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EXERTIONAL MYOPATHY IN FINNISH LANDRACE PIGS A SURVEY OF THE SITUATION AND EVALUATION OF DIFFERENT CONTROL METHODS.

Selostus: Stressilihasrappeutuma suomalaisessa maatiaisrodussa
– selvitys tilanteesta ja eri menetelmien käyttökelpoisuuden arvioiminen.

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To be presented with the permission of the College of Veterinary Medicine for public criticism in Auditorium Maximum, Hämeentie 57, Helsinki 55 on April 3 th 1981 at 12 o'clock noon.

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Preface

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CONTENTS

ABBREVIATIONS

CK	= Creatine kinase (EC 2.7.3.2.)
Phi	= Glucosephosphate isomerase (Phosphohexose isomerase) (EC 5.3.1.9.)
L	= Landrace
Y	= Yorkshire
MH	= Malignant hyperthermia
WHC	= Water-holding capacity of meat
DFD	= Dark firm dry
PSE	= Pale soft exudative
PSS	= Porcine stress syndrome
μkat/l	= Microkatal/litre (enzyme activity)
U/l	= International unit/litre (enzyme activity)
pH_1	= Meat pH 25–45 min after slaughter
pH_2	= Meat pH 24 h after slaughter

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Abstract. The exertional myopathy situation is surveyed for the top of the breeding pyramid of the Finnish Landrace breed by testing 2,003 pigs and from material on the Norwegian Landrace (86 pigs). The usefulness of the different methods as well as practical measures with regard to the breeding programme are discussed.

The halothane sensitivity frequency in the Finnish Landrace breed was found to be 12.4 %, indicating that about 58 % of all Finnish Landrace pigs at the top of breeding pyramid have the halothane sensitivity gene (Hal^n). In contrast, a frequency of only 3.2 % was found in the Norwegian material.

Of the Finnish Landrace pigs 60.7 % had the H blood group factor a, 38.0 % factor c and 16.7 % none of these factors. In the Norwegian material 62.0 % had factor a and 55.6 % factor c.

Of the Finnish hal+ pigs 91.1 % had the H blood group factor a and 3.2 % factor c, while 6.1 % had none of these factors. About 96.6 % of the hal+ pigs had the Phi enzyme type BB and 3.4 % the Phi-type AB. None of the Phi-type AA pigs were sensitive to halothane. Phi AA was found to be rare in the Finnish Landrace, with only 1.5 % of the animals having this Phi type.

The water-holding capacity measurements from muscle biopsies taken from the pigs at the end of the halothane test did not show statistically significant differences between groups of hal+ and hal– pigs.

It was concluded from the results of the present study that the measurement of CK serum activity in non-stressed pigs is not very useful for identification of the heterozygotic carriers of the Hal^n gene. The iterativeness of the CK test in non-stressed pigs was found to be poor, but muscle tissue might have infected some of the serum samples taken from the vena cava and so caused false high serum CK activity. The halothane test is reliable for the identification of Hal^n gene homozygotes when conducted on pigs older than 50 days. The Phi AA type is so rare that Phi enzyme typing in Finland is of limited value at present for the breeding programme.

A determination of the H blood group factors a and c of all pigs intended for breeding is advised. By increasing the number of pigs with the H blood group factor c it should be possible to reduce the exertional myopathy problem in the Finnish Landrace breed. Preferential use of the desirable genotype c of the H blood group system should be more attractive to breeders than selecting against the undesirable H blood group factor a, especially as many of the H a/a and H a/ pigs have a high K index and a high percentage of lean meat on the carcase. The best a/a and a/ pigs may be kept as breeding animals but have to be mated only to H c/ pigs. Because some H c/ pigs are carriers of the Hal^n gene and a high K index and percentage of lean meat on the carcase favour carriers of the Hal^n gene, it is most probable that the existing low frequency of H c/ pigs sensitive to halothane will change in the future in an unfavourable direction. It is therefore advisable to stipulate a halothane test based on a progeny test for all H c/ boars with a high K index. Halothane-sensitive sows would be especially suitable for these test matings.

I Introduction

Low stress resistance in pigs causes economic losses in pig production; when pigs are exposed to unusual environmental strain, unexpected death may occur. The cause of death can be the result of both physical and psychic strain (LUDVIGSEN 1954, RYLCKER 1968, JÖNSSON 1978, and JOHANSSON and JÖNSSON 1979). Death can occur for example during the transport of pigs to the slaughterhouse, in the slaughterhouse or when moving breeding pigs from one piggery to another. The strain of a fight can kill a pig, boars may die in mounting and sows in delivery. The effect of a high ambient temperature is also important according to WENIGER et al.

(1970), ELIZONDO et al. (1976), ANDRÉN (1977) and MALMFORS and NILSSON (1979).

Some pigs are unable to adjust to these conditions. Their muscle glycogenolysis or anaerobic metabolism increases, resulting in acidosis in which large amounts of lactic acid accumulate in their muscles. A tonic cramp is induced in muscles and the body temperature increases uncontrollably. This malignant hyperthermia (MH) and the whole complex of symptoms, called the porcine stress syndrome (PSS), is fatal, often leading to death within 10–30 minutes TOPEL et al. (1968). Physical and psychic strain causes necroses in heart muscle, which could be the final cause of death (JÖNSSON et al. 1974, JOHANSSON et al. 1974 and JÖNSSON et al. 1980). The pathogenesis of both MH and PSS has so far not been fully elucidated. Numerous theories have been put forward, and the common denominator for the primary cause of death is believed to be difficulties in mitochondrial oxygenation. This probably stems from either a defect in the internal enzyme activity of cells or a deficiency in the external hormonal function. Low stress tolerance is related to a reduced aerobic capacity (STEINHARD et al. 1974, OLLIVIER et al. 1975 and many other researchers reviewed by BICKHARDT et al. 1977 and LUDVIGSEN 1980). According to LISTER et al. (1976), the temperature rise was mainly induced by aerobic metabolism in the muscles and only to a lesser extent by anaerobic combustion.

The mitochondrial calcium metabolism was disturbed (BRITT et al. 1975 and VAN DEN HENDE 1978).

OLLIVIER et al. 1975, SMITH and BAMPTON 1977, WEBB and SMITH 1977 and SCHMITTEN and SCHEPERS 1979 reported that the cause of stress susceptibility was due to an autosomal recessively inherited gene, which had an almost complete penetrance. MINKEMA et al. (1976), ANDRÉN (1977), MABRY (1978) and SCHNEIDER et al. (1980) believed that the penetrance was complete. WEBB (1981) summarised the investigations to obtain an 0.89 penetrance. When death is caused by MH/PSS the muscles become pale, soft and watery. The result is degeneration of the stressed muscles or PSE meat (LUDVIGSEN 1954). According to LANNEK (1975), PSE is the postmortal state of PSS. RYLCKER (1968) showed that physical training tends to prevent the development of PSS.

In the meat industry it has long been known that colour and water-holding capacity of meat vary considerably in relation to the preslaughter treatment of the animal (EIKELENBOOM and SYBESMA 1968, BUTTENSCHØN 1980). A physically exhausted pig with depleted glycogen depots yields meat with a high pH, a dark colour and a dry, almost jelly-like structure (DFD meat) because of high water-holding capacity. If the pig has ample glycogen depots at the time of slaughter and is exposed to an overwhelming variety of stressors, a rapid postmortal pH decline may ensue. The result will be meat with a low pH and a pale colour and wet structure PSE meat (WISMER-PEDERSEN 1979).

The formation of PSE meat is a typical quality defect in the pig and depends on weak adjustability of muscle cells (VAN DEN HENDE et al. 1978). The disposition of the pig to develop PSE might depend on low adenosine triphosphatase activity at pH 6.7 in comparison to that of other slaughter animals. Other animals have a more efficient aerobic metabolism than pigs (BENTLER 1972). This meat quality defect depended 40–50 per cent on inheritance. These results have been summa-

rised by SCHEPER (1979).

If meat quality is not considered in breeding it will become poorer because of a positive correlation between the amount of meat and poor meat quality (LUNDSTRÖM 1975, JENSEN 1978a, MALMFORS and NILSSON 1979). This correlation, however, is not so strong that the quantity of meat cannot be increased without imparing the quality (STAUN and JENSEN 1971, LUNDSTRÖM 1975, MALMFORS and NILSSON 1979).

In addition to genetic characteristics, physical and mental stress as well as external circumstances will affect the slaughter quality of meat (SCHEPER 1979). According to SCHEPER (1979), the weather on the day of slaughter or on the day before slaughter will produce a 10 per cent effect on meat. The transport distance and the handling of the animals at the slaughterhouse before slaughter account for 15–57 per cent of PSE/DFD occurrence (SCHEPER 1971, MALMFORS and NILSSON 1979, NIELSEN 1980). A short preslaughter treatment is followed by ample PSE and a long by DFD quantity, depending on the fluctuation in the meat energy storage at the time of slaughter (WISMER-PEDERSEN 1979 and LISTER 1979).

Pale soft exudative (PSE) muscle death during transport and other exertional stress situations and the porcine stress syndrome (PSS) are all caused by the fact that in stress circumstances energy requirements in muscle are primarily met by conversion of glycogen to lactate. Both phenomena should therefore be grouped under *exertional myopathy* as proposed by BICKHARDT et al. (1972). The frequency of exertional myopathy varies greatly according to breed. The syndrome is most common in the Pietrain breed and occurs more often in the Landrace breeds than in the Yorkshire or Hampshire breeds (WEBB 1980a). When the genotype component is large, the weakness can be diminished by breeding when suitable methods are available, by which individuals with undesired hereditary characteristics can be recognized. A number of such methods have been developed and proposed for inclusion in breeding programmes (CHRISTIAN 1972, RICHTER et al. 1973, CASSENS et al. 1975, RASMUSSEN and CHRISTIAN 1976, BICKHARDT 1979, ANDRESEN 1980b, MCGLOUGHLIN 1980, ALLEN et al. 1980 and SYBESMA 1980).

II Purpose of the present study

This study endeavours to

1. test the validity of some different methods for identification of stress-susceptible pigs and pigs which produce meat of poor quality (PSE/DFD),
2. clarify the frequency of exertional myopathy in pigs at the top of the breeding pyramid of the Finnish Landrace pig using the most valid methods available, and
3. propose methods allowing improved stress resistance and meat quality in the breeding of the Finnish Landrace pig irrespective of other important breeding aims.

III Literature review of methods used for the identification of stress-susceptible pigs and pigs with poor meat quality (PSE/DFD)

1. The halothane test

HARRISON et al. (1969) showed that halothane anaesthesia produced hyperthermia and depletion of muscle adenosinephosphate in stress-susceptible pigs. The halothane reaction has subsequently been used to predict the porcine stress syndrome (PSS) and the associated condition of pale soft exudative meat (PSE) (HARRISON et al. 1969, SYBESMA and EIKELENBOOM 1969, HARRISON 1972, EIKELENBOOM and MINKEMA 1974 and WEBB 1980b). The MH/PSS symptoms usually begin within two minutes after administering anaesthesia. WEBB (1980b) concluded that narcosis lasting at least three minutes was sufficient for the test. The most common symptoms are very typical. The body temperature rises, lactic acid accumulates in the muscles followed by acidosis, the pig contacts hyperthermia and a strong, usually tonic cramp. Death results if the anaesthesia is not discontinued quickly after the onset of the symptoms (HARRISON et al. 1969).

When narcosis is interrupted before MH/PSS becomes irreversible the pig will recover rapidly from narcosis. As a result the halothane test can be used to identify stress-sensitive hogs. The halothane test is comparatively harmless. EIKELENBOOM (1977) established that only 0.68 % of all tested animals died in the course of the test. The dead test animals developed MH to such an extent that a threshold was probably passed beyond which the process was irreversible. ANDRÉN (1977) reported that in his tests on more than 2,000 Swedish Landrace pigs 15 % reacted to halothane, causing the death of five animals. According to SCHNEIDER et al. (1979) three per cent of the halothane-sensitive pigs died in the test.

The iterancy of the halothane test is good. WEBB and JORDAN (1978) verified a 5 % error in repeated tests compared to 9 % by WEBB (1980b). ANDRÉN (1977) observed that the iterancy was also good in Sweden, although occasionally a repeated test produced results aberrant from previous tests. CHRISTIAN (1972) established that the halothane test seemed to be more than 90 % accurate in diagnosing PSE. ELDIK (1975) stated that the feeding of test pigs ad libidum or with a restricted diet did not affect the results of the test.

The specific mechanism of the action of halothane in triggering the syndrome is by no means clear (LISTER 1979). The site of action of halothane appears to be within the skeletal muscle itself (BRITT and KALOW 1970, MOULDS and DENBOROUGH 1974). According to KITTLER and DZAPO (1978), the halothane reaction does not correlate with the general vitality of the animals, but does with meat quality. Smaller litters were in any case borne to halothane-positive sows. WEBB and JORDAN (1978) observed that the piglets of halothane-sensitive pigs were inferior to those of halothane-resistant pigs. The halothane test has been applied by numerous researchers in many countries to different pig breeds (ALLEN et al. 1970, OLLIVIER et al. 1976, EIKELENBOOM and MINKEMA 1974, ANDRÉN 1977, FRØYSTEIN et al. 1977, WEBB and JORDAN 1978, MABRY 1978, GERWIG et al. 1979, MCGLOUGHLIN et al. 1979, SCHNEIDER et al. 1979, WEBB 1980a, EIKELENBOOM et al. 1980, GINDELE et al. 1980,

SCHÖNNICHSEN et al. 1980, BAUMGARTNER et al. 1980 and EIKELENBOOM 1981).

WEBB (1981) has drawn up a table based on the results obtained by several investigators showing the fluctuation in halothane reactivity in different breeds (Table 1). Halothane-sensitive pigs differ from pigs not reacting to halothane in many traits related to performance. Pigs possessing the halothane gene (Hal^n) have more frequently comparatively more meat on their carcases than do pigs lacking this gene (EIKELENBOOM et al. 1978a, MABRY 1978, GERWIG et al. 1979, LUNDSTRÖM et al. 1980, SCHNEIDER et al. 1980). WEBB (1980b) has also summarised results obtained by a number of investigators regarding differences in performance traits in halothane-sensitive and halothane-resistant pigs (Table 2). WEBB (1980b) established that the halothane test should be conducted on pigs of 7 weeks of age or older. In younger pigs the test reveals a lack of halothane sensitivity.

Table 1. Summary of some reported incidences of positive halothane reaction in world pig breeds (ranked by incidence) (WEBB 1981)

Breed	Number of studies	Number of pigs tested	% halothane positive (HP)	Author* reference
Duroc	3	248	0	3,15,22
British Large White	1	764	0	21
American Yorkshire	1	225	0	22
French Large White	1	168	0	8
Australian Large White	1	140	0	13
Irish Large White	1	58	0	14
American Hampshire	2	232	2	15,22
Dutch Yorkshire	2	1394	3	4,15
Irish Landrace	1	168	5	14
Australian Landrace	1	206	5	13
Norwegian Landrace	2	576	5	7,22
Swiss Large White	1	1130	6	18
Danish Landrace	2	1990	7	9,10
Slovak White Meat	1	112	9	3
German Landrace (GDR)	1	300	10	1
British Landrace	1	1538	11	21
Swiss Landrace	1	7480	13	17
Swedish Landrace	1	1668	15	2
French Landrace	1	127	17	8
Dutch Landrace	3	4073	22	4,6,15
French Pietrain	1	335	31	16
German Landrace	2	1251	68	11,20
Belgian Landrace	5	1260	86	3,4,8,12,19
German Pietrain	1	266	87	19
Dutch Pietrain	1	101	94	5

* References: (1) Albrecht et al. (1977); (2) Andrén and Persson (1977); (3) Bulla et al. (1979); (4) Eikelenboom et al. (1976); (5) Eikelenboom et al. (1978a); (6) Eikelenboom et al. (1980); (7) Frøystein et al. (1979); (8) Guerin et al. (1980); (9) Jensen (1979; (10) Jørgensen (1979); (11) Kallweit (1979); (12) Lampo (1978); (13) McPhee et al. (1979); (14) McGloughlin et al. (1979); (15) Minkema et al. (1976); (16) Ollivier et al. (1978); (17) Schneider et al. (1980); (18) Schwörer and Blum (1979); (19) Sönnichsen et al. (1980); (20) Wagner and Pasterling (1977); (21) Webb (1980a); (22) Webb and Jordan (1978).

