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SI FAT TAILED SHEEP

The genetics of colour in fat-tailed sheep: a review

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Abstract Fat-tailed sheep come in various colours—most are either brown (tan) or black. In some, most of the body is white with the tan or black colour restricted to the front portion of the body or to just around the eyes, muzzle and parts of the legs. The Karakul breed is important for the production of lamb skins of various colours for the fashion industry. As well as the black and tan colours there are Karakuls bred for grey or roan shades, a white colour or one of the numerous Sur shades. In the Sur shades, the base of the birthcoat fibre is one of a number of dark shades and the tip a lighter or white shade. All these colours and many others are the result of the interaction of various genes that determine the specifics of the coat colour of the sheep. A number of sets of nomenclature and symbols have been used to represent the various loci and their alleles that are involved. In the 1980s and 1990s, a standardised set, based closely on those of the mouse and other species was developed. Using this as the framework, the alleles of the *Extension*, *Agouti*, *Brown*, *Spotting*, *Pigmented Head* and *Roan* loci are described using fat-tailed sheep (mainly Damara, Karakul and Persian) as examples. Further discussion includes other types of "white markings," the *Ticking* locus and the *Sur* loci.

Keywords Genetics · Coat colour · Coat pattern · Fat-tail sheep · Karakul · Damara · Persian

Introduction

Throughout the world, sheep with many different colours, patterns and white markings can be found. The study of the genetics behind this variation began in earnest around the 1920s with the work of Vasin (1928—USSR), Roberts and co-workers (Roberts 1924, 1926, 1928, 1931; Roberts and Jenkins 1926; Roberts and White 1930a, 1930b—Wales/UK), Dry (1924, 1926, 1927, 1936—UK) and others. Research into the colours of the Karakul began around the same time and was concentrated in the USSR, Germany and S.W. Africa (now Namibia).

With the exception of the Karakul, most of the research was carried out in Europe. This included work on breeds of the Northern Short-tailed group (such as the Norwegian, Icelandic, Soay, Shetland, Manx Loaghtan and Gotland), on the Merino, on British breeds (such as the Welsh Mountain, Jacob and Wensleydale) and on other European breeds (such as the Corsican, Texel and the wild Mouflon).

There has never been a review of the genetics of the coat colour as it applies to the various fat-tailed and fat-rumped breeds. While most of the research has involved the Karakul, there has been some reported in other breeds. The research that has been carried out has been reported using a number of different sets of nomenclature. There is, therefore, a need to review what is known of the genetics of coat colour as it applies to the fat-tailed and fat-rumped breeds and to present it using the standardised international nomenclature (COGNOSAG).

Nomenclature

With the initial research being carried out by various research workers working in widely spread locations, different sets of loci and allele names and symbols were developed. So, for example the basic black and brown (tan) colours of the Karakul were described using five different systems—the main three being those of Russia, Germany and Namibia (see Table 1).

The systems of nomenclature were very confusing. In the 1980s, an international committee (COGNOSAG) was set-up to produce a standardised nomenclature for sheep. Many of the rules, etc., were adapted from those that had

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Table 1 Systems of nomenclature developed to explain the genetics of coat colour in sheep—using just the systems used to explain the difference between *dominant black* and brown (tan) in the Karakul as examples

Different systems	Symbols and genes	Comments
Russian system	DD—black Dd—black dd—brown (tan)	The Russian system was based on the work of Vasin (1928). The black colour ("Arabi") of the Karakul was explained as being due to the dominant gene "D" at the D locus: the homozygous recessive genotype "dd" giving the brown ("Kambar") colour of the breed
German system	AA BB—dominant black Aa BB—dominant black aa BB—no black	In the German system (based on the work of Adametz 1917 and followed by Bonikowsky 1933), both black and brown Karakul sheep were believed to be homozygous "BB" for the brown gene. The black sheep have a dominant black gene present (normally AA BB, rarely Aa BB) and the brown sheep are recessive for the "a" gene (aa BB)
Duck (1921, 1922)	B—black b—absence of black R—red r—absence of red	Duck, working in the USA, looked at crosses of Karakuls with white longwool breeds. The lambs that were black were explained as being BB or Bb. When bb was present, those with RR were red, Rr red or spotted and rr white
Munoz (1948), Spain	N—(negro) black M—(marrón) brown	The pure arabí is NNMM. N is dominant and produces black—when it is absent (nn) the dominant M gene produces brown. When both are absent nnmm the animal is white
Nel (1967), S.W. Africa (Namibia)	E^{C}—coffee-brown E^{D}—black e^{b}—brown e^{t}—dobermann	Nel's system had its origin with the works of Sewall Wright (1917, 1918) who, in a series of 11 papers on laboratory and farm animals and man, saw the similarities between certain colour types in various species and postulated that they were probably based on similar genetically controlled chemical processes. An attempt was made to devise a uniform system of symbols for the various species—this did not include sheep Rendel (1959, 1968) adapted this system for use in various farm animals. Searle's (1968) book was a major work that dealt with the similarities that existed between the various coat colour loci of many mammalian species. Searle was able to assign a few of the sheep colours to the loci series found in other mammalian species. Adalsteinsson (1960, 1970) and Nel (1967) used it for the various colours in the Icelandic and Karakul sheep they worked with
COGNOSAG	E^{D}—*dominant black* E^{+}—*wild*	E^{D} is dominant and produces a completely eumelanic animal when present. The homozygous *wild* allele allows the full expression of the *Agouti* locus alleles where the brown (tan) colour is determined

been established for the mouse. These were finally published by Lauvergne et al. in 1996. In this article, the recommendations made for sheep coat colour genetics (Sponenberg et al. 1996) (see Table 2) are closely followed.

Pigmentation

In the sheep, as in other mammals, there are two types of pigment. Eumelanin is either black or a brown shade—determined by the *wild* and *brown* alleles, respectively, at the *Brown* locus. Phaeomelanin results in a red, tan or fawn colour.

In relation to coat colour genetics, it is the accepted convention when discussing sheep with phaeomelanin present to describe the colour as "tan" (or possibly "fawn" or "red"). The use of "brown" is restricted to the colour of eumelanin produced by the *brown* gene. This, of course, causes some confusion as in many breeds (the Karakul being one) it is customary to use "brown" to describe the tan animals—so the "brown Karakul" is, in fact, completely phaeomelanic and is a "tan" colour.

The eumelanin of a sheep is either black or brown but not both. A sheep, though, can have both eumelanin and phaeomelanin present—this can occur within the fibre (so, for example in some alleles of the *Agouti* locus, the tip may be tan and the base black) or it can occur on different regions of the body (so, again at the *Agouti* locus, some alleles are black on the body and tan on the underside, or vice versa). Sometimes, also in the *Agouti* locus alleles, where the sheep has a double-coated fleece, the coarser outer (primary) coat fibres may be a different colour to the finer inner (secondary) coat fibres.

"White" is produced by the removal of pigmentation. This can occur on some of the areas of the body (various types of "white markings") and, at its extreme, can produce a completely white animal.

The type of fibre present affects the expression of the pigmentation. In the long coarse outer-coat fibres of the double-coated fleece breeds, the contrast in expression of

Table 2 The coat colour loci of the sheep

Locus	Alleles	Comments
Agouti—A		See Table 3
Albino—C	*albino—C^c*	Causes complete inhibition of phaeomelanin and eumelanin in wool hair and skin. Eyes, bluish pink
	wild—C^+	Allows full production of eumelanin and phaeomelanin
	albino marrabel—C^{mar}	Similar to *albino* but with some persistence of tan or light yellow in hooves, leg hair and edge of iris
Australian Piebald—AsP	*wild—AsP^+*	Fleece remains white
	piebald—AsP^p	Causes sheep to have one or more black or light grey round areas in an otherwise white coat
Brown—B	*wild—B^+*	Dominant. The eumelanin pigment is black
	brown—B^b	Recessive. The eumelanin pigment is brown
Extension—E	*dominant black—E^D*	Produces a totally eumelanic sheep. It does not allow the *Agouti* locus alleles to be expressed
	wild E^+	Recessive. Allows the full expression of the *Agouti* locus alleles
Pigmented Head—Ph	*afghan lethal—Ph^{afl}*	The homozygous are white and most die soon after birth, heterozygous have pigment on parts of the head and legs
	turkish—Ph^T	Homozygous has pigmented nose, eye patches, ears and lower legs, heterozygous sheep are piebald
	persian—Ph^P	Homozygous are pigmented on the head and sometimes the neck and shoulders, rest of the body white
	wild—Ph^+	No white spotting. The colouring determined by other loci can be fully expressed
Roan—Rn	*lethal roan—Rn^{Rn}*	Dominant. Adds white hairs to the birthcoat, homozygotes are paler and often die around weaning
	wild—Rn^+	Recessive. No greying or roaning of the birthcoat
Spotting—S	*wild—S^+*	Dominant. No white spotting
	spotted—S^s	Recessive. Reasonably symmetrical white spotting, occurring on lower legs and top of head first
Sur Bukhara—SuB	*wild—SuB^+*	Dominant. Birthcoat fibre the same colour from the tip to the base
	sur bukhara—SuB^s	Recessive. Delays the initiation of pigmentation. Fibre has a fully pigmented base with white or (rarely) yellow tip
Sur Surkhandarya—SuS	*wild—SuS^+*	Dominant. Birthcoat fibre the same colour from the tip to the base
	sur surkhandarya—SuS^s	Recessive. Delays the initiation of pigmentation. Fibre has a fully pigmented base with white or (rarely) yellow tip
Ticking—Ti	*ticked—Ti^{Ti}*	Dominant. Causes the development of small pigmented spots of skin and wool/hair in areas made white by the *Spotting* locus. These spots are not present at birth but grow in later
	wild—Ti^+	Recessive. White areas produced by the *Spotting* locus remain white

Summary of the 11 loci and their alleles accepted by COGNOSAG (from Sponenberg et al. 1996)

phaeomelanin and eumelanin of the *Agouti* locus alleles is much more obvious at birth than that seen in the normal woolled breeds. In the hair breeds such as the Damara and Persian, this marked contrast can be seen throughout their life. The Karakul breed has been bred for a lamb with an intense coat colour at birth.

