The Chocolate and Lilac Colours in the Abyssinian and Somali Breeds

Marie-Bernadette Pautet, la Chacolaterie
(October 2008 version)

I want this article to be both a presentation of the chocolate and lilac colours in the abyssinian and somali breeds and a small tutorial on what the underlying genetics are. These colours are considered as "new" colours in the abyssinian and somali breeds, but remain within the wood-type colour range which suits them so well !

After a short historical summary of how these colours first appeared in the breed, and an overview of which colours are recognised by the different cat federations in the world, I present the current state of knowledge in the field of feline coat colour genetics regarding these colours.

A Brief History

In the 1970's, some breeders wanted to extend the range of basic colours found in the abyssinian breed (ruddy, sorrel, then their diluted counterparts, respectively blue and fawn).

Some cats called chocolate did exist in other breeds, and in non-agouti (solid) cats this colour appears as a beautiful dark brown. The diluted version of the chocolate colour is called lilac, or lavender. The colour of a chocolate abyssinian or somali appears as an intermediate between ruddy and sorrel, with its ticking not being black as in a ruddy or red like in a sorrel, but more dark brown (like a dark chocolate with at least 50% cocoa…) and an apricot-coloured undercoat. Similarly, the hue of a lilac abyssinian or somali can be described as intermediate between blue and fawn. One finds the terms dove grey or mushroom coloured in the descriptions: the colour is a fairly dark beige with some lavender/purple tinge.

For breeders to achieve this goal, since chocolate is a colour which is fairly common among siamese, it is often the mating of a chocolate siamese with an abyssinian who was used at the start. Among the different outcrosses, one of the most famous is the mating of LADY FAYRE[1], a chocolate siamese female carrying dilution with a sorrel abyssinian, BARENTU RED RUDY (sic), born in 1971. This mating resulted in the birth of a chocolate female, ARBOREAL CHOCOLATE KATRINA, who was used to introduce the chocolate colour in abyssinian lines. Most cats carrying the Manot affix today in the UK (Carol Ottey), or the Alexy affix in the USA (Bruce Alexy) are offspring of this mating. Looking at their pedigree, one may keep track of the chocolate over 10 to 15 generations.

Other similar outcrosses were also done elsewhere, e.g. in France and in the Netherlands. In France, this was mostly the achievement of the Bethsabée (Davaine-Chevaux family) cattery who married a chocolate siamese female to a sorrel somali to obtain a chocolate female, whose son ET UN CHOCOLAT UN DE BETHSABÉE is the founding ancestor of the chocolate somalis from this line. The picture shows a 3 months old little female from this line, NEWS DE BETHSABÉE, aka NOUGATINE.

[1] the pedigree of all cats cited in this article may be found on E.R.o'S., on-line pedigree database accessible at http://www.somali.asso.fr/eros/

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In parallel, one may cite the mating of a chocolate burmese stud, HUNTER VON DER RUHR, at the German cattery von Bardera (Bärbel Schumann) or the mating of a chocolate smoke balinese, IOWA D'AR DE L'EFA, with a sorrel somali at the French cattery Signé Cat's Eyes (Nadine Becuwe).

These examples are not exhaustive. In particular, in some abyssinian or somali lines, there are cats which are recognised by the feline judges as being chocolate (resp. lilac), but whose pedigree only contains ruddy and sorrel cats. This may be explained in different ways. One possibility takes into account the fact that black (ruddy) is dominant over chocolate; hence chocolate may remain hidden for generations before a chocolate cat appears (recessive is for ever!). Of course, one of the ruddy ancestors must have been a chocolate carrier... Another interpretation would be that some cats registered as sorrel be in fact chocolate.

One may also be wary about our own colour perception, in particular when we deal with pictures or when we see the cats under artificial light. The warmer the undercoat colour, the more the dark bands of a ticked cat will appear reddish and lighter in colour. I remember vividly my first chocolate-coated litter, with two somalis sisters (see picture), one being chocolate (PRAWLIN DE LA CHACOLATERIE), the other being chocolate silver (PYRITE DE LA CHACOLATERIE). Their appearance was really like a brown one and a grey one (with a little bit of simplification...). When looking closer at them, the colour of the ticking (and of hair at the tip of the tail, for instance) was absolutely identical. This shows that the undercoat colour changes completely our perception of the basic colour, like in those optical illusions where a grey circle will be perceived as darker or lighter depending on its surroundings.

Chocolate and Lilac Recognition

In France, LOOF[2] officially recognises chocolate and lilac abyssinians and somalis. But this is far from being the case in all cat federations throughout the world! Let's review the colours recognised for championship in CFA (USA), FIFe, TICA (USA), GCCF (UK) and LOOF (F), order being from the most restrictive to the less restrictive organisations.