Table 2. Differences in performance between halothane positive (hal +) and negative (hal −) pigs of different breeds (WEBB 1980b)

Production trait	Number of studies	Range* of reported differences hal + − hal −		Author reference[x]
PSS traits				
Post weaning mortality (and transport losses) %	3	4 7 to 10 3	W	1, 2, 3
PSE (% carcases affected)	2	22 to 41	W	1,3
Growth traits (from approx 25–95 kg)				
Growth rate (g/day)	5	0 to −45	W	1, 2, 3, 4, 5,
Daily food intake (g/day)	3	0 to −460	W	1, 2, 3
Food conversion ratio (food/live-weight gain)	5	0 to −0 30	B	1, 2, 3, 4, 5
Carcase traits (at approx 95 kg live-weight)				
Lean content (%)	5	2 3 to −0 30	B	1, 2, 3, 5, 6
Average backfat (mm)	6	0 8 to − 21	B	1, 2, 3, 4, 5, 6
Carcase length (mm)	6	0 to − 29	W	1, 2,3,4,5,7
Killing out %	4	0 to 0 8	B	1,2,3,5
Ham proportions (%)	5	0 to 1 0	B	1,2,3,4,7
Eye muscle area (cm^2)	3	0 to 3 4	B	1,3,4
Litter productivity				
Number born alive	1	−16	W	1
Piglet weights at 56 days (kg)	2	0 to − 2 6	W	1,3
Male reproductive performance				
Time to mount (minutes)	1	5	W	3
Ejaculate volume (ml)	1	−46	W	3

B and W indicate hal + better or worse than hal −

* Zero indicates that at least one study found no statistically significant difference

x Reference

1. Webb and Jordan (1978)
2. Eikelenboom (1977)
3. Christian (1977)
4. Wagner and Pasterling (1977)
5. Verstegen and others (1976)
6. Vögeli (1978)
7. Monin and others (1976)

Several investigators have shown that halothane-sensitive pigs also sustain other strains and that they more frequently develop PSE meat (EIKELENBOOM and MINKEMA 1974, ELDIK 1975, ANDRÉN and PERSSON 1977, WEBB and JORDAN 1978, EIKELENBOOM et al. 1978b, JENSEN 1978a, MABRY 1978, WEBB 1980a, BRASCAMP et al. 1980). Mortality during the fattening period and the transport of the animals to the slaughterhouse was nearly ten times higher in

hogs reacting to halothane than in Dutch Landrace pigs with no reaction to halothane (5.27 % vs 0,56 %). Of those reacting to halothane, 83 % developed more or less clearly PSE meat as opposed to only 36 % of the hogs not reacting (EIKELENBOOM et al. 1978b). According to JENSEN (1978a), Danish Landrace halothane-positive pigs had paler meat than halothane-negative pigs, the meat quality measured in KK value being 1.49 units lower. EIKELENBOOM et al. (1978a) proposed that the halothane test was most effective for minimization of stresssusceptibility and abnormal meat quality in the breeding and selection of Dutch Landrace pigs. This may not hold true for the Yorkshire breed, however. In the Yorkshire breed no correlation was found between halothane sensitivity and poor meat quality. MARBY (1978) showed experimentally that the same conditions applied to the Yorkshire breed as to Landrace hogs. Halothane-sensitive pigs produced smaller litters than the halothane-resistant pigs, and piglet mortality was greater for halothane-sensitive than for halothane-resistant sows (SCHNEIDER et al. 1980).

2. Exercise tests

Poor stress resistance is most commonly revealed through the strain caused by transport. Many different forms of transport have been experimented with in investigating exertional myopathy. Test pigs have been transported over short and long distances and for different lengths of time in different temperatures, and have also been exercised on tread mills. The consequences of this strain has been analysed by determining blood enzymes which indicate the slaughter quality of the meat or by examining the meat after slaughter. Strain, its duration and temperature all act to affect the quality of meat to a great extent (RYLCKER 1968, RICHTER et al. 1976, ELIZONDO et al. 1976, LÖVE et al. 1977, KALLWEIT and FEHRENTZ 1977, LUNDEHEIM 1977, BICKHARDT 1979, PERSSON et al. 1979, MOSS 1979, BICKHARDT et al. 1980, BUTTENSCHØN 1980).

No single applicable exercise test specially designed for breeding programmes has been developed, but examinations have demonstrated that standardizing the strain before testing is essential in order to reveal the significance of pig genotype when using blood enzyme activities or meat quality as measurement tests (BICKHARDT 1970, BARTON et al. 1977, JENSEN 1978b, PEDERSEN 1979, MOSS 1979, PFEIFFER et al. 1979).

3. Blood group systems

A survey of immunogenetics and biochemical genetics as tools in pig breeding is presented by GAHNE (1979), and the blood groups of pigs and their determinations are summarised by ANDRESEN (1963). The association between genotypes of the H blood group system and the porcine stress syndrome as detected by the halothane test was discovered by RASMUSSEN and CHRISTIAN (1976) and has been confirmed by many other workers (e.g. HOJNY et al. 1979, IMLAH and THOMSON 1979, ANDRESEN 1980b, ANDRESEN and JENSEN 1980, JÖRGENSEN 1980a). Investigations by JENSEN et al. (1976) and BARTON et al. (1977) have indicated association between genotypes of the H blood system and the porcine meat colour

score. The results show a significant correlation between inferior meat quality and the presence of the H^a allele. However, since PSE and PSS do occur in H (a—) and H—H— individuals no direct causal relationship appears to exist between the H^a allele and exertional myopathy. The frequency of the H^a allele is lower in the Yorkshire breed that in the Landrace breed. The meat colour was also darker for the Yorkshire than for the Landrace breed according to IMLAH and THOMSON (1979). There was a clear relationship between the H^a allele and the colour index in Landrace pigs. Individuals with H^a had a 13.4 % poorer meat colour compared to the mean value, but this correlation could not be significantly demonstrated in the Yorkshire breed (IMLAH and THOMSON 1979). MABRY (1978) on the other hand showed that a relationship between poor meat colour and the halothane reaction and H blood groups existed in Yorkshire pigs. The relationship between halothane positivity and the H^a allele also depended on the A blood group system (JØRGENSEN et al. 1976, MABRY 1978, IMLAH and THOMSON 1979). In H a/a pigs, which were devoid of the A system factors A and O, and in H —/— pigs, which had either A or O, a clear relationship to PSS was defined by the halothane test. MABRY (1978) found that two blood types, (+, —/—) and (—, a/a), were consistently stress susceptible, while three blood types, (+, a/a), (+, a/c) and (+, c/), were stress resistant. One blood type, (+, a/—) contained, however, both stress-susceptible and stress-resistant individuals, (+) indicating hemolysis for either A or O. MABRY (1978) also discovered that stress-susceptible animals were inferior in reproductive ability, mothering ability and preweaning growth, and that stress-positive animals were significantly more heavily muscled with larger eye muscle areas. In addition, stress susceptibility had a negative effect on muscle quality as positive pigs exhibited significantly paler colour, less marbling and greater transmission values compared to stress-negative animals. It was possible to predict correctly 84.1 % of the stress-susceptible and 79.6 % of the stress-resistant pigs using blood group factors in the H and A blood group systems (IMLAH and THOMSON 1979). According to JENSEN et al. (1976), the H^a allele could explain about a quarter of the PSE problems in Danish Landrace pigs. Results obtained with one Landrace breed cannot be directly applied to another Landrace breed. MAJOR (1968) investigated blood relationships between different populations of Landrace pigs in Denmark, the Federal Republic of Germany, Holland, Hungary, Sweden, Czechoslovakia and the Soviet Union and found differences between all these populations. He distinguished between two different subgroups, one consisting of the Landrace of Germany, Holland and Hungary and the other of Danish, Swedish, Czechoslovakian and Soviet Landrace.

4. Glucosephosphate isomerase (Phi) types

The PSS detected by the halothane test seems to be associated with the polymorphic erytrocytic enzyme system glucosephosphate isomerase (EC 5. 3. 1. 9.) (JØRGENSEN et al. 1976). This enzyme is defined by two codominate alleles (A and B) which produce three different phenotypes (AA, AB and BB). JØRGENSEN et al. (1976) showed that Phi^{BB} was present in all halothanepositive Danish Landrace pigs. JØRGENSEN (1977) additionally demonstrated the connection between the halothane reaction, the H blood group and Phi. ANDRESEN (1971), ANDRESEN and JENSEN 1977) and JØRGENSEN (1980a) showed that all these

loci are present in the same chromosome and are closely linked to each other. The Hal locus is situated between the Phi and H^a loci (ANDRESEN 1980a). In breeding, these characteristics are uncomplementary, but in fact they measure the same trait from different dimensions (JENSEN 1978b). It has been shown that in the Danish Landrace breed, pigs having the poorest meat quality were within the group of animals having both H^a and Phi^{BB} at the same time (JENSEN 1978a and b, and ANDRESEN and JENSEN 1979). ANDRESEN (1980b) found that by using the H system and the Phi system parallelly in breeding, the meat quality in Danish Landrace pigs could be improved without needless loss of many H^a pigs. Phi^{BB} is, however, so common in the Danish Landrace that it seems nearly impossible to eradicate it from this breed (ANDRESEN et al. 1979 and ANDRESEN 1980c).

5. Creatine kinase (CK) test

Many serum enzymes such as creatine-kinase, lactic-dehydrogenase and glucose-6-phosphate have been tested and summarised by PFEIFFER et al. (1979). Greatest interest has focused on creatine-kinase (CK) (EC 2. 7. 3.2.) (UNSHELM 1971, ADDIS et al. 1974, BEERMAN et al. 1975, BICKHARDT et al. 1977, HWANG et al. 1978, BICKHARDT 1981). The CK activity in blood has to indicate muscle injuries very specifically, because it is found in abundance just in muscle tissue (BICKHARDT 1970, 1979 and 1981).

Many investigators have discovered a negative correlation between CK activity in serum or in the plasma of unstressed pigs and meat quality parametres (UNSHELM 1971, SCHMIDT et al. 1971, SCHMIDT et al. 1974, BEERMAN et al. 1975, WETTERMAN 1975 and WAX et al. 1975), but after standardizing strain the correlations were even higher than before for the same animals (BICKHARDT 1970, ELIZONDO et al. 1976 and HWANG et al. 1977). CK should be analysed about eight hours after standardized exercise (BICKHARDT and RICHTER 1980). The serum CK values achieved maximum levels 10—20 hours after physical strain or muscle injury (BICKHARDT et al. 1979 and STEINESS et al. 1978). The CK activity after standard exercise follows an approximately logarithmic distribution. An increase in CK activity after exertion was higher in pigs predisposed to exertional myopathy than in stress-resistant pigs (MAXWELL et al. 1976). It would seem that the increase in CK activity in plasma after physical exertion can be attributed to enzyme escaping from skeletal muscle, following metabolic disorders in the muscle fibers. There was no indication that increased CK activity in plasma was a result of intensified enzyme synthesis. CK activities found in serum were identical to those found in plasma (BICKHARDT et al. 1979). In pigs with manifested exertional myopathy where morphological evidence of degeneration and necrosis of the muscle fibers was documented, serum CK activities up to 333 μkat/l were observed for several days. Blood samples obtained from the vena cava were suitable for CK measurement, but the fact alone that the pig had to be held steady for the blood sample to be taken caused an increase in CK activity in the plasma on the order of 10 %, attributable to haemoconcentration (BICKHARDT et al. 1979). The CK activity determination and the reliability of the CK test in the investigation of pig exertional myopathy have been reviewed by BICKHARDT et al. (1977).

BICKHARDT et al. (1980) experimented with many different exertion tests

before measuring the CK activity and recommended the administration of 8 mg of neostigmine-atropine mixture parenterally before performing the CK test. Even this exertion test could cause the death of some stress-sensitive pigs. Earlier BICKHARDT (1970) considered that a walk of a distance of 100 metres and weighing the pigs 24 hours before the CK test represented suitable standardized strain.

The heritability of the CK activity in serum was about $h^2 = 0.3$. This was somewhat lower than the parametres measuring meat quality (FLOCK 1968). According to WATANABE et al. (1978), there existed only a small degree of correlation between serum CK activity in resting pigs and meat quality measurements. BICKHARDT et al. (1977) demonstrated that the phenotypic correlation between serum CK activities and meat quality parametres was $r = 0.4$. As a negative phenotypic correlation between the CK activity of dams and the meat colour score of their daughters ($r = 0.34$) was apparent, this test was used in a breeding programme for four years. The growth rate in pigs improved and the amount of back fat thickness diminished during this time without impairing the quality of meat (BICKHARDT et al. 1979).

The results of the CK activity determination from serum obtained by automatic enzyme analyses or with the Luciferase method were very consistent (ANTONIK 1977). Occasionally observed extremely high values in pigs might anyhow complicate the use of automatic methods in determining CK activities (BICKHARDT et al. 1977 and KALLWEIT et al. 1977). The heritability of the CK activity in serum was 0.73 for the Landrace pigs and 0.37 for the Yorkshire pigs, according to SCHWÖRER et al. (1980).

BORGMAN et al. (1978) showed that the feeding level of the pig did not affect the results. When the test material was grouped so that the halothane positive and negative or PSE meat producers and good meat producers were separated into groups, a large deviation could be observed within all groups. At the same time however, a significant discrepancy was observed in the mean values for the different groups in that the mean values for halothane-reacting and PSE meat producing groups were larger than those for the halothane-resistant or groups producing good meat (BICKHARDT et al. 1977 and HWANG et al. 1978). The serum CK activity was dependent on the age of the pig and its physical activity. At the age of 1—3 months it was relatively stable (BICKHARDT et al. 1977). The applicability of the CK test in distinguishing stress-resistant and stress-susceptible pigs improved, however, when determinations were iteratively conducted for the same animals (THORÉN-TOLLING 1980).

When the CK test is used in breeding, an elimination limit must be set. Because of the large fluctuation in CK values a constant problem will be the presence of both false positive and false negative results. The range of the elimination limit naturally depends on which of these results is more harmful. HWANG et al. (1978) established the elimination limit at 6.66 μkat/l in investigations of Pietrain hogs, because they obtained the mean value of 6.60 μkat/l for halothane-resistant Yorkshire pigs. BICKHARDT et al. (1979) set the elimination limit at 29.6 μkat. SCHMIDT et al. (1974) did not find clear relationships that would allow the CK test to be used as a predictor of meat quality in live pigs.

6. Meat quality measurements

At least three different procedures are available for measuring stressed meat. It is possible to determine meat colour, water-holding capacity or pH. The meat colour determination is the one most frequently used. It has been technically the easiest to apply in routine analyses as compared to WHC and pH determinations. The determination of pH itself is relatively simple, but the pH has to be measured within a specified period of time after slaughter, which can create some difficulty. The colour measurement correlates well to other meat quality characteristics, such as pH and WHC. Its heritability is relatively good, and there are some reliable determination methods available (JENSEN 1978a, LUNDSTRÖM et al. 1979).

Meat colour

The meat colour can be evaluated either subjectively (CLAUSEN and THOMSEN 1956) or measured by reflectometres currently in use. The reflectometre measures the amount of light reflected by the meat surface; the higher the reading, the lighter is the colour of the meat. The meat colour correlated inversely to the carcase meat content, which is why one-sided breeding for more meat impairs meat quality (JENSEN 1978a). The correlation was, however, not so good that the meat content could not be improved without impairing meat quality (JENSEN et al. 1967, STAUN and JENSEN 1971, LUNDSTRÖM 1975 and MALMFORS and NILSSON 1979). Meat colour is dependent on two factors, namely the amount of meat pigment and the structure of the meat. Poor meat structure is mainly due to PSE meat (JENSEN 1978a). According to the results obtained by many investigators, the heritability of meat colour varies between 0.05 (ALLEN et. al. 1966) and 0.55 (PEASE and SCHMITH 1965), the average being 0.3 (reviewed by JENSEN, 1978b). Danish researchers showed that the inheritability improved when meat colour was measured with pretreated meat. This pretreatment, or light curing, improves meat quality. This observation indicates that meat pigmentation depends more than meat structure on the genotype (JENSEN 1978). Danish investigators have developed a meat quality index called the KK value (BARTON 1974, PEDERSEN 1979). The KK value consists of colour readings from both fresh and cured meat, corrected when necessary with the pH measured 24 hours after slaughter (pH_2). The inheritance of the KK value was calculated to be 0.5 (VESTERGÅRD 1977). The meat colour reading correlated well to other exertional myopathy meat quality measurements (LUNDSTRÖM et al. 1979). Because many external factors, such as transport and the whole preslaughter treatment, also affect meat colour to a great extent, these must be standardized in the best possible manner (LUNDSTRÖM et al. 1979, BARTON 1974). Even the stunning method affects the meat quality of stress-susceptible pigs (WAL 1971, HAMM 1972). The standardization of preslaughter treatment for Danish test pigs has been summarised by Barton (1974).

1. On the day of slaughter pigs are fed a reasonable amount of feed but are not weighed.
2. Loading utilises a hydraulic pig lift.
3. Transport, lasting about 40 min., uses a specially-designed lorry equipped with a non-slip floor, partitions and mechanical ventilation.

4. After transport the hogs are brought directly to the stunning room without using electric whip or other means of force.
5. Stunning is performed with electricity on the floor.

In Sweden the meat colour reading was taken as a minimum value in breeding selection. Colour was measured at three different points from fresh cross-sections of the M. longissimus dorsi, and the mean reading value obtained was used as the meat colour reading. Since 1. 4. 1979 attempts have been made to eliminate the share of external factors affecting the meat colour readings by selectively using deviation instead of the total reading value. Sires of elite boars are allowed a maximum of three points deviation from the mean value, and sows seven points deviation from the mean colour value of animals slaughtered at the same time. The error caused by DFD meat is eliminated by evaluating the meat as PSE meat in the case that pH_2 is$\geqq$6.0 (LUNDSTRÖM et al. 1980).