The *Extension* locus

Between them, the *Extension* and *Agouti* loci are responsible for the distribution of the eumelanin and phaeomelanin on an animal. There are two widely recognised alleles at the *Extension* locus.

The wild allele—E^+ This is the recessive allele of the pair, so when a sheep is homozygous for the *wild* allele, E^+E^+, the alleles of the *Agouti* locus are able to be seen. Therefore, a "brown Karakul" (that should be "tan Karakul") is homozygous *wild* at the *Extension* locus and the colour seen is produced by the allele(s) present at the *Agouti* locus.

The dominant black allele—E^D As the name implies, this allele is dominant and produces a eumelanic (usually black)

colour. As the examples given in Table 1 show: many authors over the years have established its presence in the Karakul breed.

The results of Davy (1927) indicate its presence in the Blackhead Persian breed (Fig. 2a). As the Dorper is the result of a cross between the Blackhead Persian and Dorset Horn breeds, it is to be expected that the black in this breed is also due to the *dominant black* allele (Fig. 3a–c). The fact that crosses between the Dorper and white breeds produce black piebald animals confirms this (Notter and Sponenberg 2002).

Vasin (1928) mentioned it being present in a number of breeds in the south and southeast of the USSR including: fat-tailed and semi-fat-tailed breeds, three fur breeds of the Ukraine (Sokolka, Reshetilovka and Chushka), the Karachaev (a fat-tail breed of the N Caucasus), the Karakul and the Mongolian (a fat-tailed breed of Mongolia and northern China). It has also been shown to be present in the White-Karaman (Akkaraman), a fat-tail breed of Turkey (Düzgünes et al. 1960).

Possibility of additional alleles at the Extension locus It is usually accepted that there are only two alleles at the *Extension* locus in sheep, E^{D}—*dominant black* and E^{+}—*wild*. In the brown (tan) Karakuls, there are a wide range of colours to be seen.

Aliev and Rachkovskiĭ (1986, 1987a, b, 1989) believed that in Asiatic sheep the frequency of the *wild* allele is very low. To explain the wide range of colours in tan Karakuls and other Tajikistan breeds such as the Hissar and Tajik, they postulated three additional alleles at the *Extension* locus in sheep: E^{bl}—*black*, E^{br}—*brown* and E^{y}—*yellow*.

When the *white/tan* gene was present at the *Agouti* locus, they suggested that E^{Bl} E^{Bl} and E^{Bl} E^{Br} produced black or blackish brown, that E^{Bl} E^{y} and E^{Br} E^{Br} produced dark brown, brown or dark red and that E^{Br} E^{y} and E^{y} E^{y} produced red, light red or tan.

Sponenberg et al. (1996) suggested that the range of tan colours in Asiatic breeds could alternatively have E^{+} E^{+} present and be due to modifications of the *white/tan* allele at the *Agouti* locus. The alleles of the *Brown* locus could also be involved.

While no one else has produced any supporting evidence for the presence of these three additional alleles, evidence from other mammalian species would suggest that it is quite possible that others could be present in the sheep.

Evidence for the black allele In the rabbit there are five alleles established at the *Extension* locus, from the most dominant to the most recessive: E^{d}—*dominant black*, E^{s}—*steel*, *E—normal extension of black*, e^{j}—*Japanese brindling* and *e—non-extension of black* (yellow). Homozygous E^{d} E^{d} is completely black whereas E^{s} E^{s} is black with a sparse distribution of agouti hairs over the back and flanks. *Steel* behaves like a weaker type of *dominant black*, so that the alleles of the *Agouti* locus have more effect in its presence than they do with *dominant black* (Searle 1968).

The *black* allele that Aliev and Rachkovskiĭ (1986, 1987a, b, 1989) propose could be comparable to the *steel* of the rabbit. If there proves to be such an allele then it could possibly also explain the colour of the Suffolk and Scottish Blackface (black), Hampshire (black/dark brown) and other similar breeds of Europe.

A completely phaeomelanic Extension locus allele A large number of mammalian species have an allele, like *e—non-extension of black* (yellow) of the rabbit and *e—recessive yellow* of the mouse (Silvers 1979), that is the most recessive at the *Extension* locus and causes a red or yellow colour.

A similar allele produces the chestnut of the horse (Sponenberg 1996) and the red of the Hereford, Simmental, etc. of cattle (Olson 1999). Aliev and Rachkovskiĭ have suggested such an allele, *yellow*, might cause the yellow colour of some Asiatic sheep.

If it were to occur, such an allele would be recessive to the *wild* (E^{+}). So if ever the mating together of two sheep with definite recognisable *Agouti* locus pattern alleles (say *badgerface*, *black and tan* or *xerus*) were to produce a completely tan/red/yellow or white lamb then this would indicate the likely presence of such a recessive phaeomelanic allele at the *Extension* locus in the sheep—so far no such result has been reported.

The *Agouti* locus

The alleles of the *Agouti* locus determine the regions that eumelanin and phaeomelanin occur in on the animal, how they may occur along particular fibres (bands of different colours) and also any differences that occur between different fibre types (outer-coat fibres compared with inner coat fibres). These changes of eumelanin and phaeomelanin lead to the alleles producing the many coat patterns to be found in the sheep.

The alleles range from completely phaeomelanic tan types (the most dominant), through those where both eumelanin and phaeomelanin occur, to *nonagouti* which is completely eumelaninic (the most recessive).

It is a feature of the alleles at this locus that when any two occur together, so that the animal is heterozygous, the areas that have phaeomelanin pigment in each allele are expressed. So, for example, a *black and tan* has a tan underside and black upper body, a *badgerface* has a tan upper body with a black underside and the heterozygous genotype *black and tan//badgerface* has tan on both the underside and upper body.

While a number of authors had worked with some of the alleles previously it was Adalsteinsson (1970), working with Icelandic sheep, who showed that six of them formed an allelic series. These are now known as *white*/*tan*, *grey*, *black and tan*, *grey and tan*, *badgerface* and *nonagouti*. Since then *wild* (Lauvergne et al. 1977), *eye patch* (Lauvergne and Adalsteinsson 1976), *blue* (Hoogschagen et al. 1978), *light grey* and *gotland grey* (Adalsteinsson et al. 1978), *light badgerface* (Sumner 1989), *swiss markings*, *light blue* and *lateral stripes* (Lundie 1984) and *english blue*, *fawn eye* and *tan eye* (Lundie 1989) have been reported. Within this author's experimental flock there appear to be another ten alleles (unpublished) and observations made of the Damara would indicate the possibility of a number of further alleles (Lundie 2007).

So, to put it briefly, there are a large number of alleles at the *Agouti* locus in the sheep. Almost all of the experimental work involving these alleles has taken place using European breeds of sheep. The Damara is a good breed to observe to find some of these alleles occurring in a fat-tailed breed (see Table 3 and Fig. 1).

The Damara breed The Damara is a fat-tailed hair sheep that was originally farmed by the Himba people in northern Namibia (du Toit 2007). Within the breed there has been no selection towards a specific colour or pattern so a very wide range of phenotypes can be seen. Because it is a hair sheep, the phaeomelanin and eumelanin appear a much more intense colour than is seen in the woolled breeds and the contrast between the two pigment types is very obvious. The intense colour and contrast remains throughout the sheep's life. Unlike many European breeds there has been no selection away from the tan to produce a white animal so the tan is very obvious.

While the Damara is excellent for viewing different colours and patterns, the extensive manner in which it is farmed makes it difficult to use to study the inheritance of these colours. While the dam is usually known, the sire is usually unknown.

Adalsteinsson (1970) found that the homozygous *grey* was a lighter grey than the heterozygous genotype and the homozygous *white*/*tan* was whiter than the heterozygous genotype. In all the *Agouti* locus alleles that this author has had dealings with, the tan (or white) markings of the patterns are more obvious/striking/extensive in the homozygous genotype compared with the heterozygous genotype.

The Agouti locus in the Karakul Nel (1967) postulated four alleles at the *Extension* locus that played a part in determining the coat colour of the Karakul: E^C—coffee-brown, E^D—black, e^b—brown and e^t—dobermann. It was noted, though, that it was possible that brown and dobermann were alleles at a separate locus to black.

It is now recognised that for the "brown" and "dobermann" groups, the homozygous $E^+ E^+$ genotype is present and the differences between colours of the two groups are caused by alleles at the *Agouti* locus (Nel and van Wyk 1982; Adalsteinsson 1982).

Nel (1967, 1968) described the majority of the "brown" Karakul lambs as being a reddish colour with some a chocolate-brown. The intensity of colour varies from a light cream shade with the chocolate-brown varying from a light brown to almost black. These have the A^{wt} (or similar—if there proves to be more than one "tan") allele at the *Agouti* locus.

