gustavsson *et al.* 1988b). They can function at maximum rates for only short periods of time. In contrast, red muscles are rich in mitochondria, thus they obtain most of their energy by oxidation of their fuels and are capable of sustained activity over longer periods. Fat is the primary fuel for light to moderate (Bechtel & Best 1985) muscular activity, while glycogen is used during a burst of high activity (Dubowitz & Pearse 1960, Pande & Blanchaer 1971). At rest, most muscle energy is derived from free fatty acids (Bechtel & Best 1985, Ganong 1987). Fatty acid composition is independent of muscle metabolic type (Sharma *et al.* 1987).

Small (red) fibers possess a high oxidative enzyme content and large (white) fibers, a high phosphorylase content (Dubowitz & Pearse 1960, Van Den Hende *et al.* 1972). The variation in oxidative enzyme capacity can be due to either mitochondrial number or higher rates of mitochondrial enzyme activity (Dubowitz & Pearse 1960). In pig, the number of mitochondria diminishes with increasing animal weight (Van Den Hende *et al.* 1972, Swatland 1975b). Cattle muscle fibers with a low mitochondrial content are the first to deplete their glycogen during postmortem contraction (Swatland 1975a).

Phosphorylase activity (a+b) increases with the "fast white" character of muscles (Monin *et al.* 1987). The glycolytic potential is related to muscle metabolic type: it is highest in "fast white" muscles. It is higher in Penshire (50% Hampshire, 35% Duroc, 15% Large White) than in Pietrain, Belgian Landrace and Large White LD, *semimembranosus* (SM) and *rectus abdominis* muscles. The activity of citrate synthase is higher in LD and SM of Penshire than in Pietrain, Belgian Landrace and Large White (Monin *et al.* 1987). Pigs fed a high protein diet have a higher glycolytic (higher lactate dehydrogenase activity in LD , *biceps femoris* and *quadriceps femoris*) and a lower oxidative capacity (lower CS activity in *quadriceps femoris*) than pigs fed a low protein diet (Karlsson *et al.* 1993). Myoglobin content of pig LD, SM and *diaphragma* muscles is lower than that of the same muscles in cattle (Hamm & El-Badawi 1991).

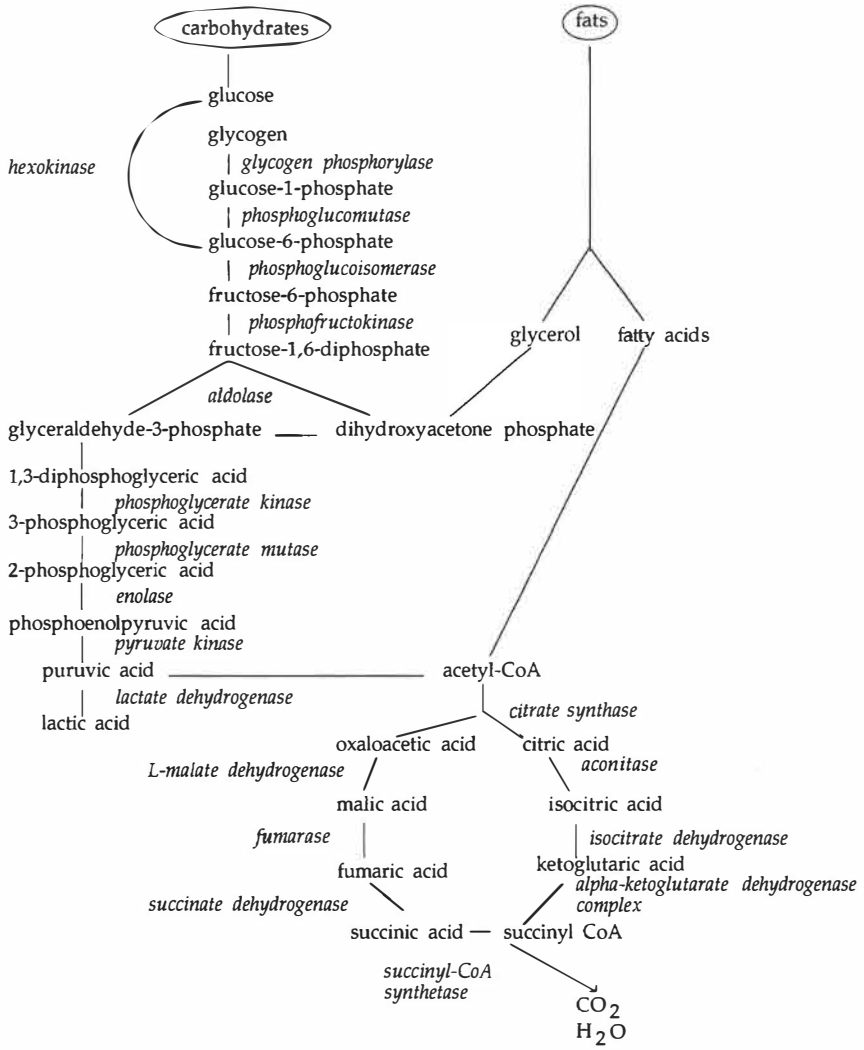

FIGURE 2 Central pathways by which nutrients enter the energy cycles in muscle. In postmortem muscle, glucose can enter the cycle only by breakdown of glycogen. The figure is modified from Lehninger (1982), Greaser (1986) and Stryer (1988).

2.4.1 Regulation of glycolysis

Glycolysis is regulated at the entry of free glucose or glucosyl residues from glycogen and the conversion of glucose-6-phosphate to pyruvate. Pyruvate is then oxidized in the citric acid cycle of the mitochondria. If oxygen is not available, lactate dehydrogenase converts pyruvate to lactic acid. One regulatory point of glycolysis is hexokinase, which phosphorylates free glucose to glucose-6-phosphate. Hexokinase

activation is regulated by the concentration of its product glucose-6-phosphate (Uyeda & Racker 1965).

Another regulatory point is glycogen phosphorylase (PHOS), which cleaves glucosyl residues from glycogen and phosphorylates them to glucose-6-phosphate (Müller 1980). Glycogen phosphorylase occurs in two catalytically different forms, a (active phosphorylated form) and b (less active dephosphorylated form). In resting muscle, PHOS occurs primarily in the b form. It also is mainly in the b form at 10 min postmortem in pig (Sayre *et al.* 1963). In muscle, the ratio of a to b regulates the conversion rate of glycogen to glucose-1-phosphate. Glucose-6-phosphate is an inhibitor of phosphorylase (Kastenscmidt 1970). Phosphorylase a phosphatase converts PHOS a to PHOS b. Phosphorylase b kinase converts PHOS b to PHOS a. The activity of phosphorylase kinase requires calcium. Adrenaline stimulates the activity of phosphorylase kinase. The activity of PHOS is also regulated in another way: the inactive form of PHOS b can be activated by its allosteric modulator AMP, whose concentration increases during ATP breakdown (Kastenschmidt 1970). The active form of PHOS b (AMP bound to it) is inhibited by ATP (Hamm 1977). Adenosine monophosphate does not stimulate PHOS a.

The regulatory points in the reactions from glucose-6-phosphate to pyruvate are phosphofructokinase (PFK) and pyruvate kinase. In skeletal muscle, phosphofructokinase is regulated allosterically by its substrates ATP and fructose-6-phosphate as well as its products ADP and fructose-1,6-diphosphate (Hamm 1977, Kastenschmidt 1970). Also, AMP, Mg^{2+}, phosphate and some other metabolites regulate PFK (Lehninger 1982). Adenosine triphosphate and citrate are the most important in inhibition, while AMP and fructose-1,6-diphosphate are in stimulation. Pyruvate kinase is inhibited by ATP, acetyl-CoA and long-chain fatty acids (Lehninger 1982).

Adenosine monophosphate deaminase, which converts AMP to IMP, is important effector of ultimate pH. It competes for nucleotides, and when AMP is no longer available, glycolysis ceases (Scopes 1974). It has been postulated, that glycolysis ceases because of enzyme denaturation. However, phosphofructokinase is the most sensitive glycolytic enzyme, and it is still active at pH 5.35 at 37°C (Scopes 1974).

Adrenaline injection before slaughter depletes muscle glycogen (Fernandez *et al.* 1992a). This leads to limited glycolysis and high ultimate pH. Adrenaline regulates muscle metabolism by cAMP, which activates glycogen phosphorylase and phosphofructokinase (Hatton *et al.* 1972).

2.4.2 Regulation of citric acid cycle and oxidative phosphorylation

The citric acid cycle is regulated by the formation rate of its fuel acetyl-CoA (Lehninger 1982). Acetyl-CoA is made by pyruvate dehydrogenase using pyruvate or by fatty acid degradation. When the cell does not need more energy, ATP stimulates pyruvate dehydrogenase kinase, which inactivates pyruvate dehydrogenase by phosphorylation. When ATP stores need repletion, pyruvate dehydrogenase phosphate phosphatase dephosphorylates inactive pyruvate dehydrogenase phosphatate to the active form pyruvate dehydrogenase. Free Mg^{2+} stimulates the activation. Pyruvate dehydrogenase complex is strongly inhibited by ATP, acetyl-CoA, fatty acids, and NADH (Lehninger 1982).

The initial steps of the citric acid cycle are rate-limiting (Stryer 1988). In the first reaction of the cycle, citrate synthase converts acetyl-CoA and oxaloacetate to citrate and CoA. The concentration of acetyl-CoA, succinyl-CoA, fatty acids, and especially, oxaloacetate regulate citrate synthase. The citric acid cycle is also regulated by the oxidation of isocitrate to a-ketoglutarate. The reaction is regulated by ADP through a NAD linked enzyme. Citrate synthase is located in the mitochondrial matrix.

Under normal aerobic conditions, neither pyruvate, lactate, nor acetyl CoA accumulate in the cell. Only as much glucose is broken down as is needed in the citric acid cycle.

Oxidative phosphorylation is regulated via ADP concentration. When ADP in cytosol is largely depleted, the rate of oxidative phosphorylation is slowed down. Mitochondrial respiration increases to its maximum rate when the concentration of ADP in cytosol increases. So ATP is formed only as fast as it is used in energy-requiring activities (Stryer 1988).

2.4.3 Lactate dehydrogenase isoenzymes

Lactate dehydrogenase is a cytosolic enzyme which reduces pyruvate to L-lactate. Pyruvate is a junction point in carbohydrate catabolism. Under aerobic conditions, NADH formed by the dehydrogenation of glyceraldehyde 3-phosphate is reoxidized to NAD^+ by O_2. Under anaerobic conditions, NADH must be reoxidized to NAD^+ by pyruvate, converting pyruvate to lactate: pyruvate + NADH + H^+ $\leftrightarrow$ lactate + NAD^+ (Lehninger 1982).

Lactate dehydrogenase occurs in five different isoenzyme forms in most tissues (Markert 1963). They are tetramers composed of two distinct

types of subunits, each having molecular weight of 33,500. The polypeptide chains, M (also designated A) and H (also designated B), are coded by two different genes (Dawson *et al.* 1964). The mixtures of chains in five isoenzymes can be: M_4, M_3H, M_2H_2, MH_3, and H_4 (also designated LDH-5, LDH-4, LDH-3, LDH-2 and LDH-1, respectively). In heart muscle, the predominant isoenzyme contains four H chains and, in skeletal muscle, four M chains (Fieldhouse & Masters 1966). The isoenzymes differ in their Michaelis constant (K_m) values for pyruvate, their maximum activities (V_{max}), and the degree of allosteric inhibition by pyruvate. The heart type isoenzyme (H_4 or LDH-1) has a lower K_m for pyruvate than the muscle type isoenzyme (M_4 or LDH-5) (Dawson *et al.* 1964, Stambauch & Post 1966). Lactate dehydrogenase-1 is strongly inhibited by excess pyruvate. It tends to favor rapid oxidation of lactate to pyruvate in heart muscle. Lactate dehydrogenase-5 is not inhibited by high levels of pyruvate and is more active catalytically. It tends to favor rapid reduction of very low pyruvate concentrations to lactic acid in skeletal muscles. The heterotetramers, in most cases, are intermediates with respect to these characteristics. It has been postulated that pyruvate and L-lactate concentrations do not occur at levels that are needed for substrate inhibition of M or H subunits in skeletal muscle (Stambauch & Post 1966). Citric acid cycle metabolites may activate some isoenzymes of LDH and thereby influence the type and rate of cell metabolism in rabbit (Fritz 1965). Pyruvate produced in red muscles during postmortem glycolysis inhibits lactate production. Also, a portion of pyruvate formed in red muscles can be transported to citric acid cycle (Beecher *et al.* 1965). It is thought that the majority of LDH binds to the myofibrillar structure as a "multi-enzyme complex" consisting of all five isoenzymes (Hamm & El-Badawi 1991).

The extremely high LDH activity of porcine skeletal muscle, as compared to tissues of many other breeds, reflects the high glycolytic rate of that tissue (Hyldgaard-Jensen 1971, Hamm & El-Badawi 1991). Light muscles show higher total LDH activity and proportion of LDH-5 with a lower proportion of isoenzymes 1, 2 and 3 than dark muscles (Beecher *et al.* 1969, Addis & Allen 1970, Cooper *et al.* 1971). So the proportion of the M subunit is higher in white muscles with high anaerobic glycolysis, than in red muscles with high aerobic metabolism in the pig (Dawson *et al.* 1964, Hamm & El-Badawi 1991), sheep (Briand *et al.* 1981) and human (Van Wijhe *et al.* 1964). Results of the determination of LDH isoenzyme distribution in LD muscle varies greatly in different studies (Beecher *et al.* 1969, El-Badawi & Hamm 1969, Hyldgaard-Jensen 1971). In the LD muscle of adult pigs, about 80% of total LDH can be LDH-5 (Addis & Allen 1970, Cooper *et al.* 1971), although as low as 40% LDH-5 has been reported (Hamm & El-Badawi 1991).

All muscle types can oxidize lactate, but oxidative muscle fibers have a greater capacity to convert lactate to pyruvate than glycolytic fibers in rats (Baldwin *et al.* 1978). Lactate oxidation is related to the total amount of LDH-1 isoenzyme.

Because of the different LDH isoenzyme patterns in different tissues, the measurement of serum LDH isoenzymes has been used as diagnostic tool to determine tissue damages. There is increased LDH-5 activity in blood as a result of stress caused by transport, exercise or adrenaline injection (Sybesma & Hessel-de Heer 1967). The total activity of LDH is increased in the blood of PSE pigs, higher LDH-5 and lower LDH-1 activity in the serum of PSE pigs has been found as compared to normal pigs (Merkel 1971). Some studies have not found any change in the distribution of serum LDH isoenzymes of PSE pigs compared to normal pigs (El-Badawi & Hamm 1969). In the blood of stress-sensitive Pietrain pigs, the proportion of muscle type LDH isoenzyme is higher than in blood in stress-resistant Large White (Sybesma & Hessel-de Heer 1967). A high positive correlation has been found between the PSE pig and LDH-5 isoenzyme pattern in serum (Merkel 1971). The proportion of LDH-5 to LDH-1 in serum of pig correlates negatively with pH measured at 45 min postmortem (Addis & Kallweit 1969). The activity of isoenzymes 1, 2 and 3 is lower in exudative than normal pig muscle (Charpentier & Goutefongea 1964).

In the pig, the specific LDH isoenzyme pattern of adult skeletal muscle develops after birth as the total activity of LDH increases. The main isoenzymes in fetuses and young piglets are LDH-1 and LDH-2, while, in slaughter animals, LDH-5 predominates (Fieldhouse & Masters 1966, te Brake 1971, Cooper *et al.* 1971).

The thermal stability of LDH isoenzymes may vary between different isoenzymes depending on storage temperature and tissue treatment. Storage at -20°C, as a whole tissue, preserves the activity of all LDH isoenzymes of human muscle for a few months at least (Zondag 1963, Kelly *et al.* 1967). The same studies reported contradictory results concerning the stability of LDH isoenzymes, especially LDH-4 and LDH-5, in tissue homogenates at the same temperature. Storage of serum at -20°C for one month can cause an increase in LDH-3 (Baustad & Tollersrud 1969). This may be explained by research reporting that freezing and thawing can cause dissociation and recombination of the original isoenzymes (Markert 1963).

2.4.4 The effect of exercise on the skeletal muscle

Physical activity has an effect on muscle characteristics. Currently, pigs do not get much exercise. They are kept in pens, where the room for each pig is less than one square meter (Alaviuhkola *et al.* 1988).

While endurance aerobic training increases the oxidative capacity and intracellular triglyceride storage in human and pig skeletal muscles (Hoppeler *et al.* 1973, Jorgensen & Hyldgaard-Jensen 1975), strength training leads to adaptations in the contractile apparatus and thus, to muscle hypertrophy (Howald 1976). During exercise, lactate is diffused from type IIB fibers to type I and IIA fibers, in which it is used for aerobic energy production (Brooks 1991). In the horse undergoing exercise, lactate also diffuses into the blood cells from the plasma in horse (Pösö & Räsänen 1993).

Endurance training increases the area of oxidative fibers (Lindholm *et al.* 1979), but does not alter the fiber type distribution determined using the myosin-ATPase activity of *biceps femoris, gracilis* (Fitts *et al.* 1973) or LD (Essén-Gustavsson & Jensen-Waern 1993) muscles of the pig. The oxidative capacity of LD (Essén-Gustavsson & Jensen-Waern 1993) and *biceps femoris* (Essén-Gustavsson *et al.* 1988a) muscles increases as a result of moderate exercise, but it has no effect on glycolytic capacity (Essén-Gustavsson & Jensen-Waern 1993). Enfält and co-workers (1993a) did not find any effect of moderate exercise on the oxidative capacity of those muscles. The effect of exercise on muscle biochemical characteristics seems to depend on the muscle studied and exercise intensity. Endurance training increases the H/M subunit ratio of lactate dehydrogenase (Jorgensen & Hyldgaard-Jensen 1975).

Training increases muscle glycogen stores (Essén-Gustavsson *et al.* 1988a), but glycogen utilization during exercise is lower in trained than in untrained pigs, and trained pigs have less slow twitch fibers devoid of glycogen after exercise than untrained pigs (Lindholm *et al.* 1979). Trained pigs have lower blood levels of lactate after exercise (Lindberg *et al.* 1973, Jorgensen & Hyldgaard-Jensen 1975, Persson *et al.* 1979) and at slaughter (Lannek *et al.* 1974) than untrained pigs. It has been shown in rats that endurance training affects lactate clearance, not lactate production (Donovan & Brooks 1983)

Pig production using larger pens has been reported to bring good results. The plasma lactate concentrations decrease in free range pigs at slaughter indicating better tolerance to preslaughter handling than conventionally raised pigs (Essén-Gustavsson & Jensen-Waern 1993). Free range pigs are easier to load (Warriss *et al.* 1983) and calmer in abattoir (Barton-Gade & Blaabjerg 1989) than the conventionally raised pigs. However, Lewis and co-workers (1989) did not find any effect of exercise

on preslaughter stress. Fiber type distribution of *semimembranosus* muscle from pigs who were raised in a large paddock did not differ from that of pigs lived in a little pen (Stecchini *et al.* 1990). The incidence of PSE have been reported to be either lower (Augustini *et al.* 1982, Stecchini *et al.* 1990) or higher (Jones *et al.* 1993) in free range pigs than in conventionally raised pigs. Meat color has been reported to be either paler (Barton-Gade & Blaablerg 1989, Enfält *et al.* 1993b) or darker (Warris *et al.* 1983) and the backfat either thinner (Warris *et al.* 1983, Lewis *et al.* 1989) or equal (Van Der Wal 1991) in pigs allowed to exercise more than commercially raised pigs. Exercise may either decrease tenderness of LD muscle (Lewis *et al.* 1989) or increase it in LD or biceps femoris muscles (Essén-Gustavsson *et al.* 1988a).

2.4.5 Postmortem reactions in the skeletal muscle

Conversion of muscle to meat comprises many metabolic, physical and structural changes. All muscles and muscle parts do not change in an uniform manner. The alteration depends on e.g. the type of muscle fibers and temperature. After death, blood flow ceases which prevents oxygen supply to cells and waste product transportation from cell. The oxygen bound to hemoglobin and myoglobin is rapidly depleted postmortem, probably within 3 min (Bendall 1973b). Postmortem metabolism depends on the concentration of glycogen, high-energy phosphate compounds (like ATP, ADP and CP) and their metabolites. Fatty acids are not used as postmortem energy sources in pigs (Currie & Wolfe 1977). The breakdown of glycogen and high energy phosphate compounds leads to lactate production, which causes a fall in pH from about neutral (pH 7.0) to about pH 5.4 in normal meat.

The rate of postmortem pH decline depends primarily on the levels of glycogen and energy rich phosphate compounds, rate of ATP turnover, buffering capacity of muscle tissue, and halothane sensitivity (Fischer & Augustini 1977, Monin & Sellier 1987, Ouali 1991). Metabolic and contractile properties, breed as well as preslaughter handling are important causes of variation in glycogen content and meat pH_u (Fernandez & Thornberg 1991). The time at which stress occurs before slaughter has an effect on meat quality via pH_1 and pH_u (Fernandez *et al.* 1992a). The central nervous system can also play a role in postmortem pH changes (Swatland & Cassens 1974).

When muscle fibers are completely depleted of ATP and creatine phosphate, they develop a state of extreme rigidity, called rigor. When this occurs after death, the condition is called rigor mortis. It starts in normal pigs 3 to 6 hours postmortem (Briskey *et al.* 1962, Sayre *et al.* 1963).

In PSE pigs, it starts sooner. The onset of rigor mortis depends e.g. on species, type of muscle, holding temperature and extent of struggling. Pig muscles reach rigor mortis sooner than horse or ox muscles (Lawrie 1960). The rigidity occurs because actomyosin is formed: when ATP and CP are no longer available, the myosin heads attach to actin, thus the thick filaments can not slide freely past the thin filaments anymore. The rigor process can be summarized by the following reactions (Bendall 1973b):

$MgATP + H_2O \rightarrow MgADP + P_i + H^+$

$MgADP + CP + H^+ \rightarrow MgATP + creatine$

$3\ MgADP + 3\ H^+ + 3\ P_i + 1\ glucose \rightarrow 3\ MgATP + 2\ lactate + 2\ H^+.$

After the onset of rigor, an increase in free Mg^{2+} is associated with ATP disappearance. The major breakdown process of ATP postmortem is: AMP→IMP→inosine→hypoxanthine (Seewald *et al.* 1993). When CP and glycogen are no longer available, the myokinase reaction (2 ADP ↔ AMP + ATP) and ammonia production by AMP deaminase (AMP ↔ IMP + NH_3) become more important in energy production (Lowenstein 1972). The total adenosine and inosine compounds remain constant postmortem (Tsai *et al.* 1972). Postmortem myokinase reactions and AMP deamination play an important role in ATP production, especially in glycogen depleted fibers. The IMP degradation product, uric acid, gives rise to free radical formation and cellular damage. This can influence meat quality, especially drip loss. Higher ammonia concentration has been found in nn pigs muscles than in NN pigs (Essén- Gustavsson *et al.* 1988b).