Colour reading inheritability is high and it correlates excellently to the halothane test and blood group information. Parallel observations of the halothane test and blood group determination in breeding contributes only very little when compared to selection based solely on colour reading (JENSEN 1978b). In Denmark meat quality improvement has for this reason been based on the KK value alone since 1972 (PEDERSEN 1977 and JENSEN and ANDRESEN 1980).

Water-Holding capacity (WHC)

Wateriness is a characteristic property of PSE meat. This condition is not caused by large amounts of water but rather by reduced water-holding capacity (WISMER-PEDERSEN 1959). The poor water-holding capacity of PSE meat is a problematic quality property for the meat industry (PUOLANNE 1980). NIINIVAARA and POHJA (1953) observed that the meat water-holding capacity is dependent on the meat pH. The lower the pH from the isoelectric point of meat, the poorer is the water-holding capacity, and vice versa (VEIJOLA 1980).

Several methods have been developed to measure the meat water-holding capacity. WEISS (1967) and RYLCKER (1968) centrifuged the bulk of meat. According to WEISS (1967), the WHC heritability was 0.54 among boars and 0.26 among sows. WENIGER et al. (1970) obtained a value of 0.57 for boars and 0.59 for sows by using a compression and filter paper method developed by GRAU and HAMM (1953 and 1956). NIINIVAARA and RYYNÄNEN (1953), GROSHE et al. (1975) and LUNDSTRÖM et al. (1979) have also used the filter paper compression method.

According to ALLEN et al. (1966), the heritability value varied between 0.48–0.77 for the Duroc and Yorkshire breeds. STAUN and JENSEN (1971) obtained a heritability value of 0.14 for boars and 0.29 for sows when using the compression method. JENSEN et al. (1967) obtained a value of 0.63. In breeding the colour reading is more widely applied than the WHC determination, although the measurement of WHC should constitute a suitable criterion for the selection of meat quality (LUNDSTRÖM et al. 1979, MALMFORS 1981).

Meat pH determination

The pH of PSE meat was significantly lower than the pH of normal meat when pH was measured 25—45 minutes after slaughter. When measuring pH 24 hours after slaughter, no difference was found (TAYLOR 1966, JENSEN 1978a). When the pH was determined 3/4 of an hour after slaughtering a strong correlation between the pH and meat colour was observed. JONSSON (1965) established this correlation to be about 0.7. It was discovered that the same difference exists in meat pH of halothane-positive and halothane-negative animals as exists between normal and PSE meat (EIKELENBOOM and MINKEMA 1974). WISMER-PEDERSEN (1959) has proposed the term pH_1 for the pH obtained 45 minutes after slaughter and pH_2 for the pH obtained 24 hours after slaughter. Adopting a meat colour reading for the identification of PSE meat is useful but not for recognizing DFD meat (JENSEN 1978a). In DFD meat the pH drop is very small, even when compared to normal meat. The pH_2 of DFD meat is significantly higher than the pH_2 of both PSE and normal meat, i.e. $\geqq 6$. In breeding selection in general, pH_1 determination is substituted by meat colour measurements, but in addition to colour reading the pH_2 should be taken in order to recognize DFD meat. This is especially important when selection is based on mean values obtained from two to four test hogs slaughter estimations (JENSEN 1978b, KANGASNIEMI 1980). According to WISMER-PEDERSEN (1980), it was not possible to state exact pH limits for detection of PSE, normal and DFD meat.

IV Conditions in Finland

In pig breeding in Finland, it has been purposefully endeavoured for more than two decades to reduce the amount of fat, mainly the back fat thickness, while increasing the amount of lean meat on the carcase with the intention to gain more back meat and ham. At the same time, feed efficiency and growth rate has been emphasized (HYVÄRINEN 1980). Until 1971 experimental hogs were slaughtered immediately after transport to the slaughterhouse, but when PSE meat emerged as a problem, this practice was changed, and the pigs were allowed to rest overnight before slaughtering. The PSE problem has since been reduced (KANGASNIEMI 1974). More attention has been paid to the quality of lean meat since the beginning of 1960. In progeny testing meat colour was first measured subjectively from a fresh surface cut from the M. longissimus dorsi. Then a supporting meat colour scale was obtained. In Finland the British colour slide was used. Since 1972 the colour reading was published in connection with test results, but the meat colour was not included in the official breeding programme (PARTANEN 1980). Since the beginning of 1977 the colour reading has been measured from a M. longissimus dorsi fresh cross-section surface by reflectometre. The results obtained from colour readings have ranged from 20—60 points, where 40 points indicates borderline meat and more than 45 points PSE meat (KANGASNIEMI 1978). Meat from Landrace hogs is lighter and the dispersion of the colour reading is wider than meat from Yorkshire pigs. During the summer higher readings are obtained in slaughtering than during the winter. Seasonal differences have been of the same order of magnitude than differences in breed

(KANGASNIEMI 1978). The heritability based on metre readings was calculated to be 0.37. The genetic correlations between colour readings and carcase quality properties were verified from the same material to be −0.28 for the back fat thickness, 0.39 for the M. longissimus dorsi cross-section area and 0.36 for the percentage of meat on the carcase (KANGASNIEMI 1978).

The Finnish Animal Breeding Association's Section for Pig Breeding imposed a threshold limit for meat colour in the spring of 1977. At first the threshold was set at 41 points, but because colour readings obtained from groups produced during summer were remarkably higher than readings taken in the winter, the threshold was increased to 44 points. The threshold is currently 44 points, but for groups produced during summer it is 46 points (Anon. 1977 and 1978). From groups produced in 1977, 11,6 % of the Landrace and 0.7 % of the Yorkshire exceeded the colour reading point of 44 (KANGASNIEMI 1979). The test groups in progeny testing consist of four pigs, two castrated and two sows.

The colour readings for the test groups have deteriorated in both breeds during 1979 (KANGASNIEMI 1980). Sudden death of normal bacon hogs during transport and in slaughterhouses before slaughter is not infrequent. In 1978, 2,320 bacon bigs died at Finnish abbatours in this way. The same year 465 carcases were rejected because of PSE meat (Anon 1979b). Readings obtained with the reflectometre have not been corrected with pH_2 determinations. The importance of pH determinations has in any case been acknowledged, and investigations of including pH_2 in breeding programme judging was begun in 1980 (KANGASNIEMI 1980). According to Alho (1980), colour reading determinations from test pigs were occasionally taken on three hour old cross-cut meat surfaces. This delay might raise the colour reading because muscle myoglobin has probably partly changed to lighter oxymyoglobin (PUOLANNE 1980).

From the beginning of 1980 colour is measured immediately after the muscle has been cut, and from the beginning of 1981 measuring of pH_2 will be included in the programme (KANGASNIEMI 1980). Alho (1980) also verified that the transport distance for test hogs from progeny testing stations to slaughterhouses was roughly the same in five cases, but very short in one case (80 km versus 4 km). The pigs were kept in slaughterhouses overnight before slaughtering. The walking distance from the pen to the stunning area varied at different slaughterhouses. The greatest variations in pre slaughter treatment was due to the fact that in one slaughterhouse very many test animals were crammed together in the same pen, while in other slaughterhouses pens were more spacious.

Since 1977 the halothane test has been used at phenotype test stations (SALONEN 1980, PÄÄLLYSAHO1980). After this boars which have reacted to halothane have not been approved for AI use.

V Material and methods

The material was selected so that all Finnish Landrace elite breeders were requested to test pigs in litters from which breeding animals were to be chosen. The elite units were asked to choose new breeding animals for their own use only from tested animals during 1979. In Finland pig breeding takes place principally in elite units ap-

proved by the Finnish Animal Breeding Association. In 1979 there were 22 Landrace elite units. The breeding value of the animals is studied by performance testing at farms and by progeny testing at progeny testing stations. The AI boars are further performance-tested at special testing stations.

The halothane test was voluntary for pig breeders. The largest number of tested pigs in one herd consisted of 404 pigs from 75 litters, and the smallest of 16 pigs from three litters. With one exception, all elite units collaborated in the operation. The smallest elite unit was excluded on the grounds that in 1979 new sows were not chosen for its breeding purposes. In addition to the elite units, ten of the most important selected Landrace units participated. Of these, some sows left for the units' use were tested, but most were boars with a breeding value high enough to attract the commercial interest of elite units. Pigs from these same herds sent to testing stations for progeny testing were tested at the stations. In this way a direct comparison between results obtained in the field test and the slaughter quality properties of the same animals was obtained. Above all it was of great interest to compare the slaughter estimation values of meat colour readings and the percentage of lean meat on the carcase with the results of the field test. The final material consisted of 2,003 Finnish Landrace pigs selected from 21 Landrace elite units, ten Landrace selected units and three testing stations. In addition 63 Norwegian Landrace pigs from the Trondheim area were tested. This material was included for the reason that Norwegian Landrace pigs were brought from Norway with the intention to breed them with the Finnish Landrace breed. All pigs excluding those in progeny tests at pig testing stations were tested in the piggeries where they were born. The age of the pigs varied between three and 23 weeks, the mean age being nine weeks. Both sexes were represented, amounting to 761 males and 1,242 females. The whole material represents the top of Finnish Landrace breeding. The tested pigs originated from 525 litters and were siblings of 154 boars.

No special measures were taken in feeding or care before the test. The fodder was generally a dry commercial complete feed, but also partly a home-mixed dry feed was used. Test pigs were handled by their keepers and assistants.

Methods

1. Material processing and statistical methods

The results from the halothane test, H blood group typing, Phi-type determinations, measurement of CK activity in serum, meat colour and WHC measurements were compared to each other as well as to the K index and to the percentage of lean meat on the carcase. The data were analysed using the computer at the Department of Animal Breeding in the Finnish Agricultural Research Centre. In the presensation of the results, the number (n), the percentage of total material (%), the mean value ($\bar{x}$) and standard deviation (S.D.) are given. Differences between means were tested for significance using the "t" test or the Chi-square method.

Calculation of method error was performed in replicates. The results of the repeated halothane test appear in table 3, and CK test results in tables 4, 5 and 6 and in appendix 1. The standard deviation of the method error from duplicate measure-

ments was calculated using the formula $S = \pm \sqrt{\frac{i^2}{2n}}$, where i is the difference between the two duplicates and n the number of samples. Method error is given as the coefficient of variation. In the statistical test, the degree of significance is stated as follows:

n.s. = not significant $p > 0.05$
\+ = significant at the 5 % level $p \leq 0.05$
++ = significant $p \leq 0.01$
+++ = highly significant $p \leq 0.001$

Other abbreviations used are:

Hal+ = halothane-sensitive pigs
Hal– = halothane-resistant pigs
Hal+ litter = litter where at least one Hal+ pig was discovered
Hal– litter = litter where no Hal+ pigs were discovered
Hal+ sire = sire from whose siblings at least one Hal+ pig was discovered
Hal– sire = sire from whose siblings no Hal+ pigs were discovered

2. Production quality measurement

The K index and the percentage of lean meat on the carcase were used as the dimensions for production quality. Growth rate, feed efficiency and meat colour deviations from test stations mean values were also included in tables 18 and 22. These data, along with the K index for the sires of tested pigs were obtained from nationwide progeny testing statistics (KANGASNIEMI 1979 and 1980). In this official progeny testing the K index employed is calculated from the formula $K = b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4 + b_5x_5 + 3.0$, where x_1 is the growth rate, x_2 is feed unit/kg, x_3 back fat thickness in millimetres, x_4 fat percentage and x_5 meat on the carcase expressed in percentages and b_1–b_5 are the corresponding coefficients, while x_1–x_5 represent deviations from each quality calculated on the basis of a 12-month moving average. Growth rate and feed efficiency deviations are obtained from test stations, and slaughter quality characteristics are represented by figures obtained from comparing individual breeds in the whole country. The percentage of lean meat on the carcase is arrived at when half of the carcase is stripped of fat, meat and bone, and the amount of meat is calculated in percentage terms for that half of the carcase. When at least three progeny groups of four pigs each have been tested a K index is calculated for their sire.

3. Halothane test

All 2,066 test pigs were anaesthetised with 4 % halothane (2-bromo-2-chloro-1, 1-trifluoro-ethane) in oxygen in a half-sealed system (Fluotex Marc II manufactured by Cyprane Ltd., England). The oxygen flow throughout narcosis was 4–5 l/min. For the test, the pigs were lifted onto a table so as to lie on their right side. The animals were kept under narcosis for three minutes or until a typical halothane reaction was achieved. Typical symptoms chiefly appead as high muscle tonus in the extremi-

ties and back muscles. Pigs developing a high muscle tonus were considered halothane positive (hal+), while animals still completely relaxed after three minutes of narcosis were classified as halothane negative (hal–). In some cases the reaction was immediately apparent. The normally narcosis-induced reduction in muscle tonus did not occur, but instead the pig began to stiffen immediately after it was lifted onto the table and the mask put on its snout. Some individuals displayed forced movements. In some of these hogs a typical hal+ reaction developed but not in all animals. Some intermediate form of hal+ or hal– reaction was confirmed. In these pigs a slight stiffness developed in the muscles but did not worsen even when narcosis continued more than five minutes. In other animals this muscle tonus gradually loosened and the animals peacefully went to sleep, while in other cases this slight muscle tonus persisted throughout narcosis. All of these twelve cases were considered to be hal–.

In calculating method error, the halothane test was repeated two weeks later with 30 hogs. In one litter consisting of 15 piglets, two hal+ pigs were detected in the first test and a third hal+ pig was found in the second. The age of the pigs was 53 days in the first test. In all other cases the repeated test yielded the same result as the first test (Table 3). One male tested at the age of nine weeks showed a hal+ reaction, and when retested at the age of 6 1/2 months reacted even then very strongly. At phenotype test stations some of the hal– males included in this study were retested. They all displayed a hal– reaction. Later a slaughter evaluation test was performed on all 86 pigs examined at test stations, and it was therefore possible in these cases to compare values obtained from live animals with the slaughter quality properties.

The potential hazard of halthane gas to investigators and their assistants was minimized by adequate ventilation and by directing the gas exhaled by pigs out of the room.

4. Blood sampling

About 5 cc of blood was withdrawn by a 1.40 × 60 mm needle from the vena cava (the needle might occasionally have been inserted into the jugular vein) immediately upon completion of the halothane test and while the pig was still under narcosis. Blood was additionally obtained immediately before narcosis from 130 pigs, and from 18 pigs 24 hours following the halothane test. Part of the blood sample was collected in tubes containing citrate for H blood group and Phi-type determinations, and another part of the samples was allowed to clot for serum CK activity determinations. The collected blood samples arrived at the laboratories the day after sampling and the serum was separated there. When the samples arrived later than this CK activity was not analysed. The Norwegian samples were processed for analysis one week after bleeding. Only H blood group and Phi-type enzymes were determined from these samples. In the experiment described in Table 6, CK activity was determined from plasma which was separated from the blood samples already in the piggeries.

5. Muscle sampling

From the first 307 halothane-tested pigs, muscle biopsies were taken from the M. longissimus dorsi to determine water-holding capacity (WHC). The biopsies were taken from the position of the last rib with a human biopsy needle (Tru-Cut Disposable needle 7.5 cm, Trevenol Lab, USA). The biopsy needle was driven 3—5 cm deep into the Musculus longissimus dorsi through a small incision. Biopsies were taken for WHC measurements immediately after the halothane test. Obvious bloody biopsies were discarded.

6. Blood group analysis

The H blood group systems Ha and Hc factors were determined from nearly all of the halothane-tested pigs, comprised of 1,991 out of the 2,003 Finnish pigs in addition to the 63 Norwegian pigs. Blood analysis was performed at the blood group laboratory of the Union of Finnish AI Associations. Ha was measured by indirect hemargglutination and Hc according to hemolytic proceedings, both described by ANDRESEN (1963).The genotypes are here described without the base letter H as follows: a/a, a/ , a/c, c/ and —/—. Because other H blood group system factors were not identified, (—) signifies only that a and c are not present. The a/a type is a homozygote in relation to a, while a/ can be either a homo- or heterozygote in relation to a, but does not contain the c-factor. The designation c/ could mean either c/c or c/—. Other H system factors were not determined, since according to the literature they have no relation to exertional myopathy (JENSEN 1978b).

7. Phi-type determinations

Phi-type determinations were performed on 1,349 pigs using electrophoresis. The tests were partly conducted at the blood group laboratory of the Union of Finnish AI Associations but mostly at the Department of Animal Breeding and Genetics at the Swedish University of Agricultural Sciences (GAHNE 1979), where Phi^{AA}, Phi^{AB} and Phi^{BB} were determined. Because of inadequate Finnish laboratory capacity, Phi determinations were not performed on all halothane-tested pigs.

