

THE 'REX' TYPE OF COAT IN THE DOMESTIC CAT

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(With Plate 22 and One Text-figure)

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INTRODUCTION

It is now over thirty years since the first description of a 'rex' mutant, by Kohler (1925), in the rabbit. This so-called 'Castorrex' has a short and velvety coat, without the guard-hairs which normally project above the general level of the fur, and with whiskers and eyelashes curled. Nachtsheim (1929) showed that it was due to a recessive gene affecting all hair-types. Later, two further rex mutants were found in the rabbit (rex-2 and rex-3), mimicking Castorrex (rex-1) but due to different genes, though rex-1 and rex-2 are linked (Castle & Nachtsheim, 1933). Since then, five recessive and two dominant genes with similar effects have been described in the mouse, and one recessive and two dominants in the rat (for references see Grüneberg, 1947, 1952; Falconer & Snell, 1952). Guard-hairs are shortened in nearly all these mutants; vibrissae and coat are waved in the young and sometimes in the adult.

Two types of rex coat have now been found in the domestic cat, one in England and the other in Germany, The former has been briefly described by Jude (1953). The present paper compares the hair structure of mutants and normal, also giving breeding data for the English rex, which is shown to be recessive.

APPEARANCE OF THE COATS

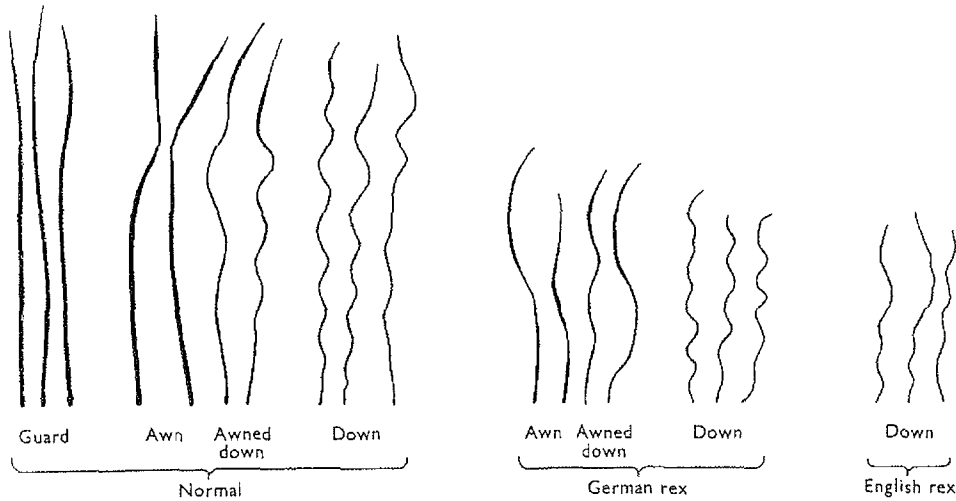
The English rex has a short plush-like coat (Pl. 22*a*) which is wavy throughout life, like that of the Astrex rabbit. It feels much finer and silkier to the touch than the coat of a normal cat. No guard-hairs can be seen projecting above the level of the main coat. Moreover, the tail looks thin and the inner surface of the ear pinna is abnormally bare in the adult, no doubt a result of this reduction or absence of guard-hairs. In the young kitten, however, the ear pinna seems to have a normal covering of hair. The owner reports that when the woolly juvenile coat is shed the tail is left bare for a time. The whiskers are curled at birth and remain in this condition.

The appearance of the German rex cat (Pl. 22*b*) is known only from photographs and the owner's description, not from personal inspection. The juvenile coat is wavy; the adult coat is short and plush-like, but is not wavy. Ears, vibrissae and tail seem to be affected as in the English rex.

HAIR STRUCTURE

The types of hair found in the coat of the normal short-haired domestic cat (Text-fig. 1) fall naturally into the same categories as those described by Thiel (1928) for the rabbit, namely:

- (a) *leithaare*; the long, straight, thick, evenly tapered guard-hairs of the overfur;
 (b) *grannenhaare*; or awn-hairs, also of the overfur. Distally these are bent and markedly thickened, before tapering fairly abruptly;
 (c) *grannenflaumhaare*; intermediate between (b) and (d), being proximally thin and crimped, but distally thickened. They can be called awned down-hairs.
 (d) *flaumhaare*; the down-hairs of the underfur, which are evenly thin and crimped.



Text-fig. 1. Drawings of hairs from the coats of normal and rex cats, to show the different types found. Natural length; about six times natural width.