CFA[3] (Cat Fancier's Association, Inc.), which presents itself as the World's largest registry of pedigreed cats, recognises abyssinians and somalis in only 4 colours: 4 ruddy, red (nothing to do with the sex-linked red), blue and fawn. Other colours, including chocolate and lilac, which are still very seldom found in the USA, are disqualified and cannot be registered at all.

FIFe[4] (Fédération Internationale Féline) accepts twice as many colours as CFA. In addition to the 4 colours above, their silver (white undercoat) varieties are also officially recognised. Here as well, no chocolate or lilac in championship class ! The EMS (Easy Mind System) coding used by FIFe, however, covers these colours, since they are recognised for some other breeds. The table on top of the next page summarises the EMS codes used by FIFe for colours other than sex-linked ones.

TICA[5] (The International Cat Association) has been recognising for a few months the 12 colours of the just-mentioned table, i.e. the three basic colours (ruddy, chocolate, and sorrel), their diluted variations (blue, lilac, fawn) and the silver varieties corresponding to these 6 colours. Cats of any of these colours may participate in Championship competition.

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[2] LOOF Breed Standards (in French): http://loof.asso.fr/loof/racine/default.asp?id=212

[3] CFA Breed Standards: http://www.cfainc.org/breeds/standards/standards-index.html

[4] FIFe Breed Standards: http://www.fifeweb.org/wp/breeds/breeds_prf_stn.html

[5] TICA Breed Standard for the abyssinian/somali group: http://www.ticaeo.com/Content/Publications/Pages/AB.pdf

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Non silver	
ruddy/usual	ABY/SOM n
sorrel	ABY/SOM o
blue	ABY/SOM a
fawn	ABY/SOM p
chocolate	ABY/SOM b
lilac	ABY/SOM c

Silver	
ABY/SOM ns	black silver
ABY/SOM os	sorrel silver
ABY/SOM as	blue silver
ABY/SOM ps	fawn silver
ABY/SOM bs	chocolate silver
ABY/SOM cs	lilac silver

Finally, LOOF in France as well as GCCF in the UK do recognise... 28 colours for abyssinians and somalis ! Describing them all would go far beyond the scope of this article, since in addition to the 12 colours already cited, one must also consider sex-linked red, its cream dilution, the corresponding silver varieties and all the tortie combinations resulting from a patchwork between the colours of the table and red (resp. cream for diluted cats). This makes a total of (2 × 12) + 4 = 28 colours ! Each one has its own EMS code, of course.

The genetic model

The genetic model used to explain the transmission of the basic coat colour in cats is well established for many years. In the previous version of this article, dating from 2003, I had formulated an alternative hypothesis to the standard model and concluded that only the identification of the involved alleles and the corresponding DNA testing could bring a definite conclusion. Now we do have this conclusion, since the studies led in several USA laboratories (see references later in this article) have identified mutations in the gene coding for a protein (TYRP1, or « tyrosinase related protein 1 ») which correlate perfectly with the classic model using three alleles ***B***, ***b*** and ***bl***. I am therefore now going to explain this model, starting with basics and then going on to describing what the new results of the genetic studies tell us.

In the nucleus of every cell in a cat, there are 19 pairs of chromosomes, except in the gametes who have half this number (19 chromosomes). Every chromosome carries thousands of genes controlling the synthesis of the various proteins needed by the cell (in fact, the whole story is more complex, the selective expression of the genes calls for many different mechanisms which we only start to understand, but for our purpose here we will consider that a gene indicates the way to build up a protein, without going into more details). The position of a gene, independently of its contents, is called a locus, and for each locus several possible expressions of the gene exist, which are called alleles. For example, on the hair length locus, one may find either of the two known alleles shorthair (generally noted ***L***) or longhair (generally noted ***l***, which is a little l, not an i).

Every somatic cell of a cat holds two copies of each gene, located on homologous loci in a pair of chromosomes. These copies are duplicated in an identical way (except for the recombinations and possible transcription errors) during each cellular division, from the original model coming from the fertilized egg. Hence, for every single locus, one allele is the copy (of the copy of the copy of the copy…) of the one in the sperm cell from the stud, and the other allele is the copy (of the copy of the copy of the copy…) of the ovule from the dam.