8. CK test

CK activity in serum and in plasma was determined at the Department of Biochemistry of the College of Vetarinary Medicine in Helsinki using a computer directed analyser (The Gilford System 3500, Gilford Instrument Laboratories Inc., Ohio, USA). The determination was carried out according to the method recommended for determination of creatine kinase in blood (Anon, 1976). CK activity is given as microkatal/litre (μkat/l) and transformed to natural logarithms. The serum samples were diluted 1:10 with 0.9 % NaCl before the test proper. As reagense CK NAC activated (Cat. no. 126357), Boehringer-Mannheim GmbH, Federal Republic of Germany, was used. The variation coefficient of method error has been calculated from 30 analyses made from one sample with a coefficient of variation of 2.0.

Because it was not possible to bring all blood samples to the laboratory within 24 hours, CK activity was not carried out on all halothane-tested pigs. Nevertheless, CK determinations were made on at least 50 % of the pigs in all elite breeding herds.

Serum CK activity was determined in 1,711 pigs from serum samples taken immediately after the halothane test. The results are summarised in the tables and represent CK values obtained from serum samples taken just after the halothane test, if not otherwise stated.

In addition, CK activity was measured from serum samples obtained from 130 pigs just prior to the halothane test and from 18 pigs 24 hours after the halothane test. CK activity was also determined from the plasma of six pigs.

9. Meat colour measurements

In the present study meat colour was determined in 86 pigs, all of which were halothane tested at the testing stations. A light reflectometre (ELL smoke stain Reflectometre, model 43, manufactured by Evans Electroselenium Ltd., England) was used for determinations at the slaughterhouses. The metre reading indicated the meat colour point.

No steps were taken to affect the measurement technique nor the handling of pigs before slaughter. Investigations conducted by ALHO (1980) on progeny testing judgment technique at different slaughterhouses showed that more care should be devoted to uniform preslaughter treatment of test animals. The meat colour determinations ought to be always measured from a fresh meat surface. A delay in colour measurement of up to three hours was occasionally observed at one of the abbatours where pigs from progeny testing were slaughtered. In the present study no attempts were made to influence the lairing and stunning of the test animals and the judging of the carcase quality.

10. Water-holding capacity

WHC measurements were made from muscle samples which were taken from the Musculus longissimus dorsi of the first 309 halothane-tested pigs immediately after the halothane test while the animals were still in a state of narcosis. The volume of the biopsy specimens varied between 2.8—25 mg. The biopsies were put on filter paper (room-dried, Schleicher & Schüll Nr 5893) and pressed in a glass compressor (trichina compressor). The glass plates were screwed firmly together for five minutes. The filter paper was then removed from the compressor and the biopsies taken off. The outlines of the moisture marks on the filter paper and the impression left on it by the biopsy specimens were drawn. Later the areas were calculated by a planimetre and the results substracted from each other. The compressed meat sample was weighed. WHC is given as cm^2/g compressed meat. The three samples (one hal+ and two hal—) with moisture marks spreading to the edge of the glass were discarded. Attempts to transport the biopsies to the laboratory to perform the weighing of fresh samples and compression thereafter were unsuccessful because many of the specimens lost so much moisture that no wet marks were apparent on

the filter paper.

Since the method mentioned above was difficult to carry out on a routine basis at piggeries in conjuction with the halothane test, WHC was also determined by another method. In these cases the biopsy specimens were put in previously weighed 2 ml glass tubes immediately after sampling, each containing a small piece of tin paper on top of a cotton plug. The tubes equipped with rubber stoppers were dried, weighed and sealed airtight at the laboratories. In the piggeries these tubes were unscrewed long enough to place the biopsy sample in the tube. The tubes were kept for 24 hours in thermos bottles containing ice. Before the tubes were weighed, they were wiped dry and the original weight of the biopsy specimen was calculated. The sample was then removed from the tube and separately weighed. The difference in weight was the amount of moisture evaporated from the specimen, where WHC was reported as the weight loss as a percentage of the original weight. Cases in which the moisture in the tubes exceeded 75 % of the original biopsy weight were omitted. According to the literature pork contains all in all 75 % water (GRAU and HAMM 1953). If the result exceeded 75 %, leakage was assumed to have occurred. Altogether 15 samples were discarded. None of these were from halothane-sensitive pigs. In six cases the biopsy specimens had stuck to the glass surface and had to be discarded. This method sought to calculate drip loss. The variation coefficients of method error were calculated in four duplicate tests, yielding a coefficient of variation of 5.4 %.

VI Results

1. Evaluation of results pertaining to methods

Halothane test

During the test, the pulse rate of the hal+ pigs increased and exceeded 200 beats/min. already in the beginning of narcosis. The handling of the pigs before the test obviously affected the hal+ pigs very strongly. Many hal+ pigs were clearly in an excited state when carried to the table. Many hal– pigs also struggled, but they did not behave as excitedly as some hal+ pigs did.

At the end of the halothane test the pulse rate of the hal– pigs was $\bar{x}$ 184±20 beats/min. and the pulse of hal+ pigs was $\bar{x}$ 221 ±38 beats/min. This difference is statistically highly significant.

Six of the halothane-tested pigs died, all of them being hal+ pigs. The cause of death was the result of prolonged narcosis. In three cases narcosis was continued for one more minute after the onset of clear symptoms in order to obtain a satisfactory electrocardiogram. For the halothane test proper, such long-lasting narcosis was not required. In two cases forced movements and gradually increasing muscle rigidity occurred in the beginning, but a typical hal+ reaction developed slowly. The test was continued until the reaction was very distinct and apparent to the pig owner. These pigs did not recuperate although narcosis was interrupted, but died ca 10 minutes later. One pig died the following night. The iterativeness of the hal+

reaction was good; only a single hal– pig produced a hal+ reaction on a repeated test (Table 3).

CK test

When the material was sorted into hal+ and hal– groups according to the results of the halothane test, the mean value of the serum CK activity of hal+ pigs was statistically significantly higher than the mean activity of hal– pigs. The most significant result was obtained when the serum was tested 24 hours after the halothane test was administered (Table 4).

Table 3. The results of some repeated serum CK activity (μkat/l) determinations in repeated halothane tests

	Number of piglets														
No of tests	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
First Hal reaction	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
CK activity	23.4	12.2	11.0	4.9	4.8	8.6	6.1	6.7	5.6	7.9	7.7	5.4	5.7	103.5	7.3
Second Hal. reaction	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–
CK activity	18.0	17.9	14.9	7.8	17.4	9.3	7.6	6.2	5.8	35.1	6.9	7.7	14.2	6.6	7.3

Table 4. Serum CK activity μkat/l and transformed to ln of hal+ and hal– pigs determined at different time intervals in conjunction with the halothane test

No of groups	Time of serum sampling	Hal+			Hal–			Level of significance
		n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	
1	Just before hal. test	20	37.75±17.62 ln 3.49±0.11		110	22.98±14.48 ln 2.95±0.18		+++
2	Just after hal. test	242	33.12±21.22 ln 3.32±0.20		1469	19.22±30.35 ln 2.68±0.29		+++
3	24 h after hal. test	11	400.73±147.05 ln 5.92±3.59		7	23.83±17.02 ln 2.93±0.10		+++
Level of significance	groups 1–2	n.s.			groups 1–2	n.s.		
	groups 2–3	+++			groups 2–3	n.s.		

The results obtained from serum CK activity determinations made just after the halothane test were usually of the same order of magnitude as those determinations made just before the test, although also large differences were apparent. In both cases, but namely for hal– pigs, some unexpectedly high CK activity values were obtained (Table 4 and appendix 1 group 2).

Serum CK activity determined from the same pig just before and immediately after the halothane test can be used to evaluate the results obtained in repetetive CK activity determinations in non-stressed pigs. The time difference between the two blood samplings is only about five minutes. The probable effect of the halothane test on serum CK activity could not possibly influence the CK values obtained in the latter serum sample. Twenty-four hours after the first halothane test, the CK activity was found to be significantly higher in the hal+ pigs. Serum CK activity determined in samples obtained just after the test were on the average lower than in samples obtained just before the test, but the difference was not prominent (Table 4).

When the serum CK activity results obtained before and after the halothane test from the same individual were compared, the serum CK activity level iterativeness was occasionally poor. According to correlation analysis, the correlation between these determinations was r=0.49, when the correlation was calculated for the same piggery. If herd space was not considered, the correlation between these two CK determinations was r=0.39. Large shifts both upwards and downwards from the mean values were observed (Table 4 and appendix 1).

To clarify the possible fluctuation in pig serum CK activities obtained from serum samples taken within short time intervals, serum samples were obtained from the same six pigs, four times every 15 minutes. This test also confirmed the poor repeatability of serum CK activity determinations (Table 5).

As the poor iterativeness of the test was suspected to be due to serum samples contaminated by muscle tissues in bleeding, the test was repeated with some pigs. In this case blood coagulation was inhibited with heparin, and the samples were immediately centrifuged after bleeding. In some blood samples small pieces of tissue could be seen floating on the plasma surface after centrifugation. Plasma CK activity was then determined in the usual way. The determination was made on separated plasma on the day of bleeding and on the following day using the plasma left in the blood tube. After centrifugation the iterativeness of the CK activity was a little better than

Table 5. CK serum activity (μkat/l) in samples taken from the same six pigs at 15 minute intervals.

Sample No.	CK activity in serum of pigs 1–6					
	pig 1	pig 2	pig 3	pig 4	pig 5	pig 6
1	8.9	76.7	6.7	11.8	31.2	14.7
2	9.7	29.1	84.2	16.0	15.0	17.0
3	12.5	41.0	11.6	12.7	33.4	71.2
4	14.1	49.4	23.2	30.9	134.0	22.6
coefficients of variation in %	21.4	41.1	114.0	49.7	101.6	85.3

that obtained with the previous test (Tables 5 and 6). It was additionally demonstrated that the CK activity in the samples incubated overnight was higher than in the previous portion of the same sample (Table 6). These pigs were not included in the halothane test.

Pig blood hemolyses very easily. To elucidate the effect of hemolysis on serum CK activity determination in a single serum sample, equal amounts of hemolysate diluted 1:11, 1:41 and 1:121 were added, whereafter the CK activity was determined. The hemolysis had no significant effect on the CK activity.

The 1:10 dilution of the serum before measurement only slightly affected the results. The coefficient of variation between results obtained from diluted and undiluted sera was 1.2 %. Repeated determinations from the same serum sample yielded identical results. The coefficients of variation were 1.1 %.

The handling of the pigs the day before the test caused large variations in serum CK activity determined at the same time from samples from different pigs at the same piggery. Pigs fought when animals from different litters were mixed in a pen on the day before the test. When testing these pigs fresh wounds such as skin scratches were apparent. The CK activity in these pigs was always high. Unexpectedly high values approaching 20 μkat/l were, however, sometimes detected in hal− pigs, although these pigs were not handled before the test (Table , appendix 1 group 1).

Serum CK activities determined in hal+ male pigs at the end of the halothane test were slightly lower than the results obtained from hal+ female pigs. This difference was, however, not statistically significant (ln 3.19 ± 0.42 contra ln 3.36 ± 0.38. On the other hand, serum CK activity was of the same order of magnitude in hal− male and female pigs $\bar{x}$ 19.0 ± 29.2 μkat/l).

In pigs with serum CK activity of less than 16.7 μkat/l (1 000 U/l), the hal+ frequency was 4.06 and in pigs with CK activities ranging from 16.7−33.3 μkat/l (1 000−2 000 U/l), the hal+ frequency was 19.36. When the CK activity was found to range between 33.3 and 116.8 μkat/l (2 000−7 000 U/l), the hal+ frequency was about 30−40 %. In the group where CK activity was above 116.8 μkat/l (7 000 U/l), only 9.1 % of hal+ pigs were detected (Table 7).

Small variations could be found in CK activity in serum from pigs with different H blood types. The differences relfected only the different numbers of hal+ pigs

Table 6. CK plasma activity (μkat/l) in samples taken from the same six pigs at 15 minute intervals. The results obtained after overnight incubation are reported in parenthesis ().

	CK activity in plasma					
Sample No.	pig 1	pig 2	pig 3	pig 4	pig 5	pig 6
1	24.2 (30.7)	46.4 (–)	33.9 (62.1)	10.7 (10.8)	8.5 (15.1)	39.5 (112)
2	21.8 (26.5)	17.4 (50.6)	15.8 (20.8)	60.8 (71.6)	30.3 (34.9)	12.9 (16.7)
3	52.5 (85.1)	46.7 (56.7)	24.2 (29.7)	16.5 (18.5)	17.9 (26.2)	16.2 (26.2)
4	91.5 (114)	50.2 (53.3)	24.1 (27.8)	57.1 (58.0)	56.5 (36.4)	56.3 (85.9)
$\bar{x}$	47.5 (64.1)	40.2 (53.5)	24.5 (35.1)	36.3 (39.7)	28.3 (28.2)	31.2 (60.3)
coefficients of variation	31.5 (49.9)	39.9 (5.7)	30.2 (52.4)	30.2 (33.5)	73.6 (34.8)	65.6 (76.7)

Table 7. Hal+ frequency in pigs with different serum CK activity

CK activity in serum		Hal+ frequency	
μkat/l	U/l	n	%
< 16.7	(< 1000)	1030	4.06
16.7–33.3	(1000–1999)	433	19.86
33.4–50.0	(2000–2999)	128	33.6
50.1–66.7	(3000–3999)	61	44.3
66.8–83.3	(4000–4999)	19	36.8
83.4–116.7	(5000–6999)	24	40.0
> 116.8	(> 7000	11	9.1
		1711	

Table 8. CK activity (μkat/l) in serum of hal+ and hal– pigs with different H blood groups

H blood groups	Hal+ n	$\bar{x}$ S.D.		Hal– n	$\bar{x}$ S.D.	
a/a	65	30.2±18.1		99	20.1±19.8	
a/	159	32.8±20.8	31.9±19.9	579	18.9±25.5	19.5±28.1
a/c	6	28.8±18.4		301	20.4±34.5	
c/	2	54.6		448	19.0±30.4	
–/–	20	40.4±16.3		311	18.7±36.9	

Table 9. CK enzyme activity transformed to ln in hal– pigs with a meat colour point higher or lower than 44

Meat colour points	n	CK activity in serum ln $\bar{x}$ S.D.
≥ 44	21	7.17±0.60
< 44	53	6.76±0.60
Level of significance		n.s.

among the H blood types. According to statistical least-square analysis, the differences were not significant (Table 8). In all hal– pigs with different H blood types the CK activity was of the same order of magnitude (Table 8). At farms where the hal+ frequency in pigs was low, the CK activity in serum was also usually low but not always. At test stations tested hal– pigs with a meat colour point of ≧ 44 showed CK activity that was not statistically significantly higher than in pigs with a meat colour point of < 44 (Table 9).

The CK activity in serum from the offspring of hal+ sires was not significantly higher than the CK activity in serum from the offpring of hal– sires (Table 10).

The CK activity in serum from Phi^{AA} pigs was comparatively low (Table 11).

Conclusion of the CK test evaluation

The CK activity was significantly higher in hal+ pigs as a group than in hal– hogs, although dispersion was great in both groups (Table 4). It was additionally

Table 10. CK activity in serum (μkat/l and ln) of hal– siblings of hal+ and hal– sires

Definition of group	sires n	siblings n	CK activity in serum calculated from sire means
Hal– pigs from hal+ sires	57	757	$\bar{x}$ S.D. μkat/l 19.2±10.1 ln 2.81±0.28
Hal– pigs from hal– sires	86	686	$\bar{x}$ S.D. μkat/l 18.9±14.2 ln 2.72±0.19
Level of significance			n.s.

Table 11. CK activity in serum (μkat/l) of hal+ and hal– pigs with different Phi enzyme types

	Hal+		Hal–		Total material
	n	$\bar{x}$ S.D.	n	$\bar{x}$ S.D.	n $\bar{x}$ S.D.
AA	0	–	20	11.2±6.9	20 11.2±6.9 ln 2.3±0.1
AB	6	30.4±17.4	285	17.8±29.9	291 18.1±29.7 ln 2.4±0.2
BB	169	31.5±17.3	869	19.6±34.6	1038 21.5±32.7 ln 2.8±0.3
Level of significance					AA/AB ++ AA/BB +++ AB/BB +

observed that when serum samples were obtained from the same pig at 5–15 minute intervals, considerable differences in CK activity could be demonstrated (Tables 5 and 6 and appendix 1). These discrepancies could not be explained as technical analytical error. Some extremely high CK activity values can be justified as a result of animal handling on the day preceding the test, but this could not, however, explain poor test repeatability. Poor iterativeness was most probably caused by the contamination of the serum samples by muscle tissue as a result of bleeding from the vena cava. The immediate centrifugation and separation of the plasma increased the repeatability of CK activity determinations, but probably did not completely correct the error caused by muscle tissue contamination.

If it were possible to expose the pigs to standardized strain the day before blood sampling for the serum CK activity detemination, it would probably yield more reliable results for breeding selection. This was demonstrated by results obtained with serum samples taken 24 hours after the halothane test (Table 4).

Meat colour determinations

The meat colour points were higher for the hal+ than for the hal– pigs (Table 12 and appendices 2, 3, 4 and 5). The percentage of lean meat on the carcase was the same in both groups. One hal+ pig had a very low meat colour point of 29 (Appendix table 3).

