

A possible genetic interpretation of the colour variants in the fleece of the *Gotland* and *Goth* sheep

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Summary

The paper describes colours of 79 adults and 184 lambs in 6 flocks of the ancient Swedish short-tailed, horned *Goth* breed of sheep. Of the adults, 36 were grey and 43 of a near-white colour, while 85 of the lambs were grey and 99 light-coloured. The light coloured lambs with limited amount of white markings showed two colour patterns, one a lightgrey with white belly, termed « grey mouflon », and the other a mixture of light steel grey and tan, termed « agouti ».

White markings were common in all flocks, and extensive white markings interfered with the classification of the main colours in some of the flocks.

On the basis of the observations, on the *Goth* sheep which contained some pedigree information, and on available observations from crosses of improved grey *Gotland* sheep and *Shetland* sheep in Scotland, together with a review of the literature, the suggestion is put forward that the grey colour in the ancient *Goth* sheep and in the improved *Gotland* sheep is caused by a new allele at the *Agouti* locus, A^{gg} (*Gotland* grey), if not A^g (icelandic grey). The « grey mouflon » colour of the *Goth* sheep is caused by another, previously unknown allele, A^{lg} (lg for light grey) at the *Agouti* locus. Some white animals may be $A^{lg}A^{lg}$ or even carry the A^{wh} gene for tan or white.

I. — Introduction

The understanding of colour inheritance in sheep has been helped by the demonstration of a multi-allelic series at the *Agouti* (*A*) locus (ADALSTEINSSON, 1960; BROOKER and DOLLING, 1969; ADALSTEINSSON, 1970) and by the recent

analysis of the extension locus (*E*) (LAUVERGNE, 1975). The studies support the conclusion of SEARLE (1968) that different mammals have homologous loci.

The colour of sheep, however, presents certain features that have not yet been elucidated, in particular the existence of several kinds of grey, the extent to which these are attributable to the *Agouti* locus not being known (ADALSTEINSSON, 1970).

Colour inheritance studies in the improved Gotland breed were first carried out by LÖFVENBERG and JOHANSSON (1952), and later by SELERUD (1955), SKARMAN (1961, 1963a, 1963b), and EBBERSTEN and SKARMAN (1976). All these studies showed a wide range of shades of grey colour, although selection against the lightest and darkest extremes have been carried out for several decades.

The predecessor of the improved grey *Gotland* breed is the old horned *Goth* breed, which was on the verge of extinction in the nineteen forties, but is now being preserved. The *Goth* sheep show a still wider range of grey shades than the improved *Gotland* breed.

The aim of the present study was to examine the type of grey in the improved *Gotland* breed and relate it to grey colour observed in other breeds, and at the same time to attempt a genetic interpretation of the wide range of grey shades in the *Goth* sheep. For this purpose the authors visited Gotland in June, 1976 and made observations on the colour variation in the *Goth* sheep. At the same time visits were made to some breeders of the improved *Gotland* breed for visual inspection of the colour shades present there. These observations, together with observations on crosses between improved *Gotland* sheep and *Shetland* sheep in Scotland form the basis for the conclusions of the present paper.

II. — Review of the grey coloration in domestic sheep, with reference to the *Gotland* breed and its various colours

A. — *The grey colour in breeds other than the Gotland*

If one regards grey as deriving from a mixture of black and white fibres, it is possible at the moment to distinguish three genetically controlled kinds of grey: lethal grey, progressive juvenile whitening, and grey as an *Agouti* factor.

Lethal grey (in which the animals are grey at birth) was first studied in the *Turcana* breed of Romania by CONSTANTINESCU (1926) then in the *Karakul* (GLEMBOTSKY *et al.*, 1934). Among numerous works devoted to it are reviews by SERRA (1948) and RAE (1956). This is a mutation which when heterozygous is epistatic to other colour genes, producing grey through an admixture of white fibres, and when homozygous is lethal. In this, gastric troubles about the time of weaning are followed by death. On a black base this gene gives grey, while on a red base it gives a kind of lilac, both colours being exploited in *Karakul* furriery.

Studies on progressive whitening were summarised by SERRA (1948) who listed several types under the names progressive whitening or silvering, which develop in breeds with dominant (*Karakul*) as well as recessive (black *Wensleydale*) pigment.