In normal pig LD muscle, CP levels drop to zero within 2 to 3 hours postmortem (Kastenschmidt 1970, Sair *et al.* 1970). When beef muscle pH has reached the value of 6.3, about one-eighth of ATP has been catabolized, one-half is depleted by pH 5.9-6.3, and when pH reaches 5.6-5.7, 90% is gone (Bendall *et al.* 1976).

Post morten preservation of enzyme activities primarily depends on temperature, pH and the amount of activators or inhibitors present. Some enzymes, e.g. AMP deaminase and phosphorylase, remain active for days postmortem, while other enzymes, such as LDH and isocitrate dehydrogenase, start to loose their activity within few hours postmortem (Bodwell *et al.* 1965, Tsai *et al.* 1972, Fischer *et al.* 1979). Creatine kinase is the most sensitive enzyme (Greaser 1986). On the other hand, it is concluded that the limiting factor in postmortem muscle metabolism is the lack of adequate substrates (Bodwell *et al.* 1965) because this lack of substrates for ATP synthesis is the rate limiting factor in resting mitochondria from living muscle (Bechtel & Best 1985).

The ability of SR to accumulate Ca^{2+} decreases postmortem. Free Ca^{2+} in sarcoplasm increases, although Ca-Mg-ATPase in SR is able to maintain a very low sarcoplasmic free Ca^{2+} concentration throughout most of the period of ATP decline in mouse (Jeacocke 1993). Greaser and

co-workers (1969a) found that the calcium-accumulating capacity declined by about 40% in the first 3 hours and by 80% at 24 hours postmortem. Swelling of SR is often apparent within 1 hr postmortem in bovine muscle (Will *et al.* 1980). Mitochondria show swelling within few hours postmortem in pigs (Cassens *et al.* 1963).

Ultimate pH not only depends on glycolytic potential, but also on the degree of transformation of this potential into lactic acid and the buffering capacity of the muscle (Sellier *et al.* 1988). In white muscles from a rested well fed animal, glycolysis stops before all glycogen has been converted to lactic acid. This limit on glycolysis occurs around pH 5.4-5.5 in pig white muscles (Monin *et al.* 1987). Talmant and co-workers (1989) did not find any difference in ultimate pH between gilts and boars. Many authors (e.g. Shorthose *et al.* 1984, Lundström *et al.* 1987) have found a higher pH_u in boars than gilts and castrates, but this could be due to the more aggressive behavior in boars before slaughter (Fernandez & Thornberg 1991). Slaughter weight does not influence pH_u (Evans *et al.* 1978). Lactate is not wholly responsible for ultimate pH (Hatton *et al.* 1972), also the amount of glucose-6-phosphate and breakdown of ATP, which releases H^+ ions during the ATPase reaction, has an effect on pH_u.

Muscle buffering capacity depends on phosphate compounds having pK values between 6.1-7.1, on creatine phosphate, on dipeptides carnosine and anserine, and on histidylimidazole residues of myofibrillar proteins (Honikel & Hamm 1974). White muscle (*longissimus dorsi*) buffering capacity in swine is higher than that of red (*triceps brachii*), although the difference is small (Kivikari 1995). Rao & Gault (1989) found the same also between white and red muscles in beef using several different muscles, but Kivikari did not found any differences in beef LD and *triceps brachii* muscles. There is no difference in buffering capacity between Hampshire, Large White, HN and HP Pietrain (Monin & Sellier 1985) nor between normal and PSE prone pigs (Bendall *et al.* 1963).

Fasting time has an influence on muscle glycogen level and ultimate pH. Fasted pigs with higher ultimate pH have lower liver and muscle (*adductor*) glycogen levels than unfasted pigs. However, other factors (e.g. exercise) than fasting time can be more important to glycogen levels (Warris *et al.* 1989). If stress is kept minimal during loading and unloading, and pigs are not hungry or mixed with unfamiliar animals, there are no differences in glycolytic potential measured from biopsies taken before and after transportation (Fernandez *et al.* 1992b).

If muscle oxidative capacity or its ability to produce energy by oxidizing fuels is low, the muscle has to make energy antemortem by lactate production, so muscle lactate concentration can already be high at slaughter (Klont 1994). Poor capillarisation of muscle and, hence, weak lactate clearance confirm this. Fast glycolytic muscles, which are muscles

with high glycolytic capacity, can be in an oxygen-deficient state prior to death (Kastenschmidt *et al.* 1968). High lactate and low ATP levels in muscles at the time of exsanguination support this hypothesis. Blood lactate level at exsanguination is higher in pigs having more slow glycolytic muscles than pigs having more fast glycolytic muscles. This can be due to the lower ability of fast glycolytic muscles to remove lactate from muscles. Stress and excitement prior exsanguination may stimulate glycolysis, and at exsanguination, porcine muscles tend to have lower pH values than most other mammalian muscles (Beecher *et al.* 1969). There are lower initial pH and glycogen levels in the light part of *semitendinosus* muscle compared to the dark area of it, indicating faster glycogen breakdown in light portion (Beecher *et al.* 1965). The initial lactic acid content does not vary, but lactic acid production is more rapid for 30 minutes postmortem in light parts. The glycogen breakdown is similar in both muscles for at least three hours postmortem.

It has been shown that there is no glycogen left in type I and IIA fibers at slaughter, whereas type IIB fibers have some glycogen still remaining (Essén-Gustavsson *et al.* 1992). In stress-susceptible nn genotype pigs, there are more glycogen depleted fibers than in NN genotype fibers (Essén-Gustavsson *et al.* 1988b). Lower glycogen levels have been found in type I fibers than in type II immediately after slaughter (Lefaucheur *et al.* 1992, Karlsson 1993).

2.5 Meat quality

Meat quality is a very broad concept. On the other hand, quality means much the same as goodness (quality meat), yet much the same as condition (meat quality) (Hofmann 1993). Goodness is a subjective value. Instead, condition is always measured objectively. Hofmann (1990) describes meat quality as "the sum of all sensory, nutritional, hygienic, toxicological and technological properties of meat". Also, animal quality has a great importance on meat quality. So genetic and metabolic factors of meat animals as well as ethical and ecological evaluations can be included in meat quality. If the muscle does not function properly, it produces poor meat.

Sensory quality includes e.g. taste, appearance and texture. Nutritional quality consists of chemical composition and physiological value. Hygienic and toxicological quality consist e.g. of microbes, residues like antibiotics, hormones and toxic heavy metals. Technological quality consists e.g. of drip loss, amount of connective tissue and fat, meat color

as well as pH value. Ethical quality refers to the well-being of animals during breeding and proper handling at the slaughter.

2.5.1 Sensory quality

The sensory quality of food consists of three properties: appearance (shape, size, color etc.), flavor (the combination of taste and odour) and texture (e.g. tenderness and juiciness) (Fjelkner-Modig 1985). The palatability of meat is influenced by animal genetic factors and treatments before, during and after slaughter. The stress caused by exercise is associated to poor meat quality (Sybesma & Hessel-de Heer 1967).

Marbling has a great influence on sensory quality. Muscle quality is negatively correlated with lean content and backfat thickness (Hovenier *et al.* 1992). The effect of intramuscular fat on palatability is the most pronounced at fat levels below 2.5% (Kirkegaard *et al.* 1979). The most tender meat occurs in the pH_1 range 6.1 to 6.5 and above 2% total lipid (Barton-Gade *et al.* 1987). About 2% intramuscular fat is needed for good sensory quality, but excessive amounts like 3% do not lead to any further improvements (Bejerholm & Barton-Gade 1986). On the other hand, consumers may adapt to the taste of low-fat meat (Mela 1990). Feeding level and diet ingredients have also an effect on sensory quality of meat. Feeding at a high level increases fat deposition and improves tenderness (Wood 1993). Fatty acids from fish in pig diets can reduce meat flavor (Jul & Zeuthen 1980).

The relationship between ultimate pH and tenderness is complex and still far from understood. It is widely believed that beef meat with a high pH_u is very tender (Purchas 1990, Jeremiah *et al.* 1991). Tenderness attained its highest value when glycolysis proceeds at an intermediate rate in beef (Smulders *et al.* 1990). Animal age, fiber diameter, intracellular fat and connective tissue also have an effect on tenderness (Herring *et al.* 1965, Fjelkner-Modig 1985, Ouali 1991). During aging, proteolytic proteases are involved in the tenderizing process (Ouali 1991). The most important of them are the lysosomal enzymes cathepsins D, B, H and L (Greaser 1986) and cytosolic calcium-dependent calpains and their regulating factors (Ouali & Talmant 1990). Both pig and beef muscles with a high proportion of type IIB fibers are more tender than muscles with high proportion of type I fibers (Totland *et al.* 1988, Karlsson *et al.* 1993), although the opposite is also reported in beef (Calkins *et al.* 1981). Muscle oxidative capacity may have an influence on the tenderness of meat (Essén-Gustavsson & Fjelkner-Modig 1985) and also, in beef, on marbling (Calkins *et al.* 1981).

Red meat has been considered to have more flavor than white meat (Ouali 1991). It has been shown, in lambs, that the slow red muscle fiber type indicates better flavor and meat juiciness, but is not directly related to the amount of fat of the carcass (Valin *et al.* 1982). The level of free amino acids and dipeptides (especially glutamine, taurine, carnosine and anserine) are also important to meat flavor. Pigs, which are leaner and have less backfat, have paler pork (McGloughlin *et al.* 1987). Kangasniemi (1993) has compared LD of Finnish Landrace, Yorkshire, Hampshire and Duroc cross (50% Duroc): Landrace LD was the lightest and most yellow, Hampshire LD the darkest and reddest, while the Yorkshire LD was the least red.

Parallel reports have been published about the effect of water holding capacity on juiciness. Water distribution in meat is an important factor in the sensory properties of pork (Fjelkner-Modig 1985). The high LDH activity is associated with exudate meat (Sybesma & Hessel-de Heer 1967).

Growing interest has been shown in use of noncastrated male pigs in meat production instead of castrates. Intact males grow faster, are leaner, more efficient and ethically more advisable than castrates. However, the palatability of intact males can be poorer because of abnormal odor and flavor caused by androsterone, skatole and other compounds (Rodbotten *et al.* 1990).

The eating quality of the three way cross (H x (Swedish Landrace x Yorkshire)) is better than that of the two breed cross (Swedish Landrace or Yorkshire x (Swedish Landrace x Yorkshire)) (Fjelkner-Modig 1985). Hampshire *longissimus dorsi* is more tender and juicy than that from Swedish Landrace and Swedish Yorkshire. *Longissimus dorsi* from Yorkshire is the least tender and juicy. At least in Swedish Landrace and Swedish Yorkshire, higher intramuscular lipid content would improve the sensory properties of meat.

2.5.2 Pale, soft and exudative (PSE), and dark, firm and dry (DFD) meat

Pale, soft and exudative (PSE) meat is, perhaps, a typical quality problem in pork. This condition in swine was first described by Ludwigsen in 1954 (Bendall *et al.* 1963). Bendall and co-workers (1963) observed two pig groups which differed from each other by the rate of pH decline. Carcasses which exhibit rapid pH decline have poorer meat quality than carcasses with a slow decrease in pH. In PSE meat, the pH value decreases more rapidly than in normal muscle postmortem, causing protein denaturation (Lawrie 1960, Enfält *et al.* 1993a). Muscles with PSE have a

high glycogen content immediately before slaughter as well as very efficient glycogenolysis and anaerobic glycolysis (Severini *et al.* 1990). Rapid breakdown of ATP and glycogen leads to lactic acid formation, and pH decreases, i.e. below value 5.8 in 30-45 min after death when carcass temperature is still high (Honikel & Kim 1986). Usually, the lower the pH_1 value, the larger the drip loss is. In normal muscle, pH decreases from approximately neutral (range 6.9-7.3) to values between 5.3 and 5.8 at 24 hours postmortem (Briskey & Wismer-Pedersen 1961). The higher the pH_u is (as long as it do not reach DFD value 6.1), the better the technological quality of the pork (Warriss & Brown 1987). High residual glycogen content may decrease meat technological value by increasing cooking loss (Fernandez *et al.* 1991). Consumers prefer, as a sign of good meat quality, dark meat color and pleasant flavor as well as a tender and juicy structure. According to Ruusunen (1994) arguments for good meat quality (concerned *longissimus dorsi*) are high pH_1 value, large loin area, high pH_{24} value (not higher than 6.1), low drip loss, dark and red color, pleasant flavor, tender and juicy structure as well as high intramuscular fat content. Arguments for good *longissimus dorsi* muscle quality are high percentage of type I and IIA fibers, high pecentage of oxidative type IIB fibers and their small cross sectional area as well as high number of capillaries (Ruusunen 1994).

Genetic factors, i.e. porcine stress syndrome or malignant hyperthermia, or poor handling of pigs before slaughter can lead to PSE meat. Calcium uptake of sarcoplasmic reticulum decreases and morphological changes are more rapid in PSE muscle than in normal muscle (Greaser 1986). If the sarcoplasmic Ca^{2+} concentration is not lowered by SR, this Ca^{2+} increase activates muscle contraction. This requires energy which is derived from both aerobic and anaerobic metabolism. The elevated Ca^{2+} level, will also activate phosphorylase kinase, resulting in an increase in glycogen breakdown (Louis *et al.* 1993). Cheah and co-workers (1994) found high correlations between Ca^{2+} accumulation by SR and pH_1 (r_g +0.663) and drip loss (r_g -0.777), respectively, in postmortem LD muscle. *Longissimus dorsi* from stress-susceptible pigs shows major ultrastructural changes immediately after stunning (Bergmann 1979). They consist of sarcoplasmic edema, glycogen loss, SR disruption, mitochondrial lysis and destruction of myofibrils. In PSE myofibrils at 24 hr postmortem, the width of Z lines has increased and the filaments appear granular when compared to normal myofibrills. Immediately after death, the mitochondria of PSE muscle are swollen and have decreased matrix density. The mitochondrial capacity for ATP synthesis is decreased in the muscles of stress-susceptible pigs (Eikelenboom & van den Bergh 1971). On the other hand, Cheah (1973) did not find any major biochemical differences in LD mitochondria from

stress-susceptible and stress-resistant pigs postmortem. Sarcoplasmic reticulum from PSE muscle shows a higher level of granular material after death (Greaser *et al.* 1969b). Large highly glycolytic fibers contribute to the severity of PSE (Merkel 1971, Sair *et al.* 1972).

The muscle metabolic defect associated with porcine halothane sensivity (also known as malignant hyperthermia, MH) can lead to PSE meat. Malignant hyperthermia is an inherited myopathy, which can be triggered by stress. Malignant hyperthermia causes abnormal regulation of the calcium concentration in muscle fibers. This depends on the hypersensitive gating of the Ca^{2+}-release channel (ryanodine receptor) on the SR (O'Brien 1987): channel opening is facilitated and closing is inhibited. The porcine MH (hal) locus has been localized in pigs to chromosome 6p11-q21 (Harbitz *et al.* 1990). A single point mutation leads to an alteration in amino acid sequence from an arginine at position 615 in the MH negative animal to a cysteine in the MH sensitive animal (Fujii *et al.* 1991). Ryanodine receptor mutation is responsible for the defective skeletal muscle Ca^{2+} regulation that is the cause of porcine MH (Shomer *et al.* 1993). This disorder parallels malignant hyperthermia in humans (MacLennan *et al.* 1990, McCarthy *et al.* 1990). There is some evidence that MH and PSE might not have the same origin. It has been shown that exercise, in pigs, causes a higher stimulation of glycogenolysis than halothane exposure (Heinze & Mitchell 1991). This may be due to a different mechanism of activation.

Stress sensitive pigs can be picked out by a halothane test: pigs are anaesthetized by 3% halothane gas for few minutes. The halothane-positive (HP or nn) pig has a strong muscle cramp, whereas a halothane-negative (HN or NN) pig sleeps calmly and has flabby muscles (Veijonen 1984). A small percentage of false halothane-negative pigs still occur as a result of the test (Gallant & Rempel 1987). Pigs carrying the halothane gene are more stress-susceptible and have a higher incidence of PSE meat than pigs without this gene. Parallel reports of the effect of halothane sensitivity on ultimate pH has been published. The pH_u is either lower (Monin & Sellier 1985, Pommier & Houde 1993) or has no effect (Renou *et al.* 1985, Monin & Sellier 1987, Lundström *et al.* 1989) on the LD from halothane-positive pigs as compared to negative animals. The pH decline in the LD from HP Pietrain is faster than in HN Pietrain for at least one hour postmortem (Renou *et al.* 1985). Breakdown of glycogen to lactate is higher in HP pigs than in HN pigs (Klont *et al.* 1993). There is only a slight difference in mitochondrial function between stress-resistant and stress-susceptible pigs (Brooks & Cassens 1973). Preslaughter glycolysis is more marked in nn and nN pigs than in NN pigs, while heterozygotes have poorer meat quality than NN pigs (Lundström *et al.* 1989). Halothane sensitivity correlates with increased drip loss (Monin & Sellier 1987).

Homozygous halothane-negative loins have darker meat and reduced free water than nN- or nn-loins (Pommier & Houde 1993).

Muscle glycogen level *in vivo* can be a more reliable predictor of PSE predisposition than halothane sensivity since the rapid pH decline after slaughter in PSE pigs may already be initiated *in vivo* (Henckel *et al.* 1992). It has been shown that muscles from PSE pigs already have a lower pH at exsanguination (Sjöblom & Lundström 1989, Enfält *et al.* 1993a). However, Kocwin-Podsiadla and co-workers (1995) have shown that the halothane genotype do not affect *in vivo* glycogen level of LD muscle, although it affects the lactate content of biopsy samples. Diffusion properties play important role in development of PSE meat. If muscle pH from stress-susceptible animals decreases before slaughter, fiber diameter and muscle blood circulation have an important role in removal of lactic acid and protons. Halothane sensitive animals have larger type IIB fibers and lower capillary densities than nonsensitive ones, so lactate diffusion into blood can be limited in stress-susceptible pigs (Essén-Gustavsson *et al.* 1988b). It has been shown that PSE muscle fibers have fewer capillaries than normal muscles (Merkel 1971). Lactate accumulates in fibers, pH decreases, myokinase and adenylate deaminase are activated, and ammonia is formed. This causes membrane damage which results in high drip loss (Honikel & Kim 1986). Using ^{31}P NMR, it has been shown that halothane-positive pigs have lower CP levels a few minutes into the slaughter process than halothane-negative animals, also ATP levels decrease more rapidly in halothane-positive than negative pigs (Lahucky *et al. 1993*).

Many explanations have been given on the enormous ATP breakdown in PSE meat, the ATP breakdown may be caused by circulation of fructose-6-phosphate via fructose-1,6-phosphate, or contraction and glycogenolysis caused by the increased $[Ca^{2+}]$ in the sarcoplasm (Honikel & Kim 1986). Schwägele and co-workers (1994) have found increased pyruvate kinase activity in the muscles of PSE pigs compared to normal pigs. Muscle fibers of PSE meat lose their ability to contract early in the postmortem state (Honikel & Kim 1986), so energy is not used to contraction. In contrast, in *longissimus dorsi* from NN genotype pigs immediately after exsanguination, the sarcomeres are longer than in nn genotype pigs (Essén-Gustavsson et al. 1992).

There is a tendency ($p<0.10$) towards higher lactate dehydrogenase and lower phosphorylase a+b activities in halothane-positive compared with halothane-negative Pietrain and Belgian Landrace pigs (Sellier *et al. 1988*). Instead, the activity of PHOS a is higher in LD of HP Pietrain than HN Pietrain, Hampshire and Large White (Monin *et al.* 1986). Lopez Buesa and co-workers (1993) and Schwägele and co-workers (1994) did not find any difference in the activity of PHOS between PSE and normal meat.

Neither breed nor halothane sensitivity had any influence on muscle glycolytic potential in *semimembranosus, rectus abdominis,* and *masseter* muscles. (Sellier *et al.* 1988). Halothane sensitivity has no influence on glycolytic potential (Monin & Sellier 1985).

Highest incidence of extreme reactions (death of animals during stressful events) is found in breeds like Pietrain, Poland China, Belgian Landrace and certain other Landrace types (Lister 1993).

Incidence of dark, firm and dry (DFD) pork is less common than the incidence of PSE pork. Dark, firm and dry meat is primarily found in beef. Muscles, which develop DFD meat, are glycogen depleted already before slaughter. So they do not have any substrates for the postmortem glycolysis, thus the ultimate pH stays higher than normal. DFD meat is more susceptible to bacterial spoilage. The absence of glucose in DFD meat allows the spoilage microflora to form odorous compounds earlier in the spoilage process (Lawrie 1985). Exhaustive stress, like fighting or starvation before slaughter, can lead to DFD meat. DFD meat is darker than normal meat (Chen *et al.* 1993).

When comparing normal, PSE and DFD prone pigs using a ^{31}NMR spectrum obtained around 30 min postmortem, muscles with a low rate of metabolism show high pH and ATP with low P_i, muscles with a fast rate of metabolism have low pH and ATP with high phosphomonoester, muscles with high ultimate pH exhibit high pH and P_i with low phosphomonoesters (Miri *et al.* 1992).

2.6 Properties of different pig breeds

2.6.1 Finnish Landrace and Finnish Yorkshire

The traditional pig breeds in Finland are Landrace and Yorkshire (Maijala 1969). The Landrace breed stems from traditional domestic swine. Earlier this century, imports from Sweden and Norway were brought to improve Finnish Landrace. Finnish Yorkshire stems from imports from England, Denmark and Sweden during the first decades of this century. Voluminous research has been done to improve the production capacity of those breeds, but there is only limited information available on the muscle quality of those breeds.