Nel (1967) groups a number of phenotypes together as "dobermann" and from the descriptions it is possible to suggest which *Agouti* alleles are involved. "The predominant black and brown zones are arranged in a particular mosaic somewhat analogous to the black dobermann dog. The proportion of black to brown varies". "Except for two isolated, lateral brown bands running lengthwise, the brown areas are restricted largely to the peripheral areas. The transition of black to brown is gradual but distinct" (the *xerus* allele). "The brown colour may be so reduced that it will only be recognised on the face, on the edges of the ears, underside and legs (the *black and tan* allele). The occurrence of brown dobermann, i.e. a reversed type, is very rare" (the *badgerface* allele). "In some instances, self-coloured (black) individuals may occur" (the *nonagouti* allele).

"Brown × brown" matings produced 879 brown (tan) and 73 "dobermann" lambs. Of these "dobermann" lambs, 15 were completely black—therefore homozygous *non-agouti* (Nel 1967). As has already been noted, where the word "brown" is used in these quotes to describe the colour of the phaeomelanin seen in the Karakul (a common practice with Karakul breeders), it would have been better to use "phaeomelanin," "tan", "fawn" or "red" and restrict the use of "brown" to the colour of the eumelanin caused by the *brown* allele at the *Brown* locus.

Later in this review, it is suggested that the *grey* may play a part in the range of shades to be seen when the *lethal roan* gene is present and the question is asked as to whether *Agouti* locus alleles, such as *eye patch* and *grey*, could play a part in some of the sur types.

The *Brown* locus

The two established alleles at the *Brown* locus of the sheep are responsible for the colour of the eumelanin pigment.

The wild allele—B^+ This is the dominant and most common allele at the locus. It results in black eumelanin pigment.

Table 3 *Agouti* locus alleles reported in European derived breeds of sheep and phenotypes observed in the Damara

Alleles identified in European woolled breeds	Phenotypes seen in the Damara of Southern Africa[b]	Comments
A^{Wt} *white/tan*[a]	*dark tan* (Figs. 1b and 2f) *tan spreading white* (Fig. 1a) *tan with extremities* *tan with saddle*	Officially *white/tan* is the only tan allele and produces a white or tan fleece. The most dominant allele at the locus. Completely white animals have been achieved by selection, over centuries, against the tan. Amongst those still tan the colour ranges from an almost yellow colour in the Icelandic (usually only the heterozygous are tan 24.4% with only 1.4% of the homozygous tan)[c] through the Portland who are all born a tan colour (and then fade to the colour of a Romney) to the dark tan shade of the Solognote. This difference in expression is explained by different modifying genes although some have wondered if there might not be different alleles involved[d, e]
	tan with muzzle	In the Damara, it is possible to recognise five different types and for the first three there is the variation within the types that would be expected if there were homozygous and heterozygous phenotypes
A^{b} *badgerface*[a]	*badgerface* (Fig. 1c)	In many breeds. Black on the underside including around the anus, underside of the tail, neck and jaw, inside the ears and black (badger like) bars on the head. [c, f, g] The non-black areas are usually white but in the Damara they are tan
A^{t} *black and tan*[a]	*black and tan* (Fig. 1d)	In many way the complete opposite of the *badgerface* colouring. So the body is black and the underside, up around the anus, underside of the tail, jaw, inside ears and short bar above the eyes is fawn or white[c, f, g]—tan in the Damara
	xerus (Fig. 1e)	All the markings of a *black and tan* with the addition of a diffuse tan area rising up behind the shoulder and going back along the side of the body. Occurs in the Damara, Persian, and Karakul breeds[b] and since seen it in a number of Indian breeds
A^{+} *wild*[a]		The allele present in the wild Mouflon of Corsica[h]
A^{g} *grey*[a]	*grey* (Fig. 1h)	Common in the Northern Short-tailed breeds of Europe but found in other breeds. In the Icelandic the outer-coat fibres are black and the undercoat mainly white. White on the muzzle, scrotum and inside the ears.[c] In the Damara has a white muzzle and produces a mahogany shade by adding a tan tip to the black fibres
A^{gt} *grey and tan*[a]		Icelandic breed. Appears the combination of the *grey* and *black and tan* alleles[c]
A^{bl} *blue*[a]		Found in the Texel. The homozygous phenotype has similarities to the *badgerface*[i]
dark blue	*dark blue* (Fig. 1f)	Studied in the Merino. Mainly black, white tear ducts, at birth a tan tip to the fibre on the body but not where the *badgerface* is black. In the Damara mahogany on body.
A^{lbl} *light blue*[a]		Found in the Perendale. Similar to a *dark blue* but lighter on the brisket, purse, around the navel and penis and on the chin. Double-coated animal becomes lighter on the base of underside[j, k]
A^{eb} *english blue*		From the English Leicester and other English breeds. Similar to a dark blue but with greying on the sides of the body and across the rear back[k]
	enblu and tan	Seen in the Damara. Appears to combine the features of the *english blue* with those of the *black and tan*. So it is tan on the rear sides of the body and across the rear back
A^{lbf} *light badgerface*[a]		From the Perendale. The same lighter areas added in the *light blue* are added to the *badgerface* type[j, k, l]
A^{lg} *light grey*[a]		A version of *grey* found within the Gotland breed[m]
A^{gg} *gotland grey*[a]		A version of *grey* found within the Gotland breed[m]
A^{sm} *swiss markings*[a]	*swiss markings*	From the Southdown breed. A distinguishing feature of the "*swiss*" type alleles is a fawn or tan band the includes all the moustache and sweeps back and up over the eyes to the horn buds and sometimes beyond. There is a frosted white tip on the belly. Grey on the rear of the hip, upper mid side and under the jaw.[k] In the Damara these grey areas become tan and so in ways the hair sheep version resembles the *black and tan*[b]
"feral Merino line"	*kaoka swiss* (Fig. 1g)	Seen in the Merino and the Damara. Much more extensive tan than in *swiss markings*
A^{ls} *lateral stripes*[a]		From the Romney. The swiss bar only goes back to the tear ducts. White frosting on the belly only in homozygous individuals. Greyish on upper mid side. A white line runs along the edge of the belly[j, k]
A^{ep} *eye patch*[a]	*eye patch* (Fig. 1i)	First seen in the Corsican breed.[n] This author has studied a number of variations of it and found that as well as having a triangular tan patch around the eye, it is tan on the outside of the ears and the body (in double fleeced lambs) is black with a tan tip. This produces a mahogany colour on the body of a Damara when present

Table 3 (continued)

Alleles identified in European woolled breeds	Phenotypes seen in the Damara of Southern Africa[b]	Comments
	ember	A phenotype seen in the Damara. Black fibres with a slight red tip on the body
	ember and bronze	The same as an *ember* but with a brown/tan on underside, muzzle, ears, around the eyes
A^a *nonagouti*[a]	*nonagouti*	Completely black. The most recessive allele at the *Agouti* locus

[a] Recognised by COGNOSAG 1989: Sponenberg et al. (1996)

[b] All Damara phenotypes (except *black and tan*) from Lundie (2007)

[c] Adalsteinsson (1970)

[d] Lauvergne and Hoogschagen (1978)

[e] Adalsteinsson et al. (1980)

[f] Roberts and White (1930a)

[g] Brooker and Dolling (1969)

[h] Lauvergne et al. (1977)

[i] Hoogschagen et al. (1978)

[j] Lundie (1984)

[k] Lundie (1989)

[l] Sumner (1989)

[m] Adalsteinsson et al. (1978)

[n] Lauvergne and Adalsteinsson (1976)

Fig. 1 Some of the *Agouti* locus alleles in the Damara. **a** *Tan spreading white*—heterozygous, **b** *dark tan*—homozygous, **c** *badgerface*, **d** *black and tan*, **e** *xerus*, **f** possibly *dark blue*, **g** *kaoka swiss*, **h** *grey* and **i** *eye patch*

The brown allele—B^b This is a rare recessive allele that when homozygous results in brown (chocolate shade) eumelanin pigment. Sometimes, the colour is referred to as "moorit" to help avoid confusion with the tan colours which in many breeds are commonly referred to as "brown".

Brown is quite common amongst the Northern Short-tailed group of breeds of Europe and found more rarely in other European breeds such as the Merino and Romney. There are only rare indications of its presence in fat-tailed breeds.

Duck (1921, 1922) reported the cross between Karakul rams and white ewes. The first cross resulted in 231 black lambs and two chocolate coloured offspring. In the F_2 generation, some red lambs were produced. The two chocolate-brown lambs could indicate the presence of the *brown* allele in both parents.

Nel (1967) reported "dobermann × dobermann" matings producing 60 dobermann and one brown offspring. This could also be the case of the presence of the *brown* allele (occurring in conjunction with the homozygous *nonagouti* of the *Agouti* locus) in the Karakul breed.

The coffee-brown allele—B^C Nel (1967) used the term "coffee-brown" to describe a peculiar black-brown colour reminiscent of black coffee without or with very little milk. A large proportion of the animals had white hairs on the ears, ventral areas, legs and tail. In some animals its incidence was so high that they appeared all over the body, thus tending towards grey (Fig. 6a).

Nikoljski and Odinzewa (1929) reported crosses between coffee-brown fat-tail sheep and black Karakuls producing equal numbers of coffee-brown and black offspring. It was concluded that the coffee-brown animals were heterozygous (Kk DD) and the blacks homozygous (kk DD). Vasin first suggested the use of K and k and a purebred coffee-brown sheep would have been KK DD (Frölich 1931).