This whitening occurs regularly in red breeds (*Solognote*) and often in black breeds (*Bizet* and *Karakul*), but not in all animals. ZAHARIA (1939) for example showed that certain *Turcana* sheep became grey, while other remained black all their life. The way in which this difference is inherited has not been studied in detail.

The *Agouti* grey factor has been demonstrated by ADALSTEINSSON (1960 and 1970) in the *Icelandic* breed. At birth, the grey animals are distinguished from all black ones by light marks around the muzzle and the eyes, as well as the presence of a white underwool on the scrotum, and in the inguinal region. The underwool develops with age to give a grey fleece at about four to five months. The expression of the gene A^g is variable, and ADALSTEINSSON (1970) distinguishes seven degrees at birth. The homozygous A^gA^g lambs were found to be born light grey, while the heterozygous lambs usually were born dark grey.

Observations and test mating carried out by RYDER *and al.* (1974) with *Orkney* sheep (thought to have affinities with the Scandinavian type) accorded with the interpretation that the grey gene A^g , originally designated A_2 by ADALSTEINSSON was also present in this breed.

In the review of Norwegian work by BERGE (1964) (summarised in English by RYDER and STEPHENSON, 1968) the mixture of black and white fibres (grey) caused by this gene is termed "black skimlet", and the mixture of brown and white fibres "brown skimlet".

B. — History of the Gotland breed

Until the nineteenth century there was in Sweden, as elsewhere in Scandinavia, a population of primitive small Sheep, with coarse wool, and a short tail, which were often horned and showed a variety of colours. This type is named the northern short-tail group of Sheep. In Sweden this original population has been gradually replaced by meat breeds mainly from Britain, so that by the nineteen forties the ancient type was found mainly on the island of Gotland (EKMAN, 1938, 1964; HALLANDER, 1976; RYDER, 1968, 1974).

Starting immediately after World War II the unimproved breed changed gradually into the improved *Gotland* which has the dual purposes of meat and furskin.

Fashion in furriery created a demand for grey skins from lambs four or five months old, and a system of performance testing and skin marketing has developed with the help of advisers from the Ministry of Agriculture. The methods used and the results obtained were described by SKÅRMAN (1961, 1963a and b) and were summarised by GAHNE *et al.* (1975).

The number of *Improved Gotland* sheep has therefore increased from 170 000 in 1962 to 300 000 today, and it now forms 90 p. 100 of the sheep population of Sweden (RYDER, 1970). In comparison with the original type, the improvement has involved a loss of horns, and the production of a fleece that has uniformity of structure and colour.

Such success has been achieved in the replacement of the old breed with the new variety that the ancient type, horned and variegated was on the verge of extinction when several enthusiasts endeavoured to safeguard it in the nineteen sixties (EDBERG, 1974).

In 1973, according to the last author, the number of mature individuals of this relic breed was around 400 animals, of which two hundred are in the island of Gotland in which it originated. These sheep retain the horns and a great variety of colour shades. Except at Skansen Zoo and in the Jakobsson flock on Lilla Karlsö small unimproved flocks often run alongside improved animals.

For the relic variety, EDBERG (1974) proposes the Swedish name *Gutejär* which in English would be called the *Goth* Sheep, instead of the previously used

name *behornade gottländska utgångsfåren* i.e. horned Gotland sheep kept outside all the time. The name given to the improved type is: *Gottlands utgångsfår*, i.e. outdoor Gotland Sheep, or more simply *Gottlands får*. In English, the improved variety is termed simply „*Gotland Sheep*” (Mason, 1969). In French we propose *Gotlandais* for the improved variety, and *Gothique* for the relic type.

C. — *The colour types of Gotland sheep
as described by previous authors*

1. *Descriptive*

EKMAN (1938, 1964) was able to place the animals in three colour categories: black, grey and white. The grey sheep were moderately variable, and the author distinguished two types; he was not, however precise about the age at which the classification was made, nor the detail of the marks on the hairy parts of the body (the face and legs).

LÖFVENBERG and JOHANSSON (1952) recognised the three main classes of EKMAN and inclined towards a scale for grey by noting that only black and white colours were definitive at birth. Grey animals on the contrary were born black, or nearly black, and did not become grey until later. In seeking criteria for distinguishing grey animals from black animals at an early age, SELERUD (1955) investigated the tongue (which is black in black animals) and the underwool which is sometimes white at birth in grey animals. Later the fleece becomes lighter in the adult, becoming almost white in some individuals.