Landrace and Yorkshire give lean carcasses. The intramuscular fat of Finnish Landrace x Yorkshire crosses is nutritionally better than that of Duroc x Landrace x Yorkshire, due to better fatty acid profile, i.e. L x Y has less saturated and more polyunsaturated fatty acids (Honkavaara 1989). Also, British Landrace has less saturated and more polyunsaturated

fatty acids than pure Duroc (Cameron & Enser 1991). The opposite is noted in back fat. The backfat thickness is smaller and LD lipid content lower in L x Large White than in Duroc and Hampshire (Warriss *et al.* 1990).

The LD of Finnish Landrace is lighter and redder than that of Finnish Yorkshire, but less red than that of Hampshire or Duroc x (Landrace or Yorkshire). *Longissimus dorsi* from Finnish Landrace and Yorkshire is lighter than Hampshire, while the Finnish Yorkshire LD is lighter than D x (L or Y) (Kangasniemi 1993). The fiber type distribution of the LD from Finnish Landrace and Yorkshire is quite glycolytic (Ruusunen 1989). Swedish Landrace has a lower glycolytic and lactate forming capacity but more glycogen than Swedish Yorkshire in LD muscle (Essén-Gustavsson & Fjelkner-Modig 1985).

2.6.2 Hampshire

Hampshire muscles typically have a high glycogen content (as far as fast-white muscles are concerned), low lactate production after slaughter and low ultimate pH compared to many other breeds (Sayre *et al.* 1963: Hampshire vs. Chester White and Poland China, Hedrick *et al.* 1968: Hampshire vs. Duroc, Monin & Sellier 1985: Hampshire vs. Large White and Pietrain, Monin *et al.* 1987: Penshire vs. Large White, Pietrain and Belgian Landrace, Barton-Gade 1988: Hampshire vs. Danish Landrace, Large white and Duroc, Krieter *et al.* 1990: Hampshire or Hampshire x Pietrain vs. Large White and Pietrain), although the ultimate pH of LD from Hampshire, Swedish Landrace and Yorkshire do not differ (Essén-Gustavsson & Fjelkner-Modig 1985). The low ultimate pH of Hampshire muscles is not associated with high lactate content or low buffering capacity, but it can be due to high glycolytic potential and high glucose-6-phosphate content (Hatton *et al.* 1972, Wax *et al.* 1975, Monin & Sellier 1985). The postmortem pH fall in Hampshire muscle takes place at a normal rate, similar to that observed in Large Whites (Monin & Sellier 1985). The high glycogen content of LD from Hampshire and Hampshire cross pigs is expressed more in glycolytic than oxidative fibers (Marinova *et al.* 1992). Hampshire pigs have high oxidative capacity, low LDH activity, high glycogen and triglyceride levels when compared with Swedish Landrace and Yorkshire (Essén-Gustavsson & Fjelkner-Modig 1985). The activity of CS is higher in Hampshire than in Large White or HP and HN Pietrain, while the activity of LDH is lower in Hampshire than in Large White (Monin *et al.* 1986). The glycolytic potential of Hampshire is higher compared to many other breeds (Krieter *et al.* 1990), but muscle lactate production in Hampshire is not higher.

High muscle glycogen content is attributed to the dominant RN- gene (Fernandez & Thornberg 1991, Fernandez *et al.* 1992d, Estrade *et al.* 1993). The activity of glycogen synthetase is higher in Hampshire than in Pietrain or Large White (Monin *et al.* 1986). Meat from Hampshire and halothane-positive Pietrains is technologically poorer than meat of Large Whites and halothane-negative Pietrains (Monin & Sellier 1985). It is concluded that poor meat quality is caused by a fast postmortem pH drop in HP Pietrains, whereas, in Hampshire, it is caused by low ultimate pH. Hampshire meat low ultimate pH is probably related to high muscle glycogen content.

Hampshire pigs have more marbling than Large White, HP or HN Pietrains (Monin *et al.* 1986), but there are no differences between Hampshire and Duroc Jersey in LD intracellular fat (Garcia *et al.* 1968). Many authors have found that Hampshire meat is paler and/or wetter than other breeds (Hedrick *et al.* 1968, Monin & Sellier 1985). The meat of Hampshire is more tender than meat from Swedish Landrace and Yorkshire (Essén-Gustavsson & Fjelkner-Modig 1985).

2.6.3 Duroc

The Duroc breed has been developed in the USA. Meat from Duroc and its crosses have high concentration of marbling fat (Barton-Gade 1988, Gu *et al.* 1992). As high as 5.5% of marbling has been reported in Duroc (Kirkegaard *et al.* 1979). The Duroc LD has more intramuscular fat than that from Hampshire (Hedrick *et al.* 1968, Wax *et al.* 1975, Warriss *et al.* 1990), British Landrace (Wood 1988, Cameron *et al.* 1990), or Large White (Wax *et al.* 1975, Wood 1988). Duroc has less (Hedrick *et al.* 1968, Warriss *et al.* 1990) or equal backfat than Hampshire, but more than Yorkshire (Wax et al. 1975). Duroc x (Irish Landrace x Large White) has more intramuscular and less subcutaneous fat than Irish Landrace and Large White crosses, but the LD of that Duroc cross is paler (McGloughlin *et al.* 1988). Duroc LD is darker, redder, less moist, more juicy, less tender and has poorer flavor than LD of British Landrace (Cameron *et al.* 1990). However, Wood (1988) did not find any difference in palatability between Duroc and British Landrace or Large White. Carcass length is shorter in Duroc than in Landrace (Wood 1988), but equal in Duroc, Hampshire and Yorkshire (Wax *et al.* 1975).

Landrace has higher incidence of PSE and DFD meat than Duroc or Hampshire (Barton-Gade 1988). Duroc has a slight PSE condition compared to Yorkshire (Allen *et al.* 1966). Crosses between Landrace and Large White are best for processing, while Hampshire and, especially, Duroc crosses for fresh meat consumption (Barton-Gade 1988). Duroc LD

has more glycogen, but lower pH_{24} value, fiber diameter, color, myoglobin concentration and percent moisture than Yorkshire (Allen *et al.* 1966).

3 AIMS OF THE STUDY

This study is part of a research project in our laboratory which has studied the relationships between muscle histology, physiology and pork quality. It has been suggested that pig breeding has led to more glycolytic muscle fibers in pigs since efficiency and rapid growth rates have been favored. Energy production by anaerobic glycolysis, particularly if it starts already before slaughter, may decrease meat quality by lowering meat pH value too fast. So, high muscle oxidative capacity and lactate clearance antemortem may have an influence to meat quality. Calcium accumulation in the sarcoplasma may activate glycogenolysis and fiber contraction, which increase lactate production also postmortem. Transportation to slaughterhouse and slaughter are very stressful events to pigs, and stress accelerates glycolysis and thus impairs meat sensory and technological quality.

The purpose of this study was to find out if there is any variation in oxidative and glycolytic capacity of muscle fibers as well as in calcium release and uptake of sarcoplasmic reticulum and mitochondria of muscle fibers and lastly, if this variation has some connection with meat pH values, sensory quality, meat color and drip loss between traditional Finnish pig breeds, Landrace and Yorkshire, and new breeds in Finland which are pure Hampshire and crossbred Hampshire or Duroc x (Landrace x Yorkshire).

4 MATERIALS AND METHODS

4.1 Animals

Breeds of the animals used in this experiment were Finnish Landrace (L), Finnish Yorkshire (Y), Hampshire (H), three-way crosses: Hampshire x (Yorkshire x Landrace) (HYL), Duroc x (Yorkshire x Landrace) (DYL), Landrace x (Yorkshire x Landrace) (LYL) and Yorkshire x (Yorkshire x Landrace) (YYL). Forefathers of Hampshires and Durocs were from Sweden. All L and all Y, except two, lived at test stations. All LYL, YYL and DYL lived on farms. Pure Hampshires and Duroc crosses lived either at test stations or farms (see Table 1). Because the pigs lived at different places, some variation may have occurred in management and feeding of these animals.

The pigs were carefully chosen. The purpose was to make sure that pigs were genetically different. As many different sires as possible were used. Artificial insemination boars as sires were favored, though farm boars were also used. Pigs from the same litter were avoided. Usually, there were more suitable pigs at the slaughterhouse than we could take, so pigs were chosen randomly. In Hampshires and Duroc crosses, these principles were impossible to fulfill, so sisters had to be used as well. Also, in other breeds, we used some sisters, though this was accidental. Two LYL and one HYL had the same dam. One L, LYL, Y, YYL and six H, HYL had the same sires. There were both castrates and gilts among pigs which were chosen (see Table 1).

In table 2, the age, live and carcass weights as well as daily weight gain of the pigs are presented. Table 3 contains the quality classes of

carcasses from the different breeds. They are based on Hennessy grading system (Hennessy GP_4, New Zealand) which was used in the abattoirs at Forssa and Nurmo, while intrascope measurements were used in the other abattoirs. With Hennessy meter, measures are done at two places. The first measuring place is behind the last rib 8 cm lateral to the midline. This fat thickness measure is the same as the measure with intrascope. The other Hennessy measure, fat thickness and muscle depth, is taken 12 cm below the first measuring place, between the third and fourth ribs and 6 cm lateral to the midline. From these values computer then calculates the carcass lean meat per cent. Table 4 shows the LD fiber type distribution in different breeds and crosses.

TABLE 1 Background data of pigs.

Breed (n)	Castrated males	Gilts	Sires[1]	Sows[1]	Litters	Pigs at test stations (number of test stations)	Pigs at farms (number of farms)
L (59)	26	33	44	52	52	59 (4)	-
Y (57[2])	26	29	44	53	53	55 (4)	2 (1)
H (52)	19	33	12	15	21	25 (1)	27 (1)
LYL (19)	8	11	11	15	15	-	19 (4)
YYL (33)	18	15	13	24	24	-	33 (4)
HYL (52)	24	28	14	49	49	-	52 (4)
DYL (52)	20	32	4	13	14	7 (1)	45 (2)

[1] Number of parents of the pigs in the study.
[2] The sex of two Y pigs was unknown.

TABLE 2 Means of age, live weight, carcass weight, and daily weight gain of the different breeds and sexes at slaughter. Mean values in the same column (between breeds or sexes) bearing the same superscript are statistically different, abcd=p<0.05, fghi=p<0.01, klmnoqrstu=p<0.001. Values are ± SD.

	Age, days (n)	Live weight, kg (n)	Carcass weight, kg (n)	Daily weight gain, g/day (n)
L	149±8^{fklmno} (59)	97.3±5.0^{cl} (59)	71.2±4.0^{fklmn} (59)	920±73^{hilno} (59)
Y	155±7^{fgqrst} (55)	97.1±3.8^{abk} (55)	71.7±3.2^{aoqrs} (56)	910±78^{afgkm} (55)
H	161±10^{gku} (50)	98.6±3.8^{f} (25)	74.5±6.0^{aft} (49)	837±85^{fo} (25)
LYL	165±9^{lq} (19)	101.4±5.2^{bc} (19)	77.4±4.2^{ko} (19)	840±66^{ai} (19)
YYL	164±8^{mr} (33)	100.3±6.5^{a} (33)	76.8±5.9^{lq} (33)	837±77^{mn} (33)
HYL	164±8^{ans} (52)	99.7±4.4^{d} (52)	76.5±3.9^{mr} (52)	829±68^{kl} (52)
DYL	169±10^{aotu} (52)	102.8±5.5^{dfkl} (51)	78.7±5.3^{nst} (51)	856±83^{gh} (51)
Castrated males	157.8±10.8^{k} (141)	99.3±5.1 (129)	74.6±5.7 (139)	895.4±87.1^{k} (129)
Gilts	161.9±10.5^{k} (180)	99.4±20.1 (164)	75.1±5.5 (180)	849.0±76.4^{k} (165)

TABLE 3 Number of carcasses belonging to different quality classes.

Breed/Quality class	E+[1]	E[1]	1[1]	1R[1]	Unknown
L	42	11	3	-	3
Y	36	9	4	-	8
H	21	10	18	-	3
LYL	6	4	9	-	-
YYL	12	9	10	1	1
HYL	15	25	11	-	1
DYL	12	11	8	-	21
Castrated males	43	40	41	1	16
Gilts	101	39	22	-	19

[1] E+ is the best quality class, then comes E, then 1 and the worst is 1R.

TABLE 4 Fiber type distribution (%) of LD from different breeds and crosses (data from Ruusunen 1994, based on method from Brooke & Kaiser 1970). Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., abc=p<0.05, fg=p<0.01, klmnoq=p<0.001. Values are ± SD.

Breed (n)	Type I	Type IIA	Type IIB
L (54)	13.2 ± 3.7^{bl}	9.0 ± 3.8	77.9 ± 3.9^{fgk}
Y (55)	9.9 ± 3.8^{afkl}	8.6 ± 3.1^{a}	81.6 ± 3.8^{cklm}
H (52)	15.2 ± 3.9^{ckmn}	9.4 ± 2.7	75.3 ± 3.1^{afmoq}
LYL (19)	12.9 ± 4.5^{a}	8.4 ± 2.9	78.8 ± 3.7^{a}
YYL (33)	10.7 ± 3.6^{bm}	8.1 ± 2.5^{f}	81.2 ± 4.0^{gno}
HYL (52)	11.6 ± 3.4^{n}	9.3 ± 2.5	79.2 ± 3.4^{bcq}
DYL (52)	12.7 ± 3.4^{cf}	10.5 ± 2.8^{af}	76.8 ± 3.8^{bln}

4.2 Slaughtering of the pigs

Pigs were slaughtered in five abattoirs: in LSO Food, Forssa, in Turun Vientiteurastamo, Turku, in Osuuskunta Pohjanmaan Liha, Vaasa, in Itikka Lihapolar, Nurmo, and in the slaughterhouse at the University of Helsinki/Department of Food Technology, Meat Section (Table 5). In all abattoirs, pigs were stunned with carbon dioxide, except in Helsinki, where they were stunned with electricity. Before slaughter, pigs were allowed to rest overnight in the abattoir, except HYL, LYL and YYL, which rested about four hours.

TABLE 5 Number of pigs slaughtered in different abattoirs.

Breed/Abattoir	Forssa	Turku	Vaasa	Nurmo	Helsinki
L	59	-	-	-	-
Y	55	-	-	-	2
H	25	-	15	12	-
LYL	19	-	-	-	-
YYL	33	-	-	-	-
HYL	52	-	-	-	-
DYL	7	45	-	-	-

4.3 pH values

pH values indirectly indicate how much lactate there is in muscle, and what the degree of postmortem reactions is. pH was measured once from each carcass at 45 min and about 24 hours after stunning using Knick Portames 752 pH-meter, Germany, equipped with Ingold Xerolyt Lot 406-M6 electrode, Switzerland. Measurements were made in *longissimus dorsi* near the place where samples for biochemical analyses were taken.

4.4 Biochemical methods

About 50 g muscle samples from *longissimus dorsi* were taken at the level of the 13th and 14th ribs on the right side of the carcass. They were quickly prepared 15 min (calcium metabolism) or 45 min (calcium metabolism and other methods) after stunning. For calcium metabolism studies, samples were cut into small pieces, put in buffer A (10 mM Hepes, 0.2 mM $CaCl_2$, pH 7.5) and kept on ice until fractionation occured a few hours later. For other studies, samples were frozen in liquid nitrogen and kept at -80° C until analyzed, usually within few months.

The homogenates for protein and enzyme assays were made with a Thomas Scientific tissue grinder, USA, using Teflon pestles (protein and enzyme assays in 50 mM Tris-HCl buffer, pH 7.6; LDH isoenzymes in 100 mM Tris-HCl , 0.9% NaCl, pH 8.0). The homogenates for membrane preparations were made with Ultra-Turrax homogenizer, Janke & Kunkel, Germany. For lactate and glycogen assays, samples were homogenized in liquid nitrogen with a Waring Blender homogenizer, USA.

Enzyme activity and the amount of metabolites from energy metabolism were assayed spectrophotometrically using Perkin Elmer Lambda 2 spectrophotometry, Germany, or LKB Novaspec-spectrophotometry, England, respectively. The enzyme analyses provide a measure of glycogen phosphorylation (glycogen phosphorylase), glycolytic capacity (lactate dehydrogenase), oxidative capacity (citrate synthase), and lipid oxidation (3-hydroxyacyl-CoA-dehydrogenase) in the *longissimus dorsi*. Lactate dehydrogenase isoenzymes were examined with Ultroscan XL -densitometry using Gel Scan^{TM} XL Software, Pharmacia LKB Biotechnology, Sweden. The details of the enzyme, metabolite and protein assays are summarized in Table 6.

Glycolytic potential (GP, μmol lactate equivalent/g muscle) was calculated according to formula proposed by Monin & Sellier (1985): GP = 2([glycogen] + [glucose] + [glucose-6-phosphate]) + [lactate]. In our

method, the concentrations of glucose and glucose-6-phosphate were not determined separately, but together. Glycolytic potential is the main compounds which produce lactic acid postmortem.

TABLE 6 The list of variables and certain aspects of methods used in various biochemical studies.

Variable	E.C. number	Substrate	Method
3-hydroxyacyl-CoA-dehydrogenase	1.1.1.35	Acetoacetyl-CoA (Sigma)	Gottesmann & Hamm 1986
Citrate synthase	4.1.3.7	Acetyl-CoA (Sigma)	Srere 1969
Glycogen phosphorylase	2.4.1.1	Glycogen (Sigma)	Bass et al. 1969
Lactate dehydrogenase	1.1.1.27	Pyruvate (Boehringer Mannheim)	Boehringer Mannheim, Kit Cat. No. 191 353
Lactate dehydrogenase isoenzymes		Lactate (Sigma)	Sigma, Kit Cat. No. 705-A
Lactate			Boehringer Mannheim, Kit Cat. No. 139 084
Glycogen, glucose, glucose-6-phosphate			Boehringer Mannheim, Kit Cat. No. 207 748
Protein			Peterson 1977

Calcium concentration in sarcoplasma regulates muscle contraction and glycogenolysis. To measure calcium release and uptake, the sarcoplasmic reticular and mitochondrial fractions were isolated using a Sorvall RC2-B, USA and Beckman L8-70M Ultracentrifuge, USA adapted to Klip & Walker (1983). Purity of the fractions were checked by measuring the activity of citrate synthase.

Calcium uptake of the fractions was measured using the ^{45}Ca method as described by Condrescu and co-workers (1987), and calcium release of the fractions using the ^{45}Ca method as described by Michelson and co-workers (1987). In both methods, a Millipore filtration technique was used, and the radioactivity of the filter was measured using a scintillation counter, either Rackbeta 1215, Wallac, Finland or Wallac 1411, Finland. Preliminary tests were made to determine the time which is needed to saturate SR and MIT fractions with calcium (data not shown). It took about one hour to saturate the fractions with calcium. After two hours, no more calcium was released. Calcium uptake was determined after 2 min incubation (at which point the rate of calcium accumulation is

still linear). For calcium release determination, the fractions were loaded for 20 min with ^{45}Ca. Calcium release was measured after a 20 min incubation.

Results of the parallel analysis of enzymes and lactic acid were tested with analysis of nested (SAS Institute Inc. 1989), using breed and the above mentioned parallel analysis of every sample as classes to determine variation dependent on the methods used. Enzyme variation was between 2.9-5.7%. Lactic acid variation was 3.3%.

4.5 Microscope methods

For electron microscopy, muscle samples from *longissimus dorsi,* at the level of 13th-14th ribs, were taken about 15 min after stunning, cut into small pieces and fixed in a formaldehyde (4%) and glutaraldehyde (1%) combination in a phosphate buffer as recommended by McDowell & Trump (1976), and stored at +4° C for one week to two months. Prolonged storage over 12 months in 4CF-1G does not affect tissue ultrastructure (McDowell & Trump 1976). The samples were post-fixed with osmium tetraoxide, stained with uranyl acetate and embedded in Epon. Thin sections were cut with diamond knives, stained with lead citrate and uranyl acetate, then examined with Jeol JEM-1200EX transmission electron microscope, Japan. To calculate the volume density of mitochondria and the amount of sarcoplasmic reticulum, 10 photographs were taken from each sample. They were taken randomly from longitudinal sections. Photographs were examined by an image analysis system using the computer program CUE 2 planomorphometry made by Olympus, Germany. The amount of SR was evaluated by numerical density of profiles on area.

4.6 Sensory analysis, color measurements, and drip loss

Sensory analysis as well as meat color and drip loss measurements were made at the Finnish Meat Research Centre, Hämeenlinna.

Meat color of *longissimus dorsi* muscle was measured in both places with Minolta CR-200 -meter, Minolta Camera Co., Japan. Fifteen minutes after the muscle sample was dissected from the pig carcass, an oxygen permeable plastic folio was put on the cut surface and the meat piece was put into a refrigerator. The color was measured after 60 minutes from

three different parts of the cut loin surface. The color values were expressed as a mean of these three measurements.

There were six trained members in the sensory analysis panel. Flavor, tenderness and juiciness were judged on a 7-point scale, where 1= weak flavor, very tough and dry, and 7= strong flavor, very tender and very juicy. The frozen muscle samples were melted for 20 to 24 h at 6 °C. The samples were cut from them just before defrosting into 2 cm thick pieces (their temperature was at that moment 0.5-2.0 °C) and baked as long as the inner temperature of samples was 68 °C.

Drip loss was measured as described by Kauffman and co-workers (1986). Samples for those analysis were taken a day after slaughter from *longissimus dorsi* between 8th and 11th ribs. One drip loss analysis was made on each sample.

4.7 Statistical methods

Three parallel analyses of the same sample were made for calcium uptake and release, two were taken for enzyme, protein, and metabolite measurements. A standard distribution test was made from the results, and the outliers were checked.

Values were expressed as mean±SD (standard deviation). All analysis were made using the Statistical Analysis System (SAS-program). Means, standard deviations, Pearson's partial correlations, and analysis of covariance, discriminant (Ranta *et al.* 1992) and nested (SAS Institute Inc. 1989) were determined. The significance of the variation between breeds or between samples taken different times postmortem for calcium uptake and release determinations was assessed using the analysis of variance. Tukey's test (Ranta *et al.* 1992) or Student's t-test was used to locate the differences. All analysis except nested were made using means of parallel analysis.

Means of pH values were calculated using hydrogen ion concentration, instead of direct pH values, in accordance with Leistner (1973) and Hofmann (1987).