Later in discussing the shoturi or camel colour in Karakuls, the symbols were reversed—black, grey, brown (tan), were all "KK" and the shoturi sheep "kk". The heterozygous "Kk" sheep were "light-brown" (Pogodin et al. 1975; Pogodin 1976).

The coffee-brown sheep that Nel (1967) studied could be traced back to a particular flock and it was assumed that this colour had been introduced from local fat-tailed sheep used in grading up. Matings of coffee-brown with black also indicated that the coffee-brown sheep had a heterozygous genotype. When coffee-browns were mated together 15 coffee-brown, one chocolate-brown and three black lambs were produced. This is close to the 25% black expected if the coffee-brown phenotype was due to a heterozygous genotype. It was thought that the chocolate-brown may have been a homozygous animal. Nel suggested that *coffee-brown—E^C* was the most dominant allele at the *Extension* locus.

Lundie (1989) reported a "dark brown" colour that originated in a Corriedale flock that also appeared to be heterozygous—leaving 50% dark brown and 50% black when mated to black. At birth the dark browns appeared either black or a dark pastel colour. It was not until 5 months that they were obviously dark brown. Amongst the three offspring of "dark brown × dark brown" matings one was born that appeared a uniform pastel grey/dark grey all over the body and belly. The hair of the legs was black but that of the head was a dark brown shade. At 5 months the wool was a pastel or silvery shade of dark brown, with the darkest colour along the backline to its lightest on its belly. Because the lamb was so different to all the others, it was assumed to be the homozygous genotype.

Nel and van Wyk (1982) discussed the different possibilities for the gene producing "coffee-brown." It could be the dominant allele at the *Extension* locus as previously proposed, it could be due to the *brown* allele at the *Brown* locus, or it could be due to another *Brown* locus allele dominant to *wild*. They favoured the last as it best explained the results of Nel (1967). They suggested it be B^{lt}: assumedly because, in the mouse the *light*, B^{lt}, gene is one of two dominant over the *wild* allele. As the homozygous *light* in the mouse is almost a white colour (Silvers 1979) *coffee-brown*, B^C, would seem to be a better name for the coffee-brown of the Karakul and "dark brown" of the Corriedale.

The *Albino* locus

No *albino* type sheep have been reported in the fat-tailed breeds. The "albinoid" (English translation of the Russian) type of grey Karakul reported in Asiatic Russia (Central Asia) has the homozygous *lethal roan* genotype and is not associated with the *Albino* locus.

The *Spotting* locus

There are two alleles accepted as being present at this locus.

The wild Allele—S^+ This allele results in a solid-coloured animal.

The spotted Allele—S^s In eumelanic animals, this usually produces some white markings on the crown of the head when heterozygous and when homozygous the area of white markings is more extensive. There is a wide range of expression—as the area of white increases on an animal, it becomes more extensive on the head, has an increasing amount on the tip of the tail, starts to occur on the lower

legs, on the bib area and underside of the neck and then on to the belly (Adalsteinsson 1970). At its most extreme, it may produce a piebald animal (such as in the Jacob breed and some coloured Merinos). This variation in expression is explained by the action of modifying genes (Adalsteinsson 1970) although, of course, there is always the possibility that more than one allele may be involved.

When the *spotted* allele occurs in a phaeomelanic background colour, it produces a piebald animal when heterozygous and a mainly white animal when homozygous (Lauvergne 1975). This gene is known to occur in the Dorset Horn/Poll Dorset, Merino, Finnish Landrace and some white Icelandic sheep where it plays a part in the removal of phaeomelanin on a *white*/*tan* background. It gives these white breeds a pink nose and white hooves. Coloured individuals in these breeds have "white markings" present.

This author does not know of any fat-tailed breeds where the *spotted* allele is obviously present. A number of otherwise solid-coloured Damara sheep have a white tip to the tail and occasionally some of these that have more white on the tail have some white on the crown. But in no cases does it extend to the underside of the neck, belly, etc. It should also be noted that in all types of "white markings" in the Damara there is a similar effect on both eumelanin and phaeomelanin pigment.

Nel (1967) discusses a small number of black Karakuls (6.58% and 12.35% in two different generations of a flock) having white markings. These markings occurred on the tail tip, occasionally on the head as well and very rarely additional flecks occurred on the legs, belly or brisket. Schmitz (1962, 1968) reported a similar level and range of markings in the Halle Karakul stud in Germany. Schmitz (1968) reported that mating sheep with white markings together resulted in 80% with markings with significantly more being piebald than other mating types.

Later (in the *persian* section) it is discussed how the Karakul background restricts the white markings in comparison with white-woolled breeds. Possibly, the *spotted* allele is present in these Karakuls with white flecks, and the Karakul background genes are restricting the extent of its expression.

On two occasions, in an attempt to produce a white Karakul pelt, these sheep with white flecks have been selected for increasing amounts of white. In Halle such an experiment was stopped in 1948 when it had only been able to progress as far as a piebald phenotype. A similar experiment was started in Namibia in 1954 and by 1963 six lambs with white encroaching on the body areas and one piebald lamb had been produced (Nel 1967). By 1982, the sheep were on average 80% white with some practically all white (Visser 1998). The heritability of the degree of whiteness was very high (0.91) which was attributed to a major gene or genes possibly being involved as well as modifying genes. Schmitz (1962, 1968) concluded that the inheritance of the white markings was polygenic and Nel (1967) showed that more than one recessive gene was involved. Could one of these have been the *spotted* gene?

The *Pigmented Head* locus

Four alleles are postulated as being present at this locus—*wild*, *persian*, *turkish* and *afghan lethal*.

The wild allele—Ph^+ This allele produces a solid-coloured animal—no white markings are present.

The persian allele—Ph^P When homozygous, this allele restricts the colour of the animal to the front portion of the animal. It is present in many breeds in Africa and Asia. When considering the colour of the animal, do not think of it as a white animal with a coloured front section, but rather as a coloured animal with a huge white spot on its rear section.

The position of the demarcation line between white and colour varies between breeds. In the Uda and Bali Bali breeds (hairy thin-tailed breeds of the Sahel type found in northern Nigeria, Southern Niger, Central Chad, Northern Cameroon and western Sudan—Porter 2002; Epstein 1971), it is around the midriff or even just in front of the hind legs. In the Somali and the Persian (Fig. 2a, b) (derived from the Somali), it is in front of the front legs and in the Dorper (Fig. 3a) and the Awassi half way up the neck.

Because the Dorper is the result of a cross between the Blackhead Persian and the Dorset Horn breeds the difference seen between it and the Somali and Blackhead Persian can be explained by the action of modifiers. No doubt the modifiers that built up over the centuries to produce the pure white of the Dorset Horn are having an effect to enlarge the white spot of the Dorper. The *spotted* gene of the *Spotting* locus is known to be one of these and its effect can occasionally be seen in the Dorper when the white extends forward to include the crown (Fig. 3b). This phenotype is often seen in the Namaqua Afrikaner breed as well (Fig. 3d).

Modifiers are most likely also responsible for the difference seen between the Blackhead Persian and the Udi and Bali Bali sheep, although the possibility of there being a different allele in the thin-tailed sheep cannot be entirely ruled out as no one has ever investigated it.

Breed modifiers also have an effect on the expression of the *wild*//*persian* heterozygous phenotype. When the Persian is crossed with the Karakul half (51%) of the lambs born are completely black. A few (10%) were born piebald, and this is similar to the number of pure Karakuls that normally have white flecks. The rest (39%) have white flecks (Nel 1967). So in half of the first cross offspring the

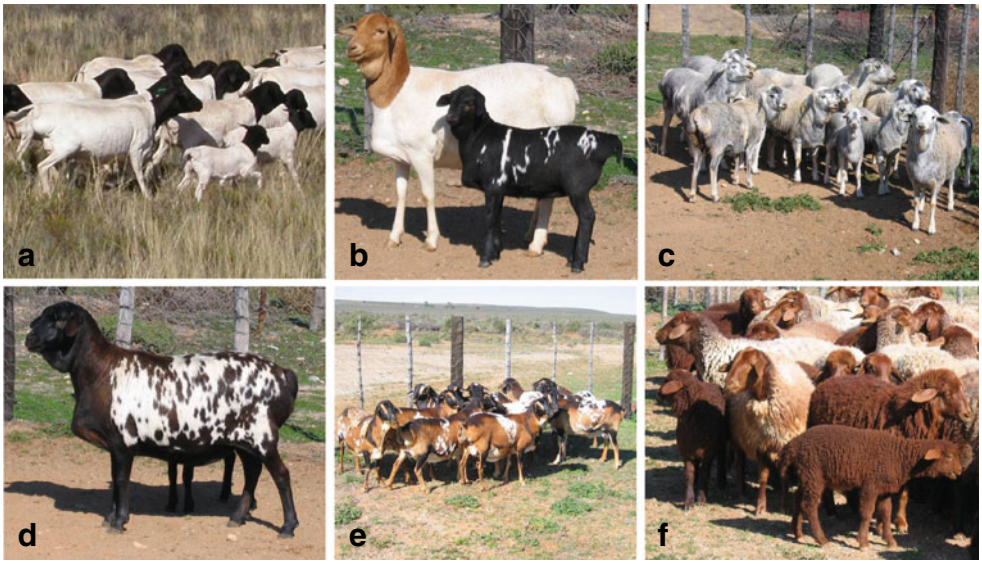

Fig. 2 The Persian sheep of Southern Africa. **a** Blackhead Persian—black due to the *dominant black* gene—colour restricted to the front by the homozygous *persian* gene. **b** Redhead Persian—red due to *wild* at the *Extension* locus and probably *dark tan* at the *Agouti* plus a black Speckled lamb. **c** Blue (Blou) Persians—probably due to the *lethal roan* gene (heterozygous). **d** Speckled (Skilder) Persian. **e** Speckled "briqwa" Persians that are probably homozygous *xerus* at the *Agouti* locus. **f** Russian Red Wooled Persian—probably homozygous *dark tan* at the *Agouti* locus

wild allele is dominant and where piebald and white flecked lambs are born it may be due to an interaction with the gene(s) in the Karakul causing white flecks.