All the analysis of genetic segregation carried out by LÖFVENBERG and JOHANSSON, however, relied on classifications made at or before the age of sale (between two and five months) without taking account of the colour on the head and feet.

Following these authors, SKÅRMAN recorded the colour shade on the scrotum and tongue, the presence of white underwool at birth and studied their correlation with different shades of grey at four to five months, but as with the previous authors his colour description at four to five months referred to the colour on the woolly parts of the animals only. In the interval, however, the scale of grey had become extended; LÖFVENBERG and JOHANSSON (1952) recognised three grades: light grey, grey and dark grey; there are now five: white-grey, light-grey, grey, dark-grey and grey-black.

2. *Genetic interpretation*

LÖFVENBERG and JOHANSSON (1952) thought at first that the recessive black which they observed was due to a mutant (*g*) at the locus for wild coloration which they named *G*; and that the white was given by an allele (*W*) at another locus. They proposed two alternatives to explain grey: an allele or several alleles either at the *G* locus or the *W*, without being able to distinguish between the two.

Later genetic interpretations by EBBERSTEN and SKÅRMAN (1976), can be summarised as follows:

- i) A quantitative inheritance was suggested for the shade of grey with a heritability of shade varying from 0.35 to 0.70 depending on the method of estimation.
- ii) A marked effect was found of genes for white markings on fleece colour, increased white markings being in general accompanied by a lighter wool colour.

- iii) The white colour, which is sometimes observed among the *Gotland* sheep is most likely due to the combined effects of genes for white markings and lack of darkening modifiers.
- iv) Black colour in the *Gotland* sheep may be either due to homozygosity for a gene which is recessive to the gene for grey, or it may be the result of a darkening modifier, which suppresses grey colour.
- v) The grey colour of the *Gotland* breed was found to be recessive to the white colour of the *Swedish Landrace* sheep.

III. — Material and methods

Following the preceding analyses we approached the problem as follows : animals of the improved type were examined to see what colours or colour shades the improved stock had in common with the ancient stock and animals of the latter were examined to see which colour variants could be identified within this breed and which of the variants described by LÖFVENBERG and JOHANSSON (1952) were still in existence.

The flocks of *Goth* sheep available are generally small and dispersed, with a greater concentration in Gotland than on the Swedish mainland, those on the island of their origin were therefore naturally chosen for investigation; this also allowed improved flocks to be visited.

Flocks of the *Goth* breed surveyed are shown in Table I.

TABLEAU I

Flocks of Goth sheep inspected in June 1976 on Gotland (G) and in Stockholm (S) and number of animals grouped by main colour

Troupeaux de moutons Gothiques examinés en juin 1976 dans l'île de Gotland (G) et à Stockholm (S) avec la distribution des animaux selon leur couleur

Flocks	Rams			Ewes			Lambs		
	Grey	Light	Sum	Grey	Light	Sum	Grey	Light	Sum
Lilla Karlsö (G) ^a	7	0	7	101	57	41	98
Sven GUTEMARK, Furillen, Rute (G)	1	2	3	4	10	14	8	6	14
Erik OHLSSON, Vallstena, Dalhem (G)	5	4	9	4	12	16
Fredrik WEHTJE, Klintebys (G)	2	3	5	6	8	14	7	7	14
Sven WAHLBY, Gullgårde, Rome (G)	0	1 ⁽¹⁾	1	10	11	21	7	30	37
Skansen Zoo (S)	1	4	5	2	3	5
Total	10	6	16	164	85	99	184
All. exc. Lilla Karlsö . . .	3	6	9	26	37	63	28	58	86

⁽¹⁾ Only a colour slide available for inspection.

In the Lilla Karlsö flock all the lambs were described with respect to colour, but the colour of individual ewes in that flock was not recorded. In the Gullgårde flock the colour of both ewes and lambs was recorded, and pedigree records were available on all lambs in that flock. They were all sired by the same sire. In the remaining four flocks, ewes and lambs were classified into the two groups *grey* and « *light* » only. Several of these classifications were made at a distance in the pasture.