Let's come back to our example of the "coat length" gene. For a given cat, depending on the alleles inherited from his parents, there are 3 possible combinations ***LL***, ***Ll*** and ***ll***. The look of the cat (its phenotype) will be determined by the combination he carries. It's easy to imagine that a ***LL*** cat will be a short-haired cat, or that an ***ll*** cat will be a long-haired cat. But what about a cat carrying the combination ***Ll*** ? This is when the concept of dominant allele and recessive allele comes in. To just go on with the hair length example, one may say that the shorthair allele is dominant over the longhair allele, which means that in a cat carrying both alleles, the shorthair character will win and the phenotype of the ***Ll*** cat will be that of a short-haired cat. People familiar with the conventions used in the notation will have already guessed this, since upper-case letters are generally used for dominant traits and lower-case ones for recessive traits.

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The genotype of an abyssinian for the “hair length” locus is ***LL*** (his/her two alleles are “shorthair” ones). The genotype of a somali for this same locus is ***ll*** (his/her two alleles are “longhair” ones). An abyssinian can therefore only transmit a “shorthair” allele to his offspring, whereas a somali can only transmit a “longhair” allele. The mating of an abyssinian with a somali results in kittens which are heterozygote for the “coat length” locus. These cats are called “aby variant” in France. Their look is very close (sometimes even undistinguishable) from homozygous abys ***LL***, since the ***L*** allele is dominant over ***l***. They are of no interest in an abyssinian breeding programme, since the breeder will not be able to distinguish homozygous abys ***LL*** from heterozygous ones ***Ll***. The issue is quite different in a somali breeding programme, since already at birth it is easy to visually distinguish between a shorthair ***Ll*** kitten and a longhair somali ***ll***. It would therefore seem more appropriate to call these cats “shorthair somalis” like it is done in a few countries.

But let’s come back to our colours ! On the base colour locus (B), the identified choice is between, not two, but three possible alleles:

- ***B*** = black ;
- ***b*** = chocolate, b standing in fact for brown ;
- ***bl*** = cinnamon, bl standing for brown light.

B is dominant over the other two, and ***b*** is (possibly not fully) dominant over ***bl***. This means that a ruddy (black) cat may genotypically be ***BB***, ***Bb*** or ***Bbl*** (i.e. this cat may carry chocolate or cinnamon — we remain in a gourmet vocabulary...), that a chocolate cat may genotypically be ***bb*** or ***bbl*** (i.e. this cat may carry cinnamon), but that a sorrel (cinnamon) cat may only have one genotype: ***blbl***. Indeed, if one of the two alleles carried by this cat was ***B*** or ***b***, the cat would be ruddy or chocolate !

In practice, between a real chocolate cat and a real sorrel cat, a continuum of colour variation exists. This also holds true for the silver varieties, the diluted ones (lilac vs. fawn), and the silver diluted ones. So, how can this be explained ? Of course, one often hears that the variability results from the action of polygenes. This means that, instead of having a character expressing itself according to one of two very different modes, a whole series of other characters intervenes to change a bit the look of the cat, which cannot be modelled easily as bi-modal recessive and dominant genes.

Left picture:
chocolate and ruddy

Right picture:
chocolate and sorrel

Until now, we have only talked about fully-coloured cats (ruddy, chocolate or sorrel/cinnamon). If we want to cover the so-called “diluted” colours (respectively blue, lilac and fawn), we must take into account another independent locus, called D for dilution. On the D locus, only two alleles are known: the dominant allele D allows full expression of the colour intensity, whereas the recessive allele d gives the cat an appearance of paler colour, hence the “diluted” term. The genetic formula of an intense-coloured cat for the D locus will be either ***DD*** (homozygous for the dominant allele) or ***Dd*** (carrying dilution), but a diluted cat will always be ***dd*** (homozygous for the recessive allele).

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The B and D loci are located on different chromosomes and their transmission is totally independent one from the other. Hence, when taking them both into account, we get the following combinations:

ruddy	***B- D-***	blue	***B- dd***
chocolate	***bb D-*** *OR* ***bbl D-***	lilac	***bb dd*** *OR* ***bbl dd***
sorrel	***blbl D-***	fawn	***blbl dd***

The hyphens in this little table represent any one of the possible alleles. For instance, B- means that the cat has one ***B*** allele and that the second allele may be any one among ***B***, ***b*** and ***bl***. Hence, writing ***B-*** is the same as writing "***BB*** or ***Bb*** or ***Bbl***".

The genetic formula for a blue cat (considering only the B and D loci), which is written as ***B- dd***, can then be either ***BB dd***, ***Bb dd*** or ***Bbl dd***. If one of the parents of this blue cat is sorrel or fawn, then this gives us more information and we can be sure that the genetic formula of the kitten is ***Bbl dd***, since the sorrel or fawn parent could only pass on a ***bl*** allele to his/her offspring. As of today (May 2007), genetic tests exist both for the B and the D loci. When the analysis of the pedigree and collateral branches is not sufficient to determine the alleles the cat is carrying, and if this information is useful for the breeder, then it is very easy to determine the genotype of the cat for the B and D loci. For example, such testing will tell whether a ruddy cat carries chocolate or cinnamon, whether he/she carries dilution, or whether a chocolate cat is homozygous for this colour or whether he/she carries cinnamon.