When the Persian (Davy 1927) and the Dorper (Notter and Sponenberg 2002; Lundie 2007) are crossed with white-woolled breeds black (due to the presence of the *dominant black* gene in the Persian and Dorper) piebald animal are produced, usually with most of the front section coloured. The cross reported by Davy (1927) was with the Merino, and it was noted that all the lambs had a white spot on top of the head—this will be due to the presence of the *spotted* gene (heterozygous in the cross) which is known to be present in the Merino.

The turkish allele—Ph^T The homozygous *turkish* phenotype appears as a white animal with coloured areas around the eye, on the nose, penis and udder areas and on parts of the legs. Again, as with the *persian*, it should be thought of as a coloured animal with very extensive areas of white on it. It is the usual colour in many fat-tail breeds such as the Akkaraman (or White Karaman) of Turkey—hence the name.

The genetics of the allele have been reported in this breed. When the Akkaraman is crossed with the Red Karaman (a solid-coloured breed) piebald animals are born (Mason 1967). Also, when the Akkaraman was crossed with the white German Mutton Merino, it was again

Fig. 3 The Dorper. **a** The colour of the Dorper is black due to the *dominant black* gene—it is restricted to the front of the animal by the homozygous *persian* gene. **b** It is likely that the white on the crown is due to the *spotted* gene from the Dorset Horn ancestor. **c** The *ticked* gene causes small pigmented spots to grow on areas where "white markings" have removed the colour. **d** The Namaqua Afrikaner—in some the white extends forward on to the crown. The Damara. **e** The homozygous *turkish* phenotype. **f** A ewe with the *turkish* phenotype and her lamb with what is likely the heterozygous phenotype as it occurs in the Damara

reported that piebald lambs were born (Düzgünes et al. 1960; Lauvergne 1976).

When Lundie (2007) noted the offspring of some of the Damara with the homozygous *turkish* phenotype he observed both piebald and another peculiar type of white markings (similar to his "*encroaching white*") (Fig. 3e, f). The German Mutton Merino would have introduced the *spotted* gene into the cross with the Akkaraman which would/could have had a modifying effect on the crossbred. Possibly the "*encroaching white*" type markings of the Damara is the heterozygous *wild*//*turkish* phenotype when the *spotted* gene and other white-woolled breed modifiers are absent.

The afghan lethal Allele—Ph^{afl} Discussed as part of the *Roan* locus.

The *Roan* locus

Two alleles have been established at this locus—*wild* and *lethal roan*, and there is evidence that the *afghan lethal* is also situated here rather than at the *Pigmented Head* locus.

The wild allele—Rn^{+} This is the most common allele and when present and homozygous the animal is a solid colour.

The lethal roan allele—Rn^{Rn} In the German system of nomenclature, the *lethal roan* and *wild* alleles are symbolised "*G*" and "*g*", respectively, in the Russian system "*We*" and "*we*" and by Nel (1967) "W^{R}" and "*w*".

The *lethal roan* allele is present in a number of breeds where it is important in the production of grey pelts for the fur trade. It is best known within the Karakul breed (Fig. 4) (where in Russia it is known as "shirazi"). It occurs in two grey breeds: the Grey Shirazi of Iran (a fat-tailed breed with a similar origin to the Karakul—Monem et al. 2005) and the Sokolki (a fur breed) of the Ukraine (Semyonov and Selkin 1989). As well it is one of the colours found within the Ţurcana breed (a Zackel type) of Romania, Malich breed (a fat-tailed fur type) of the Crimea and the Ukraine and the Mongolian breed (a fat-tailed breed—Baatar 1990) (Nel 1967; Ghighineisvili 1975; Porter 2002).

Lethal roan in the Karakul Prior to the study of the genetics of coat colour in sheep, Russian Karakul farmers avoided mating "grey to grey" claiming it was contrary to their custom. Sinizyn recorded this back in 1900 (Adametz 1917; Nel and Louw 1953). It is now known that the gene that causes the grey colour, *lethal roan*, is sub-lethal when homozygous, which explains why the "grey to grey" matings were avoided.

Nel and Louw (1953), Nel (1967) and Ghighineisvili (1975) detail much of the research that has been undertaken on the *lethal roan* gene—from finding the gene is dominant, through realising that the homozygous genotype is sub-lethal, to being able to fairly accurately identify the homozygous phenotype at birth.

The grey colour is described by Nel (1967) as: "the coat consists of black and white fibres, intermingled with each other. Some areas of the coat, particularly the anterior-dorsal region (shoulder area), are a lighter shade which results in a pelt with a lighter centrepiece with darker surrounding areas. The face, ears, tail tip and lower parts of the legs are also often lighter in colour. The relative proportions of black and white fibres and their relative lengths determine the shade of grey. The intensity of colour varies from white-grey to almost completely black with grey on the extremities, i.e. black with grey points".

A feature of the homozygous genotype, Rn^{Rn} Rn^{Rn}, is that the individual usually dies at a relatively young age. These sheep usually become pot-bellied, emaciated and anaemic and this leads to death in a few days. On post-mortem it is revealed that they have problems in the rumen, abomasums and intestines. Deaths occur between 32 and 888 days of age with a median value of 174 days (Nel 1967).

Very occasionally a homozygous individual will live long enough to produce offspring: Contescu and Leagu (1941)—some Zurkana (Ţurcana) ewes produced up to six and eight lambs, Nel (1950)—a Karakul ewe produced two lambs, and Nel and Louw (1953)—a Karakul ram produced 12 grey lambs when mated to black ewes.

Because the homozygous individuals will not survive the Karakul breeders need to be able to identify these lambs so that, if they occur, they can be used for the production of pelts. The distinguishing features of a homozygous *lethal roan* are "a pale coat colour, unpigmented tongue, absence

Fig. 4 The *lethal roan* gene in the Karakul. All three lambs are black due to the *dominant black* at the *Extension* locus and grey due to the *lethal roan*//*wild* at the *Roan* locus. **c** Notice that this lamb has a white muzzle whereas the others do not

of black hairs on the chin and presence of white flecks inside the ears" (Nel 1967). Being able to identify the homozygous lambs at birth allows "grey to grey" matings to be used. This is an advantage over the "grey to black" matings as it not only produces more grey lambs, but also allows both parents to be selected for the ideal traits of a grey birthcoat (Ghighineisvili 1975).

The *lethal roan* allele acts on the basic colour of the animal, so when it occurs on a brown (tan) Karakul a roan or brown-roan colour is produced. This colour is known as "gulgas" in Russia and is variously translated as grey-brown, roan, rose, lilac and occasionally pink. The "shoruri" or camel colour of Pogodin et al. (1975) and Pogodin (1976) is assumedly the "coffee-brown" colour with the heterozygous *lethal roan* gene present.

Lethal roan in the Damara There is a rather similar grey colouring occasionally seen in the Damara that, after extensive discussion, this author previously concluded was probably not due to the *lethal roan* allele, but was more likely similar to the colouring seen in the Herdwick breed and suggested calling it "whitening" (Lundie 2007). Subsequently, the same phenotype was seen in a line of Persian sheep, the Blue Persian (Fig. 2c), where it is also occurring on a hair sheep background. There were no unexplained deaths that would indicate the presence of the *lethal roan* allele (Deon Volk, personal communication). Since that time, the author has discovered (Campbell 2003, 2006) that the colour was introduced into the Persian in the 1980s, by way of an outcross to the grey Karakul. So, it must be concluded that the colouring seen in both the Damara and Persian is most likely due to the *lethal roan* gene as well. The reason there have been no *lethal roan* deaths seen in the Persian sheep will be the continual backcrossing to the Blackhead Persian that has occurred so that all grey offspring produced will be heterozygous.

A number of different phenotypes were noted in the Damara where, what now must be assumed to be, the *lethal roan* occurred (Lundie 2007). Interactions were noted between *lethal roan* and some alleles of the *Agouti* locus. For example, the *tan spreading white* in combination with the *lethal roan* produces an almost pink colour (Fig. 5d); this is similar to the situation in the Karakul.