A. — *The observations*

1. *The Gotland sheep*

In the Gahne flock, which according to Swedish experts is a good average example of present fur producers, the adults appear as follows: the head and legs are black, with lighter areas around the muzzle and the eyes (cf. fig. 1a). White markings on the head are present in only few animals. A high proportion of the wool fibres is white, giving the body a near white appearance, but an admixture of black hairs is invariably found.

Lambs observed some time after birth had the same coloration on the feet and the head as their mothers. The coat was grey, the lightness depending on age, consisting basically of a black outer coat with a white underwool. The same descriptions apply equally well to the flock in Scotland.

2. *The Goth sheep*

a) The adults could be classified into two main categories with respect to body colour. The first was a dark grey type, comparable to the improved *Gotland*, but on the whole showing somewhat darker grey colour on the body, presumably

Fig. 1. — *Colours of the Goth Sheep*

- a) dark grey *Goth* ewe at Lilla Karlsö. One can see the lighter areas around the muzzle and eyes. The colour is very similar with that of the improved *Gotland* which, has perhaps, a smaller extension of lighter areas.
 - b) dark grey *Goth* ewe in Erik OHLSSON's flock Vallstena, with the light adult fleece and white markings.
 - c) Light grey *Goth* ewe at Lilla Karlsö. One can still distinguish an indistinct type of a grey mouflon pattern.
 - d) nearly white *Goth* ewe at Erik OHLSSON's flock, most likely of the lightgrey type, with extensive white markings.
 - e) dark grey *Goth* Lamb at Seven GUTEMARK's flock, Furillen.
 - f) grey mouflon *Goth* Lamb (Links) and agouti *Goth* Lamb at Lilla Karlsö.
- (a, b, c, d, f) photographs by Anna Lena WASSBERG.

Les couleurs du mouton Gothique

- a) Brebis *gothique* gris foncé à Lilla Karlsö. On voit les zones éclaircies autour du museau et des yeux. La coloration du *Gotland* amélioré est très semblable avec peut-être des zones éclaircies plus limitées.
- b) Brebis *Gothique* gris foncé dans le troupeau d'Erik OHLSSON, avec la toison claire d'adulte et les marques blanches.
- c) Brebis *Gothique* gris clair à Lilla Karlsö. On peut encore distinguer les marques d'un patron mouflon gris.
- d) Brebis *Gothique* presque blanche du troupeau d'Erik OHLSSON, probablement du type gris clair avec des marques blanches très étendues.
- e) Agneau *Gothique* gris foncé du troupeau de Sven GUTEMARK.
- d) Agneaux *Gothiques* à Lilla Karlsö : à gauche mouflon gris, à droite agouti.

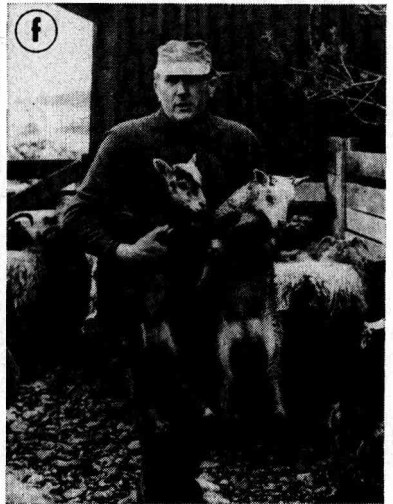
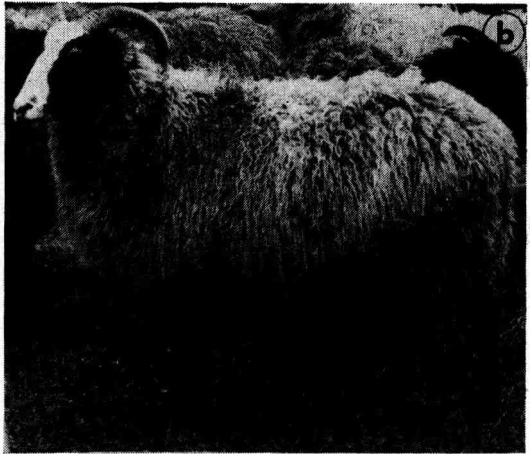


TABLE 2

Distribution of lambs at Lilla Karlsö by sex and colour classes
Distribution des agneaux à Lilla Karlsö selon le sexe et la couleur

Main colour of lamb	Male			Female			Both sexes		
	+(¹)	—	Sum	+	—	Sum	+	—	Sum
Grey	26	1	27	29	1	30	55	2	57
Grey mouflon	20	0	20	17	0	17	37	0	37
« Agouti »	3	0	3	1	0	1	4	0	4
Total	49	1	50	47	1	48	96	2	98

(¹) + means presence of white markings.