Thus there are no zigzag hairs, such as are found in the rat and mouse; for although cat down-hairs are thin hairs of the underfur, like zigzags, they have neither the sharp bends nor the constrictions of the latter. The two types have much in common, however; for instance, there is a small area behind a cat's ear which is covered with down-hairs only, while the same region in a mouse has only zigzags (Falconer, Fraser & King, 1951). Mouse auchenes are similar to cat awn-hairs; both have a single constriction distally. Cat and mouse guard-hairs closely resemble each other; in an agouti area cat guard-hairs are solid black, with no yellow band, just like the guard-hairs of an agouti mouse (Dry, 1928).

Fraser's (1953) paper on rex and angora rabbits does not distinguish by name between types (a), (b) and (c) above, apparently grouping them all together as guard-hairs. But we consider that this name should be reserved for the thick straight hairs which in so many mammals can be seen projecting above the general level of the coat; Thiel's *leithaare*, in fact. In the cat this type of hair is certainly distinct from all the others. A few intergrades are found, however, between the other three types, so their boundaries must be arbitrary to some extent. We only classed down-hairs as being awned if there was no doubt at all about the distal thickening; similarly, hairs which were clearly awned had to be markedly thin and crimped proximally before being classified as awned down-hairs.

A comparison of hair plucked from short-haired (i.e. non-Persian) normal, English rex and German rex cats (Table I and Text-fig. 1) showed that neither rex sample had any guard-hairs. This absence of guard-hairs has been confirmed by the examination of other larger samples than those of Table 1, without making further counts. The German

rex and normal hair samples show very close agreement in the proportions of the other three hair types ($\chi^2=0.16$, $n=2$, $0.95 > P > 0.90$). The absence of awn-hairs and awned down-hairs from the English rex sample is clearly a highly significant difference from the situation in the German rex. About 1-2% of the English rex hairs were, however, decidedly thicker than the rest, and somewhat less crimped. Since they showed no marked distal thickening and were clearly not guard-hairs, it was decided to class them as down-hairs too, though somewhat atypical ones. Both types of German rex awned hairs were often atypical, for the distal thicker area tended to be longer than normal and tapered more gradually. It is interesting to note that 'furless' in the house mouse has a similar effect on auchenes, according to the drawing in Green's (1954) paper. German rex awned hairs also showed abnormal curvature.

Table 1. *Distribution of hair types in samples of normal and rex cat fur*

	Guard	Awn	Awned down	Down	Total
Normal	4	15	45	190	254
English rex	0	0	0	250	250
German rex	0	17	46	187	250

Table 2. *Mean lengths in mm. of normal and rex hairs, with standard errors*

	Guard-hairs	Awned hairs	Down-hairs
Normal	42.1 ± 0.81	40.1 ± 1.29	41.3 ± 1.74
English rex	—	—	20.4 ± 0.47
German rex	—	23.0 ± 1.23	20.6 ± 1.15

Twelve intact fully developed hairs of each type were mounted in glycerine and projection drawings made, from which hair-lengths could be calculated. Both types of awned hairs were included in one category. Table 2 shows that rex hairs are only about half the length of normal hairs in the same category. The three categories of normal hair do not differ significantly in length, suggesting that they all grow at about the same rate. The guard-hairs appear longer mainly because they are straighter and more erect.

The thickness of rex and normal down-hairs was measured from high power camera lucida drawings. Ten hairs of each type were studied in this way. Since the shaft of an individual rex cat hair usually varies appreciably in thickness throughout its length, all measurements were made at about fifty medullary cells from the root end of the hair. Table 3 shows that down-hairs from both rex mutants are significantly thinner than normal, but there is no significant difference between the two rex types. The waviness, or amount of crimping, in rex down-hairs seems no greater than in normal down-hairs.

Table 3. *Thickness in μ of normal and rex down-hairs*

	Mean diameter	s.e. of mean
Normal	25.8	1.32
English rex	16.2	0.54
German rex	17.0	0.50

GENETICS

Kalli, the first English rex cat to be recognized, was one of a litter of four, the other three being normal. His father was probably his mother's brother. Kalli has been mated systematically, in confinement, with his mother and subsequently with his non-rex

daughters; these females have also been crossed with a rex son of Kalli. Sixty-four offspring have been produced from these matings so far, of which twenty-nine have been normal and thirty-five rex, in good agreement with the 1:1 ratio expected from this type of cross whether the rex character is due to a single fully penetrant recessive or dominant gene. Information on the dominance or recessivity of rex is best sought from outcrosses of the mutant to unrelated cats and from rex \times rex matings. We have been told that Kalli has had at least twenty offspring, all normal, from uncontrolled outcrosses. With dominance, the probability of such an event is less than one in a million, which would indicate that rex is recessive. But no records were kept of these matings, and it is notoriously difficult to be sure of the paternity of kittens. So this evidence cannot settle the mode of inheritance beyond doubt. However, sixteen offspring have now been born as a result of controlled rex \times rex matings; all have been rex. The probability of such an event if rex is due to a fully penetrant dominant gene is only 0.01. Therefore it can be concluded that the English rex character is due to a single fully penetrant recessive gene. We suggest that it is given the symbol *r*.