This was most probably a case of DFD meat, but it was not confirmed because no pH determinations were made. A meat colour reading of $\geqq 44$ was obtained for 71.5 % of the hal+ and for 29.5 % of the hal– pigs (Table 12).

Table 12. Percentage of lean meat on carcase and meat colour points of hal+ and hal– pigs tested at pig testing stations and percentage of pigs with meat colour points ≥ 44

	Hal+ $\bar{x}$ S.D.	Hal– $\bar{x}$ S.D.	Level of significance	Total material
Percentage lean meat on carcase	n= 6 49.3±2.6	n= 48 49.5±2.9	n.s.	n= 54 49.4
Meat colour points	n= 7 48.7±7.5	n= 70 41.5±6.2	++	n= 77 45.2
Percentage pigs with meat colour ≥ 44	n= 5/7 71.5	n= 21/70 30.0	+	n= 77 33.2

Table 13. Meat colour points, percentage of lean meat on carcase and K index of progeny-tested hal+ and hal– litters

Halothane reaction	Tested litters n	Meat colour points $\bar{x}$ S.D.	K index $\bar{x}$ S.D.	Percentage lean meat S.D.
Hal+	14	42.6±6.1	8.7±7.6	51.6±2.3
Hal–	63	40.9±4.9	4.3±8.4	50.4±1.4
Level of significance		n.s.	n.s.	n.s.

In group one at the progeny testing station in southwestern Finland one hal+ pig was found. This group was given the highest meat colour reading, although this hal+ pig was killed in a fight before slaughter and was therefore not included in the slaughter evaluation. The H blood group factor a/ was demonstrated for all pigs included in this group but not factor c. Group three, in which most of the animals had factor c, received a lower colour reading but also at the same time the lowest K index values (Appendix table 2). Group one tested at the progeny testing station in east and central Finland included two hal+ pigs. All pigs in this group had the H blood group factor a. The group obtained a higher K index as well as a higher colour reading (Appendix table 3). It was also found among pigs tested at the swine research station in Hyvinkää that the hal+ pigs generally had a high meat colour reading (Appendix tables 4 and 5) and that hal+ and H a usually followed each other.

For some of the pigs tested on breeding farms, the meat colour points could be calculated as mean values from four litter mates raised as one group at one of the progeny testing stations. In these cases colour readings were obtained from normal progeny testing. Higher colour readings were in these cases demontrated among hal+ litters as compared to those among the hal– litters. The difference was, however, not statistically significant (Table 13). Large dispersion within and between groups was verified (Appendix tables 2, 3, 4 and 5).

The hal– pigs from hal+ litters had a higher colour reading than pigs from hal– litters. The reading was 43.5 compared to 41.1, but the difference was not statistically significant.

Table 14. Determination by two different methods of water-holding capacity (WHC) in muscle biopsies of hal+ and hal– pigs

Hal. reaction	WHC by filter paper press method cm^2/g		WHC by drip loss method % weight loss	
	n	$\bar{x}\pm$S.D.	n	$\bar{x}\pm$S.D.
Hal+	8	61.8±11.5	39	61.5±12.3
Hal–	52	54.1±19.7	186	57.6±11.5
Level of significance	n.s.		n.s.	

Table 15. Water-holding capacity (WHC) in pigs with different H blood groups determined by the drip loss method. % of weight loss

WHC % weight loss	H blood groups					Level of significance
	a/a n = 22	a/ n = 85	a/c n = 39	c/ n = 62	–/– n = 29	
$\bar{x}$ S.D.	63.1±9.9	63.3±11.0	60.3±12.0	58.0±13.2	57.6±16.8	n.s.

Determination of the meat water-holding capacity (WHC)

WHC was the same in both hal+ and hal– pigs (Table 14). No significant differences in WHC could be demonstrated in pigs with different H blood types (Table 15).

2. Epidemiological results

The halothane test

Totally 251 halothane sensitive (hal+) pigs were found. This means a hal+ frequency of 12.4 % for the Finnish Landrace and 3.2 % for the Norwegian material (Table 16). The hal^n gene frequency in the Finnish Landrace breed is thus calculated to be 0.35, according to the Hardy–Weinberg law and assuming that halothane susceptibility is induced by one recessive autosomal gene which has a complete penetrance.

The Finnish material consisted of:

249 hal+ pigs
1 754 hal– pigs

Of the Finnish pigs, 10.4 % of the males and 13.5 % of the females produced a positive halothane reaction. The hal+ frequency remained low when pigs less than 51 days old were tested in comparison to results obtained with pigs tested at an older age (Table 17). Halothane-sensitivity remained below 20 % in the Finnish Landrace, but on some single farms, however, quite high values could be demonstrated (Appendix table 6). The animals included in this study represent the top of the Finnish Landrace breed. The growth rate of the sires exceeded the mean, measured in progeny testing during the same period of time. Hal+ pigs were discovered among the progeny of 64 sires (hal+ sires).

Table 16. Frequency of halothane-sensitive pigs in the Finnish Landrace breed and in some Norwegian Landrace pigs

Origin of sample	Number of tested pigs	Halothane-sensitive pigs (hal+ pigs) n	%
Finnish Landrace	2003	249	12.4
Norwegian Landrace	63	2	3.2
	2066	251	

Table 17. Halothane frequency in pigs of different ages

Age in days	n	Hal+ pigs in different age groups. n	frequency in % of age group
below 30	44	2	4.5
31–40	146	12	8.2
41–50	231	11	4.2
51–60	473	53	11.2
61–90	850	131	15.4
91–120	232	36	15.5
over 120	27	4	14.8
	2003	249	12.4

Table 18. K index, percentage of lean meat on carcase and meat colour points of hal+ and hal– sires and percentage of sires with high or low K index, lean meat on carcase and meat colour

	Hal+ $\bar{x}$ S.D.	Hal– $\bar{x}$ S.D.	Level of significance
	n = 49	n = 60	
K index	7.49±4.9	4.81±6.3	+
Percentage lean meat on carcase	50.65±1.1	50.16±1.2	+
Meat colour points	40.42±2.3	39.56±3.6	n.s.
Percentage boars with meat colour points ≥ 44	n= 109 18.6	13.1	n.s.
Percentage boars with K index + 8.0	53.5	29.4	+
Percentage boars with negative K index	5.5	26.1	++
Percentage boars with growth rate better than station mean	78.5	60.0	n.s. (p= 0.057)
Percentage boars with meat colour lower than station mean	16.4	32.7	n.s.

Only hal– pigs were found to spring from 90 sires (hal– sires). From hal+ sires an average of 20 offspring were tested and from hal– sires 17.2. The greatest number of hal+ sires were found among those with a high K index, when again hal– sires were more frequent among those with a low or negative index value (Tables 18 and 26 and appendix 7). Only few hal– sires had a high K index. The mean K index among hal+ sires was 7.46 compared to only 4.81 among hal– sires. The percentage of lean meat on the carcase was also greater for hal+ sires than for hal– sires. The meat colour was lighter in hal+ sires than in hal– sires (Tables 18 and 26 and appendix 7), but this difference was not statistically significant. A better growth rate was also a more prominently inherited characteristic among hal+ sires than among hal– sires (Table 18 and 26.)

H blood group factors

The H blood group factors were determined from 1,991 Finnish and 63 Norwegian pigs, 38 % being males and 62 % females. The Ha factor was present in 60.7 % of the Finnish Landrace and in 62 % of the Norwegian pigs (Table 19).

Of the Finnish Landrace hogs 38.0 % had the c factor as opposed to 55.6 % of the Norwegian animals. In the Finnish Landrace pigs the H blood group could be traced over two generations, and also especially in pigs which were selected by breeders as parents for the third generation. A slight decrease in the a factor was discovered in these selected animals, while a clear increase was seen in pigs with the c factor (Table 20).

Pigs with the a factor tested at test stations had a higher percentage of lean meat on the carcase than had pigs without the a factor. The meat colour reading did not deviate significantly among hogs with the a factor from the value determined in pigs without it (Table 21). Hal+ pigs had a tendency to produce lighter meat than hal– pigs.

Sires with factor a had a higher K index, a higher lean meat percentage on the carcase as well as higher colour readings than sires without factor a. Sires with a fac-

Table 19. Distribution of different H blood group factors in the Finnish Landrace breed and in some Norwegian Landrace pigs

H blood group factors	Finnish Landrace			Norwegian Landrace		
	n	%		n	%	
a/a	164	8.2		5	8	
a/	739	37.1		17	27	
a/c	307	15.4		17	27	
a total			60.7			62
c/	450	22.6		18	29	
c total			38.0			56
–/–	331	16.7		6	9	
	1991	100		63	100	
H blood group not determined	12					
	2003					

Table 20. H blood group factors in two generations of Finnish Landrace pigs

H blood group factors	I generation Landrace boars			II generation Landrace pigs			Pigs chosen for breeding	
	n	%		n	%		n	%
a/a	8	8.5		164	8.3		3	1.4
a/	40	42.6		739	37.1		83	38.6
a/c	15	16.0		307	15.4		37	17.2
a total			67.0			60.7		57.2
c/	17	18.0		450	22.6		60	28.0
c total			34.0			38.0		45.2
–/–	14	14.9		331	16.7		32	14.8
	94	100		1991	100		215	100

Table 21. Percentage of lean meat on carcase and meat colour points in pigs with the H blood group factor a and in pigs without this factor

	H blood group factors a/a, a/, a/c	H blood group factors c/, –/–	Level of significance
	n=33	n=20	
Percentage lean meat $\bar{x}$ S.D.	50.16±2.63	48.17±2.97	++
Meat colour points $\bar{x}$ S.D.	42.8±6.6	41.9±6.8	n.s. (p=9.9)

Table 22. K index, percentage of lean meat on carcase, meat colour points and determination of growth rate and feed efficiency for sires with and without the H blood group factor a

		H blood groups a genotypes a/a	a/	a/c	non a genotypes c/	–/–	Level of significance	Total material
		n = 49		(n = 11)	n = 29			
K index	$\bar{x}$	+7.8±5.7		(8.9)	+4.7±7.6		n.s. p = 0.056	6.8
% lean meat on carcase	$\bar{x}$	50.79±1.2		(50.4)	50.37±1.2		n.s.	50.64
Meat colour points	$\bar{x}$	41.43±3.4		(40.1)	39.0±3.3		++	40.56
Percentage sires with growth rate better than station mean		83.0			56.0		++	
Percentage sires with feed efficiency better than station mean		81.3			60.0		+	

Table 23. Frequency of different H blood groups in hal+ and hal– pigs

Halothane reaction		H blood groups							
		a/a	a/	a/c	a total	c/	c total	–/–	
Hal+	n	65	154	6	(225)	2	(8)	20	247
	%	39.6	20.7	1.9	91.1	0.4	2.3	6.1	
Hal–	n	99	585	301	(985)	448	(749)	311	1744
	%	60.4	79.3	98.1	56.4	99.6	42.9	93.9	
Total material	n	164	739	307	(1210)	450	(757)	331	1991
	%	8.3	36.8	15.6	60.7	22.6	38.0	16.7	

tor also possessed a better growth rate and better feed efficiency than sires without it (Table 22).

A high correlation between the H blood group factor a and the hal+ reaction was confirmed. Of the a/a pigs 39.6 % were halothane sensitive as were 20.7 % of the a/ pigs. Only 1.9 % of the a/c pigs and 0.4 % of the c/ pigs reacted to halothane, compared to 6.1 % of the –/– pigs (Table 23).

The correlation of H blood group factors and the hal+ frequency fluctuated greatly between different farms. In general a high Ha and a low Hc frequency was followed by a high hal+ frequency, but exceptions to this rule also occurred (Appendix table 6).

Phi enzyme types

All three Phi types were present in the Finnish Landrace, the AA being rarest and the BB most prevalent (Table 24). The BB also dominated in the Norvegian material (Table 24).

Hal+ pigs usually had the Phi-type BB, but some hal+ pigs with type AB were also discovered. In contrast no AA type was detected in hal+ pigs (Table 25). Of the hal+ pigs 96,6 % had the BB type and 3.4 % the AB type, whereas of hal– pigs 74 % had the BB type and 24 % the AB type. Of the hal+ pigs 90 % with the BB type had the H blood group factor a, but the H blood group factor a occurred in 52 % of hal– pigs with the BB type (Table 25).

Table 24. Frequency of Phi types in the Finnish Landrace breed and in some Norwegian Landrace pigs

Origin of sample	Phi types							
		AA			AB		BB	
	n	n	%		n	%	n	%
Finnish Landrace	1349	20	1.5		291	21.6	1038	76.9
				qA 0.12				pB 0.87
Norwegian Landrace	63	9	0		10	15.9	53	84.1
				qA 0.08				pB 0.92

Table 25. Phi type and H blood groups in hal+ and hal– pigs

Phi types	Hal+							Hal–						
			a/a	a/	a/c	c/	–/–			a/a	a/	a/c	c/	–/–
	n	%	n	n	n	n	n	n	%	n	n	n	n	n
AA								20	1	1	8	6	5	0
AB	6	3.4	2	2	0	0	2	285	24.2	14	79	55	101	36
BB	169	96.6	41	106	5	1	15	869	74.1	40	280	131	234	174
				149	(90 %)						451	(52 %)		

Table 26. K index, percentage of lean meat on carcase and meat colour points in hal+ and hal– sires calculated for all test groups and for test groups from hal– litters only

		Hal+ sires		Hal– sires
		Hal+ and hal– litters n = 32	Hal– litters only n = 18	Hal– litters n = 44
		A	B	C
K index	$\bar{x}$ S.D.	7.4±7.0	6.4±7.6	3.9±7.9
% lean meat	$\bar{x}$ S.D.	51.6±2.3	50.7±1.3	50.2±1.4
Meat colour points	$\bar{x}$ S.D.	41.6±7.0	42.8±5.7	39.5±4.1

Level of significance		
	K index	A/C +, B/C n.s., A/B n.s.
	% lean meat	A/C ++, B/C n.s., A/B n.s.
	Meat colour points	A/C (+), B/C +, A/B n.s.

The serum CK activity was markedly low in pigs with the AA type. This was also observed when only hal– hogs were compared (Table 11).

VII Discussion

Exertional myopathy frequency

A knowledge of conditions at the top of the breeding pyramid gives some picture of the future of the breed as a whole. If the stock is to be changed by breeding, then action has naturally to be focused on the top of the pyramid, and for this reason it is important to know the prevailing situation.

The results of material consisting of more than 2,000 pigs presented in this study will reliably reflect the situation for exertional myopathy at the top of the Finnish Landrace breed in 1979. Breeding pigs from all elite herds excluding one were investigated. In addition, pigs from ten more breeding piggeries were studied where the breeding level of the animals was so high that they could be accepted as aspirant herds for elite breeding. The K index for the sires of these test pigs was 2.6 points higher than the mean value obtained for the whole Landrace breed in 1979. Of these sires about 70 % were used in the artificial insemination service. It was additionally verified that two-thirds of the breeding animals for the next generation in the elite herds were included in this study.

Susceptibility to exertional myopathy as determined by the halothane test was confirmed in 12.4 % of the hogs tested, being so far the second highest hal+ frequency demonstrated in Scandinavia. The halothane sensitivity frequency could most probably have been still higher, in that case approaching the hal+ frequency verified in the Swedish Landrace breed, if all the pigs used in the halothane test had been more than seven weeks old. The present investigation includes 421 pigs under 51 days of age at the time of testing, and among these pigs the halothane frequency was only about half of the value obtained for the 1,582 pigs tested at the age of 51 days or older. WEBB (1980 b) also showed that the hal+ frequency was lower when pigs were exposed to the halothane test at an age of under seven weeks than when the same pigs were tested at an older age.

VAN DEN HENDE et al. (1976) demonstrated that the muscles of younger pigs had a more efficient aerobic metabolism than those of older pigs, and this might be the reason why younger individuals endure halothane better than older animals. The hal+ frequency among male pigs was slightly lower (10.4 %) than among female pigs (13.5 %). A contributing factor for this could be that male pigs were more often tested at the breeding piggeries while nearly all female pigs were tested in elite herds. Accordingly, the breeding level was most likely better among sows in general than among boars.

The hal+ frequency in Swedish Landrace pigs was 15 % (ANDRÉN 1977), in the Danish Landrace breed 7 % (JENSEN 1978b), in the Norwegian Landrace breed 5 % (WEBB & SMITH 1977) or 5,4 % (FRØYSTEIN et al. 1981). The hal+ frequency in Finnish Landrace pigs now demonstrated is markedly lower than that in the Central European Landrace breeds (WEBB 1981). The two subgroups of Landrace breeds were characterized by MAJOR (1968) with the help of blood group analyses. The Finnish Landrace seems to be more closely related to the subgroup of Scandinavian Landrace breeds than to the Landrace breeds on the European continent. This is not surprising because of the active exchange of breeding animals between Finland, Sweden and Norway. Norway especially has exported a rather large number of Landrace hogs to Finland.