5 RESULTS

5.1 pH values

pH values were measured at 45 min (pH_1) and about 24 hours (pH_{24}) after stunning. Measurements were made in *longissimus dorsi* at the last rib, near the place where samples for biochemical analyses were taken. There was no correlation between these two pH values. pH_1 was lower in LYL than in Yorkshire ($p<0.05$), Hampshire ($p<0.01$), YYL ($p<0.05$) or HYL ($p<0.01$). Between other breeds, there were no differences in pH_1 (Table 7).

pH_{24} was lower in Hampshire than in Landrace ($p<0.001$), Yorkshire ($p<0.01$), LYL ($p<0.05$), YYL ($p<0.001$), and DYL ($p<0.01$). It was also lower in HYL than in Landrace ($p<0.05$), Yorkshire ($p<0.05$), YYL ($p<0.001$), and DYL ($p<0.01$). Low pH_{24} is typical for Hampshire and its crosses.

Among the pigs in this study, there were six (1.9%) PSE pigs ($pH_1<5.8$). There was one in the L, Y, YYL, DYL groups and two among LYL pigs. On the average, the incidence of PSE may be over 10% in Finland (Honkavaara 1989). No DFD pigs ($pH_{24}\geq6.0$) were observed.

The average pH_1 of Hampshire pigs slaughtered in Forssa was higher than in pigs slaughtered in Vaasa ($p<0.01$) or in Nurmo ($p<0.001$) (Table 8). There were no other differences in pH values between pigs slaughtered in different abattoirs.

In winter, slaughtered pigs had the lowest pH_1 and the highest pH_{24} (Table 9).

TABLE 7 Means of pH values from different pig breeds at 45 min (pH_1) and 24 hours (pH_{24}) after stunning. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., abc=p<0.05, fg=p<0.01, klmn=p<0.001. Values are ± SD.

Breed	pH_1 (n)	pH_{24} (n)
L	6.22±0.24 (55)	5.49 ± 0.10^{bk} (59)
Y	6.31 ± 0.25^{b} (55)	5.49 ± 0.13^{cf} (57)
H	6.33 ± 0.17^{f} (49)	5.41 ± 0.09^{afklm} (44)
LYL	6.10 ± 0.32^{abfg} (19)	5.49 ± 0.12^{a} (18)
YYL	6.29 ± 0.24^{a} (33)	5.56 ± 0.16^{mn} (33)
HYL	6.36 ± 0.19^{g} (52)	5.43 ± 0.08^{bcgn} (46)
DYL	6.25±0.25 (52)	5.50 ± 0.08^{lg} (48)

TABLE 8 Means of pH values from Hampshire pigs slaughtered in different abattoirs at 45 min after stunning. Mean values bearing the same superscript are statistically different, f=p<0.01, k=p<0.001. Values are ± SD.

Abattoir	pH_1 (n)
Forssa	6.47 ± 0.16^{fk} (22)
Vaasa	6.32 ± 0.15^{f} (15)
Nurmo	6.23 ± 0.10^{k} (12)

TABLE 9 Means of pH values from pigs slaughtered in different seasons at 45 min (pH_1) and 24 hours (pH_{24}) after stunning. Mean values in the same column bearing the same superscript are statistically different, a=p<0.05, f=p<0.01. Values are ± SD.

Season	pH_1 (n)	pH_{24} (n)
Summer	6.35±0.26 (93)	5.47 ± 0.09^{f} (84)
Autumn	6.44 ± 0.19^{af} (58)	5.45 ± 0.09^{a} (55)
Winter	6.31 ± 0.24^{f} (97)	5.52 ± 0.11^{af} (97)
Spring	6.33±0.22 (67)	5.48±0.12 (67)

5.2 Enzyme activities

The differences in biochemical characteristics show metabolic heterogeneity within the species. Hampshire LD was the most oxidative muscle and YYL LD was the most glycolytic muscle (see Figure 3). There were some differences in enzyme activities among the breeds when pigs were raised at different places (Tables 11, 12 and 13).

The activity of glycogen phosphorylase was higher in YYL than in Landrace (p<0.01), Yorkshire (p<0.001), and DYL (p<0.01) (Table 10). It was also higher in Hampshire than Yorkshire (p<0.05). There were no differences between L, Y, HYL, or DYL. The total activity of PHOS has been reported to be higher in Hampshire than in Chester White and Poland China (Sayre *et al.* 1963), but similar to that in Large White or

Pietrain (Monin *et al.* 1986). The total phosphorylase activity as well as forms a and b is five times higher between pH 5.5 and 6.1 than above 6.1 (Schwägele & Honikel 1988). Among our samples, there were 52 specimens in which the pH was in the range 5.5-6.1 at sampling for the PHOS measurements. The activity of PHOS in these specimens did not differ from those whose pH was above 6.1.

The activity of LDH was the highest in DYL and the lowest in Hampshire. It was higher in DYL than in Landrace ($p<0.05$), Hampshire ($p<0.001$), LYL ($p<0.001$) or HYL ($p<0.001$). It was lower in Hampshire than in Landrace ($p<0.01$), Yorkshire ($p<0.001$), YYL ($p<0.001$) and as previously mentioned, in DYL ($p<0.001$). It was higher in YYL than in LYL ($p<0.05$) or HYL ($p<0.01$), and lower in HYL than in Landrace ($p<0.05$) or Yorkshire ($p<0.001$). The activity was higher in Landrace than in LYL ($p<0.001$). There were no differences between Landrace and Yorkshire, between Yorkshire and DYL, and between Hampshire and HYL. The Hampshire crosses had lower LDH activity than Yorkshire and Landrace, but similar oxidative enzyme activities. The Duroc crosses also had similar oxidative enzyme activities as Yorkshire and Landrace, but higher LDH activity than Landrace. Low LDH activity is typical for Hampshire (Fjelkner-Modig 1985). HYL pigs seemed to inherit this property. The activity of LDH was higher ($p<0.05$) in gilts than in castrated males (Table 14).

The values of LDH activity were little lower and the values of CS activity at the same level as in the study of Oksbjerg and co-workers (1995; crosses of Danish Yorkshire and Danish Landrace). The activities of CS and HADH were at the same level as in studies of Essén-Gustavsson and co-workers (1988a; crosses of Swedish Landrace and Yorkshire) and Enfält and co-workers (1993b; crosses of Hampshire, Swedish Landrace and Swedish Yorkshire), and little higher than the HADH value in studies of Kiessling & Hansson (1983; cross pigs) as well as Oksbjerg and co-workers (1995; crosses of Danish Yorkshire and Danish Landrace). The activities of HADH and CS were higher in Hampshire than in all other breeds ($p<0.001$ and $p<0.01$, respectively). There were no other differences in activity of HADH between breeds, except it was higher in HYL than in YYL ($p<0.05$). The activity of CS was lower in YYL than in Landrace ($p<0.01$), Yorkshire ($p<0.01$), the previously mentioned Hampshire ($p<0.01$), HYL ($p<0.001$), and DYL ($p<0.01$). *Longissimus dorsi* of Hampshire pigs is typically more oxidative, i.e. activities of HADH and CS are higher, than in many other breeds (Fjelkner-Modig 1985).

TABLE 10 The activity of PHOS, LDH, HADH and CS (U/g muscle) in different breeds. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., abc=p<0.05, fg=p<0.01, klmnogrs=p<0.001. Values are ± SD. PHOS=glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH =lactate dehydrogenase; CS=citrate synthase.

Breed (n)	PHOS	LDH	HADH	CS
L (59)	21.5±3.5^{l}	2334±346^{bcf}	8.66±1.65^{k}	6.55±1.27^{ks}
Y (57)	21.0±3.0^{ak}	2508±432^{knq}	8.24±1.34^{l}	6.04±1.21^{fo}
H (50)	23.7±5.0^{a}	2055±281^{fklm}	11.23±2.24^{klmnoq}	8.27±1.84^{lnoqrs}
LYL (19)	22.0±4.6	2097±295^{ano}	7.68±1.30^{m}	5.80±1.16^{n}
YYL (33)	25.9±6.4^{fkl}	2419±369^{agl}	7.80±1.58^{an}	4.98±1.09^{fgklm}
HYL (52)	23.3±6.0	2100±444^{bgqr}	8.96±1.93^{ao}	6.36±1.49^{mr}
DYL (52)	22.1±5.1^{f}	2568±285^{cmor}	8.14±1.50^{q}	6.09±1.26^{gq}

TABLE 11 The activity of PHOS (U/g muscle) and the amount of lactic acid (µmol/g muscle) in Landrace and Yorkshire pigs raised at different farms or test stations. Mean values in the same row bearing the same superscript are statistically different, no superscript means n.s., ab=p<0.05, f=p<0.01. Values are ± SD. PHOS=glycogen phosphorylase; LACT=lactic acid.

Breed	Enzyme or metabolite	Farm or test station Hyvinkää (n)	Tampere (n)	Panelia (n)	Paimio (n)	unknown (n)
L	PHOS	23.2±3.3^{f} (21)	19.7±3.5^{f} (20)	21.8±3.5 (7)	21.2±2.5 (11)	-
Y	PHOS	21.7±1.8^{b} (14)	19.8±1.7 (8)	22.0±2.3^{a} (14)	20.8±3.6 (19)	15.1±6.6^{ab} (2)
Y	LACT	38.4±10.0 (12)	43.6±20.7 (7)	37.2±11.6^{a} (14)	45.5±15.2 (19)	72.9^{a} (1)

TABLE 12 The activity of PHOS, HADH, CS and LDH (U/g muscle) in HYL, LYL and YYL pigs raised at different farms. Mean values in the same row bearing the same superscript are statistically different, no superscript means n.s., a=p<0.05. Values are ± SD. PHOS=glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH =lactate dehydrogenase; CS=citrate synthase.

Breed	Enzyme	Farm Takala (n)	Hakanpää (n)	Uusi-Kraapo (n)	Mäkelä (n)
HYL	PHOS	22.3±6.7 (24)	20.7±5.0^{a} (12)	27.2±3.6^{a} (12)	25.9±3.3 (4)
HYL	HADH	9.22±1.89 (24)	7.63±1.82^{a} (12)	9.88±1.81^{a} (12)	8.66±0.96 (4)
LYL	CS	4.99±0.69^{a} (8)	6.02±1.25 (5)	7.55±0.95^{a} (2)	6.28±0.62 (4)
YYL	LDH	2619±340^{a} (16)	2171±366^{a} (7)	2278±263 (9)	2245 (1)

TABLE 13 The activity of PHOS, HADH, CS and LDH (U/g muscle) and the amount of lactic acid (μmol/g muscle) in DYL pigs raised at different farms or test stations. Mean values in the same row bearing the same superscript are statistically different, no superscript means n.s., ab=p<0.05, fg=p<0.01, kl=p<0.001. Values are ± SD. PHOS =glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH=lactate dehydrogenase; CS=citrate synthase; LACT=lactic acid.

Breed	Enzyme or metabolite	Test station or farm Panelia (n)	Farm 1 (n)	Farm 2 (n)
DYL	PHOS	28.8±3.4^{fk} (7)	23.4±3.5^{fg} (21)	19.1±4.3^{gk} (24)
DYL	HADH	7.70±0.87^{a} (7)	9.20±1.20^{ak} (21)	7.35±1.34^{k} (24)
DYL	CS	7.66±0.73^{ak} (7)	6.58±1.02^{al} (21)	5.20±0.81^{kl} (24)
DYL	LDH	2253±143^{l} (7)	2462±194^{k} (21)	2753±258^{kl} (24)
DYL	LACT	45.7±5.5 (7)	52.8±14.0^{k} (21)	36.1±8.0^{k} (24)

TABLE 14 The activity of LDH (U/g muscle) of male and gilt pigs. Mean values bearing the same superscript are statistically different, a=p<0.05. Values are ± SD. LDH=lactate dehydrogenase.

Sex	LDH (n)
Castrated males	2253±405^{a} (141)
Gilts	2359±407^{a} (178)

5.3 Lactate dehydrogenase isoenzymes

The LDH isoenzyme content was calculated as the per cent of each isoenzyme band density to the total density of all bands (Table 15). The activity of different lactate dehydrogenase isoenzymes was measured as a percentage of the total activity (Table 16).

The main findings from LDH isoenzyme measurements were that the proportions of LDH-1 and LDH-2 were higher and the proportion of LDH-5 lower (all at least at the level of p<0.05) in Hampshire or Duroc crosses than in nearly all other breeds or crosses (Table 15). Hampshire and DYL did not differ from each other in proportion of isoenzymes. However, the activities of LDH-1 and LDH-2 were higher (p<0.001) in Duroc crosses than in Hampshire and all other breeds or crosses (Table 16). The activity of LDH-5 in Hampshire was lower than that in Duroc crosses (p<0.01) and in many other breeds or crosses (p<0.001). This indicates that Duroc crosses, which have high total LDH activity, may have more efficient lactate clearance prior to slaughter than other breeds due to lactate oxidation. Postmortem, the exceptional isoenzyme

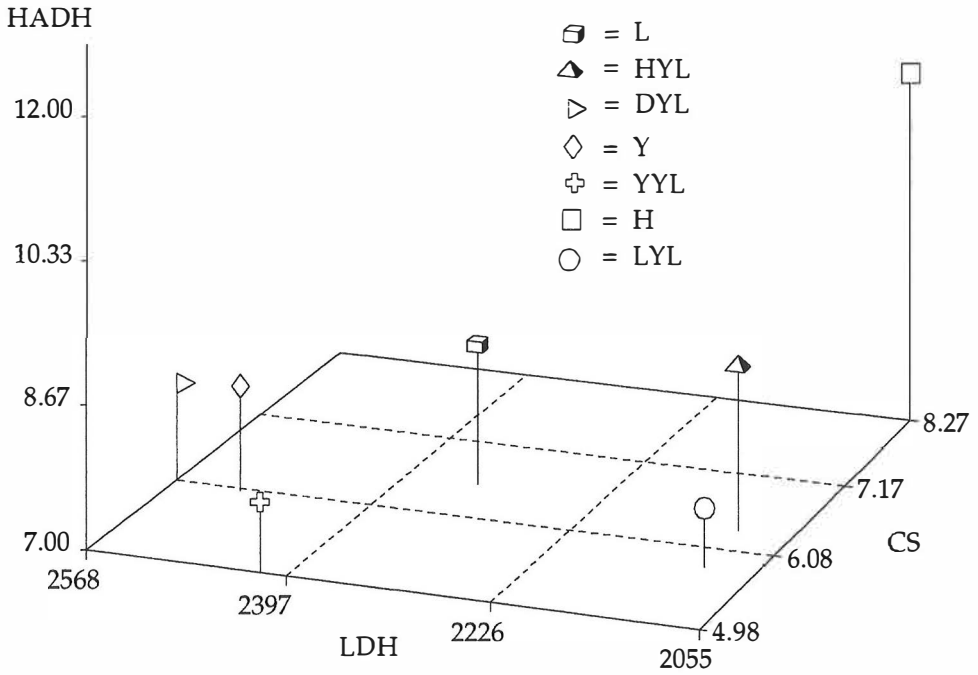

FIGURE 3 The summary of the enzyme data in different pig breeds (means are in U/g muscle). HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH= lactate dehydrogenase; CS=citrate synthase.

distribution of Duroc crosses does not decrease their lactate production compared to other breeds, as may be the case in Hampshire pigs. Landrace and Yorkshire pigs did not differ from each other in the distribution or activity of LDH isoenzymes, except the proportion of LDH-1 was higher ($p<0.05$) in Landrace than in Yorkshire.

The summary of LDH isoenzymes is presented in Figure 4.

TABLE 15 Lactate dehydrogenase (LDH) isoenzymes as percentage of total LDH in different breeds. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., abc= $p<0.05$, fgh=$p<0.01$, klmnoqr=$p<0.001$. Values are ± SD.

Breed (n)	LDH-1	LDH-2	LDH-3	LDH-4	LDH-5
L (44)	7.6±2.3^{ag}	8.5±1.5^{br}	11.4±2.2	21.0±3.4	51.5±6.3^{a}
Y (42)	6.0±2.4^{akl}	7.7±2.0^{lm}	11.1±2.4^{ab}	21.4±4.0	53.8±7.4^{kl}
H (43)	9.1±2.7^{flnr}	9.8±2.4^{abfgm}	12.9±2.7^{a}	20.5±3.7	47.8±7.0^{bcdl}
LYL (14)	6.2±2.6^{fo}	7.5±2.5^{fk}	10.8±2.4	21.4±3.0	54.1±5.9^{bf}
YYL (29)	6.2±2.0^{mn}	8.0±1.4^{go}	12.1±2.5	21.2±4.3	52.5±7.7^{dh}
HYL (40)	6.8±2.3^{qr}	8.3±1.8^{aq}	11.4±2.4	20.9±3.2	52.6±5.9^{cg}
DYL (42)	9.5±2.6^{gkmoq}	10.3±2.4^{kloqr}	12.9±2.7^{b}	20.4±3.4	46.9±6.1^{afghk}

TABLE 16 The activity of lactate dehydrogenase (LDH) isoenzymes in different breeds (U/g muscle). Mean values in the same column bearing a same superscript are statistically different, no superscript means n.s., abc=p<0.05, fgh=p<0.01, klmnoq=p<0.001. Values are ± SD.

Breed (n)	LDH-1	LDH-2	LDH-3	LDH-4	LDH-5
L (44)	181 ± 65^{o}	202 ± 53^{q}	270 ± 70^{g}	490 ± 87^{a}	1214 ± 260^{m}
Y (42)	150 ± 66^{n}	190 ± 61^{m}	275 ± 75^{h}	530 ± 133^{gk}	1336 ± 330^{gk}
H (43)	185 ± 61^{aq}	201 ± 59^{o}	263 ± 71^{m}	417 ± 87^{afkl}	978 ± 210^{fklm}
LYL (14)	124 ± 56^{ak}	152 ± 53^{k}	216 ± 49^{fk}	435 ± 81	1111 ± 245
YYL (29)	150 ± 50^{m}	196 ± 43^{n}	298 ± 75^{af}	522 ± 127^{cf}	1294 ± 285^{l}
HYL (40)	145 ± 65^{l}	177 ± 59^{l}	239 ± 69^{al}	442 ± 120^{bcg}	1108 ± 261^{g}
DYL (42)	241 ± 63^{klmnoq}	262 ± 57^{klmnoq}	330 ± 75^{ghklm}	526 ± 113^{bl}	1206 ± 210^{f}

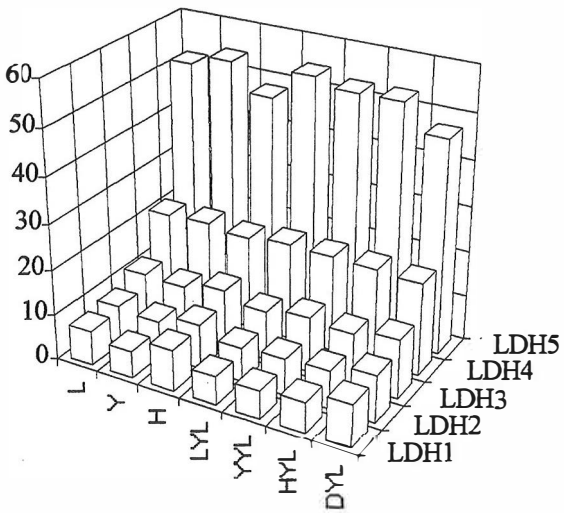

FIGURE 4 Relative proportions of lactate dehydrogenase (LDH) isoenzymes in different breeds (%).

5.4 Glycogen and lactate content

The glycogen and lactate contents as well as glycolytic potential of LD were measured from samples taken 45 min after stunning. Although the LD of Hampshire has the highest amount of glycogen and highest value of glycolytic potential, it has the lowest amount of lactate at the same time. This is typical for fast white muscles as LD from Hampshire pigs (Monin & Sellier 1985, Barton-Gade 1988). Lactate dehydrogenase-5 is a key enzyme for the conversion of pyruvate to lactate in postmortem muscle. The proportion and the activity of that isoenzyme was lower in Hampshire than in nearly all other groups. The isoenzyme distribution may have some connection to low trend of lactate content in Hampshire.

The activities of LDH-1 and LDH-2 in Duroc was higher than in other groups. So antemortem, lactate clearance by lactate conversion back to pyruvate may play a role in lactate content of Duroc crosses, which is similar to that in the other groups, although the total activity of lactate dehydrogenase was higher in Duroc crosses.

In the Hampshire LD, there was more glycogen than in Landrace ($p<0.01$), Yorkshire ($p<0.001$), LYL ($p<0.01$), YYL ($p<0.01$), and DYL ($p<0.001$) (Table 17). The HYL LD had more glycogen than DYL ($p<0.01$). Lactic acid content was higher in LYL than in Hampshire ($p<0.01$) and HYL ($p<0.05$). LD of Landrace and Yorkshire had similar glycogen and lactate content. Glycogen and lactate levels did not correlate with each other. The glycogen content in pigs used in this study was lower than measured by Honkavaara (1989) 45 min postmortem in LD of pigs having different halothane genotypes. Those pigs were Finnish Landrace, Finnish Yorkshire or their crosses.

The glycolytic potential was higher in Hampshire than in Landrace ($p<0.01$), Yorkshire ($p<0.01$), YYL ($p<0.01$), and DYL ($p<0.001$) (Table 17).

TABLE 17 The amount of glycogen (µmol/g muscle), lactic acid (µmol/g muscle) and the glycolytic potential (µmol lactate equivalent/g muscle) from different breeds. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., a=$p<0.05$, fghi=$p<0.01$, kl=$p<0.001$. Values are ± SD.

Breed	Glycogen (n)	Lactic acid[1] (n)	Lactic acid[2] (n)	Glycolytic potential
L	11.1 ± 5.2^{i} (15)	44.5±13.0 (15)	44.1±14.8 (54)	73 ± 18^{f} (15)
Y	9.3 ± 4.6^{l} (15)	42.3±16.8 (15)	42.1±14.9 (53)	69 ± 14^{l} (15)
H	21.8 ± 11.2^{ghkli} (15)	37.2 ± 8.7^{a} (15)	37.3 ± 9.7^{f} (50)	105 ± 26^{fgkl} (15)
LYL	7.5 ± 6.6^{g} (6)	60.8 ± 22.7^{ab} (6)	51.4 ± 19.7^{af} (19)	84±21 (6)
YYL	10.5 ± 9.4^{h} (9)	39.8±22.1 (8)	41.7±15.3 (32)	67 ± 32^{g} (9)
HYL	16.3 ± 7.5^{f} (15)	38.7 ± 9.5^{b} (15)	39.0 ± 11.5^{a} (52)	83±20 (15)
DYL	5.6 ± 5.7^{fk} (15)	46.5±11.2 (15)	44.1±13.1 (52)	70 ± 16^{k} (15)

[1]Same pigs as in glycogen measurements.
[2]All possible pigs are included.