The underlying biology

The model described in the above section with three possible alleles for the B « base colour » locus is totally in line with what is seen is the real world: for instance, two sorrel cats will never have kittens of other basic colours than sorrel (or fawn if they carry dilution), whereas a ruddy cat carrying cinnamon (***Bbl***), mated with a sorrel cat (***blbl***) will statistically give birth to half ruddy (or blue if both parents carry dilution) and half sorrel (or fawn if both parents carry dilution) kittens.

But what is the nature of the modification which changes the coat colour from black (the wild-type) to other shades such as e.g. brown (for chocolate cats) or grey (for blue cats) ?

Our knowledge of the mammal pigmentation biology is currently progressing fast, but we are still far from having solved all its secrets. However, some things were already known for several years. First, observation of cat's hair with a microscope reveals that the aspect of melanosomes (the pigment granules produced by the melanocytes and which migrate then towards neighbouring cells) is different for ruddy, chocolate and sorrel cats. They become more and more elongated[6]. Mutations on the B locus have therefore an impact on the shape of melanosomes.

As for dilution, it doesn't change the aspect of individual melanosomes, but it causes them to clump together rather than be spread more evenly. The large zones of the hair in between these clumps do not absorb as much light and the colour of the cat appears of a lighter shade, even though the amount of pigment is the same as with a non-dilute cat.[7].

On the picture at left, we can see a lilac somali, BUCCI KID DE BUFFAVAND. On the picture at right, one can see a fawn silver somali SAMIOLE DE LA CHACOLATERIE. Even though it is difficult to compare pictures, especially when they have been taken in different light conditions, we can see that the lilac has mauve shades where the fawn has orange shades. Depending on the cats, the difference may be very slight.

(photo C.Hermeline)

To make things more visual, here is a schematic representation of the

[6] Feline Color Genetics, 3rd edition, Diana Brown

[7] See Heather E. Lorimer's article, with pictures of hair under the microscope, at http://cc.ysu.edu/~helorime/BasicCol.html

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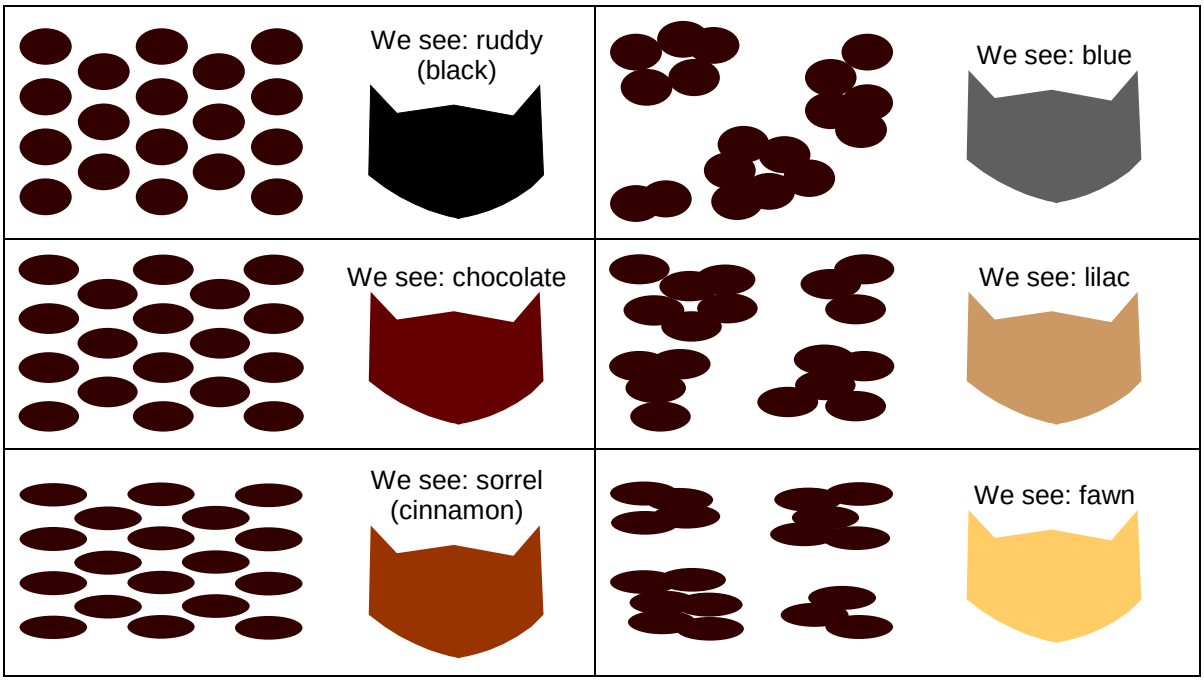
shape and spread of melanosomes for each of the 6 basic colours found in abyssinians and somalis.