What is unexpected is that in two of the Damara phenotypes an interaction with an *Agouti* locus allele can also be seen where the *dominant black* gene is assumed to be present. So, in the Damara, when the *lethal roan* occurs along with the *grey* allele of the *Agouti* locus a "dark

Fig. 5 The *lethal roan* Gene in the Damara. All the sheep are *lethal roan*//*wild* at the *Roan* locus. **a**, **b** and **d** are homozygous *wild* at the *Extension* locus so the alleles at the *Agouti* locus are able to be expressed. **a** *grey* at the *Agouti* locus which produces a dark mahogany shade which the *lethal roan* then acts upon—notice the white muzzle. **b** Probably *dark tan*//*grey* at the *Agouti* locus—the body is a dark tan shade with it darker on the head—the *lethal roan* acts on this—again notice the white muzzle. **c** This ram has the same features as (**a**) and (**b**) but has no sign of phaeomelanin (tan colouring)—so is a grey colour rather than a roan colour—this will be because the *dominant black* gene is present—the significant feature is that the white muzzle is still present indicating the *grey* of the *Agouti* locus is able to be expressed in the presence of the *dominant black* gene. **d** Probably heterozygous *tan spreading white* at the *Agouti* locus. **e** Ewe and lamb both probably homozygous *tan spreading white* at the *Agouti* locus—with the *dominant black* turning it from a roan shade into a dark grey shade. **f** A completely grey colour—so *dominant black* at the *Extension* locus—the alleles at the *Agouti* locus having no effect (so not *grey* or *tan spreading white*)

mahogany roan" phenotype is produced with *lethal roan* characteristics along with the large white muzzle of the *grey* (Fig. 5a). A "dark tan roan" lamb with similar features was assumed to be produced by the *dark tan*/*grey* and the *lethal roan* genotypes interacting (Fig. 5b). When identical features are seen in a grey lamb (not dark mahogany roan or dark tan roan) it has to be assumed that the *dominant black* gene is present as well as the *grey* of the *Agouti* locus and *lethal roan* (Fig. 5c).

This same large whitish muzzle is seen amongst some, but not all, grey Karakul lambs where the *dominant black* gene would also be present (Fig. 4c). This would seem to indicate not only that the *grey* allele of the *Agouti* locus might be present in the Karakul but, also, that when the *lethal roan* gene is present the *grey* allele of the *Agouti* locus is able to be expressed even though the *dominant black* gene is present.

Another interesting phenotype seen had a white head and legs and a very dark grey body—much darker at birth than the ones just discussed with *grey* present. Lundie (2007) had reasoned that it was homozygous "whitening" on a *nonagouti* background. It is obviously not homozygous *lethal roan* as the ewe is now 4 years old and has an identical lamb by a grey ram (Fig. 5e). Could they be heterozygous or (more likely) homozygous *tan spreading white* in conjunction with both *lethal roan* and *dominant black*? If correct this is the second case of an *Agouti* locus allele being expressed in the presence of the *dominant black* gene when *lethal roan* is present.

In both cases (*grey* and *tan spreading white*), the *Agouti* locus alleles are not recognised because of the presence of characteristic phaeomelanic and eumelanic areas—the *dominant black* gene has converted all of these to black eumelanin. Instead, it is the areas where white fibres are present that are the distinguishing features.

Shades of grey in the Karakul Nel (1967), using seven shades, found the shade of grey to have a high heritability, 0.54, so it is possible to select in whatever direction the pelt market dictates.

Ghighineisvili (1975) described work by various Russian workers where the range of the shade of grey seen was divided into eight different "tints"; milky, light-steel, silver, pearl coloured, light-blue, mother-of-pearl, grey and black-grey. Because of their appearances, some were much more valuable than others. Some tints were highly heritable whereas others were hard to produce—mating light-blues together produced up to 94% light-blue whereas pearls mated together only produced 34% pearls.

Speculation concerning the grey Karakul colour Could it be that some of the *Agouti* locus alleles, such as *grey*, play a role in producing the range of grey shades to be seen in the Karakul?

As has already been stated, the phenotypes of grey Karakul lambs would indicate that the *grey* is likely present in some (Fig. 4c) but not in others (Fig. 4a, b).

In European woolled breeds where *grey* is present, it leads to the addition of white fibres on the body of the animal—particularly changing the undercoat fibres. Homozygous animals are a lighter (whiter) shade than heterozygous individuals (Adalsteinsson 1970).

In spite of the differences in the background colours of the Karakul (centuries of selection towards an intense black or tan shade) and the woolled European breeds (centuries removing the tan from *white*/*tan*), it is to be expected that if the *grey* gene were to combine with the *lethal roan* it would interact to produce a somewhat lighter shade of grey. And an individual with homozygous *grey* would be expected to be lighter than the one that was heterozygous. While the *Agouti* locus *grey* gene is probably only at an extremely low frequency within black Karakul flocks, if it helps in producing an ideal shade of grey, it may have risen to a higher frequency in grey Karakul flocks.

Nel (1967) observed that Karakul "grey × brown" matings usually produced "exceptionally dark grey lambs". He suggested that possibly some modifying genes increase the pigmentation of the coat and other parts of the body.

Within animals that are heterozygous *lethal roan* and *dominant black*: could the presence of the *grey Agouti* locus allele in some grey Karakuls be playing a part in the production of these "exceptionally dark grey lambs"? If they had the homozygous *grey* allele present, then mating them to a "tan" Karakul, say *dark tan*, would produce darker heterozygous *dark tan*/*grey* individuals—the heterozygous phenotype being darker than the homozygous. If the grey Karakuls happened to be heterozygous *grey* at the *Agouti* locus then 50% of the offspring would be homozygous *dark tan* and so a much darker shade of grey.

There may be other modifying genes also present that help in producing an ideal grey shade. Not all grey Karakuls have the phenotype that would suggest the possible presence of the *grey* allele at the *Agouti* locus.

If the suggestion that the *Agouti* locus *grey* gene plays a part in some of the grey Karakuls is correct, then the question arises: if the *grey* gene were to occur in a *dominant black* animal without the *lethal roan* being present, would it be expressed in the phenotype? Again, there are some results reported by Nel (1967) that indicate that possibly it would be.

When "grey × grey" matings are carried out in the Karakul, 25% of the offspring are black and referred to as "black ex grey" [so $E^D E^D\ Rn^+\ Rn^+$]. Mating these "black ex grey" sheep back to "grey" produced 108 grey and 71 black offspring. This is significantly different ($P<0.01$) to the 1:1 ratio expected. To explain the excess of grey lambs, Nel suggested three possibilities. The one he favoured was a

modifying complex causing the grey colour to appear where it was not expected. So could the excess of greys be due to some being *grey* at the *Agouti* locus while homozygous *wild* at the *Roan* locus? If this were the case, then an excess of greys should also be expected in the "grey × grey" matings. Overall, when all the grey shades were combined, these matings closely fitted the 3:1 ratio expected. If, as has already been discussed, a sheep were to carry both the *grey* and *lethal roan* genes, it could be assumed they would probably have an additive effect and so produce a lighter shade of grey. It was found that matings involving the lighter shades of grey gave 39 grey:8 black ($P>0.20$) and one particular "light grey" ram gave 46 grey:8 black ($P>0.05$). In both cases, there are an excess of greys but not enough to be significantly different to the 3:1 ratio expected.

If the *Agouti* locus *grey* gene were able to be expressed on the *dominant black* background without the presence of the *lethal roan*, then it should be possible to breed grey Karakuls without the sub-lethal problem. Whether they could be bred a desired shade would be another matter.

The afghan lethal allele—Ph^{afl} or Rn^{afl} The *afghan lethal* gene has been studied in India, Namibia and the USSR.

Beginning in 1912, in India, an attempt was made to produce a white line of sheep within the Bellary breed. In the attempt, they worked with three phenotypes: completely black, a colour that looked very similar to the homozygous *turkish* that they called "black-face-white" (white with black on the nose area, around the eyes and on the ears) and a completely white colour. Their results indicated that the "black-face-white" phenotype was heterozygous and that the white was homozygous. The white sheep had a weak constitution and most died at a young age. In later years, they drenched the whites with cod-liver oil and were able to keep a few through to breeding age (Murari 1932; Littlewood 1936).

It was felt that the raising of a pure breeding white flock had failed. From 1938 to 1952, two lines were bred. One was a pure Bellary "black-face-white" line which continued to produce white, black-face-white and black offspring. Of the 64 pure white lambs born, 57.8% were dead within a year (Das and Rajagopalan 1956).

In Namibia, the gene was introduced to the black Karakul by crossing with the white Wooled Persian. They found the same three phenotypes and called the heterozygous "usual white" and the homozygous "pure white". While there was only the occasional death amongst the "pure whites", it was found that they never contributed much as rams (Nel 1967). They termed them "sub-vital".

In an attempt to produce a completely white Karakul in Namibia, they scored the "usual whites" on a four-point scale from "D" (piebald) through to "A" (completely white and termed a "safe white"). In selecting and breeding the "safe whites", they have been able to modify the heterozygous phenotype to be much whiter (Fig. 6b, c).

The Jaidara is a fat-rumped breed of Uzbekistan. These are usually black or dark brown with some of the "shirazi" (*lethal roan*) type. Whites are very rare, and these have coloured spots on the head and neck (Kurganov 1938). These white types with black on their ears, face and lower limbs that occasionally occur in the Karakul and fat-rumped breeds of Asiatic Russia (now Central Asia) are known as "afghan pieds" or "Karakulaks" (Kijatkin 1968). Vasin (1928), using "Ph" first described and named the colouring in the Afghan breed and reported that crosses between the Afghan and Merino indicated that it was a dominant trait.

In an attempt to produce a white Karakul, a white Karakul (with black on the head and legs) was mated to black Karakuls—half the offspring were white with black on the head and legs and the other half were black. As well, white Jaidara rams were used over black Karakul ewes (Bioko 1962). No lambs were spotted and both black and white lambs had a similar survival rate (Koševiõ et al. 1964) (of course these were the first cross and so heterozygous).

When "afghan pied" ewes and rams were mated together, they produced "afghan pied" and black in a 3:1 ratio (Kijatkin 1968; Stoyanovskaya and Islamov 1977).