5.5 The volume density of mitochondria and the number of sarcoplasmic reticulum

The Hampshire mitochondrial volume density was higher than that of YYL ($p<0.05$) (Table 18). Although there was no other statistically significant differences between groups, there was a clear trend toward higher V_{vmit} in Hampshire than the other breeds or crosses. This is in agreement with the higher CS and HADH activities in Hampshire than in the other groups. Mitochondria take part in oxidative metabolism by offering a place for the citric acid cycle and fatty acid oxidation to occur. Thus, CS and HADH are mitochondrial enzymes. There were no differences in the amount of SR in different breeds. The sarcoplasmic reticulum is an intracellular store of calcium.

TABLE 18 The volume density of mitochondria (V_{vmit}) as percentage of cell volume (%) and the amount of sarcoplasmic reticulum (SR) as numerical density of profiles on area (numbers/μm^2) in *longissimus dorsi* from different breeds. Mean values in the same column bearing a same superscript are statistically different, no superscript means n.s., a=$p<0.05$. Values are ± SD.

Breed (n)	SR	V_{vmit}
L (11)	1.2±0.4	1.90±1.17
Y (11)	1.2±0.2	1.98±1.58
H (11)	1.2±0.2	2.91±1.73[a]
LYL (4)	1.1±0.2	0.88±0.28
YYL (8)	1.4±0.2	0.91±0.54[a]
HYL (12)	1.1±0.2	2.27±1.09
DYL (12)	1.3±0.2	1.85±0.80

5.6 Calcium uptake and release

To check the purity of SR and MIT fractions, CS activity was measured in all samples. Cross contamination between the fractions was about 20 per cent, as calculated on the basis of the results of the CS assay (Table 19). The cross contamination was quite high, although it was lower than the cross contamination in the report of Klip and Walker (1983), in which they published the fractionation method used in this study. Also, a few EM photographs were taken of the fractions; they showed some impurities (data not shown).

TABLE 19 The activity of CSSP (U/mg protein) in SR and MIT fractions. Mean values bearing the same superscript are statistically different, a=p<0.05, klmn=p<0.001. Values are ± SD. CSSP=specific activity of citrate synthate; SR15=sarcoplasmic reticular fraction, samples taken 15 min after stunning; SR45=sarcoplasmic reticular fraction, samples taken 45 min after stunning; M15=mitochondrial fraction, samples taken 15 min after stunning; M45=mitochondrial fraction, samples taken 45 min after stunning.

Fraction	CSSP (n)
SR15	0.02 ± 0.01^{kl} (63)
SR45	0.02 ± 0.02^{mn} (62)
M15	0.11 ± 0.05^{akm} (61)
M45	0.09 ± 0.03^{aln} (64)

In the calcium uptake and release work, there was a large inter-individual variation both in SR and MIT (Tables 20 and 21). Uptake and release correlated positively (r_g +0.31 $p<0.05$) with each other in SR samples taken 45 min after stunning. They did not correlate in SR samples taken 15 min after stunning or in MIT samples taken either 15 or 45 min after stunning.

Calcium uptake and release were measured in samples which were taken 15 and 45 minutes after stunning. Calcium uptake either decreased or increased postmortem both in SR and mitochondria depending on breed. Calcium release either decreased or increased postmortem, depending on breed, in mitochondria, but in SR, it increased in all breeds (Tables 20 and 21). Differences between samples taken 15 or 45 min after stunning were not statistically significant in any breed.

TABLE 20 Calcium uptake of SR and mitochondrial samples taken 15 and 45 minutes after stunning. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., ab=p<0.05. Values are ± SD. Causr15=calcium uptake of sarcoplasmic reticular fraction, samples taken 15 min after stunning; Causr45= calcium uptake of sarcoplasmic reticular fraction, samples taken 45 min after stunning; Caum15=calcium uptake of mitochondrial fraction, samples taken 15 min after stunning; Caum45=calcium uptake of mitochondrial fraction, samples taken 45 min after stunning.

	Calcium uptake nmol/min x mg prot			
Breed	Causr15 (n)	Causr45 (n)	Caum15 (n)	Caum45 (n)
L	234±200 (10)	344±276 (11)	346 ± 205^{ab} (11)	338±213 (11)
Y	214±172 (11)	202±150 (11)	267±141 (11)	292±239 (11)
H	336 ± 180^{a} (11)	313±160 (11)	265±155 (11)	268±164 (11)
LYL	59±47 (3)	174±60 (2)	139±154 (3)	168±147 (3)
YYL	97 ± 123^{a} (6)	120±56 (6)	102 ± 82^{a} (7)	143±155 (6)
HYL	165±100 (11)	136±72 (11)	157 ± 79^{b} (11)	149±91 (10)
DYL	133±119 (9)	126±147 (10)	176±137 (10)	233±203 (9)

TABLE 21 Calcium release in SR and mitochondrial samples taken 15 and 45 minutes after stunning. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., a=p<0.05. Values are ± SD. Carsr15=calcium release of sarcoplasmic reticular fraction, samples taken 15 min after stunning; Carsr45 =calcium release of sarcoplasmic reticular fraction, samples taken 45 min after stunning; Carm15=calcium release of mitochondrial fraction, samples taken 15 min after stunning; Carm45=calcium release of mitochondrial fraction, samples taken 45 min after stunning.

	Calcium release (nmol/min x mg prot)			
Breed	Carsr15 (n)	Carsr45 (n)	Carm15 (n)	Carm45 (n)
L	18.2±18.6 (10)	31.7±25.7 (11)	24.8±19.5 (11)	23.0±18.9 (11)
Y	27.2±25.3 (11)	36.4±38.1 (11)	36.7±25.5[a] (11)	25.3±19.8 (11)
H	24.2±20.0 (11)	32.8±30.1 (11)	13.4±9.4 (11)	17.1±11.8 (11)
LYL	7.3±12.6 (3)	26.1±17.1 (2)	0.2±0.4[a] (3)	2.8±3.7 (3)
YYL	14.3±16.1 (6)	25.4±25.1 (6)	11.7±11.7 (7)	22.7±10.7 (6)
HYL	15.4±16.6 (11)	19.2±29.2 (11)	17.2±13.7 (11)	19.4±14.5 (10)
DYL	16.8±22.4 (9)	29.2±37.7 (10)	17.6±22.5 (10)	20.7±16.7 (9)

Hampshire SR calcium uptake was higher than YYL ($p<0.05$). Uptake of MIT was higher in Landrace than in YYL ($p<0.05$) and HYL ($p<0.05$). Calcium release in MIT was higher in Yorkshire than in LYL ($p<0.05$). There were no other differences in calcium release or uptake in SR or MIT.

In crosses (HYL, DYL, LYL and YYL), both SR (Causr15, $p<0.01$; Causr45, $p<0.001$) and mitochondria (Caum15, $p<0.001$; Caum45, $p<0.05$) uptakes were lower than in purebred pigs (L, Y and H). Release in MIT was also lower in crosses than in purebred pigs (Carm15, $p<0.05$).

The standard deviations were quite large, even bigger than means, especially in release in some breeds. This may depend on methods used or individual differences between pigs.

5.7 Variation in Duroc crosses

Duroc cross pigs were progenies of only four boars. Those four boars were not close relatives. Progenies of boars 572 and 573 lived either at a test station (7 pigs) or at a farm (the rest). Progenies of the other two boars were all lived at a different than the previously mentioned farm. All DYL pigs were slaughtered at the same abattoir, except those pigs which lived at the test station.

There were large variations between groups of progenies with different sires (see Tables 22 and 23). In many properties measured, there were two pairs (boars 572/573 and boars 577/578) in those groups which differed from each other (Figure 5). Because it is not known if these differences are inherited or due to growth place, further research is needed to discern the answer.

TABLE 22 pH values of Duroc cross pigs are classified according to their sires. Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., f=p<0.01. Values are ± SD. pH_1 measured 45 min after stunning; pH_{24} measured 24 hours after stunning.

Boar	pH_1 (n)	pH_{24} (n)
572	6.10 ± 0.18^{f} (8)	5.54±0.05 (8)
573	6.33±0.32 (20)	5.51±0.09 (20)
577	6.35±0.17 (13)	5.50±0.07 (10)
578	6.47 ± 0.12^{f} (11)	5.48±0.07 (10)

TABLE 23 The activities of PHOS, LDH, HADH and CS (U/g muscle) and the amount of lactate (µmol/g muscle) in Duroc cross pigs classified according to their sires. Mean values in the same column bearing a same superscript are statistically different, no superscript means n.s., abc=p<0.05, fg=p<0.01, klm=p<0.001. Values are ± SD. PHOS =glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH=lactate dehydrogenase; CS=citrate synthase.

Boar (n)	PHOS	LDH	HADH	CS	LACT
572 (8)	21.6 ± 2.6^{ac}	2470 ± 167^{g}	9.45 ± 1.24^{bf}	6.52 ± 1.24^{af}	62.9 ± 11.8^{klm}
573 (20)	26.0 ± 4.0^{cek}	2386 ± 214^{fk}	8.58 ± 1.26^{a}	6.98 ± 0.98^{kl}	46.3 ± 9.7^{abm}
577 (13)	16.9 ± 3.6^{abk}	2653 ± 183^{f}	7.09 ± 1.28^{af}	5.18 ± 0.75^{ak}	36.7 ± 8.9^{ak}
578 (11)	21.6 ± 3.8^{be}	2871 ± 291^{kg}	7.66 ± 1.41^{b}	5.21 ± 0.92^{fl}	35.4 ± 7.2^{bl}

5.8 Sensory analysis, meat color, and drip loss measurements

Hampshire meat had the highest scores in flavor, juiciness and tenderness (Table 24). Landrace, Yorkshire, HYL and DYL did not differ from each other in flavor, juiciness and tenderness.

Hampshire meat color was darker than Landrace ($p<0.05$) and LYL ($p<0.01$) (Table 25). Meat of LYL was also paler than meat from HYL and YYL ($p<0.05$). Hampshire meat was redder than that of Landrace ($p<0.01$), Yorkshire ($p<0.001$), LYL ($p<0.05$), YYL ($p<0.001$) or DYL ($p<0.05$). The meat of HYL was redder than that of YYL ($p<0.05$), while Landrace meat had more red color than Yorkshire ($p<0.05$). Meat from LYL was more yellow than that of Yorkshire ($p<0.05$) or DYL ($p<0.05$).

Drip loss in Hampshire meat was lower than in meat of Landrace ($p<0.01$), LYL ($p<0.01$) and DYL ($p<0.01$) (Table 26). Meat drip loss in HYL was lower than in DYL ($p<0.01$), Landrace ($p<0.01$) or LYL ($p<0.01$). There were no difference in drip loss of meat from Landrace and Yorkshire.

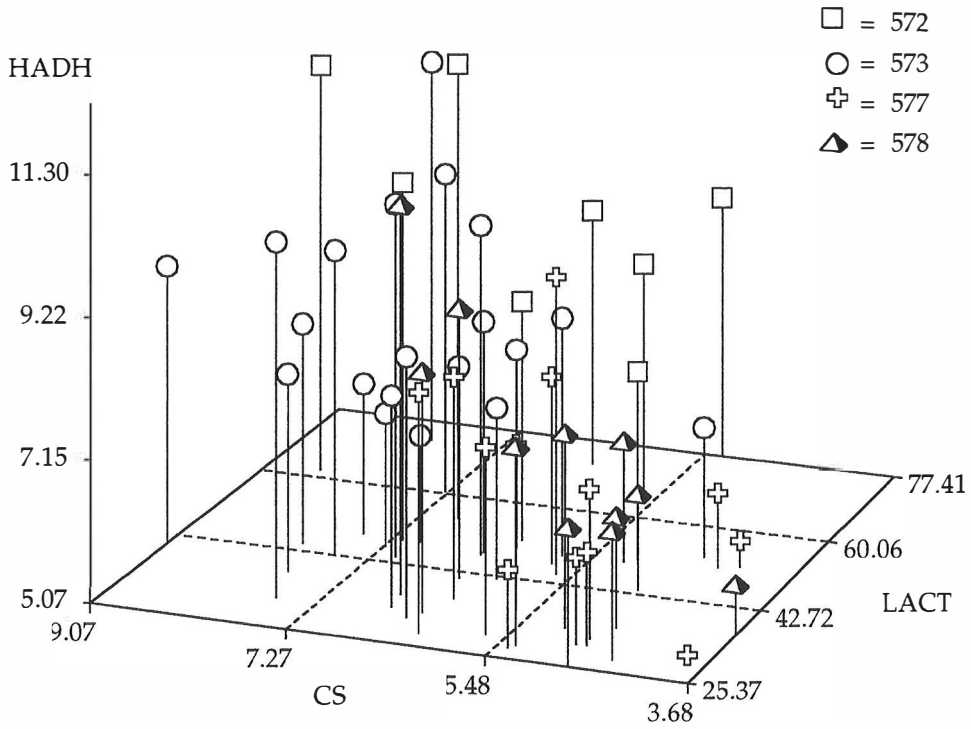

FIGURE 5 The summary of Duroc cross data. Citrate synthase (CS), 3-hydroxyacyl-CoA-dehydrogenase (HADH) are in U/g muscle; lactate (LACT) is in µmol/g muscle.

TABLE 24 Results of sensory analysis (data from Pajari 1994), the values are means of a 6 member sensory panel. The scale of each variable is 0-7 (1= weak flavor, very tough and dry; 7= strong flavor, very tender and very juicy). Mean values in the same column bearing the same superscript are statistically different, no superscript means n.s., ab= $p<0.05$, f=$p<0.01$, kl=$p<0.001$. Values are ± SD.

Breed (n)	Flavor	Juiciness	Tenderness
L (25)	5.0±0.5	5.0±0.4[a]	4.6±0.8[a]
Y (25)	5.0±0.4	4.9±0.4[g]	4.6±0.7[b]
H (40)	5.3±0.5	5.4±0.5[afgk]	5.3±1.0[ab]
LYL (15)	5.1±0.5	4.8±0.4[f]	4.7±0.8
YYL (28)	5.0±0.3	4.8±0.6[k]	4.7±0.6
HYL (43)	5.2±0.5	5.1±0.6	5.1±0.7
DYL (48)	5.2±0.5	5.1±0.5	4.8±0.7
all pigs (224)	5.1±0.5	5.0±0.5	4.9±0.8

TABLE 25 Means of meat color measurements (data from Pajari 1994), values in the same column bearing the same superscript are statistically different, no superscript means n.s., abcde=p<0.05, f=p<0.01, klmn= p<0.001. Values are ± SD.

Breed (n)	L* value[1]	a* value[2]	b* value[3]
L (27)	52.4±2.8^{a}	6.6±1.7^{af}	3.8±1.2
Y (28)	51.1±3.0	5.5±1.1^{abklm}	3.3±0.8^{a}
H (27)	50.1±2.4^{af}	8.0±1.1^{defmn}	3.8±0.8
LYL (18)	53.2±4.0^{bcf}	6.7±1.5^{bd}	4.3±1.2^{ab}
YYL (32)	50.5±2.7^{b}	6.1±1.4^{cn}	3.4±1.2
HYL (52)	50.7±2.6^{c}	7.1±1.3^{cl}	3.9±0.8
DYL (46)	51.5±2.4	6.9±1.1^{ek}	3.4±1.3^{b}
all pigs (230)	51.2±2.9	6.7±1.5	3.7±1.1

[1] Degree of meat lightness. The higher the number, the paler the meat appears.
[2] Degree of meat redness.
[3] Degree of meat yellowness.

TABLE 26 Means of LD drip loss (mg/filter paper) in different breeds (data from Pajari 1994). Mean values bearing the same superscript are statistically different, no superscript means n.s., abc=p<0.05, fghijk=p<0.01. Values are ± SD.

Breed (n)	Drip loss
L (25)	65.9±27.5^{bgj}
Y (24)	50.5±15.6
H (29)	41.4±19.4^{fgh}
LYL (19)	67.9±32.2^{chk}
YYL (32)	47.1±18.0^{abc}
HYL (52)	46.3±21.2^{ijk}
DYL (35)	63.7±23.8^{afi}
all pigs (216)	53.2±24.1

All statistically significant correlations between muscle metabolic characteristics, meat sensory and technological quality were small. There was, however, clear tendency to favor oxidative characteristics in better sensory quality of meat. The activities of CS and HADH were positively correlated with flavor (r_g 0.26 p<0.001 and 0.18 p<0.01, respectively) and juiciness (r_g 0.14 p<0.05 and 0.17 p<0.05, respectively) (Table 27). The higher the activities of CS and HADH, the redder the meat was (r_g 0.26 p<0.001 and 0.27 p<0.001, respectively). The proportion of LDH isoenzymes 1 and 2 correlated positively with a* value (r_g 0.21 p<0.01 and 0.23 p<0.01 respectively) (Table 28).

When muscle lactate content at 45 min after stunning was high, pH_1 was low (r_g -0.53 p<0.001), while pH_{24} (r_g 0.12 p<0.05) and drip loss (r_g 0.53 p<0.001) were high (Tables 27 and 30). The glycolytic characteristics, i.e. LDH activity, glycolytic potential, lactate or glycogen content, did not seem to have any effect on sensory quality. However, they may have some connection with meat color. Lactate content was positively correlated with L*-, a*- and b* values (r_g 0.28 p<0.001, 0.27 p<0.001 and 0.30 p<0.001, respectively) and LDH was negatively correlated with a*

and b* values (r_g -0.28 p<0.001 and -0.24 p<0.001, respectively). Lactate dehydrogenase-5 correlated positively (r_g 0.15 p<0.05) with L* value and negatively (r_g -0.16 p<0.05) with a* value (Table 28).

The activity of PHOS was negatively correlated with L* and b* values as well as drip loss (r_g -0.18 p<0.01, -0.16 p<0.05 and -0.14 p<0.05, respectively), but positively correlated with flavor (r_g 0.17 p<0.05) and tenderness (r_g 0.16 p<0.05) (Table 27).

TABLE 27 Statistically significant Pearson's partial correlation coefficients (effects of breed, test station or farm and abattoir are eliminated). * p<0.05, ** p<0.01, *** p<0.001. Glycpot=glycolytic potential; LACT=lactic acid; PHOS=glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH=lactate dehydrogenase; CS=citrate synthase; L* value=lightness of meat; a* value=redness of meat; b* value =yellowness of meat.

	Drip loss (n)	Flavor (n)	Juiciness (n)	Tenderness (n)	L* value (n)	a* value (n)	b* value (n)
Glycpot						0.41*** (71)	
LACT	0.53*** (211)				0.28*** (223)	0.27*** (223)	0.30*** (223)
PHOS	-0.14* (195)	0.17* (275)		0.16* (275)	-0.18** (210)		-0.16* (210)
LDH						-0.28*** (228)	-0.24*** (228)
HADH		0.18** (275)	0.17* (275)			0.27*** (210)	
CS		0.26*** (275)	0.14* (275)			0.26*** (210)	

TABLE 28 Statistically significant Pearson's partial correlation coefficients (effects of breed, test station or farm and abattoir are eliminated). *p<0.05, **p<0.01. LDH=lactate dehydrogenase; L* value=lightness of meat; a* value=redness of meat.

	Tenderness (n)	L* value (n)	a* value (n)
LDH-1			0.21** (188)
LDH-2			0.23** (188)
LDH-3			
LDH-4	0.15* (191)		
LDH-5		0.15* (188)	-0.16* (188)

5.9 Summary of comparisons of different breeds

The Hampshire LD muscle, of those breeds studied, was the most oxidative. This was observed in CS, HADH and LDH activities as well as in volume density of mitochondria and distribution of LDH isoenzymes. Although the oxidative capacity was high in Hampshire LD, its glycolytic

potential was also higher than in most other breeds or crosses. Between the other breeds, the differences were not so pronounced.

The traditional Finnish pig breeds, Landrace and Yorkshire, did not differ from each other in the muscle properties measured in this study. Only the *longissimus dorsi* of Landrace had a higher LDH-1 proportion than in Yorkshire. There were no other significant differences between breeds. Nevertheless, there was a clear trend toward a higher oxidative capacity in LD of Landrace than Yorkshire. This is hardly significant in practice. Both breeds have quite a glycolytic LD.

The *longissimus dorsi* of Hampshire and Duroc crosses was distinguished from each other by glycogen and lactate content as well as different distribution of LDH isoenzymes. The higher ($p<0.01$) glycogen content in HYL LD is inherited from Hampshire. Although the activity of LDH was higher in DYL than in HYL ($p<0.001$), their lactate contents at 45 min postmortem were similar. The lower ($p<0.01$) proportion of LDH-5 in DYL, but a similar LDH-5 activity in both crosses may explain this. They have similar ability to produce lactic acid postmortem. The ability of DYL LD muscle to oxidize lactate to pyruvate antemortem is higher ($p<0.001$).

Crossbreeding impaired the oxidative properties of Hampshire, but affected the glycolytic properties less. Hampshire CS and HADH activity was higher ($p<0.001$) than HYL. The glycogen content of HYL was between Hampshire and the other breeds or crosses. Hampshire cross pigs did not seem to inherit the LDH isoenzyme distribution from Hampshire, although they had lower a total LDH activity than most other groups except Hampshire. The Hampshire cross resembled Landrace and Yorkshire considerably. Only LDH activity was lower in HYL than in Landrace ($p<0.05$) and Yorkshire ($p<0.001$). Calcium uptake, in MIT samples taken 15 min after stunning, was higher in Landrace than in HYL ($p<0.05$).

The Duroc cross differed from Landrace and Yorkshire only in LDH activity as well as LDH isoenzymes distribution, which consisted of more "heart" isoenzymes and less "muscle" isoenzyme in DYL. The total activity of LDH in DYL was lower than in Landrace ($p<0.05$) and similar to Yorkshire. However, the activities of LDH-1, LDH-2 and LDH-3 were lower in Landrace and Yorkshire than in DYL, but the activity of LDH-5 was similar in all three groups. So their ability to produce lactate postmortem is similar. The lactic acid content at 45 min postmortem was similar in those groups.