Some of the crosses made between rex and normal cats allow one to test for linkage between rex and 'dilute'. Kalli is homozygous from these two genes,* also hemizygous for sex-linked yellow; that is, he is *r/r d/d y* (symbols as in Searle, 1949). Those of his daughters which are intense and non-rex must be heterozygous for *r* and *d* in coupling; offspring of these females backcrossed to Kalli or to other *r/r d/d* males give the required data. Totals for each phenotype are as follows: 9 ++, 5 *rd*, 3 +*d*, 8 *r*+, which is eleven recombinants out of twenty-five. Thus there is no evidence for linkage between these factors.

The original German rex cat, a female, is the only one known of this type. So far she has not been systematically bred, so the mode of inheritance of this character is uncertain, if it is inherited at all.

DISCUSSION

Thiel (1928) found that the rex rabbit has no guard-hairs, while there is a marked shortening of the other hair types, so that all tend to be the same length. There is also a reduction in the thickness of individual hairs. His findings are thus very similar to ours for both types of rex cat, except that the situation is more extreme in the English rex, with only the down-hairs left. The cat rex genes have a more drastic effect on hair-length than those of the rabbits examined by Thiel. In the rex rabbit, awn-hairs are 65% and down-hairs 83% of the normal length; for the German rex cat the corresponding figures are 57% and 50%.

Nachtsheim (1929) considered that the rex rabbit did not actually lack guard-hairs; they were merely so much shortened that they no longer overlapped the general fur level. It seems that he, like Fraser (1953), classified as guard-hairs all the hair-types of the overfur, so his findings do not necessarily contradict those of Thiel. Nachtsheim also found that the medulla of rex rabbit guard-hairs was unevenly developed, showing constrictions and interruptions, which he believed responsible for some waviness of the fur. This unevenness of the hair also occurs in rex cat hairs; sometimes the hair medulla is

* Microscopical examination of individual hairs has shown that 'dilute' in the cat clumps pigment granules, as do 'dilute' and 'leaden' in the house mouse (Grüneberg, 1952). Such large clumps may result that the whole hair shaft is swollen.

absent for a short distance. The presence of these irregularities in the German rex hair, which is not wavy, suggests that the waviness of English rex fur has some other cause. It may be just a result of the natural waviness of individual down-hairs, not hidden by the straight hairs of the overfur. One type of rex rabbit, the Astrex, also has wavy hair throughout life. Pickard (1941) has shown that this is due to the action of a recessive gene 'waved' on the rex coat; its morphological basis, however, does not seem to be known. Curling of the eyelashes often leads to corneal keratitis in the rex rabbit (Létard, 1929); the cat has no eyelashes, so this side-effect of the rex gene is not to be expected.

'Rex' in the cat (especially English rex) resembles 'crinkled' in the house mouse (Falconer *et al.* 1951) in that certain types of hair disappear. In crinkled mice there are no guard or zigzag hairs; in the English rex cat there are no guard or awned hairs. Rex down-hairs are shorter and thinner than normal, so are the hairs on the ear pinna of the crinkled mouse. The main hairs of the crinkled coat, which resemble the awls of normal mice, show marked irregularities of thickness, which are also found to some extent in rex hair. The data available on crinkled hairs also indicate that they may be slightly shorter and thinner than normal awls, although the effect (if any) is small. The crinkled gene suppresses the formation of some hair follicles and retards the growth of others. The problem which arises is whether guard and awned hair follicles are suppressed in the English rex cat, or whether they are merely changed, so as to produce down-hairs (and some atypical hairs). One clue is provided by the median inner surface of the ear pinna, which in normal adult cats is covered with guard-hairs. This area is bare in the English rex; the guard hairs have not been replaced by down-hairs. There is an obvious analogy with the bald patch found behind the ears of crinkled mice, due to the absence of zigzags, which are the only hairs found in this region in normal mice. This suggests that, in the adult English rex mutant at least, there is complete suppression of certain hair-types, as in crinkled mice. The ear pinna is not bare in the juvenile rex coat: hair succession in the cat must be studied further before this fact can be explained. There is no conclusive evidence on the situation in the German rex cat, but it is probably similar.