The Norwegian Landrace breed material included in this study revealed a halothane sensitivity of 3.2 %, which was considerably lower than the frequency demonstrated in the Finnish Landrace, and even lower than the figure of 5 % reported by WEBB and SMITH (1977). The present Norwegian material was tested in breeding herds in the Trondheim area and probably does not represent the top of the Norwegian Landrace breed as well as the material tested by WEBB and SMITH (1977). Halothane sensitivity is a characteristic inherited by the recessive Hal^n gene, which has complete or nearly complete penetrance (SIMON 1980). The halothane test reveals about 90 % of the homozygotes, but heterozygotes are not revealed. When the hal+ frequency was 12.4 %, it was possible to calculate using the Hardy-Weinberg law that at least 45.6 % of the Landrace pigs carry the Hal^n gene and that about 58 % of the Finnish Landrace pigs are either homozygotes or heterozygous carriers of this gene.

Carcase quality

In the present study the correlation between the Hal^n gene and good production qualities was not clearly verified in the pigs from the test stations but was demonstrated in the much more extensive material from the breeding farms. The percentage of lean meat on the carcase of hal+ (Hal^nHal^n) pigs was not significantly higher than that of hal– (Hal^NHal^N) and (Hal^NHal^n) pigs, but the K index and lean meat percentage on the carcase of hal+ (Hal^nHal^n) and (Hal^NHal^n) sires were higher than those of hal– (Hal^NHal^N) and (Hal^NHal^n) sires.

It has been demonstrated that halothane-sensitive pigs usually have more meat on their carcases than pigs not sensitive to halothane. Effective breeding for more meat on the carcase in a population where the Hal^n gene is present will most probably increase the frequency. OLLIVIER et al. (1975) and MABRY (1978) have experimentally shown in selection tests that this calculated increase in fact occurs. Their selection tests also confirmed that the meat quality was poorer in hal+ pigs than in hal– pigs.

The reason why FRØYSTEIN et al. (1978) were unable to demonstrate an increase in the number of hal+ pigs in the meaty line with low back fat compared to the high back fat line in the Norwegian selection experiment may result from the fact that the Hal^n gene is rare in the Norwegian Landrace breed. The lack of an increased hal+ frequency could also partly arise from the fact that in the selection test in question more effort was devoted to thinning back fat than to increasing meatiness (VANGEN 1979). Selection for reduced back fat would affect meat quality less than selection for increased muscularity (LUNDSTRÖM 1975).

Meat quality

The poor meat quality of hal+ pigs compared to meat quality in hal– pigs has been verified by many but not all investigators (WEBB 1981), and this was also confirmed in the present study where it was shown that hal+ pigs and the offspring of hal+ sires had a higher meat colour reading than the offspring of hal– sires. The difference in the meat colour readings of hal+ and hal– sires was not statistically significant, however. When meat quality is reliably determined and is taken comprehensively enough into the breeding programme, the spread of the Hal^n gene can be prevented. These proceedings have been effectively practised in Denmark (JENSEN 1978b) Norway (HEMMA 1978) and are now also employed in Sweden (LUNDSTRÖM et al. 1980).

Crossbreeding may be used for improving meat quality but in crossbreeds meat quality appears to be intermediate between the two parent breeds, suggesting that no beneficial effect is to be gained from heterosis (WALSTRA et al. 1971, LEAN et al. 1972). Results by EIKELENBOOM et al. (1980) and JENSEN and ANDRESEN (1980) indicated that carriers which were themselves stress-resistant were intermediate to the two homozygotes in meat quality and percentage of lean meat on the carcase.

H blood group system

The H blood group system factor a is more common in the Finnish Landrace breed than in the Finnish Yorkshire breed. According to the present study the frequency of the Ha blood factor in the Landrace was 60.7 %, while in Finnish Yorkshire boars it was 48.0 % (LINDSTRÖM 1980). A bigger difference was, however, seen in the frequency of the c factor, which was 38.0 % in the Landrace and 76.8 % in the Yorkshire breed. The c factor was present in 55.6 % of the Norwegian Landrace pigs tested in this study. Halothane sensitivity was shown to be very rare in Landrace pigs which had the c factor. Halothane sensitivity was also low in the populations where the c factor was common as was demonstrated both in the Finnish Yorkshire breed (0.2 %) and in the Norwegian Landrace breed (3.2 %).

The extremely low hal+ frequency in Finnish Landrace pigs having the H blood group factor c but not factor a provides no evidence that the same situation also prevails in other breeds nor that this positive stress-resistant situation in Hc pigs is permanent in the Finnish Landrace breed. JØRGENSEN'S (1979) investigation including 531 Danish Landrace pigs showed a hal+ frequency of 5.5 % among Hc pigs.

Differences evident between breeds are probably an indication that Hal and H blood group loci are not so closely linked that it should be impossible for a chromosomal crossover to occur between them. Evidence of this also shown by JØRGENSEN (1981) reduces the usefulness of the role of H blood group factors as markers of stress resistance in breeding programmes, and requires that the halothane test is also used so that a change in the once established relationship between the marker and marking factors is not hidden from the breeders.

Exertional myopathy in breeding

The halothane sensitivity gene

Poor meat quality caused by a poor stress resistance of genetical origin could be improved by eliminating the Hal^n gene. Before such a procedure can be proposed, all properties, both good and bad, of the Hal^n gene should be estimated and weighed against one another. In the pig population "ABRO" which WEBB investigated, the negative properties, or higher mortality and poorer reproductivity connected to the Hal^n gene, were so much more significant than the relatively greater meatiness of the carcase that the effect due to the Hal^n gene was negative and created a loss of £ 3.60 for every bacon pig produced. It would have been feasible to eliminate the Hal^n gene completely at least from the "ABRO" stock (WEBB 1980a).

By removing the Hal^n gene from the Finnish Landrace it is possible to reduce mortality due to the stress syndrome. The death rate of Landrace pigs at test stations and during transport from test stations to slaughterhouses could be reduced to at least half of the present death rate. The same positive development should take place at fattening piggeries and during transport from there to abbatoirs. EIKELENBOOM et al. (1978) showed that the death rate of hal+ pigs during transport and preslaughter treatment was nearly ten times higher than the death rate of hal– pigs. In the progeny testing of Finnish Landrace pigs, most probably more than 10 % (12.4

%) are hal+ pigs and the death rate of these pigs corresponds to at least 50 % of the total "stress deaths" of Landrace pigs. A comparison of the death rate for Hal^n heterozygotes and the death rate for pigs without the Hal^n gene has not been performed, but it is most likely that death from stress is greater among heterozygote pigs than among pigs which have no Hal^n gene at all. In Hal^n gene homozygotes (hal+) and also in the group which had the greatest number of Hal^n heterozygotes (hal+ litters hal– pigs), it was demonstrated that the meat colour reading was higher than in pigs from hal– litters and the offspring of hal– sires, both of which represent groups with few hal^n gene carriers among them. Meat colour readings would thus certainly improve if fewer Hal^n gene-carrying pigs were brought to the test stations.

When 33.2 % of all pigs at test stations included in this study were given a colour reading of more than 44 points, 71.5 % of the hal+ pigs had the same high colour reading compared to only 29.5 % of the hal– pigs. If the hal+ pigs were excluded from breeding, all colour readings would improve so that only 29.5 %, or 3.7 percentage units less, of groups would receive a colour reading of more than 44 points. The improvement in meat quality should, however, be greater than 3.7 percentage units, as also the Hal^n gene heterozygous pigs would begin to disappear. The meat quality of these pigs is an intermediate between the meat quality of the two previously mentioned groups. This has been pointed out by many researchers and summarised by JØRGENSEN (1980 b and 1981) and SCHNEIDER et al. (1980), and the results obtained in this study are also in agreement.

Carcase quality

Differences in the meatiness of hal+ and hal– pigs were not observed in the test station material. Due to this it could be assumed that elimination of the hal+ pigs would improve meat quality without reducing the amount of lean meat on the carcase. However, it has generally been demonstrated that hal+ pigs and pigs carrying the Hal^n gene have more meat on their carcases than pigs without the Hal^n gene (LUNDSTRÖM 1975, JENSEN 1978a and EIKELENBOOM et al. 1978b and 1980). In this investigation it was also discovered in sires that the K index of hal+ sires and the percentage of carcase lean meat were higher than the K index and lean meat on the carcases of hal– sires. Although the eradication of the Hal^n gene improves meat quality according to results obtained from test station material without reducing the amount of lean meat on the carcase, a reduction is to be expected. Improving meatiness will be possible, however, because even among hal– sires there are individuals with a high K index and a high percentage of lean meat on the carcase. Some of these sires in all probability do not have the Hal^n gene, although certainly only a small number of such individuals exist.

The Hal^n gene is present in approximately 58.0 % in all of the best breeding pigs. The complete destruction of the Hal^n gene would therefore be problematic. The impediments caused by the Hal^n gene, i.e. sensitivity to stress called "stress death" and the formation of PSE/DFD meat, pose such large risks that the eradication of the gene becomes necessary. If nothing is done, the gene will be increasingly prevalent as long as the breeding programme for more meaty pigs is continued. Even the theoretical assumption of the total eradication of the gene might not be re-

alistic because no method is available so far for direct identification of the heterozygotes. With the help of the halothane test and suitable test matings this becomes possible (WEBB 1980 b, JØRGENSEN 1981 and SMITH 1981).

H blood group factors

The use of H blood groups, the Phi-type determination and the CK test have been proposed as methods to reveal Hal^n gene heterozygous individuals. Results from the present study show that the Ha factor is closely linked to the hal+ reaction. Of the a/a pigs and a/ pigs, 39.6 % and 20.7 %, respectively, were hal+ hogs. The H blood group system factor a is not, however, casually associated with the halothane reaction, since all hal+ pigs do not have the a factor. This has been demonstrated by BARTON et al. (1977) and JØRGENSEN (1977). In this study it was also shown that of the —/— pigs and the c/ pigs, 6.1 % and 0.4 %, respectively, were hal+ individuals. If the H blood group factor a is completely removed from the Finnish Landrace, it would first of all be a very radical action, because 60.7 % of the best breeding animals possess this factor. This share is about the same as the percentage of Landrace pigs estimated to have the Hal^n gene (58.0 %). The eradication of factor Ha should lower the hal+ frequency very effectively, since about 91 % of the hal+ pigs would disappear if the a factor is removed. The hal+ genotype frequency would be reduced from 12.4 % to 1.12 %. Most of the Hal^n gene heterozygotes would also disappear, and the Hal^n gene frequency would decline from 0.35 to 0.11.

If Ha individuals having both a and c factors were preserved, it would be possible by selective eradication of 45.4 % but not 60.7 % of the breeding animals to diminish the number of hal+ pigs to nearly the same degree, or 88.7 %. This alternative should at any rate leave in breeding a little higher percentage of Hal^n heterozygotes than the previous alternative. The eradication of Ha should lead to a 50 % reduction in stress death compared to the present situation. No statistically significant differences in meatiness or meat colour were demonstrated in pigs carrying the Ha factor or in pigs without the factor when these measurements were performed at test stations. However, Ha pigs tended to have more meat, but their meat was lighter than the meat from pigs without the Ha factor. Many investigators have shown that the amount of lean meat on the carcase is greater and the meat colour lighter in pigs with the factor a than in pigs without it (BARTON et al. 1977 and LUNDSTRÖM et al. 1980 and JØRGENSEN 1981).

In this study a difference was discovered between sires with different H blood groups. Sires with the Ha factor had a K index 3.1 points higher than sires without the Ha factor. The dispersion within groups was large, however, and therefore the difference was not statistically significant. Both lean meat on the carcase, growth rate and ability to utilise fodder were above the mean average value in Ha sires. If Ha pigs were removed, the K index and meatiness would diminish, but the meat colour points would improve by about one index point. Breeding for meatiness and growth improvement could continue successfully because some individuals with a high K index are to be found among both Hc/ and H—/— sires. As their number is low, a momentary setback in breeding results would inevitably occur.

Evaluation of the different methods used

Halothane test

The halothane test was quite harmless to pigs. Of the 2,066 pigs tested only six died. These were all sensitive to halothane. Of these animals at least three could have been saved if the halothane test had not been conducted in conjunotion with other tests. The iterativeness of the halothane test was good but not 100 % successful. The interpretation of a positive result was in most cases easy, although some ambiguous cases appeared. The typical hal+ reaction in pigs is so dramatic on the basis of obtained results that there was no difficulty to convince the pig breeders to use the results of the halothane test in their breeding programmes. Because the nature of the material used in this investigation, the results obtained with the halothane test could only be repeated with few pigs. The test pigs were either the owners' best breeding animals or pigs from the progeny testing. In test repeatability, a less than 5 % error was confirmed. This corresponds to levels presented in the literature (WEBB and JORDAN 1978 and WEBB 1980a). When pigs at an age of 51 days or younger were tested, however, a lower hal+ frequency was found than in older pigs. The obtained hal+ frequency of 12.4 % is slightly underestimated to represent the situation for the whole breed. On the other hand, the hal+ frequency among individuals with lower breeding value is most probably somewhat lower than the situation apparent at the top of the breeding pyramid.

The possibility to reduce the Hal^n gene frequency in a breed above all depends on how high the hal+ frequency is in the population in question. In the Finnish Landrace breed the hal+ frequency of 12.4 % fell below 20 %, considered by some researchers (LUNDSTRÖM et al. 1980) to be a borderline above which the hal+ frequency must lie before the use of halothane test becomes profitable. Although the frequency for the whole breed remained below 20 %, some individual piggeries were observed to have a frequency above this borderline value. Conducting the halothane test in these piggeries would at least be profitable, and a rapid improvement in stress resistance is expected in the beginning, assuming that all breeding animals are tested and that all the reactors are rejected.

If all animals intended for breeding, including both males and females, are halothane tested in a population where the Hal^n frequency is 0.35 and all reactors are rejected, the gene frequency should decrease to 0.127 by the fifth generation and the share of hal+ pigs to 1.6 %. This change in gene frequency was calculated according to the formula $\Delta q = \frac{sq^2(1-q)}{1-sq^2}$ where q is the gene frequency and s the coefficient of selection as introduced by FALCONER (1960).

If only male pigs were to be tested, the gene frequency in the fifth generation would be 0.2 and the share of hal+ animals 4 %. This calculation is based on the same formula. Taking into account more precisely the differences in gene frequencies between the male and female population does not yield a significantly different result.

In the calculations it has been assumed that halothane sensitivity is caused by one recessive gene with the property of complete penetrance in the halothane test. An additional assumption is that the effect of all males and females is of the same order of magnitude on building the next generation. No adjustment has been made for

Table 27. Decrease in halothane-sensitivity frequency when all breeding animals are halothane-tested

Generation of selection	Hal+ frequency (%) in different generations						
0	40	25	20	15	10	5	2.5
1	15	11.1	9.5	7.8	5.7	3.3	1.8
2	7.8	6.1	5.3	4.3	3.6	2.3	1.4
3	4.3	3.9	3.5	2.9	2.4	1.7	1.1
4	2.9	2.6	2.5	2.1	1.7	1.3	0.9
5	1.6	1.9	1.8	1.6	1.3	1.0	0.8

Table 28. Decrease in halothane-sensitivity frequency when the coefficient of selection is 0.5

Generation of selection	Hal+ frequency (%) in different generations						
0	40	25	20	15	10	5	2.5
1	29	18	15	11	7.8	4.1	2.2
2	25	13	11	8.5	6.2	3.4	1.9
3	18	10	8.5	6.7	5.1	2.9	1.7
4	13	7.8	6.7	5.4	4.2	2.5	1.5
5	10	6.2	5.4	4.4	3.5	2.2	1.3

the fact that some boars are used in artificial insemination and can affect the whole population, while other boars on farms will affect only a small subpopulation. The possible weaker reproductivity of halothane-sensitive animals has also not been taken in consideration. If all breeding animals were tested and the reactors rejected, then the gene frequency in the first generation of selection would be reduced from 0.35 to 0.26. In the fifth generation of selection the reduction would be much smaller, or from 0.17 to 0.15. This would first correspond to a reduction of the hal+ frequency from 12.4 % to 6.7 % and then only from 2.92 to 2.12, respectively, and in this way indicates that the rate of progress decreases as selection continues.

Breeders who have the chance to use the halothane test on all breeding animals and choose only non-reacting females and males for breeding could under optimal circumstances expect a reduction in halothane-sensitive pigs in the manner calculated in table 27. All breeders do not have the opportunity to use the halothane test on their pigs, but all breeders can use artificial insemination, and the boars used in the artificial insemination service are halothane-tested. By using artificial insemination, it is conceivable that with an unselected female population progress can be achieved as indicated in table 28.

In tables 27 and 28 improvement is calculated according to the same FALCONER (1960) formula used in the previous calculations. In table 28 the figure 0.5 is used as a coefficient of selection, and primarily corresponds to the selection of males only. The progress demonstrated above occurs only when the heterozygotes are not selected for breeding more frequently than pigs completely free from this gene. However, these Hal^n heterozygotes have been found to be meatier than individuals without this gene (EIKELENBOOM et al. 1976 and 1980 and SCHNEIDER et al. 1980), and thus they are in fact in a better position to be more often chosen for

breeding purposes (OLLIVIER et al. 1976 and ANDRESEN and JENSEN 1980). This investigation showed that both the hal+ and hal– litters of hal+ sires had a better K index and more lean meat on the carcase than litters of hal– sires. The fall in halothane frequency shown in tables 27 and 28 should certainly not occur, because when selecting sires for artificial insemination the Hal^n heterozygotes are favoured although the Hal^n homozygotes will be eliminated. Since females are not halothane-tested, both hetero- and homozygotes will be favoured among them. Actual progress towards better stress-resistance would then be slower.