— means absence of white markings.

due to a coarser outercoat than is found in the improved type. The other type is light grey or near white. The distribution of the adult sheep by these colour classes is shown in Table 1. See also pictures in fig. 1*a.b.c.*

White markings were common in both types. The white markings were limited to head and feet only in most of the dark types, but covered larger areas in the lighter types. In some of the lightcoloured adults with the least developed white markings one could distinguish and indistinct type of a grey mouflon pattern (or grey reversed badger face). In light-coloured animals with extensive white markings this pattern was possibly present, but obscured. Some of the white sheep like those recorded by LÖRVENBERG and JOHANSSON were perhaps of the lightgrey type with extensive white markings (fig. 1*d*).

b) It was possible to identify three colour classes in lambs which showed limited amount of white markings. The first of these was a dark grey type, similar to the improved type, but sometimes showing white kemp on the belly (fig. 1*b*). A second type was a distinct type of a grey mouflon pattern with the following characteristics (fig. 1*f*): the upper part of the body was light grey or steel grey in colour, the head showed white colour inside the ear, above the eyebrow and under the chin, and the belly colour was white, all borderlines between grey and white were rather diffuse, which distinguishes this type of grey mouflon from the grey mouflon described in Iceland. The third type of lambs colour was termed « agouti » by the present observers (fig. 1*f*). This type showed a steel grey colour on the shoulders, which sometimes extended downwards to the flanks. The sides were tan-coloured at the wool tips, while the staple colour varied from steel grey to very light grey. The belly was white with no clearcut borderline between the sides and the belly.

When the lambs showed extensive white markings, it became very difficult to distinguish between the grey mouflon and the « agouti » patterns. They were then only termed « light ».

The distribution of the lambs in all the flocks visited on the two classes grey and « light » is shown in Table 1, and Table 2 shows the distribution of the lambs

at Lilla Karlsö by sex and the three colour classes grey, grey mouflon and « agouti ». It is evident from Table 1 that the frequency of grey lambs is significantly higher in the Lilla Karlsö flock than in the other flocks ($\chi^2_1 = 12.08$; $P < 0.001$).

By assuming that the grey colour in the lambs is due to homozygosity for a recessive gene, the grey mouflon being the heterozygote and the « agouti » the other homozygote, the frequency of the gene for grey is found to be 0.77 in the Lilla Karlsö flock and 0.57 in the other flocks combined. For the Lilla Karlsö flock the expected numbers of grey, grey mouflon and « agouti » lambs are 58.1, 34.7 and 5.2 respectively, which is in good agreement with the observed numbers ($\chi^2_1 = 0.45$; $P > 0.05$).

The grey mouflon and « agouti » patterns were not observed among the improved *Gotland* sheep. No black animals were seen.

c) The white markings observed in darkgrey lambs and adults were usually a star or a blaze, and in several instances white socks on the feet and a white tail tip was also observed. Extensive piebaldness was rare among the dark greys. In the lighter coloured types the white markings were more extended. The head was sometimes almost completely white, except for some dark around the eyes, and white markings on feet and tail were common.

White markings on head (H), feet (S), tail (T) and body (P) are shown in Tables 2 and 3 for the Lilla Karlsö flock, and in Tables 4 and 5 for the Gullgarde flock. Only 2 lambs were found without white markings, both on Lilla Karlsö. This gives the frequency of *s*, the recessive gene for white markings, of 0.99 at Lilla Karlsö, and 1.00 elsewhere within the *Goth* breed.

The main colour of the lambs on Lilla Karlsö was found to affect the extent of the white markings significantly, the HST-combination (white head spot socks white tail tip) occurring among only 5 grey lambs out of 55, compared to 12 HST lambs out of 41 with the colours grey mouflon and « agouti » ($\chi^2_1 = 6.56$; $P < 0.05$).