With the enormous progress in DNA sequencing for different mammalian species (man, mouse, dog, cat among others), and by exploiting syntenic groups[8] between species which are phylogenetically close to each other, we can locate more and more individual genes on the DNA strings and we can make a catalogue of their variants (the different alleles found). This is the case today for the B and D locus which we are interested in here.

The publication of the studies led by the University of California at Davis[9] explains how the search for the B locus was performed and it gives the results of the sequencing analysis. Another study, led by a pre-doctoral student at George Washington University, Washington, DC in collaboration with the National Cancer Institute of Frederick, MD[10] gives similar results. Both studies identify the B locus as being the same as the locus on the D4 chromosome of the cat which codes for a protein called "Tyrosinase Related Protein 1", hence the TYRP1 label given to this locus. The study listed in note 9 has identified 16 mutations, each one applying on a single DNA base, and therefore called SNPs, for "single nucleotide polymorphism". 15 among these occur in chocolate/lilac-coloured cats ("chocolate-coated cats" for gourmet people…!) or cats carrying chocolate on one of their chromosomes, and one occurs in cinnamon/fawn cats.

Among the 15 SNPs associated with chocolate, only 7 are in coding areas, and among these a single one leads to a change in the corresponding amino acid: a cytosine replaced by a guanine at the 8th position along the DNA strand in exon[11] 2 leads to the incorporation of glycine instead of alanine in the resulting protein. The other SNPs are silent mutations (without any effect on the protein).

The SNP linked with the cinnamon phenotype is the replacement of a cytosine by a thymine at position 298 of exon 2 along the DNA strand. It translates into a "stop" codon instead of an arginine amino acid, resulting in the premature stop of the protein build-up.

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[8] Synteny is the simultaneous presence of several loci on the same chromosome. The closer two species, the more syntenic groups they will share. This knowledge is very useful to know where to search for specific loci when studies have already been done on related species.

[9] Chocolate-coated cats : TYRP1 mutations for brown color in domestic cats, Leslie A. Lyons, Ian T. Foe, Hyung Chul Rah, Robert A. Grahn, University of California, Davis, published in "Mammalian Genome", vol. 16, 2005.

[10] Tyrosinase and Tyrosinase Related Protein I alleles specify domestic cat coat color phenotypes of the albino and brown loci, A. Schmidt-Küntzel, E. Eizirik, S.J. O'Brien, M. Menotti-Raymond, published in "Journal of Heredity", 2005.

[11] An exon is the portion of the gene which is transcribed in the final messenger RNA (the portions removed are called introns). Exons therefore define the structure of the protein built from the gene in question. Genes from eucaryot cells are often made of a sequence of exons separated by introns.

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After having identified these mutations and proven their correlation with the cat phenotypes in many different breeds, the UC Davis laboratory has developed a test which is commercially available through VGL[12]. The results of their research having been made public, other laboratories throughout the world may have developed a similar test, even though they didn't do the original research.

As for the dilution locus (D), it has also been identified by the same laboratory and the corresponding DNA test is available commercially since spring 2007.

Epilogue, or why did I get interested in these colours ?

As you may have noticed, when I start talking about feline genetics, I can't stop ! Thanks to my scientific background, and having always been interested by biology (though my profession is in a very different domain), I am thrilled by the questions raised by feline genetics. But I had no particular reason to bear attention to the chocolate or lilac colours until one day, being at last able to adopt the cat I had been dreaming of for years, I fell in love with a little somali female... can you guess which colour she was? Chocolate of course!

Unfortunately, Nougatine (it was her pet name) walked away much too soon to look for other colours on the other side of the rainbow, on 7 January 2000. We had named our small family breeding "la Chacolaterie" to honour her memory and it is with a lump in my throat that I dedicate this article to her.

Babette PAUTET, la Chacolaterie
www.chacolaterie.com

[12] VGL (Veterinary Genetics Laboratory) reinvests all the money earned by testing in new research projects. I therefore encourage you to help them by submitting your DNA tests to them: http://www.vgl.ucdavis.edu/service/cat/index.html

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