The Landrace and Yorkshire crosses, LYL and YYL, lived in same conditions as Hampshire crosses. *Longissimus dorsi* from YYL and LYL strongly resembled those of L or Y. The LD of HYL was more oxidative than that of YYL, whose CS activity was lower ($p<0.001$) and LDH activity

higher ($p<0.01$) than in HYL. There was more lactate in LYL than HYL ($p<0.05$).

5.10 Reclassification of pig breeds by discriminant analysis

The purpose of discriminant analysis is the classification of an item into one of the several mutually exclusive groups on the basis of its measured response variables (Ranta *et al.* 1992) .

Discriminant analysis was made to determine the heterogeneity or inter-individual variation in different pig breeds in this study, and to find out how those breeds resemble each other. The analysis was made using CS, HADH, PHOS, LDH, LACT as variables with or without pH_1, pH_{24}, LDH-1, and LDH-5. They were chosen because they characterize cell energy metabolism and the data was available from nearly all of the pigs used in this study.

There were many pigs in the Landrace (42; total 53 in the analysis) and Yorkshire (35; 53) breeds that can be classified, based on the results of this analysis, to other breeds, even to the Hampshire breed (5 of Landrace and 1 of Yorkshire). Also, DYL was a very heterogeneous group, many DYL resembled Yorkshire (18/48). Hampshire and LYL were the most homogeneous groups in properties used in this analysis.

Figures 6 and 9 show that Yorkshire and DYL were quite similar in CS, HADH, PHOS, LDH capacity and LACT, but differed in the share of LDH-1 and LDH-5. When LDH-1 and LDH-5 were added to the variables, the amount of DYL pigs classified to their own breed increased from below 30 to over 60%. About 70-80% (depending on variables used in the analysis) of Landrace could be classified to other breeds. Landrace was the most heterogeneous breed. Only about 30% of Hampshire could be classified to other breeds. There were no big difference in that number even when LDH-1 and LDH-5 were included in the analysis. Therefore, the values of HADH, CS, PHOS, LDH and LACT were enough to classify Hampshire. The Hampshire breed was the most homogenous. The inclusion of pH_1 and pH_{24} to the analysis did not appreciably affect most of the results.

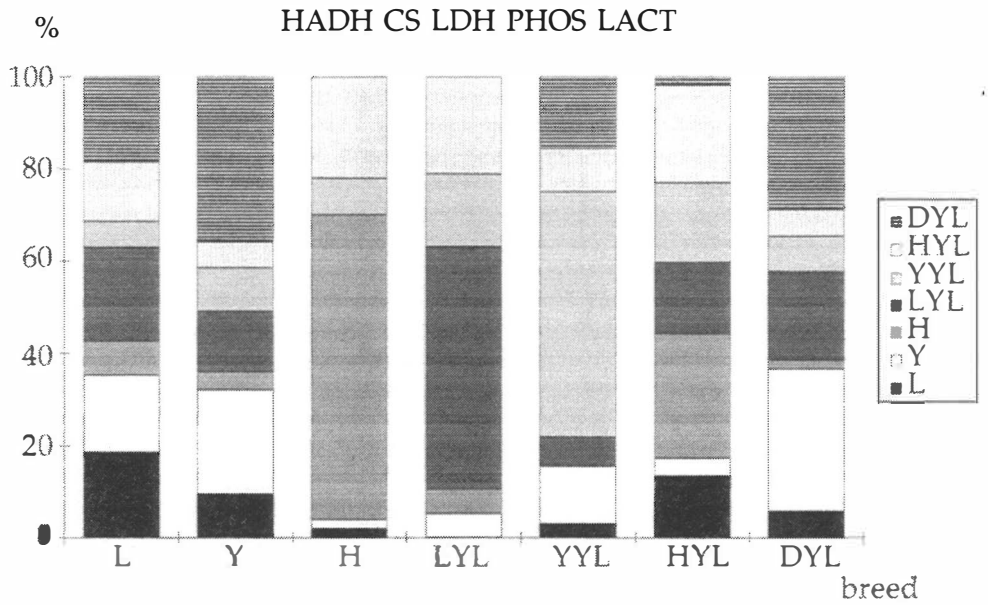

FIGURE 6 Outcome of discriminant analysis showing the classification of pigs to new breeds (%).Variables which were used in the analysis were: CS, HADH, PHOS, LDH and LACT (n=312).

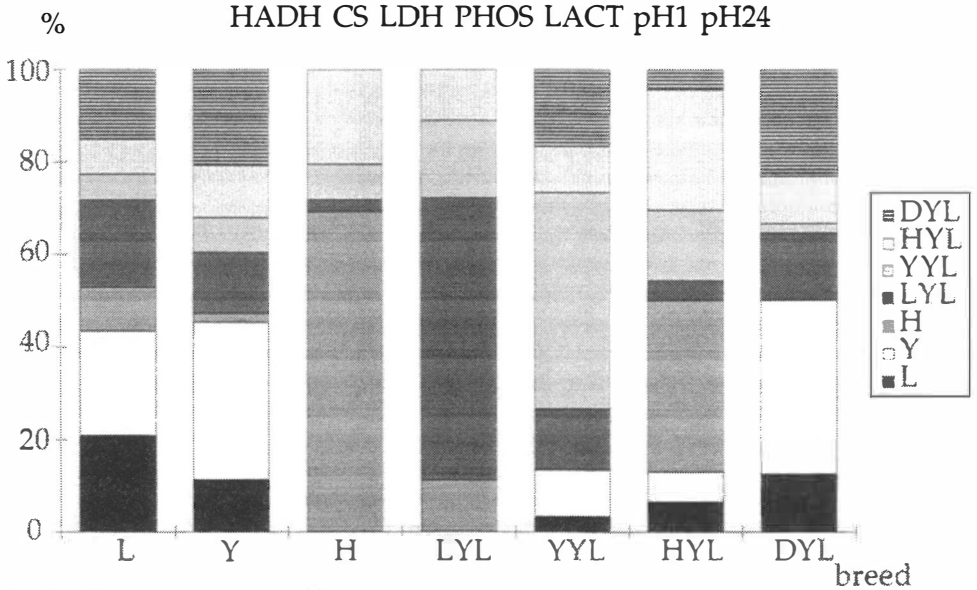

FIGURE 7 Outcome of discriminant analysis showing the classification of pigs to new breeds (%).Variables which were used in the analysis were: CS, HADH, PHOS, LDH, LACT, pH_1 and pH_{24} (n=287).

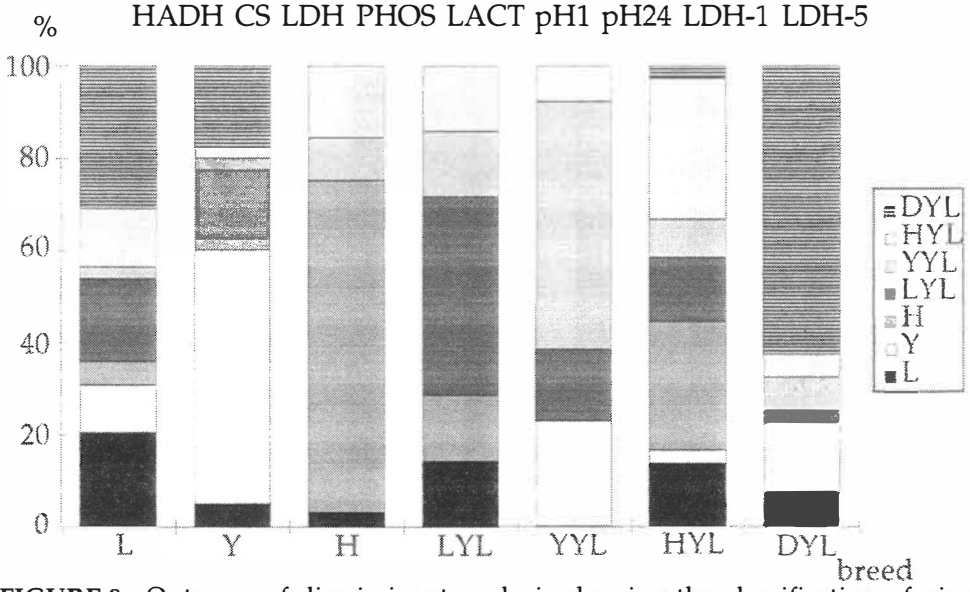

FIGURE 8 Outcome of discriminant analysis showing the classification of pigs to new breeds (%).Variables which were used in the analysis were: CS, HADH, PHOS, LDH, LACT, LDH-1, LDH-5, pH_1 and pH_{24} (n=227).

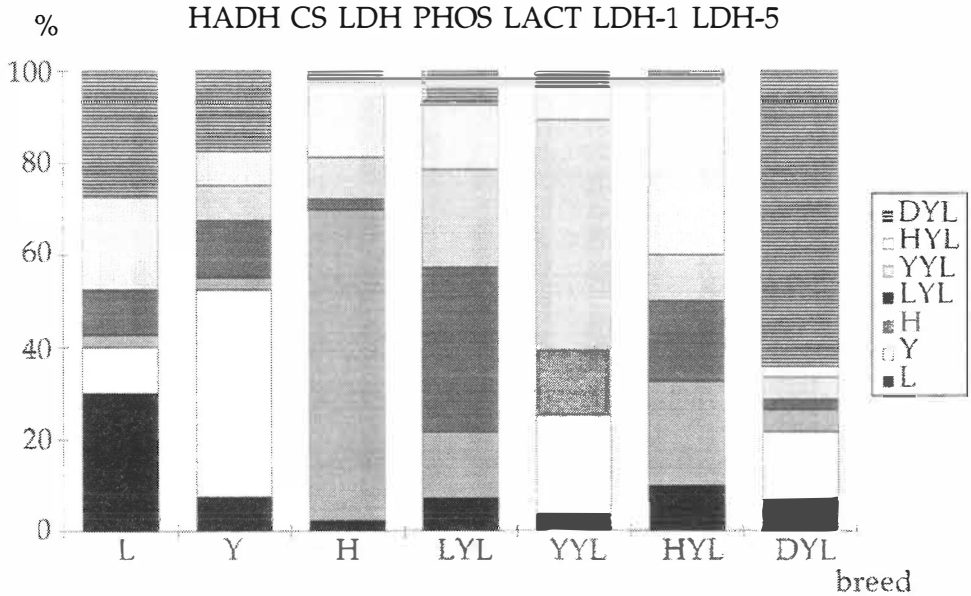

FIGURE 9 Outcome of discriminant analysis showing the classification of pigs to new breeds (%).Variables which were used in the analysis were: CS, HADH, PHOS, LDH, LACT, LDH-1 and LDH-5 (n=247).

5.11 Classification of pig breeds according to certain good quality properties of *longissimus dorsi* measured in this study

To make this classification, the following parameters were selected: high CS, HADH, LDH-1 activity, volume density of mitochondria and low lactate level. High CS, HADH and LDH-1 activities as well as high V_{vmit} are important antemortem, so that muscle can produce energy by oxidizing fuel instead of lactate formation. Because there was no DFD pigs among pigs in this study, low lactate level at 45 min postmortem can be considered as a good selection criterion. The resulting ranges in these parameters from every pig in this study were divided in three parts of equal size. Every parameter mean from each breed was classified to one of these parts. If the mean belonged to the first third (the best), it received three point, if to the second third, it was given two points and if to the bottom third (the worst), it was assigned one point. Points were added together for each breed, the more points, the "better" the breed.

According to this classification, the best breed was Hampshire (Figure 10). This classification accentuates oxidative properties of muscles, hence this "test" indicates that the Hampshire LD was the most oxidative muscle in these breeds. HYL and DYL were little "better" than Landrace and Yorkshire. Landrace was "better" than Yorkshire. The DYL cross placed high due to its elevated distribution of "heart" LDH isoenzymes and low distribution of "muscle" isoenzymes.

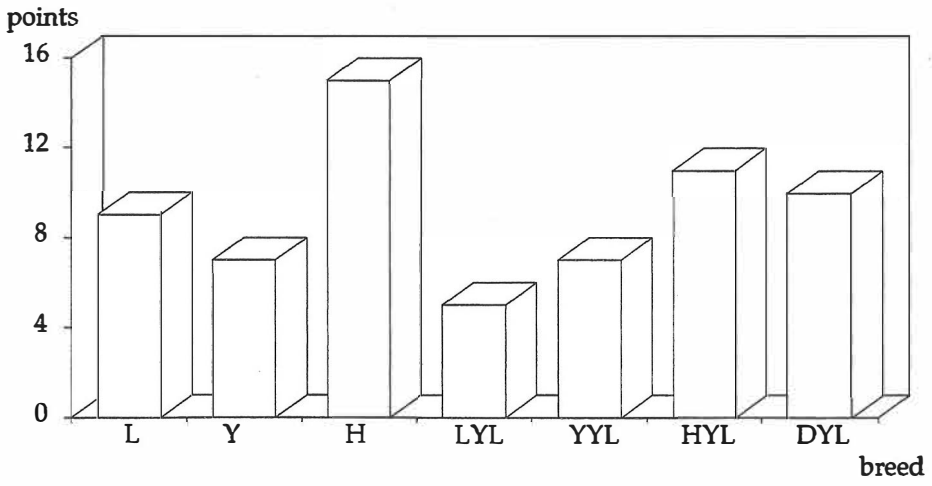

FIGURE 10 Breeds were classified according to CS, HADH and LDH-1 activity, mitochondrial volume density as well as lactate level in LD using a point system. High pillar height indicates "better" breeds (For further details, see text).

6 DISCUSSION AND CONCLUSIONS

6.1 General considerations on pig backgrounds and methods used in this study

Longissimus dorsi muscle, the pork loin, is economically one of the most valuable muscles in the carcass. Research has focused on increasing the size of this muscle. For example the average loin area of Finnish test station pigs has increased many square centimetres: in 1981 (at live weight of 88 kg), it was 35.3 cm^2 in Landrace and 33.8 cm^2 in Yorkshire; in 1988 (at the same live weight), it was 38.7 cm^2 in Landrace and 37.4 cm^2 in Yorkshire (Puonti 1983, Puonti 1989). *Longissimus dorsi* is a widely studied muscle with many research papers available on it. It is a large muscle, from which samples are quite easy to take under slaughterhouse conditions. This study attempted to carefully take muscle samples at the same place and depth (from the midportion) in each pig despite difficulties caused by variations in individual backfat thickness. Studies with rats have shown that a greater proportion of red fibers as well as higher succinic dehydrogenase activities are located in the internal muscle areas than in superficial layers (Srèter & Woo 1963, Romanul 1964).

Because only the *longissimus dorsi* was used, these results may not be generalized to the whole animal. Since only a small sample of LD was used, these results may not fully reflect the situation throughout the entire LD muscle. However, Ruusunen (1994) found positive correlations between *longissimus dorsi* and *adductor* muscles in the percentage or cross sectional area of different fiber types. Pigs used in the Ruusunen study were same as in this study.

The individual animals were carefully chosen. Pig selection did not accommodate any particular property, however offspring from artificial insemination were favored. Relatives were avoided, if possible. Unfortunately, all Duroc crosses were the offspring of only four boars. Therefore, samples from the same litter had to be taken. Thus, there were differences between the various sire lines in enzyme activities and lactate content in DYL pigs. Also in the HYL group, there were some siblings used. To determine the number of pigs needed for the study, preliminary tests (enzyme measurements) were made using ten randomly chosen meat pigs and four wild pigs (Appendix 1). The variation between individual pigs was theorized to be large, thus the number of pigs in each groups (about 50) was chosen by following instructions of Kastenbaum & Hoel (1970) and Day & Graham (1989). For practical reasons, morphometric analysis, glycogen contents and measurements of calcium metabolism had to be done from smaller populations.

In this study, all samples were taken postmortem. Some decrease in enzyme activities may occur when compared to *in vivo* state. Also, differences in calcium accumulation and release may occur when compared to the antemortem state. All slaughterhouses were commercial, except for the one at the University of Helsinki. Pigs in the study were slaughtered in a common slaughter line. We had to choose the sampling times based on the above, thus muscle samples for this study were taken either after scalding and dehanging (15 min after stunning) or after slaughter line (45 min after stunning), 45 minutes after stunning was the average time (range of approximately 15 minutes), although most samples were taken 45 minutes after stunning. The range of the first sampling time is, at most, five minutes. Preliminary tests with one pig (even biopsies before slaughter were taken) were performed to determine the dependence of the sampling time on enzyme activities and EM samples. Decreased enzyme activities have been reported in samples taken 45 min postmortem as compared to samples taken prior to slaughter (Essén-Gustavsson & Jensen-Waern 1993). However, in this study enzyme activities were well preserved in pig samples taken even twenty hours postmortem (Appendix 2). Samples in Essén-Gustavsson & Jensen-Waern (1993) study were not taken from exactly the same site as samples in this study. Severini and co-workers (1990) did not find any phosphorylase activity in PSE muscles 2 hours postmortem. They thought that this may have been caused by metabolites which had inhibited enzyme activity. Klont and co-workers (1993) did not find any decrease in glycogen content of LD samples taken 45 min after slaughter compared to samples taken 25 min after slaughter in NN or Nn pigs. In nn pigs, there was a little decrease in that time. Honkavaara (1989) has shown that the most prominent decrease in muscle glycogen occurs during scalding with a

minor decline afterwards, 17.4% of muscle glycogen is broken down 45 min postmortem in Finnish Landrace, Yorkshire or crossbred pigs. However, the time elapsed between stunning and carcass chilling had a minor effect on muscle glycogen and lactate content. Sayre and co-workers (1963) found a 20 % decrease in muscle glycogen content of Hampshire and Chester White pigs at one hour after slaughter compared to the value obtained immediately after slaughter. The small variation in sampling time between individual pigs may have some influence on the large standard deviations in many of the properties measured in this study. If the sampling time has some influence on these properties, then this influence probably has the greatest effect on the glycogen and lactate values.

Pigs were grown at either test stations or farms. It was impossible to choose only pigs which were grown at the same place, under the same conditions, in the available time period. No Hampshire and only a few Duroc crosses were available at the test stations. At those farms, where Hampshire and Duroc crosses lived, pure Landrace and Yorkshire pigs were unavailable. LYL and YYL pigs were grown at the same farms and were slaughtered in the same abattoir as the Hampshire crosses. So they can be regarded as controls to HYL. Landrace and Yorkshire pigs (except two Yorkshire pigs) were raised at test stations and were slaughtered in the same slaughterhouse as HYL, YYL and LYL. Carcass quality of the test pigs were, on average, a little better than carcass quality from normal farm pigs. In our study, 71% of Landrace and 63% of Yorkshire carcasses belonged to the best E^+ quality class, whereas at most, only 40% of carcasses of other breeds or crosses belonged to it. Unfortunately, the quality class from 40% of the DYL carcasses is unknown. The test station pigs represented "the best Finnish pigs". Ruusunen (1994) found (using same pigs as in this study) that if the carcass belonged to a better quality class, a higher area percentage of type IIB fibers was noted, but this could not be the only reason for better quality class of Landrace and Yorkshire pigs. Landrace and Yorkshire pigs were younger and little lighter at slaughter than other breeds or crosses. Their daily weight gain was higher than the others.

There were some significant differences among certain breeds or crosses between growth place or slaughterhouses. Slaughter age of pigs grown at different places diverged little. The average pH_1 of Hampshire pigs slaughtered at Forssa was higher than in pigs slaughtered at Vaasa ($p<0.01$) or Nurmo ($p<0.001$) (Table 8). Hampshires slaughtered at Forssa had been raised at a test station, while Hampshires slaughtered at Vaasa and Nurmo on a farm. There were differences in some enzyme activities and the amount of metabolites between growth places in some breeds or crosses: PHOS, CS, LDH, HADH and LACT in DYL; PHOS in L; PHOS

and LACT in Y; PHOS and HADH in HYL; CS in LYL; LDH in YYL (Tables 11, 12 and 13). Differences between Duroc pigs raised at different farms may also be explained by different sire lines at each farm. Because the pigs were raised at several farms or test stations, differences in management styles are therefore likely to occur to some extent, which could have had an effect on the intramuscular substrate stores. Diet and physical activity are factors which may influence storage of glycogen (Fernandez & Thornberg 1991). However, variations in the composition of different pig feeds or in the level of physical activity are small. The HYL, LYL and YYL pigs arrived at the abattoir the same morning they were slaughtered. The others arrived the day before slaughter. Feed was not given at slaughterhouse. This means that the others had fasted (at most 10 hours longer) and rested longer than HYL, LYL and YYL. Fasting reduces muscle and liver glycogen stores (Warriss *et al.* 1989). Honkavaara (1989) found a twenty-four hour fast reduses glycocen stores and increases lactate content of LD from pigs. Although Fischer and co-workers (1988) did not find any decrease in the glycogen content of LD from pigs withheld from feed for up to three days. Also, Fernandez and co-workers (1992c) found that losses of muscle glycogen after fasting for 2h or 24h were similar. Riis & Grummer (1969) have shown that pigs fed restricted rations show more variation in glycogen utilization when compared to pigs fed *ad libitum*. Pigs in this study were fed twice a day. There were no differences between HYL, LYL or YYL pigs and the longer fasted breeds or crosses in the muscle lactate level. The glycogen content of Hampshire LD muscle was higher than that of LYL or YYL, even though Hampshire pigs were fasted longer. The glycogen content of HYL was between that of Hampshire and other groups, but was nearly three times higher than that of DYL. However, DYL pigs had fasted, at most, ten hours longer, which may have influenced glycogen stores. All pigs, except two Y, were stunned with CO_2. Carbon dioxide stunning can induce stress in pigs even if it is properly done (Lambooy 1990). Both carbon dioxide and electrical stunning lower the pH_1 compared to unstunned animals (McLoughlin 1971). Although there were differences in some muscle properties between pigs raised or slaughtered at different places, these differences were small, and they hardly explain the changes between breeds or crosses. When the relationships between muscle and meat properties were calculated, the partial correlation coefficient was always used, so the effect of growth and slaughter place as well as breed or cross were adjusted for.