TABLE 3

Relation between main colour of lambs at Lilla Karlsö and the extent of white markings
Corrélation entre la couleur pigmentaire des agneaux à Lilla Karlsö et l'extension des marques blanches

Main colour of lambs	White markings on lambs ⁽¹⁾				
	H	HT	HS	HST	Sum
Grey	30	14	6	5 ⁽²⁾	55
Grey mouflon	14	9	3	11 ⁽²⁾	37
« Agouti »	1	1	1	1	4
Total	35	24	10	17	96

⁽¹⁾ H : white on top of head.

T : white on tip of tail.

S : white socks on feet.

⁽²⁾ On male lamb showing white spots on side.

⁽³⁾ One male lamb showing white spots on flanks.

TABLE 4

Classification of lambs at Gullgårde farm according to colour and extent of white markings and by colour class of dam

Classification des agneaux de Gullgårde selon la couleur, l'extension des marques blanches et la couleur de leur mère

Colour of dams No. of dams		Colour of lambs ⁽¹⁾									No. of lambs
		Grey			Grey mouflon			Light			
		H, HS HT	HST	Sum	H, HS HT	HST	Sum	H, HS HT	HST	Sum	
Darkgrey	6	4	2	6	0	6	6	0	0	0	12
Grey	4	0	1	1	1	2	3	0	1	1	5
Grey (mouflon ?)	3	0	0	0	0	2	2	1	1	2	4
Grey mouflon	2	0	0	0	1	2	3	0	1	1	4
Lightgrey	3	0	0	0	1	4	5	0	1	1	6
Lightgrey piebald	2	0	0	0	0	3	3	0	1	1	4
Lightgrey tan	1	0	0	0	0	0	0	0	2	2	2
Total	21	4	3	7	3	19	22	1	7	8	37

⁽¹⁾ See footnote; to Table 3.

The same was found to hold for the Gullgårde flock, where 3 grey lambs out of 7 showed the HST combination compared to 26 HST lambs out of the remaining 30 ($\chi^2_1 = 6.43$; $P < 0.05$). On the other hand the HST combination was significantly more frequent at Gullgårde than at Lilla Karlsö within the same main colour. For the grey lambs the HST combination occurred among 5 out of 55 at Lilla Karlsö, but among 3 out of 7 grey at Gullgårde ($\chi^2_1 = 6.30$; $P < 0.05$), and among the non-grey lambs, 12 out of 41 at Lilla Karlsö and 26 out of 30 at Gullgårde showed the HST combination ($\chi^2_1 = 22.94$; $P < 0.001$). The concurrence of piebaldness was also found to be significantly more frequent in the Gullgårde flock ($\chi^2_1 = 59.45$; $P < 0.001$). This is consistent with a high frequency of modifiers which limit the extent of white markings in the Lilla Karlsö flock and a high frequency of modifiers which increase the extent of white markings in the Gullgårde flock. This is in agreement with the adopted selection practices in the two flocks, emphasis being placed on the dark types on Lilla Karlsö and on the piebald types in the Gullgårde flock.

B. — *The segregations*

The classification of the colour of the lambs at the Gullgårde farm by colour classes of the dam is shown in Tables 4 and 5. The ram used was most likely of the grey mouflon type, but it was dead by the time of the visit, and only a

colour slide was available for inspection. The classification of the ewes was uncertain, as seen from the tables. The most clearcut category was the dark grey colour. The 12 lambs out of the darkgrey ewes showed only two colours, i.e. 6 were grey and 6 grey mouflon, which is a perfect fit under the assumption that the ram used was a grey/grey mouflon heterozygote. The other results in Tables 4 and 5 are in general agreement with this hypothesis, except for the lack of grey lambs in the lower parts of Tables 4 and 5.

Observations in the MacDonald flock in Scotland suggested that the relatively dark grey *Gotland* rams used for breeding there were homozygous grey, because no black lambs were born. A cross made between *Gotland* rams and 102 black or brown (moorit) *Shetland* ewes produced only grey lambs. The lambs were mostly dark, but some were light.

105 white *Shetland* ewes mated with a *Gotland* ram produced white and grey lambs roughly in the proportion 1 : 1, indicating that a high proportion of the ewes were heterozygous white.