Fig. 6 Karakuls. **a** A coffee-brown lamb descended from the animals studied by Nel (1967). **b**, **c** The *afghan lethal* gene in the Karakuls of Namibia. All animals shown are heterozygous *afghan lethal*//*wild*. Those two in (**b**) are the result of a recent cross of a white ram to black Karakul ewes so the normal heterozygous phenotype is seen. Those in (**c**) show the result of continual selection against black in the heterozygous animals—these are termed "safe whites"—the homozygous "pure whites" are recognisable at birth and used for their pelts

In Namibia, the colour of an animal that is heterozygous for both *lethal roan* and *afghan lethal* is termed "silkara". Nel (1967) described such a ram lamb at birth as "pure white–grey spots around the eyes, lips, horn seats, sheath and teats—tongue light grey speckles at the point and the palate striped medium grey".

Nel mated this ram to a number of black Karakul ewes and obtained seven with the *lethal roan* phenotype and nine with the "usual white" phenotype. This 1:1 ratio is that expected if both genes were at the same locus. If they had been at two different loci, a 1:1:1:1 ratio (black/"usual white"/heterozygous *lethal roan*/heterozygous *afghan lethal* with heterozygous *lethal roan*) would have been expected.

At the moment *afghan lethal* is placed at the *Pigmented Head* locus based mainly on the fact that the phenotypes of *persian*, *turkish* and *afghan lethal* visually seem to form a series. There are similarities between *lethal roan* and *afghan lethal* (the homozygous genotypes of both have a weaker constitution) and this along with Nel's results indicate it is more likely to be situated at the *Roan* locus.

Other types of "white markings"

There is a huge range of "white markings" to be seen within the Damara breed. Lundie (2007), from observation alone, grouped them into a number of main types, each of which formed a series.

White tip to the tail While some animals are completely coloured, most are seen to have a white tip to the tail. As this area enlarges, some have a small area of white on the crown as well. It is always possible that the *spotted* gene is involved, but with that gene, white usually occurs on the head first. Many of the sheep in the following series have the white tail tip as well.

Encroaching white This is seen in a large number of Damaras. The white markings are first seen on the belly and upper underside of the neck. As it becomes more extensive, its spread seems to occur first into the shoulder area and then it spreads forward, up and back from there as well as down on to the upper legs. The upper rear body area and parts of the head are the last places to keep their colour.

Scattered on the edge of the white and coloured areas, there are always a large number of coloured spots. The spread of white appears to be similar on either side of the animal but is not identical in the fine detail (Fig. 7a). A couple of ewes with the homozygous *turkish* phenotype had lambs that were very similar to the encroaching white phenotype—rather than having coloured spots at the edge of the colour change the two had more of a streaking of colour and white. It is possible, though, that the sheep with the encroaching white phenotype are all heterozygous *wild*//*turkish*.

Broken white This series is not as common as the first. In these, the removal of white seems to start on the lower front side of the sheep and spreads up and back from there. The edge between the colour and white would best be described as being "broken". The shoulders, neck and legs do not seem to be affected (Fig. 7b).

White belted Also quite common in the Damara is a large white spot which occurs first in the central region of the body. In animals in which this white area is larger, it extends forward, backward and down. Roughly equal amounts of white occur on either side although the shape is not identical. In many it completely circles the body to form a white belt. There is a clear-cut smooth boundary between the colour and white (Fig. 7c).

White patched In this series, there are very large patched areas of white mainly situated on the lower side of the body and sometimes on part of the neck and head. There is a relatively smooth border between the colour and white, and there are no scattered pigmented areas within the white area (Fig. 7d).

It should be noted that Henseler (1913), reporting on a cross between the Somali (*dominant black* and homozygous *persian*) and Merino breeds, shows an F_1 ewe and her F_2 lamb with a white patched phenotype but with the white not extending in front of the shoulders. A second F_2 lamb had the belted phenotype.

Mottled Rather rare in the Damara. Within one flock, there were four ewes with most of the body covered with extensive speckling/mottling. In other flocks, there were the odd sheep with a similar colouring but the area covered was not as extensive (Fig. 7e).

Flowing droplets Some Damara have the white area of the body completely covered with fairly uniformly sized droplets that are shaped in the direction of the flow of the lie of the hairs. This flow is down and back from the backline and towards a whorl situated on each edge of the belly mid way between the front and rear legs. The author is not sure whether the gene that causes the droplets also causes the white area of the body or whether another gene produces the white area and the "flowing droplets" are like *ticking* and acting within that white area. Some animals have the white area over all the body and much of the points so that flowing droplets occur on all this area.

The Speckled Persian This is also known as the Skilder Persian and is bred on a black or (more rarely) red background colour (Fig. 2b, d and e). From the results of

Fig. 7 Types of "white markings" seen in the Damara. **a** "Encroaching white"—there is a possibility that this is the heterozygous *turkish*//*wild* phenotype as it occurs in the Damara. **b** "Broken white". **c** "White belted". **d** "White patched". **e** "Mottled". **f** In most cases where there are "white markings" present, it is possible to place them into one of the series which would suggest that in most cases there is only one series present in each animal. The author wondered previously (Lundie 2007) if this may be due to the fact that many solid-coloured rams are used in the flocks. This family group consists of a "white patched" ram, a ewe in which it is not easy to recognise the series present (so may be a combination) and their pure white lamb—where the genes inherited have been enough to completely remove all colour. Such white lambs are rare in the Damara

a survey of some breeders, Lundie (2007) came to the conclusion that there were probably two pairs of genes involved in the production of the speckled phenotype. The head, neck, legs and underside retain the solid colour. Initially it was felt that this could be the phenotype of the *persian*//*wild* genotype on the Persian background. The fact that 1–10% of the lambs born had the homozygous *persian* phenotype indicates that some of the speckled sheep are heterozygous *persian*//*wild* but certainly not all of them.

It was felt that a second gene pair must be involved and it was suggested that it could be the gene causing "broken white" in the Damara. It was felt that it was different to the "mottled" phenotype as the "mottled" mottling extended on to the neck and head. Some of the Speckled Persian flocks can trace back to an outcross with the Namaqua Afrikaner while others were of pure Persian breeding.

The *Ticking* locus

There are two alleles at this locus: *ticked*—Ti^{Ti} and *wild*—Ti^{+}.

The ticked allele The *ticked* allele is assumed to be dominant and causes small pigmented spots on the skin and wool to develop in regions that are white due to the action of one of the white markings genes. The area is white at birth and the spots develop later. It has been recorded in the Icelandic breed, where the amount of pigmented spotting has a hereditability of 0.55 (Adalsteinsson 1978, 1984). The Dorper is white on most of the body due to being homozygous for the *persian* gene. Normally this remains white but if the *ticked* gene is present then spots develop (Fig. 3c).

The *Sur* loci

Sur colouration is a common trait in the Karakul breed of Asiatic Russia (now Central Asia). The birthcoat of lambs born with sur colouration has a lighter or white colour on the fibre tip (Fig. 8b, c). Sur colours vary in two ways. There is variation in the basic colour of the fibres, this being seen on the base section of the fibres, and there is also variation in the shade and extent of the colour of the fibre tip. Both of these variable traits are believed to be under separate genetic control.

The sur colours are not expressed if the *dominant black* gene is present although one of the hypotheses used to explain the genetics of silvery sur would, if correct, make it an exception.

The different combinations of base colour and the shade and extent of the tip colour lead to a number of sur colours, each of which has been given a specific name. There are three groups of sur colours: Bukhara Sur includes golden

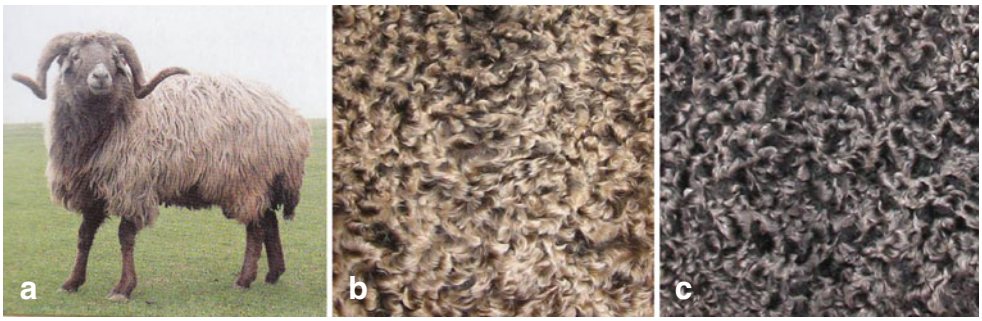

Fig. 8 Sur colouring in the Karakul. **a** A Bukhara type sur ram from Kazakhstan. (From: Medeubekov et al. 2008). **b**, **c** A close-up view of two sur lamb pelts from Uzbekistan showing the lighter colour on the fibre tip

and silvery, Surkhandarya Sur includes platinum, amber, bronze, and anthracite and Karakalpak Sur includes steel, flame and apricot.

The Bukhara Sur (Fig. 8a) Considering the golden sur first it consists of a rust red-coloured base and a lighter tip giving it a golden sheen. Vasin (1946), using the Russian system of nomenclature, gave the genotype of a *golden* sur lamb as dd GG or dd Gg (Mukhamedov 1974, 1976). When the *dominant black* gene, "D", is absent (dd) a brown (tan) Karakul lamb is produced—this producing the basic colour of the fibre (in the COGNOSAG nomenclature, $E^{D}E^{D}$ $A^{wt}A^{wt}$ and $E^{D}E^{+}$ $A^{wt}A^{wt}$ are black and $E^{+}E^{+}$ $A^{wt}A^{wt}$ is tan).