The 'furless' mouse (Green 1954) resembles the German rex cat in having all hair-types shortened, as well as in the abnormal appearance of its achenes, mentioned earlier. The furless gene also causes baldness, thus providing a link between the rex type of mutant and the various kinds of hereditary hair loss. There is, in fact, a large group of mammalian hair mutants, each member of which shares with other members one or more of the following effects: waviness of coat and vibrissae in the young and sometimes in the adult, hairs shortened, hairs thinner than normal, loss of hairs, breakage of hairs, absence or deficiency of certain hair-types. Table 4 gives examples of such mutants in the mouse, rabbit and cat; genes causing hair loss or breakage have only been included if they show other of the effects listed. The question-mark after German rex indicates that its mutant character has not been proved. A blank space does not necessarily mean that the mutant concerned lacks that particular character, but only that such an effect has not been reported. For instance, occasional hair breakage due to deficient keratinization may well be more widespread than it appears; the same is true for a reduction in hair diameter. Mutants making hairs thicker have not been found in this group of animals, although presumably they are present in the wire-coated breeds of dogs. Neither are hair-lengthening genes known in the mouse; they are present in the Persian cat and Angora rabbit, but seem to be devoid of pleiotropic effects. No doubt some of the similarities in

gene action which Table 4 shows are really only superficial, but, taken as a whole, this list suggests that a number of these genes act at different levels and in different ways on a single important developmental process, which has changed little since the early days of mammalian evolution.

Table 4. *Mutants in the mouse, rabbit and cat with similar pleiotropic effects on the hair*

Mouse:	Coat waved	Short hairs	Thin hairs	Hairs lost	Hairs broken	Hair-types lacking
Waved-1	+	+	.	.	+	.
Waved-2	+	+
Wellhaarig	+	+	+	.	.	.
Caracul	+
Rex	+	+
Frizzy	+	+	+	.	.	+
Fuzzy	+	.	+	.	.	+
Ragged	.	+	.	.	.	+
Furless	.	+	.	+	.	.
Naked	.	.	+	.	+	.
Hairless	.	.	+	+	.	.
Crinkled	+
Tabby	+
Rabbit:						
Rex-1	+	+	+	.	.	+
Cat:						
English rex	+	+	+	.	.	+
German rex (?)	+	+	+	.	.	+

Note. For references see Grüneberg, 1952 (waved-1, waved-2, wellhaarig, caracul, rex, fuzzy, naked, hairless); Carter & Phillips, 1954 (ragged); Falconer, 1952 (tabby). Other references in text.

Rex cat down-hairs are about 65% the thickness and 50% the length of normal down-hairs; their volume is therefore about one-fifth normal. Fraser (1953) has suggested that in the rabbit the rex gene increases the density of hair follicles, resulting in a decrease in the amount of substrate for each follicle and thus a slowing down of growth. If this were to happen in English rex cats one would expect hair density to be at least five times normal, to compensate for the decreased volume of each down-hair and the disappearance of other hairs. Suitable material for testing this is not yet available, but preliminary counts on equal areas of preserved rex and normal kitten skin, cleared in xylol and mounted in Canada balsam, gave 78 rex follicles to 33 normal ones, which is 2.4:1. This does suggest some increase in the rex follicle density, but various errors may have arisen (due to unequal shrinkage of the skins, etc.) and only more favourable material could give conclusive results.

SUMMARY

1. Two types of rex coat are described, one ('English rex') with a wavy coat throughout life, the other ('German rex') with a straight adult coat, but a wavy juvenile one.
2. Both lack guard-hairs; other hairs are about half the normal length. In the English rex, awn-hairs and awned down-hairs are also absent; only the down-hairs of the underfur remain, with a few atypical thicker hairs. Down-hairs are much thinner than usual in both types of rex.
3. The English rex character is due to a single fully penetrant recessive gene, for which the symbol *r* is proposed.

4. A comparison of rex cats and 'crinkled' mice suggests that in the former there is a complete suppression of the missing hair-types rather than a change into those hair-types which remain.

5. Similarities between a number of genes affecting hair in the mouse, rabbit and cat are discussed, and listed in Table 4.

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EXPLANATION OF PLATE

Fig. 1a. 'English rex' male cat, showing short wavy coat, thin tail, curved whiskers and bare ears. The rex character masks the dilute tabby pattern.

Fig. 1b. 'German rex' female cat. The coat is short, but not wavy; the tabby pattern is again masked.