TABLE 5

Classification of lambs at Gullgårde farm according to colour and occurrence of piebaldness, and by colour class of dam

Classification des agneaux de Gullgårde selon leur couleur, la présence de panachures et la couleur de leur mère

Colour of dams	Colour of lambs ⁽¹⁾									No. of lambs
	Grey			Grey mouflon			Grey			
	P	S	Sum	P	S	Sum	P	S	Sum	
Darkgrey	0	6	6	1	5	6	0	0	0	12
Grey	1	0	1	3	0	3	1	0	1	5
Grey (mouflon?)	0	0	0	2	0	2	2	0	2	4
Grey mouflon	0	0	0	2	1	3	1	0	1	4
Lightgrey	0	0	0	3	2	5	1	0	1	6
Lightgrey piebald	0	0	0	3	0	3	1	0	1	4
Lightgrey tan	0	0	0	0	0	0	1	1	2	2
Total	1	6	7	14	8	22	7	1	8	37

⁽¹⁾ P : means piebald, i.e. white patches on body.

S : means solid colour, i.e. no white patches on body.

Discussion

It was shown by ADALSTEINSSON (1970) that nonwhite *Icelandic* sheep possessed either black or brown pigment (presumably eumelanin), the black pigment being produced by a dominant gene *B* and the brown pigment by the recessive allele, *b*. The recessive brown genotype *bb*, is found in the brown *Icelandic* sheep and in the moorit *Shetland* sheep (for the link between past and present gene symbols see ADALSTEINSSON, 1974).

Genes at the *Agouti* locus modify the pigment produced by the genes at the *B*-locus to a greater or less extent. The top dominant allele at the *A*-locus, *A^{wh}*, produces white or tan (red) colour, the intermediate alleles *A^b*, *A^w* and *A^g*

produce the patterns or colours badgerface, mouflon (reversed badgerface) and grey, and the bottom recessive allele, *a*, has no effect on black or brown pigment, producing selfcolour (black or brown) when homozygous.

It will be assumed that the above rules hold for the breeds under discussion in the present study except where otherwise stated.

I. — *The Gotland sheep*

The grey of the improved type has several of the characteristics of the grey at the *Agouti* locus found in Iceland, but differs from it some aspects.

The results from the cross made in Scotland between grey *Gotland* rams and black and brown *Shetland* ewes show that the grey gene is dominant to lack of grey in the black or brown *Shetland* ewes, that the rams used were most likely homozygous, *BB*, for the gene for black pigment, and that the relatively dark grey *Gotland* rams were most likely homozygous for the gene producing the *Gotland* grey colour. This last piece of evidence possibly indicates that the *Gotland* grey is not produced by *A^g* (*A₂*) found in Iceland, because one the characteristic features of *A^g* is the much lighter colour of the homozygotes than the heterozygotes (ADALSTEINSSON, 1970).

EBBERSTEN and SKÅRMAN (1976) inferred that they had found rams which were heterozygous for the grey gene within the *Gotland* breed. These rams were themselves darker than other rams, and their grey progeny was also on the average darker than the progeny of other rams. This indicates that the effect of the grey gene within the improved *Gotland* breed is comparable to the *A^g*-gene within the Icelandic breed, i.e. that neither gene is completely dominant to the recessive *a*, which in homozygous form gives black colour.

EBBERSTEN and SKÅRMAN further showed that the *Gotland* grey colour was recessive to the white colour of the short-tailed *Swedish Landrace* sheep. Their backcross of white (*Swedish-Landrace* × *Gotland*) ewes to grey *Gotland* rams produced only two colours, i.e. white (or tan piebald) and grey in the ratio 1 : 1.

Two independent pieces of evidence suggest that selection for darkening modifiers of grey has been carried out within the improved *Gotland* breed. EBBERSTEN and SKÅRMAN (1976) found that grey lambs from the cross white (*Landrace* × *Gotland*) ewes × *Gotland* rams were of an appreciably lighter shade than the average within the improved *Gotland*. In the MacDonald flock in Scotland it was also observed that the backcross white (*Shetland* × *Gotland*) × *Gotland* produced grey lambs which were mainly light grey.

This, viewed in light of the selection against light types described by EBBERSTEN and SKÅRMAN (1976), together with the relatively high heritability they found for shade of grey, mentioned previously, also points to selection for darkening modifiers. From the evidence presented here one feels that the following conclusions are permissible.