The toxicity of halothane

Long-lasting (more than 20 minutes) or repeated halothane narcoses have been shown to be dangerous to both humans and several animal species, such as monkey, mouse, rat mink and dog. It can cause liver and kidney damage appearing as centrolobular necrosis in the liver and tubular necrosis in the kidneys (GREENHAM and WARE 1979 and COUSINS 1980). It has been demonstrated that halothane produces a teratogenic as well as mutagenic effect (V. BASFORD and FINK 1968, GRANT et al. 1977 and FÖRSTER and BUTLER 1978). An above-normal abortion frequency has been reported in women working in operating rooms (COHEN et al. 1977). The halothane test when narcosis lasts 3–5 minutes is of no danger to pigs, and no analogous damage has been reported.

Malignant hypertermia (MH) can also be induced in sensitive pigs by other narcotic agents, as shown with chloroform by HARRISON et al. (1969) and with Suxamenthonium. MH can in addition be induced with caffein (VAN DEN HENDE et al. 1978).

Hal^n heterozygotes

Effective elimination assumes that in addition to Hal^n homozygote (hal+)pigs it is possible to identify Hal^n gene heterozygotes. These are not revealed by the halothane test. If no other tests than the halothane test are available, elimination based on progeny testing as proposed by WEBB (1980b) and SMITH (1981) should be performed, and all sires and dams with even only one hal+ offspring eliminated.

A–O blood type system

JØRGENSEN (1977) and IMLAH and THOMSON (1979) demonstrated that halothane sensitivity is dependent not only on the H blood group system factor a but also on the A–O blood group system. When both systems were taken into account, it became possible to indicate hal+ pigs with 84.1 % certainty and hal– pigs with 79.6 % certainty. MABRY (1978) showed that hal+ individuals could be found among the H blood group system a/a pigs which did not react to the A–O system nor to A or O, and without exception found among H–/– pigs which reacted to A or O. Of Ha/– pigs reacting in the A–O system to A or O, some were hal+ pigs and some hal– pigs. The A–O blood group factors were not investigated

in any greater detail in the present study. Knowledge about these factors in relation to H system factors would have contributed further needed information to the elimination process, but according to results reported by MABRY (1978) proposing the A–O factors for consideration in the breeding programme further study was not practical. As for the elimination of hal+ pigs, both the addition and elimination of pigs with the A–O factors would be necessary.

Phi enzyme

JØRGENSEN (1977) demonstrated that all hal+ pigs in the Danish Landrace breed had the Phi enzyme type Phi^{BB}, while JENSEN (1978 b) reported that more hal+ pigs and poorer meat quality were found in pigs which simultaneously had both Ha and Phi^{BB}. By considering the Phi-polymorphism, breeding against stress sensitivity and poor meat quality can be intensified (JØRGENSEN 1980 a).

In this study it was demonstrated that the Phi^{BB} is present more commonly in hal+ pigs, but also among Phi^{AB} pigs some hal+ individuals were discovered. No hal+ reaction was observed among Phi^{AA} pigs, but the Phi^{AA} was very rare in this material. Only 1.5 % of the pigs tested had the Phi^{AA}. On this basis, Phi typing in Finland at present only has small practical value for the breeding programme. As Phi^{BB} is present in 76.9 % of all pigs tested, there exists in fact no reason to propose selection against it. Further studies indicate that eliminating Phi^{BB} would not remove all Hal^{n} gene-carrying individuals. ANDRESEN (1980a) substantiates on the same ground that elimination of the Phi^{BB} genotype in the Danish Landrace breed is neither advisable nor adequate. This investigation showed that pigs with Phi^{AA} had a markedly lower CK serum activity level. The CK activity of Phi^{AB} pigs were also lower than those of the Phi^{BB} pigs, and this difference persisted when pure hal– pigs were compared to each other.

CK test

Many investigators (reviewed by BICKHARDT et al. 1977) have emphasized the use of the serum CK enzyme activity determination (CK test) to recognize stress-sensitive pigs, but only BICKHARDT et al. (1979) have applied it in a breeding programme. HWANG et al. (1978) demonstrated that the CK test separated hal+ and hal– pigs into groups but that at the same time the fluctuation in CK activity within the groups was large. Due to this fluctuation it was difficult to impose elimination limits needed in breeding programmes. Many other investigators have also shown this (BICKHARDT et al. 1977). The results obtained in this study were also in full agreement with these findings.

The fact that extremely high serum CK activity values are sometimes demonstrated in pigs poses difficulties in using automatic analyses, as has been pointed out both by BICKHARDT et al. (1977) and KALLWEIT et al. (1977). The test error was also observed to increase along with a rise in the CK activity level. Test errors of the same type but much larger were demonstrated when the CK activity was determined in serum samples taken from the same pigs on different occasions. The reason for the poor iterativeness of the CK test probably mostly lay in the fact that very fre-

quently serum samples were contaminated with muscle tissue, and these contaminations could cause false high CK activity values. False positive CK activity values have also caused difficulties for other investigators (HWANG et al. 1976, BICKHARDT 1979). THORÉN–TOLLING (1980) showed that individual judgement improved as judgement was passed on repeated determinations.

From the breeding point of view, it would be of principal value to know if the CK test could be used to identify Hal^n gene heterozygotes. Despite some technical drawbacks to the procedures, hal+ pigs or Hal^n homozygotes clearly deviated from the hal– pig group in this investigation. But among hal– pigs it was not feasable to form a group representing the Hal^n heterozygotes. It was expected that hal– offspring of hal+ sires would deviate from the offspring of hal– sires. The same CK activities were, however, obtained in both groups, and no remarkable differences in CK activity could be demonstrated in hal– pigs representing different H blood group types. The conclusion was accordingly that the CK test performed on "non-stressed" pigs was of no value for the demonstration of Hal^n heterozygotes. LUECHER et al. (1979) and SCHNEIDER et al. (1980) proposed, however, that the heterozygote CK activity fell between the values obtained for homozygotes and for the group lacking the Hal^n gene. Perhaps they stressed the pigs before the serum CK activity was determined and were more careful in collecting blood samples.

BICKHARDT et al. (1980) have emphasized the importance of standardized straining before the CK test determination. BICKHARDT et al. (1979) proposed that the serum CK activity be analysed about eight hours after standardized exercise. It was also shown in this investigation that the activity of hal+ pigs increased radically 24 hours after the halothane test. In this study no attempt was made to elucidate the type of strain test necessary to cover the high CK fluctautions observed in resting pigs. BICKHARDT et al. (1980) previously used an exercise test and later drugs suited for parenteral administration.

Meat colour

The investigations conducted in this study also show that the colour of the meat correlates very well with other test results used to demonstrate exertional myopathy. Because of this high correlation and the relatively good inheritability of meat colour, it has become the most important method to suppress exertional myopathy by using meat colour determination both in Denmark and Sweden (PEDERSEN 1979 and LUNDSTRÖM et al. 1980). JENSEN and ANDRESEN (1980) showed that although the other tests, primarily the halothane test, the H blood group system factor a and Phi enzyme typing, yield more information speeding up breeding progress, the contribution is, however, so small that it is most practical for Danish purposes to concentrate on meat colour. LUNDSTRÖM et al. (1980) demonstrated that in the Swedish breeding programme too little attention has been paid so far to meat colour to make any progress. Both in Denmark and Sweden much importance has been attached to improving the reliability of the results obtained from meat colour determinations. The Danes have effectively standardized the transport of test pigs and the entire preslaughter treatment and have also developed the KK index as a measure for meat quality (BARTON 1974). In Sweden rejection is based on average deviations from numerical colour points measured from all test pigs slaughtered at the same ti-

me (LUNDSTRÖM et al. 1980). In both countries the colour readings are corrected with results obtained in pH_2 determinations so that DFD meat does not disturb the evaluation principles. In this study problems related to meat colour determinations have not been investigated. The results obtained indicate, however, that criticism of meat colour readings in the Finnish progeny testing has been too severe, although deficiences which need rapid correction were found. Above all, the errors caused by DFD meat have to be rectified. The evaluation procedure should be modified so that DFD meat is evaluated as PSE meat. In order to reveal DFD meat the pH_2 should be determined. Perhaps a change in preslaughter treatment favouring PSE meat and not DFD meat should also be taken into consideration, as is the procedure in Denmark (BARTON 1974).

Water-holding capacity of meat

In this study, efforts were made to apply the meat water-holding capacity measurement to live animals, but without success. The obtained results did not correspond to results obtained in other tests determining exertional myopathy. The actual reason for unreliable results might be that too small biopsy specimens were taken. In the methods used to determine WHC, the processing of small samples magnified technical errors so that no real differences in WHC could be reliably measured. WALSTRA et al. (1977) also failed in their efforts to use determinations on muscle biopsies from live animals as general criteria for meat quality characteristics. Results could, however, be improved with larger biopsy specimens (PFEIFFER 1981).

Implications for the breeding programme

The results obtained in this investigation indicate that the quickest and easiest means to reduce the hal+ frequency and improve the meat colour reading would be to favour the H blood group factor c. By increasing the number of pigs with the c factor, the hal+ frequency should decrease rapidly. In this group more than 88 % of the pigs were free of the Hal^n gene. The meatiest individuals carrying the Ha blood group factor could be retained but should be mated to Hc individuals. In most piggeries using this method halothane-sensitive individuals would completely disappear as soon as the first generation of selection. A small number of Hal^n carriers exist among Hc pigs, however, so the halothane test should be used at phenotype stations to exclude the possibility of getting Hc Hal^nHal^n pigs for artificial insemination. Additionally it would be necessary to expose the Hc/Hal^nHal^N pigs with great degree of reliability. This is possible only if test matings are carried out and a halothane test is made on the offspring. This should be done at least to all sires carrying the Hc/ blood group and additionally having a high K index. When in test matings hal+ dams are mated to sires carrying the Hal^n gene, half of the piglets born will be hal+ pigs. In a litter consisting of at least five piglets, the halothane test will reveal if the sire used carries the Hal^n gene or is free of the gene with 95 % confidence, and in a litter with seven piglets do so with 99 % confidence. If a test dam known to be a Hal^n gene heterozygote or known to have at least one hal+ offspring is mated to a Hal^n gene carrier boar, 25 % of the offspring born will be homozygotes or hal+

pigs. In this case only one litter with 11 piglets has to be halothane-tested to reveal the sire genotype with 95 % confidence. To obtain a 99 % probability the litter should contain 16 piglets (PIRCHNER 1969). If the test is performed on the litters of daughters of the sire or on daughters of known heterozygous sires or dams, offspring from the litters of five dams should be tested before it can be confirmed whether or not the sire has the Hal^n gene.

VIII Conclusions and application of practical measures for the breeding programme

As long as breeding for more meat is carried out in the Finnish Landrace breed where the Hal^n gene and the drawbacks caused by it are present, the quantity of PSS and PSE/DFD will continue to increase. In order to prevent this it is necessary to include in the breeding programme clear procedures to restrain the dissemination of the Hal^n gene. In a long term programme it seems to be profitable to try to eradicate the Hal^n gene completely.

In 1979 the Hal^n gene was present in at least 58 % of the most advanced Finnish Landrace pigs, and 12.4 % of them were homozygotes in regard to that gene. The halothane test has to be performed on pigs older than seven weeks to reliably reveal Hal^n gene homozygotes. A fully satisfactory test identifying Hal^n gene heterozygotes has to date not been demonstrated.

The iterativeness of the CK test was poor when the test was conducted without prior exertion. No real proof that the CK test performed on "rested" pigs identified Hal^n gene heterozygotes was demonstrated. Of the Phi enzyme types the Phi AA very seldom follows the Hal^n gene, but the Phi AA is rare. Only 1.5 % of all pigs tested had this Phi type. The determination of the H blood group system factor a and c provides in addition to the meat colour measurement and the halothane test the most advanced information to identify Hal^n gene-carrying individuals. Of the Ha-carrying pigs most probably 91 % have the Hal^n gene. No casual relationship exists, however, between the H blood group factor a and the Hal^n gene. Of Hc pigs 0.4 %, of –/– pigs 6,1 % and of Ha/c pigs 1.9 % reacted to the halothane test.

The Hal^n gene-carrying pigs both homo- and heterozygotes generally have lighter meat than pigs free of this gene. The meat colour reading follows the results obtained in determining exertional myopathy. The mean value of the meat colour from four test pigs cannot be a reliable basis for selection if the probable presence of DFD meat is not observed. DFD meat has to be judged as PSE meat. Hal^n gene-carrying pigs were not identified with water-holding capacity determinations performed in muscle biopsies from living pigs.

A breeding programme for the Finnish Landrace breed should according to the results of this study contain the following measures.

1. In progeny testing the meat colour should be correlated to the results obtained in pH_2 determinations and strongly pointed out in order not to aggravate the current exertional myopathy situation.
2. The breeding herds could resist exertional myopathy by employing the H blood group system factor c. The meatiest a/a and a/ pigs could be saved, but they

should not be mated to each other. The Ha (a/a and a/—) pigs should be mated to c pigs. If c pigs are not available, a/c or —/— pigs should be used, and of these a/c pigs are more suitable.

3. The halothane test should be used

— at phenotype testing stations when selecting sires for artificial insemination
— when selecting breeding animals in piggeries where the hal+ frequency is higher than 15 %
— as a progeny test on all c sires having a high K index

It is enough to test only one litter of seven pigs if the dam is a hal+ dam, or 11 pigs if the dam is known to give birth to hal+ offspring. If such dams are not available, the test should be conducted on daughters of hal+ dams or sires, or on the boars' own daughters. In this case whole litters from five dams have to be halothanetested before it is reliably guaranteed that the sire used is free of the Hal^n gene.

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X Selostus (Summary in Finnish)

Tutkimuksessa tarkastellaan sian puutteellisen stressinkestävyyden ja siihen liittyvän huonon lihanlaadun, PSE, esiintymistä suomalaisen maatiaisrodun pisimmälle jalostetussa osassa.

Eri menetelmien käyttökelpoisuutta huonoa stressinkestävyyttä periyttävien porsaiden tunnistamisessa selvitetään ja tulosten sekä käytettyjen tutkimusmenetelmien soveltuvuutta sikaloissa tapahtuvaan käytännön jalostustoimintaan pohditaan.

Tutkimusaineisto käsittää 2003 porsasta 21 jalostus- ja 10 siitossikalasta sekä 86 norjalaisen maatiaissian porsasta. Suomalaisista porsaista 84 kpl tutkittiin sikatalouskoeasemilla, jotta saatiin suora vertailu elävillä sioilla tehdyn tutkimuksen tulosten ja samojen yksilöiden lihan laatuominaisuuksien välille.

Sikojen huono stressinsietokyky paljastettiin halotaaninukutuksella. Tähän halotaanitestiin reagoi 12.4 % porsaista. Edellyttäen, että halotaaniherkkyys on yhden resessiivin geenin aiheuttama ja että halotaanitesti paljastaa kaikki homozygootit yksilöt laskettiin, että ainakin 58 %:lla maatiaisrodun pisimmälle jalostetuista sioista on tämä geeni. Luku 58 % on ilmeisesti hieman alempi kuin hal^n geenin omaavien yksilöiden todellinen määrä.

Alle 50 vrk:n ikäisinä testattujen 421 porsaan joukossa todettiin vähemmän halotaaniherkkiä yksilöitä kuin tätä vanhempina testattujen 1582 porsaan joukossa. Tästä päätellen luotettava homozygoottien paljastaminen edellyttää, että porsaat halotaanitestataan vasta, kun ne ovat yli 7 viikon ikäisiä.

H veriryhmäjärjestelmän tekijät a ja c määritettiin 1991 porsaalta. Suomalaisista porsaista oli 60.7 %:lla tekijä a ja 38 %:lla tekijä c. 16.7 %:lla porsaista ei esiintynyt kumpaakaan näistä tekijöistä.

Norjalaisista porsaista oli 62 %:lla a ja 55 %:lla tekijä c. Halotaaniin reagoineista porsaista oli 91 %:lla tekijä a ja 6.1 %:lla tekijä c. H a/a sioista reagoi halotaaniin 39.6 % ja H a/ sioista 20.7 %. H a/c sioista reagoi 1.9 % ja H c/ sioista vain 0.4 %. H –/– sioista reagoi 6.1 %.

Halotaaniin reagoineista porsaista oli 96 %:lla Phi enzyymi tyyppi BB ja 3.4 %:lla tyyppi AB. Phi tyyppi AA porsaista ei yksikään ollut herkkä halotaanille. Phi tyyppi AA oli harvinainen sillä se todettiin vain 1.5 %:lla porsaista.