Vasin's "G" gene produces the lighter tip to the fibre and he believed it to be dominant. Mukhamedov (1974, 1976) presented his and other results as confirming Vasin's hypothesis. When golden sur rams were mated to black Karakul ewes, most lambs born were black (95.5%) with only the occasional sur (4.2%) and brown (tan) (0.3%) (the sur and tan lambs occurred because some of the ewes were heterozygous Dd [$E^{D}E^{+}$] and the tan lambs because some of the sur rams were heterozygous Gg). It should be noted that Vasin (1928) had believed that "agouti", which he equated to sur, was recessive and used "g" as its symbol, with "G" for its absence—the reverse of Vasin (1946)).

All authors agree that it is only in the backcross of the F_1 to sur that larger numbers of sur lambs were produced.

If all the golden sur rams were homozygous then 50% black and 50% golden sur lambs would be expected in the second generation (backcrossing the F_1 to golden sur rams). From 490 lambs produced, they obtained 49.8% black, 49.2% sur and 1% brown (tan) (Mukhamedov 1974). This would indicate not only that the sur gene (of the golden sur) is dominant but also that most of the golden sur rams were homozygous. If, on the other hand, the sur gene was recessive the backcross would have been expected to yield 50% black, 25% golden sur and 25% brown (tan).

Other authors had previously obtained conflicting results. For example Mukhamedov (1974) refers to Yudin and Kotov (1953) (Judin et al. (1953)) obtaining close to 3 black:1 sur in the backcross of golden sur rams over the F_1: but in these results other types of sur (notably silvery sur) were also involved. Likewise, Mukhamedov (1976) also reports an excess of black ewes (69.8%) in the second generation and an excess of sur (69.9%) in another second generation cross—he puts the variation from the 1:1 ratio expected down to some silvery sur adult animals being wrongly classified as golden sur and involved.

Mukhamedov (1976) measured the length of the tip on golden sur lambs and scored them into nine classes ranging from a tenth to a half of the length. As the proportion of golden sur parentage increased, the average tip length increased. It was suggested that the increase in length of the lighter tip was under the control of a number of genes (what was not suggested was that lambs homozygous for the sur gene involved might have a longer tip than those heterozygous—surely a possibility).

Vasin (1946) believed that the silvery sur had the dominant black gene "D" [E^{D}] present. He postulated that this black colour is turned into a dark smoky shade by the presence of a second dominant gene "O"—this gene "O" having no effect on the rust red or brown colours. When the sur gene that produced the golden sur is also present it gives the dark smoky fibres a light silvery shade to the fibre tip—silvery sur (Mukhamedov 1974, 1976).

The Sur Bukhara locus Aliev and Rachkovskiĭ (1986, 1987a, b, 1989) carried out an extensive analysis of the literature on the sur colours and suggested that the sur tip of the Bukhara Sur group was recessive and determined by three alleles at the *Sur Bukhara* (*Sb*) locus: *Sb*—solid colour, Sb^{i}—*intense expression* and Sb^{m}—*middle expression*. Both golden sur and silvery sur being homozygous Sb^{i} Sb^{i}.

COGNOSAG changed the *Sur Bukhara* symbol to *SuB* and suggested two alleles SuB^{+}—*wild* and SuB^{s}—*sur bukhara* (Sponenberg et al. 1996).

The genetics of the basic colour Aliev and Rachkovskiĭ (1986, 1987a, b, 1989) believed that the basic colour of the fibre in all types of sur lambs was determined by the interaction of alleles at the *Agouti* and *Extension* loci. Having said that, they believed that almost all sur types were homozygous A^{wt} A^{wt} at the *Agouti* locus. So they were proposing that the differences in the basic colour were

actually determined by different *Extension* locus alleles. They proposed three additional *Extension* locus alleles—E^{bl}—*black*, E^{br}—*brown* and E^{y}—*yellow* (see "The *Extension* locus" section) to explain the differences in the base colour seen.

It was suggested that silvery sur sheep were homozygous—E^{bl} E^{bl} and the golden sur sheep—E^{br} E^{br}. So silvery sur—E^{bl} E^{bl} A^{wt} A^{wt} SuB^{s} SuB^{s} and golden sur—E^{br} E^{br} A^{wt} A^{wt} SuB^{s} SuB^{s}.

The Surkhandarya Sur Bronze sur has chestnut (red) fibres with a light bronze tip and platinum sur coffee-coloured fibres with an almost colourless tip. (Gigineišvili 1956). When the length of the depigmented tip was measured against the total length, it was found that for anthracite it was 10%, for bronze up to 40% (mostly 10–20%), for amber up to 60% (mostly 30–40%) and for platinum up to 70% (mostly 20–40%) (Salovatov 1991).

When the four Surkhandarya were pure mated (e.g. "bronze × bronze") in all cases, all four types occurred in the offspring. By selection within the colour types, it was possible to raise the percentage of the required type (e.g. within the bronze matings the bronze rose to 61.7% and the platinums in the platinum matings to 39.7%). Anthracite by anthracite matings yielded 71.1% anthracite surs (Gigineschvyli 1973). Muradov and Ismailov (1987) gave similar results.

The Karakalpak Sur Apricot sur has black fibres changing to a golden yellow with the very tip white. Dusky sur has black fibres tipped with white and steel blue has black fibres shading to steel grey (Belobrova and Dzumanijazov 1958).

The Sur Surkhandarya Locus Zakirov (1965) reported that when silvery and golden (Bukhara sur types) ewes were mated to Karakalpak Sur rams 94.9% and 93.6%, respectively, were black.

Gigineišvili and Ukbaev (1983) reported that mating Bukhara and Surkhandarya types together (reciprocal crosses) yielded 90.5% and 90.7% black lambs, 2.3% and 2.7% Surkhandarya Sur types and 2.3% and 4.6% Bukhara Sur types. The same cross by Ukbaev et al. (1992) produced 81% black, 7% brown (tan) and 11% sur types.

Going on the results of these three sets of crossings and other evidence, it is assumed that the Surkhandarya and Karakalpak Sur types are under completely different genetic control to the Bukahara type.

Aliev and Rachkovskiĭ (1986, 1987a, b, 1989) suggested that the sur tip in both the Surkhandarya and Karakulpak Sur types was due to recessive alleles at the *Sur Surkhandarya* (*Ss*) locus. Again, to account for the variation in length between the different surs, they proposed three alleles: *Ss*—solid colour, Ss^{i}—*surkhandarya intensive expression* and Ss^{m}—*surkhandarya middle expression*.

COGNOSAG changed the *Sur Surkhandarya* symbol to *SuS* and suggested two alleles SuS^{+}—*wild* and SuS^{s}—*sur surkhandarya* (Sponenberg et al. 1996).

For a lamb to show the sur colouring, it has to be homozygous SuB^{s} SuB^{s} or SuS^{s} SuS^{s}. A lamb heterozygous at both loci would not have a sur tip.

The basic colour of the fibres is under the same genetic control as seen with the Bukhara Sur types. Using the interpretation of Aliev and Rachkovsky (1989), the bronze sur would be E^{br} E^{br} A^{wt} A^{wt} SuS^{s} SuS^{s} SuB^{+} SuB^{+}.

Could other Agouti locus alleles be involved? For a long time, Vasin (1928) and other early researchers referred to the "sur" colouring as "agouti". This was because of the banding of the fibres which is a characteristic of the alleles at the *Agouti* locus. In the above proposals the only *Agouti* locus allele suggested is *white*/*tan*.

In types such as the apricot sur ("black fibres changing to a golden yellow with the very tip white"), is it possible a different *Agouti* locus allele could be involved? At birth various alleles of the "*eye patch*" type, when they occur in a double-coated fleece, are characterised by outer-coat fibres that are black at the base and an extensive tan on the tip. Could one of the "*eye patch*" alleles and possibly even a "*grey*" allele be playing a part in some of the sur types?

Conclusions

The alleles of ten of the recognised sheep coat colour loci have been discussed in relation to the fat-tailed and fat-rumped breeds—the *Extension*, *Agouti*, *Brown*, *Albino*, *Spotting*, *Pigmented Head*, *Roan*, *Ticking*, *Sur Bukhara* and *Sur Surkhandarya* loci.

The presence of some genes such as *dominant black* (at the *Extension* locus) and *lethal roan* (at the *Roan* locus) are very well documented. Because many of the *Agouti* locus patterns are so easily identified, it has been possible to discuss alleles at this locus even though no *Agouti* locus research has been carried out with fat-tailed sheep—similarly with the *ticked* allele at the *Ticking* locus. The *coffee-brown* gene has been assigned to the *Brown* locus without any experimental evidence to show it is an allele with *brown*.

There are research results available for the *persian* and *turkish* genes (both officially assigned to the *Pigmented Head* locus) but no research to prove they are both alleles at the same locus. The *afghan lethal* gene has also been officially assigned to the *Pigmented Head* locus (because its phenotype seems to form a series with *persian* and *turkish*) although there is more evidence that it is an allele with the *lethal roan* (at the *Roan* locus).

The research results for the Sur colours are sometimes conflicting and this author feels there are questions that still need answering. Instead of *white/tan* being the *Agouti* locus allele involved in almost all Sur types, could there be others such as *eye patch* or even *grey*? What changes the change in colour at the base of the Sur fibres (is it due to different *Extension* locus alleles, different *Brown* locus alleles, different modifications of a tan allele at the *Agouti* locus, different *Agouti* locus alleles or a combination of some of these)? Another question raised is whether the *grey* allele at the *Agouti* locus plays any part in the variation in shade of grey produced by the *lethal roan* gene.

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