- i) The *Gotland* grey is situated at the *Agouti* locus.
- ii) It may and often does produce a dark grey colour in the homozygote.
- iii) Selection for darkening modifiers has been carried out within the *Gotland* breed.
- iv) The *Gotland* grey is produced by an allele which is very similar from *A^g* (*A₂*) found in the *Icelandic* sheep and possibly also in Corsica (LAUVERGNE and ADALSTEINSSON 1976) but perhaps distinct. Provisionally we propose the name *A^{gg}* (*gg* for (improved) *Gotland* grey) for this apparently new allele at the *Agouti* locus.



Erratum

Fréquence du syndrome d'hyperthermie maligne dans des populations porcines françaises; relation avec le développement musculaire

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avec la collaboration technique de Marie-Reine LANGLOIS, P. DANDO, C. FELGINES, A. TALMANT (*),
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Page 197 : 3^e ligne et suivantes lire :

...Pour le *Large White*, la limite supérieure de l'intervalle de confiance de la fréquence génique, correspondant à une probabilité inférieure à 5 p. 100 de ne trouver aucun positif dans l'échantillon étudié, est égale à 0,17 en supposant une pénétrance complète. Les estimations...

2. — *The Goth sheep*

The *Goth* sheep shows a considerably greater variation than the improved type, as mentioned earlier. The three phenotypes observed among the lambs at Lilla Karlsö are consistent with a two-allele case, the dark grey lambs being homozygous $A^{gg}A^{gg}$, the grey mouflon lambs being $A^{gg}A^{lg}$ (*lg* for light grey) and the « agouti » lambs being homozygous $A^{lg}A^{lg}$.

It is obvious from the studies on the improved *Gotland* sheep cited earlier that a more pronounced colour variation was encountered in the study of LÖFVENBERG and JOHANSSON (1952) than one finds today. The grey mouflon pattern found in the *Goth* sheep of today might for example have existed in the flock that LÖFVENBERG and JOHANSSON studied, but selection against unfavourable, highly heritable traits would soon have eradicated such a gene if it had occurred at a low frequency.

The segregation of the two alleles postulated in the *Goth* sheep at Gulgärde near Roma is not clearcut. One should bear in mind that white markings were found to be more pronounced in the Gulgärde flock than in the Lilla Karlsö flock, and this may have obscured the picture.

The existence of a separate allele producing the light colour which the present authors have termed grey mouflon is not at all firmly established, but the type of grey mouflon pattern observed in the Lilla Karlsö lambs is consistent with the hypothesis that this light colour is produced by a single gene.

It is also possible that the gene for tan or white A^{wh} quite common in Iceland which probably was in the genetic formula of the white animals described by LÖFVENBERG and JOHANSSON (1952) is still present in some flocks we have checked even if sometimes A^{wh} it is mimicked by ($A^{lg}A^{lg}$).

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Résumé

Possible interprétation génétique des variants colorés de la toison des moutons Gothique et Gotlandais

On décrit la couleur de 79 adultes et de 184 agneaux en provenance de 6 troupeaux de l'ancienne race suédoise cornue, à queue courte, le mouton *Gothique*. Parmi les adultes il y avait 36 gris et 43 presque blancs, cependant que 85 des agneaux étaient gris et 99 de couleur claire. Les agneaux de couleur claire avec une extension limitée de taches blanches présentait soit un patron gris clair avec le ventre blanc appelé « mouflon gris » soit un mélange de gris acier clair et de fauve appelé « agouti ».

Les marques blanches étaient fréquentes dans tous les troupeaux, et lorsqu'elles étaient étendues, elles rendaient parfois difficile l'identification du patron pigmenté.

Sur la base d'observations sur le mouton *Gothique* avec quelques examens de croisés *Gotlandais* gris et *Shetland* faits en Écosse et d'une revue de la littérature on pense que la couleur grise de l'ancien mouton *Gothique* et du *Gotlandais* amélioré est due à un nouvel allèle en *Agouti* A^{10} (gg pour *Gotland grey*) à moins que ce ne soit le même allèle que A^9 (icelandic grey). La couleur mouflon gris du mouton *Gothique* serait due à un autre allèle encore non décrit A^{10} (lg pour *Light grey*) au locus *Agouti*. Quelques animaux blancs peuvent être $A^{10} A^{10}$ ou même porter le gène A^{wh} pour le fauve ou le blanc.

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