Castrated male pigs were younger ($p<0.001$) at slaughter, their daily gain ($p<0.001$) and LDH activity ($p<0.05$) was lower than in female pigs (Tables 2 and 14). A higher portion of females carcasses belonged to the best quality class than carcasses of males (Table 3). The sex

distribution was: 181 females, 141 males and 2 unknowns. There were no differences between sexes in oxidative or glycolytic characteristics (except in the activity of LDH) of LD muscle. Monin and co-workers (1986) either did not find any difference in oxidative or glycolytic capacity between sexes, but the lipid content was higher in castrated males than in females. Castrated males are fatter than gilts (Warriss *et al.* 1990).

pH_1 was lower in pigs slaughtered during the winter than in those slaughtered in autumn ($p<0.01$) (Table 9). pH_{24} was higher in pigs slaughtered during the winter than in pigs slaughtered in autumn ($p<0.05$) or summer ($p<0.01$). This can not be explained by breed, because a large proportion of Hampshire pigs were slaughtered during the winter. Also pH_1 of Hampshires slaughtered during the winter was lower than in those slaughtered in autumn ($p<0.05$). The effect of winter on pH_1 values may be associated with different climatic conditions, particularly the lower temperature. Cold stress has been shown to accelerate the rate of metabolism, causing hyperglycemia (Kolb 1974). The pH_1 results are in agreement, while pH_{24} results disagree with Pospiech and co-workers (1989), who found the pH_1 in pigs slaughtered in spring and autumn in Poland to be higher than in those slaughtered during the summer or winter; pH_{24} was higher in pigs slaughtered in autumn than in those slaughtered in spring, summer or winter. The slaughter days of pigs in this study were distributed quite uniformly throughout the year.

The reliability of enzyme activity was tested using the analysis of nested SAS-program. The variation due to method was quite low for the enzyme activity measurements (from 2.9 to 5.7%). The LDH, CS and HADH activities were in accordance with many earlier reports concerning pig LD muscle (Kiessling & Hansson 1983, Lefaucheur & Vigneron 1986, Essén-Gustavsson & Jensen-Waern 1993, Karlsson *et al.* 1993). The sampling methods and conditions may influence enzyme activities, metabolite contents and pH value. Sampling may affect PHOS activity (Ren & Hultman 1988). The Ca^{2+} release during sampling may cause the conversion of PHOS b to PHOS a. After a few minutes, the activity of PHOS a drops to the initial level. In this study, the total PHOS activity was measured, thus it is not affected by Ca^{2+} release during sampling. Mitochondrial activity declines during storage, and no biologically active mitochondria can be isolated when muscle pH is below 5.5 (Cheah 1973). In the present study, muscle pH was probably above 6.0 at the time of sampling. Freezing the sample in liquid nitrogen improves the preservation of HADH activity (Chen *et al.* 1990). The activity of PHOS does not decrease if the muscle is stored at -20°C for four months (Müller 1980). The insertion of the electrode into muscle tissue can influence postmortem glycolysis and pH (Hofmann 1987). Glycogen content of

white muscle may decrease more rapidly than in red muscles during sample preparation (Beecher *et al.* 1969).

There were some weak positive or negative correlations (range of r_g from 0.12 to 0.38) between fiber type distribution and capillary density as measured by Ruusunen (1994) and the muscle properties measured in this study (Table 29). A positive correlation was found between type I fiber content and CS activity, HADH activity as well as the proportion of LDH-1 and LDH-2, between IIB fiber content and lactate as well as the proportion of LDH-5, and lastly, between capillary density and CS activity, HADH activity, glycogen as well as glycolytic potential. A negative correlation was found between type I fiber content and LDH activity as well as the proportion of LDH-5, between IIB fiber content and CS activity, HADH activity as well as the proportion of LDH-1 and LDH-2, and lastly, between capillary density and LDH activity, lactate as well as the proportion of LDH-5. Kiessling & Hansson (1983) found correlations along the same lines, but closer between the activity of HADH and type I or type IIB fiber content. They also found a weak positive correlation between the activity of LDH and IIB fiber content. The fiber types in this study were measured using myosin ATPase activity, which reflects a contractile property. This may explain the weak correlations between fiber types and metabolism in our study. It is important to remember that a marked variation in oxidative and glycolytic capacity as well as glycogen and lipid content may occur between fibers even if they demonstrate similar staining intensity for myosin-ATPase (Essén & Henriksson 1974, Essén-Gustavsson *et al.* 1988b, Ruusunen 1994). The number of capillaries around type I fibers is greater than that around type IIB fibers (Essén-Gustavsson *et al.* 1992, Ruusunen 1994). Maxwell and co-workers (1980) did not find any correlation between the capillarity and the oxidative metabolic capacity (succinate oxidase activity) of muscle fibers in many species, while Ruusunen (1994) found a positive correlation between them (using NADH-tetrazolium reductase for oxidative capacity) in some Landrace, Yorkshire and Duroc crosses. Fast growing pigs have more red fibers and a smaller average fiber diameter than slow growing pigs (Sevón-Aimonen & Kettunen 1993). The activity of HADH is closely related to the red fiber content (Kiessling & Hansson 1983).

In crosses, the F_1 generation is generally more vigorous than their parents (Schneider *et al.* 1982). This effect is apparent when litter size is analyzed (Flen & Hassinen 1992). Heterosis is more obvious when the parent breeds are not closely related. This does not remain true for the F_2 generation which can decline to the level of parents or even below. The LD of LYL and YYL pigs was shown to have a quite low oxidative, but high glycolytic metabolism. These animals were used as the control group to HYL pigs.

TABLE 29 Statistically significant Pearson's partial correlation coefficients are shown below, the effects of breed, test station or farm and abattoir are eliminated. * p<0.05, ** p<0.01, *** p<0.001. Data for fiber type distribution and capillary density from Ruusunen 1994.

	Fiber types			
	I (n)	IIA (n)	IIB (n)	Capillary density (n)
PHOS		+0.12* (315)		
LDH	-0.12* (315)			-0.38*** (315)
CS	+0.14* (315)	+0.15** (315)	-0.25*** (315)	+0.27*** (315)
HADH	+0.30*** (315)		-0.25*** (315)	+0.36*** (315)
LDH-1	+0.26*** (249)		-0.27*** (249)	
LDH-2	+0.25*** (249)		-0.29*** (249)	
LDH-3				+0.13* (249)
LDH-4				
LDH-5	-0.21** (249)		+0.20** (249)	-0.13* (249)
LACT			+0.12* (310)	-0.15** (310)
glycogen				+0.29** (89)
glycpot				+0.29** (88)

6.2 Muscle quality

6.2.1 The oxidative and glycolytic capacity of *longissimus dorsi*

Meat-producing animals react to their environment, and if they react strongly enough, the effect may well be reflected in the biochemical reactions of the muscle. Transportation of pigs to the slaughterhouse and the slaughter process itself can produce undesirable postmortem changes, such as high lactate content and a rapid rate of decline in muscle's pH (Honkavaara 1989). So the durability of stress is an important factor which has to be taken account in pig breeding. Muscle metabolic characteristics play an important role in this.

Longissimus dorsi is a muscle whose fibers have to rely primarily on anaerobic carbohydrate metabolism for energy production, because of its high proportion of IIB fibers (Essén-Gustavsson & Lindholm 1984). In this study, the proportion of IIB fibers in LD of different breeds or crosses varied from 75 to 82% (Ruusunen 1994).

The rate of pH decline postmortem has a great influence on meat quality. If lactate production starts at a high level antemortem, the pH may be decreased at the time of slaughter (Kivikari & Puolanne 1989, Essén-Gustavsson *et al.* 1992). If a muscle relies on oxidative energy metabolism *in vivo* and has a good vascular system to remove waste products from muscle to blood, the pH may not be changed at the time of slaughter. Before slaughter, lactate clearance may play a greater role than lactate production.

TABLE 30 Statistically significant Pearson's partial correlation coefficients are shown below, the effect of breed, test station or farm and abattoir is eliminated. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	pH1 (n)	pH24 (n)	PHOS (n)	LDH (n)	CS (n)	HADH (n)	LDH-1 (n)	LDH-2 (n)	LDH-3 (n)	LDH-4 (n)	glycogen (n)	LACT (n)	Causr15 (n)	Causr45 (n)	Caum15 (n)	Caum45 (n)	Carm15 (n)
LDH	0.18** (313)	0.24*** (301)	0.19*** (322)														
CS		-0.12* (301)	0.21*** (322)	-0.19*** (322)													
HADH		-0.15** (301)		-0.19*** (322)	0.69*** (322)												
LDH-1					0.24*** (254)	0.21*** (254)											
LDH-2					0.18** (254)	0.18** (254)	0.85*** (254)										
LDH-3							0.33*** (254)	0.61*** (254)									
LDH-4		-0.15* (238)						-0.20** (254)									
LDH-5						-0.14* (254)	-0.71*** (254)	-0.74*** (254)	-0.71*** (254)	-0.46*** (254)							
glycogen	0.22* (88)	-0.27* (85)			0.31** (90)	0.23* (90)											
LACT	-0.53*** (298)	0.12* (291)															
glycpot		-0.28* (84)			0.43*** (89)	0.25* (89)					0.61*** (89)	0.44*** (89)					
Causr45	0.36** (59)												0.31* (60)				
Caum15	0.29* (61)												0.38** (61)	0.43*** (62)			
Caum45	0.31* (58)			0.37** (59)										0.53*** (60)	0.38** (61)		
Carsr45														0.34** (62)		0.30* (60)	
Carm45																	0.31* (61)

The biochemical differences in muscle from the seven pig breeds or crosses show a large metabolic heterogeneity within the species. The different metabolic profiles seen between the breeds might be related to either genetic or environmental factors. Sevon-Aimonen (1994) found the heritability of type I muscle fibers to be 5% and that of IIA and IIB fibers to be 20-30%. Pigs in this study came from several farms or test stations. In all places, they were housed in similar manner in conventional pens. Differences in management and diet are likely to occur. These small variations in pen size hardly have an effect on intramuscular substrate stores or muscle oxidative capacity, since moderate indoor exercise does not affect glycogen content or oxidative capacity of LD (Enfält *et al.* 1993b).

The Hampshire LD clearly differed from that of other breeds in oxidative and glycolytic capacity. Hampshire pigs had both greater oxidative capacity and glycogen storage. High muscle glycogen content, typical for Hampshire or Hampshire crosses, is attributed to the dominant RN- gene (Fernandez *et al.* 1992d). The activity of glycogen synthase in the muscle of Hampshire and its crosses is higher than in many other breeds (Monin *et al.* 1986, Monin *et al.* 1987). Although Hampshire pigs had the lowest activity of LDH, they had the highest glycolytic potential. In situations such as exercise and stress, Hampshire pigs may produce less lactate. The Hampshire lactate level was the lowest. Because of the high oxidative capacity of Hampshire pig muscle, lactate production may not start before slaughter. The ability of Hampshire LD muscle to oxidize lactate back to pyruvate is higher than in many other breeds because of their high percentage and activity of LDH-1. Although this study could not find any correlation between LDH activity or isoenzyme distribution and lactate content in muscle. Hampshire-type muscle fibers are able to produce the energy they need before slaughter by oxidizing fuels. As Hampshire capillary density is higher than in many other breeds (Ruusunen 1994), the antemortem lactate clearance may be more efficient. Hence, lactate accumulation may not start in Hampshire-type muscles as easily before slaughter as in many other type muscles. The high glycolytic potential typical for Hampshire muscles does not affect the pH decline just after slaughter, but it does lower pH_u. This may increase cooking loss, since water bound to glycogen is released during meat processing.

Hampshire parentage seemed to give the crosses some low glycolytic characteristics, but not the high oxidative ones. The Hampshire cross had lower LDH activity than Yorkshire and Landrace, but similar oxidative enzyme activity. It has been suggested that the high glycolytic potential may exhibit a dominant mode of inheritance in the Hampshire cross via the dominant RN- gene (Monin *et al.* 1987, Fernandez 1992d). Sellier (1987) found that the same may be true for low ultimate pH. There

was not an increase in glycolytic potential in the LD of HYL pigs compared to Landrace and Yorkshire in this study.

The breed differences in CS and LDH activities determined in this study are similar to the results of Essén-Gustavsson & Fjelkner-Modig (1985), who reported that Hampshire pigs have higher CS but lower LDH activities in LD muscle than Swedish Yorkshire, while Swedish Landrace have activities of those enzymes between the other breeds. There is also a tendency (not statistically significant) to higher HADH activity in Hampshire than in Swedish Yorkshire and Swedish Landrace as well as higher activity in Swedish Landrace than Yorkshire. The same tendency in activities of CS, HADH and LDH between Finnish Landrace and Yorkshire occured in this study, although differences were not statistically significant. Generally, CS and HADH activities in LD muscles are higher in Hampshire than in many other breeds (Monin *et al.* 1986: Hampshire vs. Large White and Pietrain, Monin *et al.* 1987: Hampshire vs. Large White, Pietrain and Belgian Landrace). There was no correlation between the activity of HADH and intramuscular fat content (fat data from Pajari 1994; data not shown), although HADH is a mitochondrial enzyme, which takes part in the oxidation of fatty acids to acetyl-CoA. This is then oxidized in the citric acid cycle. The composition of fatty acids does not influence the function of HADH (Lehninger 1982).

The glycogen level at slaughter determines, to a large extent, the meat ultimate pH (Warris *et al.* 1989, Karlsson *et al.* 1993), whereas the rate of pH decline is primarily influenced by halothane sensitivity (Monin & Sellier 1985). Muscle glycogen level can influence the technological quality of pig meat independent of its effect on pH_u. Glycogen is able to bind water to a large extent. This water can be freed postmortem which decreases the technological yield of the processed meat (Fernandez & Thornberg 1991, Fernandez *et al.* 1991). There was a slight negative correlation between ultimate pH and glycolytic potential (r_g -0.28 $p<0.05$) or glycogen (r_g -0.28 $p<0.05$) in this study, which is in agreement with Warriss and co-workers (1989). It is known that, in some muscles of well-fed and rested animals, glycolysis stops at a "limit value", even in the presence of large amounts of residual glycogen (Bendall 1973a). Glycolysis ceases and there is no longer any ADP available for rephosphorylation. Normally, this "limit value" is at a pH of 5.3 to 5.5 (Greaser 1976). Meat color and drip loss are known to be dependent, at least partly, upon the extent of the pH drop postmortem. The glycolytic potential, which takes into account the main compounds likely to produce lactic acid postmortem, may be considered as a good approximation of the glycogen level just before slaughter (Monin *et al.* 1987). Breed, muscle metabolic type, preslaughter stress and fasting are the main causes of variation in the glycogen level of muscles (Fernandez & Thornberg 1991).

In this study sex had no effect on the glycolytic potential, which is in agreement with results of Talmant and co-workers (1989). A two hour trip to the abattoir does not affect glycogen stores (Fernandez *et al.* 1992b). The postmortem metabolism is dependent on the time at which stress occurs before slaughter (Fernandez *et al.* 1992a).

The glycolytic potential values obtained in this study (Table 17) were much lower than those generally reported in LD, for instance: 172 μmol g^{-1} in Large White and 301 μmol g^{-1} in Pen Ar Lan (Marinova *et al.* 1992), 136 μmol g^{-1} in Large White and 229 μmol g^{-1} in Hampshire (Monin & Sellier 1985). The glycogen content of pigs at 45 min postmortem in this study was at the same level as in studies of Fischer & Augustini (1977) and Klont *et al.* (1993), but a little lower than in the studies of Honkavaara (1989) and Monin & Sellier (1985). Reasons, which may explain lower glycolytic potential values in this study, are differences in sampling place and procedure, different determination method used in this study than in the other studies, the level of stress or genetic background. Landrace, Yorkshire, Hampshire, and DYL had fasted longer than HYL, LYL, and YYL. The glycolytic potential was higher in Hampshire than in the other breeds, except for HYL and LYL. This is in agreement with other studies (Monin *et al.* 1987, Marinova *et al.* 1992). The glycolytic potential of Hampshire and Hampshire crosses is generally higher than that of other breeds. This is evident in "fast white" muscles, but not in "slow red" muscles (Monin *et al.* 1987).

Glycogen phosphorylase catalyzes glycogen degradation by transferring a glucose residue from the nonreducing end of the glycogen chain to inorganic phosphate. The activity of PHOS is related to the rate of postmortem glycolysis (Kraeling *et al.* 1975). In this study, only the total activity of PHOS was measured. There were a slight positive correlation between PHOS activity and CS or LDH activities (r_g 0.21 $p<0.001$ and 0.19 $p<0.001$ respectively). The activity of PHOS in Hampshire pigs was higher than in Yorkshire. Sayre and co-workers (1963) reported higher total PHOS activity in LD of Hampshire than in Chester White or Poland China. Monin and co-workers (1986) did not find any differences in total PHOS activity between Hampshire, Large White or HP and HN Pietrain pigs, but PHOS a activity was higher in Hampshire and HP Pietrain than in HN Pietrain. In halothane-positive animals, a higher degree of PHOS activity is related to a higher intracellular free calcium level compared to halothane-negative pigs (Cheah *et al.* 1984), because calcium activates phosphorylase kinase, which converts PHOS b to PHOS a. In Hampshire pigs, which show a normal rate of pH fall after death, PHOS is maybe activated by other mechanism, i.e. by stress-induced catecholamine release (Monin *et al.* 1986).

In this study, there was a positive correlation between the oxidative capacity of a muscle and its glycolytic potential. Also, the higher the activity of CS and HADH, the more glycogen was left in LD muscle at 45 min postmortem. These can not be explained by Hampshire breed, because the effect of breed was eliminated using Pearson's partial correlation procedure. It may be that if muscle is able to produce energy aerobically, it need not to use as much glycogen as when producing energy anaerobically. Lactate production yields two ATP molecules, as oxidization of pyruvate yields 38 ATP molecules (Lehninger 1982). The glycolytic potential is related to the metabolic type of muscle. It is lower in slow red muscles, like *masseter* and *trapezius*, than in fast white muscles, such as LD and white part of *semimembranosus* in the Hampshire cross Penshire (Monin *et al.* 1987). In Pietrain, Large White and Belgian Landrace, the glycolytic potential is similar regardless of muscle type. Unfortunately, only LD muscle was used in this study. Further research is needed to find out if the oxidative capacity and glycolytic potential as well as glycogen content are positively related to each other in different kinds of muscles.

The rate of enzymatic glycogen catabolism to lactic acid in muscle perimortally, i.e. immediately before, at or after animal slaughter, is of great importance to meat quality. Lactate dehydrogenase plays an important role in anaerobic glycolysis. The relative share of the different LDH isoenzymes correlates with the metabolic requirements of the tissue. In white muscle, there is a higher proportion of isoenzymes 4 and 5 as well as a lower proportion of isoenzymes 1, 2, and 3 than occur in dark muscle (Beecher *et al.* 1969, Hamm 1991). In this study, LDH-1 and LDH-2 were positively correlated with the activities of CS (r_g 0.24 $p< 0.001$ and 0.18 $p<0.01$, respectively) and HADH (r_g 0.21 $p<0.001$ and 0.18 $p<0.01$, respectively), while LDH-5 was negatively correlated with HADH activity (r_g -0.14 $p<0.05$) (Table 30). The correlations were small, but the direction was clear: the higher the activity of oxidative enzymes, the higher the proportion of LDH-1 and the lower the proportion of LDH-5.

The total LDH activity in the Duroc cross was higher than in most of the other breeds. However, the distribution of LDH isoenzymes in DYL was similar to that in Hampshires: a higher proportion of LDH-1 and LDH-2, as well as a lower proportion of LDH-5 than in the other breeds. Concerning the activity of LDH isoenzymes, the difference between the Duroc cross and other breeds was even clearer where isoenzymes 1, 2, and 3 were concerned. The LDH-5 activity was similar in the Duroc cross as in other breeds. The conversion of lactate to pyruvate is related to the amount of "heart" LDH isoenzyme in rats and rabbits (Stambaugh & Post 1966, Baldwin *et al.* 1978). The higher proportion of LDH-1 may play a role in lactic acid clearance before slaughter, when oxygen is available. In

postmortem muscle, when oxygen is not available, the amount of LDH-1 may not be of importance anymore. Then the ability of LDH to produce lactic acid is more important, and thus the activity of LDH-5 is significant. The lactic acid content of the Duroc LD was similar to that of the other breeds, although its total LDH activity was higher than in many other breeds or crosses. This may be explained by the higher activity of LDH-1 and LDH-2 in DYL pigs than in all other pigs. However, the LDH-5 activity was similar across breeds and crosses with the exception of Hampshire which had lower LDH-5 activity. In Hampshire, the lactic acid content was lower than in LYL, but equal to the other breeds. There was not any differences between Hampshire and the other breeds or crosses, except for DYL, in the activity of LDH-1 or LDH-2. Although, the activity of LDH-5 in Hampshire was lower than in many other breeds. However, it is not clear whether the small difference in the LDH isoenzyme pattern has any significant meaning in practice. On the other hand, red muscles, when compared to white ones, show PSE signs less frequently and the LDH isoenzyme distribution is different between these two muscle-types (El-Badawi & Hamm 1969). In PSE muscle and blood, the proportion of muscle type isoenzymes is higher than in normal animals (Charpentier & Goutefongea 1964, Addis & Kallweit 1969).

The proportion of LDH-4 was fairly constant in all breeds. There was no correlation between the total activity of LDH and isoenzyme distribution. Briand and co-workers (1981) have found that the greater the total LDH activity is, the higher the proportion of LDH-5, and the lower the proportions of LDH-1 and LDH-2 in sheep. The distribution of LDH isoenzymes was quite alike in Landrace, Yorkshire, and HYL.

Among Duroc crosses, there was variation in pH_1, lactate content and activities of PHOS, LDH, CS and HADH between progenies of different fathers (Tables 22 and 23). The DYL pigs were progenies of only four boars. There were two pairs of boars, which differed from each other in many properties measured. Those pairs lived at different places, one pair on the same farm and the other pair at another farm and one of the test stations. Nearly all DYL pigs were slaughtered in the same abattoir, only seven of 28 pigs from the other pair were slaughtered in a different abattoir. So the difference in pH_1 values between two boar groups in DYL can not be explained by slaughterhouse, but it may be inherited or dependent on variation in growth environments or both factors may have had an effect. The same is true for the differences in enzyme activity. One pair of boars produced progeny, which had lower activities of CS and HADH, higher activity of LDH, and lower lactate content than progeny from the other boar pair. The number of pigs in each of the progeny groups were rather low, so this needs further research.