CK testillä (seerumin kreatiini kinaasi aktiviteetin mittaus) voitiin erottaa halotaaniherkät ja halotaaniin reagoimattomat porsaat ryhminä toisistaan, mutta halotaaniherkkyys geeniä piilevänä kantavien yksilöiden muodostamaa ryhmää ei voitu osoittaa. CK testin antamat tulokset vaihtelivat paljon sekä halotaaniherkkien että -kestävien porsaiden joukossa. Jalostuskarsintaa varten tarvittavaa karsintarajaa oli tästä syystä vaikea asettaa.

CK testissä toisinaan saatuihin odottamattoman korkeisiin lukemiin todettiin kaksi syytä. Ensinnä vaikutti porsaiden käsittely testiä edeltäneenä päivänä tulokseen. Jos eri pahnueiden porsaita oli siirretty yhteiseen karsinaan odottamaan testaajaa ne olivat tapelleet ja tämän seurauksena niillä todettiin korkea CK aktiviteetti.

Toisaalta todettiin, että verenoton yhteydessä joutui joihinkin näytteisiin kudospalanen, josta seerumiin vuoti kreatiini kinaasia. Verinäytteet otettiin kaulalaskimosta ja seerumi irrotettiin vasta seuraavana päivänä. Verinäytteiden sentrifugointi heti verenoton jälkeen paransi jonkin verran CK testin antamien tulosten toistettavuutta.

Eläviltä porsailta heti halotaanitestin jälkeen otettujen lihasnäytteiden vedenpidätyskyvyn mittaamisella ei kyetty erottamaan halotaaniherkkiä yksilöitä halotaaniin reagoimattomista.

Halotaaniherkkien yksilöiden liha todettiin väriltään vaaleammaksi, kuin halotaania kestävien sikojen. Lihan värin mittaamista voidaan siis käyttää stressiä huonosti kestävien sikojen tunnistamiseen. Joku hyvin tummalihainen halotaaniherkkä sika kuitenkin todettiin. Tämä osoittaa, että kantakokeissa ei koeryhmien väripisteenä voida käyttää ryhmien jäsenten värilukemien keskiarvoa ellei tervalihan mahdollista esiintymistä huomioida.

Kaikkien siitokseen tarkoitettujen sikojen H veriryhmän määrittämistä suositetaan. Suosimalla H c tekijän omaavia sikoja pitäisi olla mahdollista nopeasti alentaa halotaaniherkkien sikojen määrää suomalaisessa maatiais-

rodussa. Parhaat H a/a ja H a/ siat voitaisiin pitää kunhan ne aina paritettaisiin H c sikojen kanssa.

Koska jotkut H c siat kuitenkin ovat stressiheikkousgeenin kantajia ja korkea K-indeksi ja suuri lihaksikkuus suosii tämän heikkoustekijän kantajia, on odotettavissa, että nyt H c sioilla todettu matala stressiherkkyysfrekvenssi muuttuu tulevaisuudessa epäedulliseen suuntaan. Tästä syystä olisi ainakin kaikki korkean K-indeksin saavuttavat H c karjut voitava osoittaa vapaiksi stressiheikkoustekijästä. Tämä voidaan osoittaa vain halotaanitestaamalla riittävä määrä tutkittavan karjun jälkeläisiä. Jos karju voidaan koeparittaa emakolla joka tunnetaan heikkoustekijän kantajaksi, joko homo- tai heterozygootiksi, saavutetaan jo yhden normaalikokoisen pahnueen porsaiden halotaanitestaamisella riittävän luotettava tieto karjun perintöasusta. Jos testaus suoritetaan karjun omien tyttärien tai stressiheikkoustekijää kantavan karjun tyttärien porsailla olisi halotaanitestattava viiden tyttären pahnueet.

XI Appendix

Appendix Table 1. Serum CK activity levels μkat/l determined from the same pigs at different times

No of group	No of pig	Halothane reaction	Time of serum sampling compared to the time of halothane test			
			Two months before	Just before	Just after	24 h after
	1	+	12.1		32.3	
	2	+	23.4		18.0	
	3	+	12.2		17.9	
	4	–	7.4		23.5	
1	5	–	19.4		117.4	
	6	–	12.0		118.7	
	7	–	18.8		19.8	
	8	–	6.7		6.2	
	9	–	4.9		7.8	
	10	–	4.8		19.4	
	11	–	8.6		9.3	
	12	–	6.1		7.1	
	1	+		18.8	7.95	
	2	+		15.2	17.5	
	3	+		23.7	13.1	
	4	+		60.7	47.8	
2	5	+		19.0	18.1	
	6	+		49.9	23.5	
	7	–		24.1	53.2	
	8	–		5.3	12.9	
	9	–		7.8	16.2	
	10	–		13.9	10.3	
	11	–		25.9	57.9	
	12	–		32.1	19.2	
	13	–		22.8	51.0	
	14	–		19.6	7.0	
	15	–		44.4	39.2	
	16	–		16.4	14.8	
	17	–		17.6	14.5	
	18	–		6.6	15.8	
	19	–		8.5	7.9	
	1	+			30.3	473.6
	2	+			45.8	340.6
	3	+			24.8	195.3
	4	+			18.8	636.3
3	5	+			119.8	532.7
	6	+			62.3	224.6
	7	+			137.5	367.2
	8	+			142.9	373.1
	9	+			85.2	542.5
	10	+			19.5	223.7
	11	+			16.8	498.7
	12	–			6.6	9.4
	13	–			36.5	46.4
	14	–			10.0	10.4
	15	–			13.5	41.0
	16	–			8.1	10.1
	17	–			77.1	38.2
	18	–			90.5	11.4

Appendix Table 2. Meat colour points, H blood group, halothane reaction, percentage of lean meat on carcase and K index of pigs tested at Pig Progeny Testing Station in southwestern Finland

No of group	No of pigs	Meat colour points of groups	Meat colour points of pigs	Hal. reaction	H blood group	Percentage lean meat on carcase	K index
	1		died	+	a/		
	2		49	–	a/		
1	3	46	45	–	a/	50.4	+6.3
	4		43	–	a/		
	1		46	–	a/		
	2		44	–	–/–		
2	3	45	45	–	–/–	51.8	+10.6
	4		46	–	a/		
	1		43	–	a/c		
	2		50	–	a/		
3	3	41	42	–	a/	51.5	+14.2
	4		40	–	a/a		
	1		37	–	–/–		
	2		52	–	–/–		
4	3	41	41	–	a/	49.9	–0.4
	4		37	–	a/		
	1		41	–	c/		
	2		45	–	c/		
5	3	40	38	–	c/	50.2	–1.7
	4		36	–	a/		

Appendix Table 3. Meat colour points, H blood group, halothane reaction, percentage of lean meat on carcase and K index of pigs tested at Pig Progeny Testing Station in east and central Finland

No of group	No of pigs	Meat colour points for groups	Meat colour points for pigs	Hal. reaction	H blood group	% lean meat on carcase	K index
	1		51	+	a/a		
	2		50	–	a/		
1	3	46	45	+	a/a	51.7	+7.4
	4		37	–	a/		
	1		30	–	a/		
	2		48	–	a/		
2	3	42	42	–	–/–	51.7	+5.1
	4		48	–	a/		
	1		died	–	c/		
	2		41	–	–/–		
3	3	41	41	–	c/	49.9	–0.6
	4		41	–	–/–		
	1		42	–	–/–		
	2		37	–	c/		
4	3	38	39	–	–/–	49.4	+2.4
	4		35	–	c/		
	1		died	–	–/–		
	2		41	–	a/		
5	3	37	40	–	a/	49.3	+4.2
	4		29	+	–/–		

Appendix Table 4. Meat colour points, H blood group, Phi-type and CK activity in serum before (CK I) and after (CK II) halothane test and halothane reaction of pigs tested at Swine Research Station in Hyvinkää on 22. 2. 1979

No of pigs	Meat colour points	Hal. reaction	H blood group	Phi-type	CK in serum μkat/l		WHC %
					CK I	CK II	
1	58	+	a/	BB	22.8	50.9	72.4
2	58	–	c/	AB	–	55.3	69.5
3	55	+	a/a	AB	54.8	55.3	59.7
4	53	–	a/	BB	–	–	–
5	52	–	c/	AB	11.3	17.8	66.3
6	51	–	a/c	AB	18.4	8.1	69.8
7	47	–	a/c	BB	11.0	13.6	–
8	45	–	c/	AB	–	–	52.7
9	43	–	a/	BB	33.1	5.0	–
10	41	–	c/	BB	31.5	9.8	79.5
11	40	–	a/c	AB	15.2	17.5	62.0
12	39	–	a/c	BB	19.6	6.9	68.7
13	39	–	a/c	BB	–	16.4	54.5
14	39	–	a/	BB	18.6	8.0	70.6
15	39	–	a/c	BB	44.4	39.2	43.6
16	39	–	a/	BB	13.0	9.3	78.5
17	37	–	c/	BB	10.5	8.7	70.2
18	37	–	a/c	BB	12.8	6.0	–
19	35	–	a/c	BB	7.1	8.3	–

Appendix Table 5. Meat colour points, Halothane reaction, H blood group, Phi-type and CK serum activity in pigs tested at Swine Research Station in Hyvinkää on 24. 9. 1979

No of pigs	Meat colour points	Hal. reaction	H blood group	Phi-type	CK in serum μkat/l
1	60	–	a/		15.2
2	58	–	c/		11.2
3	52	+	a/	BB	31.1
4	49	–	a/		27.4
5	47	–	–/–		9.6
6	44	–	–/–		9.5
7	42	–	a/c	BB	11.9
8	42	–	c/	AB	30.3
9	40	–	a/		7.7
10	39	–	a/	AB	14.1
11	39	(+)–	a/	BB	14.9
12	38	–	a/c		16.4
13	37	–	a/		35.0
14	36	+	a/	BB	13.6
15	35	–	c/	BB	8.1
16	34	–	a/c		15.3
17	34	–	c/	BB	9.6
18	33	–	c/	AB	4.6
19	33	–	c/		5.0
20	33	–	c/	BB	7.9
21	28	–	a/	AB	6.8

Appendix Table 6. Frequency of halothane reactivity and H blood group factors a and c in pigs from different farms and ages of pigs at the time of halothane test

Code number of farm	Tested pigs	Hal+ pigs in %	Frequency in % of a and c factors		hal^n gene frequencies	Mean ages in days of hal+ and hal– pigs at the time of halothane test	
						hal+	hal–
	n		a	c			
2117	24	0	45.0	8.3		–	51.5
2919	80	0	15.0	85.0		–	70.5
6040	14	0	57.1	42.8		–	60.4
2764	25	0	25.0	75.0		–	72.0
807	79	1.3	68.0	15.1	0.11	100.0	55.8
5540	69	1.4	62.3	34.7	0.12	66.0	65.0
3386	56	1.8	30.9	87.0	0.13	69.0	58.0
4402	49	2.0	66.0	30.6	0.14	60.0	44.6
271	86	4.7	43.0	25.5	0.22	84.5	66.5
1808	75	5.3	60.0	17.3	0.23	71.0	66.5
2029	12	8.3	83.3	0.0	0.29	67.0	67.4
457	23	8.9	80.0	0.0	0.30	78.1	78.1
2788	45	8.9	55.6	11.1	0.30	90.5	78.8
4063	42	9.5	61.9	30.9	0.31	98.0	84.0
1135	30	10.0	63.3	36.6	0.32	40.7	48.1
6359	404	10.4	59.5	21.6	0.33	71.5	65.8
3391	43	11.6	65.1	2.2	0.34	75.4	66.4
2095	34	11.8	82.3	0.0	0.34	62.9	67.4
294	113	12.4	70.8	16.0	0.35	49.2	58.2
2032	23	13.0	47.8	39.1	0.36	64.3	89.4
134	45	13.3	80.0	8.9	0.36	82.2	75.3
3063	58	13.8	67.2	17.2	0.37	53.4	47.7
2387	68	17.6	35.3	32.4	0.42	81.4	85.2
5425	16	18.6	56.2	43.7	0.43	52.0	51.5
3303	218	19.3	77.0	16.0	0.44	69.2	60.5
4594	88	20.5	60.2	19.3	0.45	77.7	64.1
312	4	25.0	50.0	0.0	0.50	91.0	91.0
1961	17	29.4	82.3	0.0	0.54	82.0	80.3
2652	98	33.6	75.5	7.1	0.58	72.2	66.9
584	21	40.0	90.0	9.5	0.63	85.3	82.3
4488	32	59.3	87.5	0.0	0.77	70.8	73.6

Appendix Table 7. Sires, their H blood group, K index, percentage of lean meat on carcase and meat colour points compared to halothane reaction of their offspring. Sires with K index higher than 8.6 and those with a negative K index are listed

Name and pedigree no	H blood group	No of test groups	K index	% lean meat on carcase	Meat colour points	No of halo. tested offspring	No of hal+ pigs	No of tested litters	No of Hal+ litters	Hal+ or hal− boar
Karelia 4520	a/	6	20.8	53.9	42.4	11	2	2	1	+
Pulkka 4662	−/−	7	17.3	51.5	42.0	43		6		−
Ekra 4367	a/c	3	16.3	50.4	42.3	5		1		−
Penta 5100	a/	15	15.8	53.1	43.9	92	24	17	11	+
Jahvetti 4719	a/	3	15.2	52.7	48.7	6		1		−
Pahka 4779	a/	11	14.8	52.2	38.7	16	9	2	2	+
Pilot 4777	a/	23	14.4	52.1	43.7	67	18	17	7	+
Parka 4961	a/	9	13.7	52.1	41.3	53	2	9	1	+
Paholainen 4790	a/	8	13.2	51.2	43.1	142	17	26	12	+
Polska 4781	a/	8	12.7	51.5	44.1	15	3	3	2	+
Pako 5071	c/	3	12.5	52.2	37.0	7		1		−
Pateri 5154	c/	4	12.5	50.9	44.7	10		1		−
Horatius 4740	a/	7	12.5	52.0	35.9	19	1	4	1	+
Kiekko 4722	a/	11	12.2	51.7	37.3	10		1		−
Elmeri 4894	a/a	4	11.8	51.8	41.7	10		2 (c,c)		−
Taso 4712	c/	3	11.7	52.4	38.8	41		6		−
Rysky 4778	a/	6	11.6	51.7	41.8	16	2	5	1	+
Senaattori 5001	a/	4	11.5	51.1	41.5	8	1	2	1	+
Baneli 4649	a/c	4	11.4	52.1	42.3	45	13	9	7	+
Pover 4927	−/−	6	10.9	51.5	43.0	42	9	7	4	+
Panu 5-254	a/a	4	10.8	50.7	41.8	12	12	2	2	+
Kuula 4724		4	10.8	51.0	40.3	1		1		−
Justeeri 4607	a/a	4	10.9	49.7	41.1	11	3	2	1	+
Panta 5044	a/	7	10.4	51.4	40.9	32		4		−
Mölli 4770	a/	5	10.3	51.0	38.3	16	2	5	1	+
Jermu 5186	a/c	3	10.2	50.8	38.5	10	4	3	2	+
Käämi 4595	a/c	4	10.0	49.6	42.2	1	1	1	1	+
Idea 5004		6	9.9	51.4	38.0	3	2	1	1	+
Heko 5236	−/−	5	9.9	51.1	41.9	4		2		−
Patu 4970	c/	6	9.8	50.8	38.0	98		13		−
Joiku 4956	c/	3	9.2	51.1	40.0	9		2		−
Kääne 4600		10	9.2	50.6	41.6	1		1		−
Pultsa 4637	−/−	8	9.1	51.2	38.4	8	1	3	1	+
Inssi 5003	a/c	6	9.1	51.5	40.2	6	2	1	1	+
Jäli 5163	a/c	10	9.0	50.7	40.4	34		9		−
Nykytys 4384		5	8.8	51.2	38.6	9		9		−
Pankkiiri 4801	a/	5	8.7	51.8	31.7	37	4	7	3	+
Jokunen 5142	c/	5	8.7	51.2	42.8	47	12	14	7	+
Kiero 5258	a/	3	−1.2	49.6	38.9	4		1		−
Jyrä 5131		4	−1.4	49.8	40.0	4	1		−	
Parka 5168	c/	6	−1.7	49.5	40.5	7		4		−
Doro 4225		3	−2.0	47.9	41.5	7		2		−
Rasu 4967		3	−2.0	49.7	40.4	5		1		−
Pösö 4713		5	−2.2	48.1	29.6	1		1		−
Nipo 4916		3	−2.5	49.0	40.2	2	1	1	1	+
Heka 4815		3	−4.7	48.2	35.0	2		1		−
Ukko 4899		3	−5.4	47.9	33.8	7		2		−
Pappo 5151	a/	7	−5.0	48.2	42.9	5	1	2	1	+
Esu 4905	c/	3	−6.4	48.8	46.6	3		1		−
Ikko 5056	−/−	6	−7.0	48.6	39.5	4		1		−
Kompi 5155		5	−7.0	48.3	39.4	16		4		−
Riski 4430	−/−	4	−9.2	47.9	35.8	15		4		−