There are more mitochondria and less sarcoplasmic reticulum in oxidative muscle fibers than in glycolytic fibers (Leeson & Leeson 1981). The amount of mitochondria is important to living cells, because citric acid cycle and fatty acid oxidation occur in mitochondria. Sarcoplasmic reticulum is important storage site for calcium. The rather high standard deviation values from the volume density of mitochondria in this study maybe caused by the heterogenity of muscle fiber structure, the difficulty in the determination of which fiber type V_{vmit} is counted from, the low number of counting places and the number of pigs used. The V_{vmit} was highest in Hampshire pigs, although the difference was statistically significant only when compared to YYL pigs. The high mitochondrial volume density of Hampshire fibers is in agreement with their high oxidative capacity. The amount of SR was similar in every breed or cross.

Landrace and Yorkshire were very similar in characteristics measured in this study, although there was a trend toward a higher oxidative capacity in Landrace than in Yorkshire. The results of discriminant analysis show, depending on properties taken into the analysis, that at least 70% of Landrace pigs have characteristics of the other breeds or crosses in this study. So there is a high inter-individual variation between Landrace pigs as a result of many muscle properties being examined together. In Yorkshire pigs, this inter-individual variation is also high, but not so pronounced as in Landrace breed. Thus, there is a lot of variation among traditional Finnish pig breeds in muscle properties studied, and this can be used to breed those breeds in the desired direction. The big difference between Hampshire and the other breeds or crosses in many muscle properties found in this study was also verified by discriminant analysis. Although standard deviations in HADH and CS determinations were highest in Hampshire pigs compared to the other pure breeds, most of Hampshire pigs were classified to their own breed. As was expected, a lot of Hampshire and Duroc crosses were classified to many other breeds or crosses. Only the LDH isoenzyme distribution seemed to differentiate most of DYL pigs from the other breeds.

6.2.2 Calcium uptake and release

Calcium concentration in the cytoplasma regulates the function and activity of a wide variety of tissues. In skeletal muscle, the main processes regulated by Ca^{2+} are thick and thin filaments interactions, glycogenolysis, mitochondrial oxidative metabolism and protein turnover. Elevated calcium level in sarcoplasma will activate muscle to contract or it may activate the phosphorylase kinase, the key Ca^{2+}-dependent enzyme of glycogenolysis, which results in an increased glycogen breakdown

(Louis *et al.* 1993). Cell death modifies the homeostasis of cell membrane fluidity, making the membrane more rigid (Rock 1993). This may be associated with enhanced calcium permeability.

Calcium is localized primarily in the skeletal muscle fiber sarcoplasmic reticulum and in minute quantities in the mitochondria (Pearson & Young 1989). However, Borgers and co-workers (1984) found calcium to be localized in the junctional SR of white skeletal muscle of rats as well as the sarcolemma and its T-tubular invaginations in red skeletal muscle of rats. The ability of muscle to regulate its sarcoplasmic Ca^{2+} concentration is due to the activity of specific Ca^{2+} pumps, transporters, and channels located in the surface membranes (sarcolemma and T-tubules), SR and mitochondria (Pearson & Young 1989). During muscle contraction, the SR is primarily responsible for the regulation of sarcoplasmic Ca^{2+} concentration. The relaxation rates of slow and fast muscles differ *in vivo*, as do the Ca^{2+} uptake capabilities of SR from these muscles *in vitro* in rats and cats (Briggs *et al.* 1977). It has been proposed that mitochondrial Ca^{2+} transport is required for regulation of mitochondrial enzyme activities rather than for the regulation of cytoplasmic Ca^{2+} (McCormack *et al.* 1981). The rate of calcium release from mitochondria correlates positively with the lactate content and drip loss (Cheah & Cheah 1979). Mitochondrial calcium release is also related to cold shortening in beef (Buege & Marsh 1975). The larger the cell's ability to accumulate calcium in the SR, the higher the pH_1 and the lower the drip loss are (Cheah *et al.* 1994).

Because the excessive amount of calcium in sarcoplasma may cause elevated glycogenolysis and energy utilization in muscle cell postmortem, the intensity of sarcoplasmic reticular and mitochondrial calcium uptake and release were determined in different breeds. Calcium uptake and release was similar in every breed and cross, except that uptake was higher in Hampshire than in YYL pigs 15 min after stunning in SR and higher in Landrace than in YYL or HYL pigs 15 min after stunning in MIT. So the faster postmortem glycogenolysis in LYL pigs as determined by lower pH_1 value and higher lactate content at 45 min after stunning may not be explained by elevated calcium metabolism in SR and MIT, although there was clear tendency toward high uptake and low release in the oxidative LD, but low uptake and high release in the more glycolytic LD. There was large variation between individual pigs within groups. So, it could not be proved any differences between breeds or crosses. Although, calcium uptake was lower in crossbreds than in purebred pigs in both SR and MIT. The calcium uptake and release from SR and MIT, as detected in this study, was a little lower than noted by Greaser and co-workers (1969a) in Poland China pigs (uptake), Cheah & Cheah (1976) in Pietrain, Poland China and Large White pigs (release) as

well as Condrescu and co-workers (1987) from the human muscles (uptake). The calcium uptake of SR, as detected by Robinson & Tombs (1981), was lower than that found in this study.

Stress-susceptible pigs have high sarcoplasmic Ca^{2+} levels. This may be due to increased calcium release from calcium stores (Cheah & Cheah 1976, Cheah *et al.* 1984). The three halothane genotypes (NN, Nn and nn) can be identified by measuring the Ca^{2+} accumulation capacity of SR (Cheah *et al.* 1994). Only one Yorkshire pig in calcium metabolism studies showed signs of PSE. Unfortunately, the halothane genotype of pigs in this study was unknown. Because of the very low incidence of halothane-positive Yorkshire and Landrace pigs in Finland as well as halothane-positive Hampshire and Duroc hogs in Sweden, it is clear that most of our pigs were halothane-negative. Both calcium uptake and release were quite low in that PSE-prone pig.

There was a slight positive correlation (r_g 0.34 $p<0.01$) between calcium release and uptake in SR samples taken 45 min after stunning. No other significant correlations were found between uptake and release.

The ability of SR and MIT to accumulate calcium decreases with time postmortem (Greaser 1974). There was no significant decrease or increase in calcium uptake or release 15-45 min postmortem in SR or MIT in any breed in this study.

6.2.3 Finnish Landrace and Yorkshire pigs which had higher activity of CS and HADH as well as a lower lactate level than the means

The interindividual variation in every breed or cross was marked in nearly every characteristic determined in this study. The results of discriminant analysis showed the populations of Landrace and Yorkshire to be very heterogeneous groups. Therefore, it was concluded that there may be individuals that have some characteristics similar to Hampshire. Landrace and Yorkshire pigs, whose CS and HADH activity was higher and lactate lower than means of those breeds, were selected and compared to Hampshires. Those selected pigs (ten Landrace and twelve Yorkshire) mimicked Hampshire in the activity of CS and HADH as well as in lactate content (Figures 11 and 12).

There were no differences in meat quality between the "better than means" pigs and the rest of the population, except that the pH_1 was higher in the "better than means" Yorkshire pigs than the other Yorkshire pigs, also the ultimate pH was lower in Landrace and higher in the Yorkshire "better than means" pigs than in the others. Kangasniemi & Honkavaara (1989) stated that because of the high interindividual variation in

Yorkshire and Landrace pigs, it would be possible to increase the intramuscular fat content of those breeds by selection. It also seems possible that breeding may be able to increase the oxidative capacity of Landrace and Yorkshire.

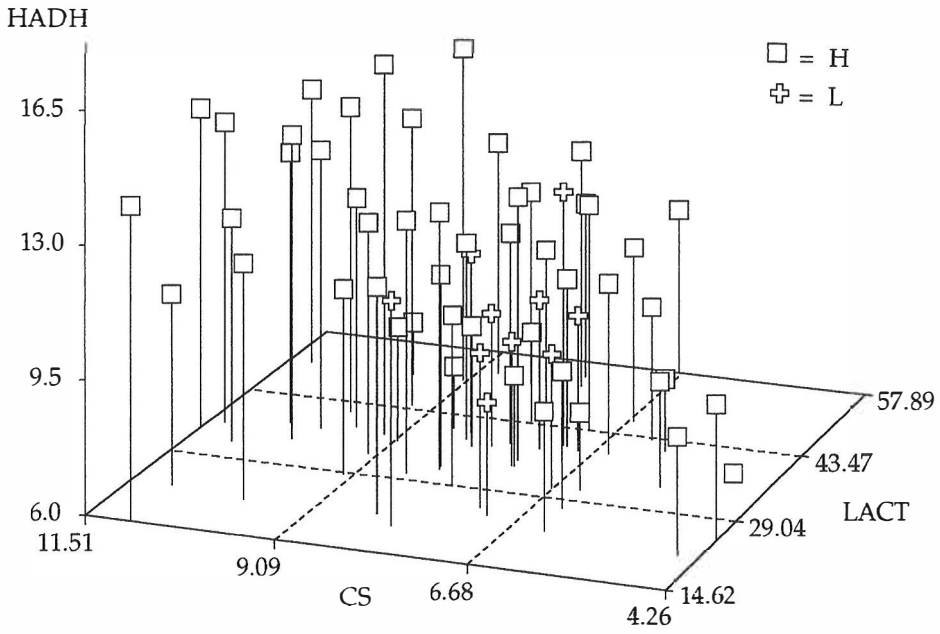

FIGURE 11 Landrace "better than means" pigs compared to Hampshires. CS and HADH U/g muscle; LACT µmol/g muscle.

6.3 Relationships between muscle biochemical properties and meat quality

Meat quality is related to perimortem muscle metabolism, which is influenced by both genetic and environmental factors. In pigs, *longissimus dorsi* is the most frequently used indicator muscle in meat quality studies. As mentioned earlier, this muscle has a low oxidative capacity and a high proportion of IIB fibers (Essén-Gustavsson *et al.* 1992, Ruusunen 1994). In this study, muscle biochemical properties were compared with meat flavor, juiciness, tenderness, color and drip loss.

Meat flavor did not differ between the various pig breeds or crosses, but Hampshire meat was more juicy than meat from the other

breeds, except that of HYL and DYL. Essén-Gustavsson & Fjelkner-Modig (1985) did not find any differences between the meat of Hampshire, Swedish Landrace or Yorkshire in flavor and juiciness, but Hampshire meat was more tender than meat from those other two breeds. In this study, Hampshire meat was also tender than meat of Finnish Landrace or Yorkshire.

This study found that if the glycolytic potential or glycogen content of muscle at 45 min postmortem was high, then the ultimate pH was low. If the glycogen content at 45 min postmortem was high, then the pH_1 was also high. The low ultimate pH means that much of the glycogen has been used, although the ultimate pH is also affected by muscle buffering capacity (Sellier *et al.* 1988). Glycogen depletion in

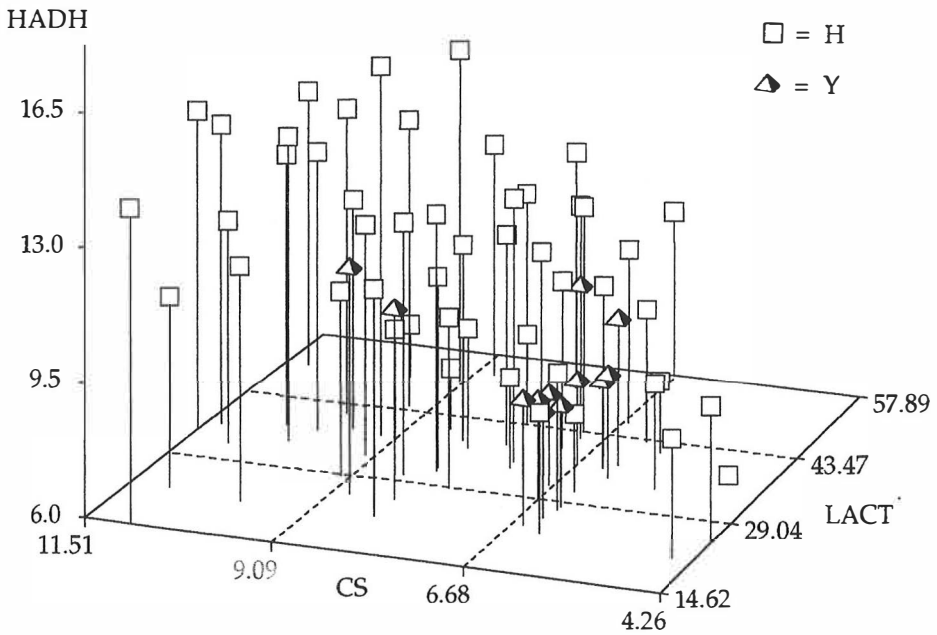

FIGURE 12 Yorkshire "better than means" pigs compared to Hampshires. CS and HADH U/g muscle; LACT µmol/g muscle.

muscle fibers, especially from IIB fibers, can impair the technological quality of muscle (Karlsson *et al.* 1993). The ultimate pH was the lowest in Hampshire and HYL. Low pH_u is typical for Hampshire or its crosses (Sayre *et al.* 1963, Monin & Sellier 1985, Barton-Gade 1988). The pH_u was negatively related to oxidative metabolism of the muscle. This disagrees

with Karlsson (1993) who found a positive correlation between oxidative capacity and ultimate pH. In this study, the pH_u was positively related to lactate content at 45 min postmortem. Although the correlation was low (r_g 0.12 $p<0.05$), it agrees with Hatton and co-workers (1972), who found that a build-up of lactate is not wholly responsible for the ultimate muscle pH.

Drip loss is related to the lactate content and pH value (Briskey & Wismer-Pedersen 1961, Essén-Gustavsson *et al.* 1992, Kocwin-Podsiadla *et al.* 1995). The low pH may activate both myokinase and adenylate deaminase which would produce IMP and ammonia, this may cause muscle cell membrane damage and lead to high drip loss (Honikel & Kim 1986). Drip loss and lactate content were the lowest in Hampshire and the highest in LYL pigs. Also, high glycogen content may increase drip loss. Unfortunately, the residual glycogen content of pigs in this study is unknown. In LYL pigs, pH_1 was lower than in most other breeds. The meat of LYL was paler than that of Hampshire, HYL or YYL. Also, meat of Landrace was paler than that of Hampshire. Monin & Sellier (1985) found Hampshire LD to be paler than that of Large White or halothane-negative Pietrains. However, the total LDH activity was similar in LYL than in Hampshire and HYL. Generally, increased muscle lactate caused lower pH_1 and higher drip loss.

This study showed that if the oxidative capacity or glycolytic potential of the LD muscle was high, the meat was redder in color than if they were low ($p<0.001$). The glycolytic potential had no correlation with meat flavor, juiciness or tenderness.

In this study, no correlation was found between tenderness and oxidative capacity of muscle, but the oxidative capacity was positively related to flavor and juiciness. Essén-Gustavsson and Fjelkner-Modig (1985) have suggested that the oxidative capacity of the muscle may be of importance for the tenderness rating. Calkins and co-workers (1981) found a positive correlation between fibers with a high oxidative capacity (αR and βR fibres) and tenderness in bovine muscles. Although the correlation coefficients in this study were low, the tendency was clear: oxidative characteristics of muscle improve meat quality.

The proportion of inherited properties and environmental factors to meat quality needs further research. However, if muscle functions properly, animals can handle more stress without producing meat of low quality. On the other hand, if animals are treated badly, no amount muscle function can guarantee good meat quality.

The results show that the seven breeds or crosses studied have advantages and disadvantages with respect to meat technological and sensory quality. Just as a high muscle glycogen content may have a negative effect on the technological quality of meat (Fernandez *et al.* 1991),

a low oxidative capacity may have a negative effect on the sensory quality of meat. Ruusunen (1994) found that good muscle quality does not necessarily lead to good carcass and meat quality. Barton-Gade (1988) concluded that crosses between Landrace and Large White are best for processing, whereas the use of Duroc and Hampshire as sire breeds is the best for fresh meat consumption, and lastly, it is difficult to find a breed which is ideal for all purposes.

6.4 Conclusions

1. There is a high inter-individual variation in every breed and cross in the oxidative and glycolytic characteristics of muscle fibers. This may provide opportunities for improving desired characteristics in the Finnish pig population by choosing the right pigs to breed.

2. Hampshire LD has a higher oxidative capacity and glycolytic potential than the other breeds or crosses. *Longissimus dorsi* from the three-way crosses do not differ significantly from Landrace and Yorkshire in the capacities measured in this study. Crossing with Hampshire or Duroc do not improve the oxidative capacity of Landrace and Yorkshire.

3. The higher the oxidative capacity of muscle, the higher its glycolytic potential is and the more glycogen is left 45 min postmortem.

4. The oxidative capacity of muscle is positively related to meat flavor, juiciness and red color. Glycolytic capacity has no correlation to sensory quality of meat.

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Yhteenveto (Résumé in Finnish)

Longissimus dorsi lihaksen oksidatiivinen ja glykolyyttinen kapasiteetti ja niiden yhteys lihan laatuun verrattaessa eri sikarotuja ja risteytyksiä

Tämä väitöskirja selvitti seitsemän eri sikarodun tai risteytyksen, jotka olivat Maatiainen, Yorkshire, Hampshire, Hampshire x (Yorkshire x Maatiainen), Duroc x (Yorkshire x Maatiainen), Maatiainen x (Yorkshire x Maatiainen) ja Yorkshire x (Yorkshire x Maatiainen), *longissimus dorsi* -lihaksen (LD), oksidatiivista ja glykolyyttistä kapasiteettia. Myös LD:sta eristettyjen sarkoplasmisen kalvoston ja mitokondrioiden kykyä sitoa ja vapauttaa kalsiumia mitattiin. Lisäksi selvitettiin näiden periytyvien lihaksen ominaisuuksien yhteyttä lihan laatuun.

Lihaksen oksidatiivisen kapasiteetin selvittämiseksi määritettiin sitraattisyntaasin ja 3-hydroksiasyyli-CoA-dehydrogenaasin aktiivisuudet ja mitokondrioiden tilavuusosuus. Lihaksen glykolyyttistä kapasiteetia varten määritettiin glykogeenifosforylaasin ja laktaattidehydrogenaasin (LDH) aktiivisuudet, maitohapon ja glykogeenin pitoisuudet sekä glykolyyttinen potentiaali. Myös LDH:n isoentsyymien prosenttiset osuudet mitattiin.

Maatiaisen ja Yorkshiren LD-lihakset muistuttivat suuresti toisiaan. Hampshire-kolmirodun LD:n laktaattipitoisuus oli matalampi ja Duroc-kolmirodun korkeampi kuin Maatiaisen ja Yorkshiren. Muissa ominaisuuksissa kolmirodut eivät eronneet Maatiaisesta ja Yorkshiresta. Hampshire-kolmirodussa oli suurempi glykogeenipitoisuus ja pienempi laktaattipitoisuus kuin Duroc-kolmirodussa. LDH-1:n osuus oli suurempi ja LDH-5:n osuus pienempi Duroc-kolmirodussa ja Hampshiressä kuin muissa roduissa tai risteytyksissä. LD oli selvästi oksidatiivisin Hampshiressä. Hampshiren glykolyyttinen potentiaali oli suurempi kuin muissa roduissa tai risteytyksissä, vaikka sen laktaattipitoisuus oli pienin. Sarkoplasmisen kalvoston ja mitokondrioiden kyky vapauttaa kalsiumia ja mitokondrioiden kyky sitoa kalsiumia oli suurempi puhtaissa roduissa kuin risteytyksissä.

Hampshiren ja Hampshire-kolmirodun loppu-pH-arvot olivat alhaisemmat kuin muissa roduissa tai risteytyksissä. Liha oli sitä punaisempaa, mitä suurempi oli lihaksen oksidatiivinen kapasiteetti ja glykolyyttinen potentiaali. Sen sijaan glykolyyttisellä potentiaalilla ei ollut vaikutusta lihan aistinvaraiseen laatuun. Lihan suurempi oksidatiivinen kapasiteetti näytti parantavan lihan makua ja mehukkuutta.

Tämä tutkimus koski vain yhtä lihasta, sian ulkofilettä, joten tuloksia ei voi yleistää koskemaan koko sikaa. Kolmirodut eivät

oleellisesti parantaneet LD-lihaksen ominaisuuksia verrattuna Maatiaiseen ja Yorkhireen. Sen sijaan Hampshiren LD-lihas oli selvästi oksidatiivisempi kuin muiden rotujen tai risteytysten. Lihaksen korkeampi oksidatiivisuus näytti parantavan lihan aistinvaraista laatua. Yhteenvetona tuloksista voidaan sanoa, että yksittäisten sikojen välinen vaihtelu oli suurta kaikissa roduissa tai risteytyksissä. Tämä saattaa antaa mahdollisuuksia jalostusvalinnalle.

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APPENDIX 1

Preliminary test. The activity of PHOS, HADH, LDH and CS (U/g muscle) in randomly chosen meat pigs (L, Y or their cross; right breed unknown) and in wild pigs. Samples were taken from longissimus dorsi at the level of the fourth and fifth ribs on the right side of the carcass. Mean values in the same column bearing the same superscript are statistically different, k $p<0.001$. Values are ± SD. PHOS=glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH=lactate dehydrogenase; CS=citrate synthase.

Breed (n)	PHOS	LDH	HADH	CS
meat pigs[1] (10)	6.8±1.4[k]	827±269[k]	6.0±2.4[k]	4.9±1.4[k]
wild pig[2] (4)	20.2±5.7[k]	1482±71[k]	19.7±1.8[k]	16.8±1.1[k]

[1]Pigs were slaughtered in Helsingin kaupungin elintarviketukkukaupan keskuksen teurastamo, Helsinki.
[2]Pigs lived and were slaughtered at Erkki Aaltonen's wild pig farm in Pukkila.

APPENDIX 2

Preliminary test. The activity of PHOS, HADH, LDH and CS (U/g muscle) in one meat pig (breed unknown). Samples were taken from longissimus dorsi at the level of the fourth and fifth ribs on the right side of the carcass four days before slaughter, after bleeding, one hour after stunning and twenty hours after stunning. PHOS=glycogen phosphorylase; HADH=3-hydroxyacyl-CoA-dehydrogenase; LDH=lactate dehydrogenase; CS=citrate synthase.

Sampling time[1]	PHOS	LDH	HADH	CS
biopsy	-	1071	7.1	4.2
after bleeding	13.3	1900	7.1	5.0
1 hour	11.5	1757	8.1	5.8
20 hours	13.6	1757	8.1	6.1

[1]The pig was slaughter in the slaughterhouse at the University of Helsinki/Department of Food Technology, Meat Section.