

ON THE GENETICS OF ROSETTE PATTERN IN GUINEA PIGS

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Among the most familiar of the types of cavy bred by fanciers are those with conspicuous rosettes or whorls in the coat. This character has been studied principally by CASTLE and myself in America and by PICTET and FERRERO in Switzerland. The conclusions reached by the latter authors have seemed decidedly at variance with those which we had reported (cp. reviews by LANDAUER 1926, 1929). Their recent paper, however, (PICTET & FERRERO, 1934) presents data which seem to make the relation between the two sets of results somewhat clearer.

CASTLE (1905) found a practically continuous series of grades from the normal smooth furred type to the full fancier's rough. He found evidence that the broad category „rough” differs from smooth by a single dominant gene (designated R). He did not reach a Mendelian interpretation of the wide variations of the rough pattern, but noted that there was some sort of genetic basis. In particular, he found that matings of full rough with certain „prepotent” smooths gave young with feeble development of the character, although with most smooths, dominance of full rough seemed complete. DETLEFSEN (1914) found that, the wild Brazilian species, *Cavia rufescens* (smooth furred) when mated with full rough guinea pigs produced young with only a slight dorsal crest and thus resembled „prepotent” smooth guinea pigs in its influence on the character. This recalled also the similar result observed by NEHRING (1894) from matings between the wild species *C. aperia* of Argentina and rough guinea pigs.

In my experiments with the stocks in Dr. CASTLE's laboratory (WRIGHT, 1916) I found that the full rough type differed from the wild species *C. cutleri* of Peru, from *C. rufescens* of Brazil and also from certain smooth guinea pigs by two major factors. One of these was a completely dominant one, identified with CASTLE's R and necessary for any development of this type of roughness. The other, called s in that paper, was an incomplete recessive, necessary for full development of the character. In later papers this second factor has been called m to avoid confusion with the principal white spotting factor, also designated s.

For a detailed comparison with the results of PICTET and FERRERO, it will be necessary to define the grades which I used.

GRADES OF ROUGHNESS

Grade E. Smooth furred except for reversal of hair direction on the toes, especially the hind toes. Typical of R-MM.

Grade D. A crest along the middorsal line and roughness of at least the hind toes, but no rosettes. Usually R-Mm.

Grade C. A single rosette on each side (occasionally on only one side) of the back and roughness of toes. Usually a crest between the ears. Typical of R-Mm.

Grade B. Various conditions intermediate between grades C and A. There may, for example, be 4 or even 6 dorsal rosettes but little or no development of head rosettes, or the latter may be well developed but associated with only 2 or 3 dorsal rosettes. Usually R-mm.

Grade A. At least two widely separated pairs of rosettes on the dorsal side of the body and well developed head rosettes (forehead, eyes). There are also always irregularities of hair direction on the belly, as well as the crest between the ears and the reversal on the toes found in lower grades. Typical of R-mm.

Grade A might well have been divided, since it covers a wide range, from individuals which barely meet the requirements to ones with as many as 12 more or less distinct rosettes on the back.

While the major variations were found to depend on the two pairs of genes R, r and M, m it was noted that there are minor variations clearly dependent on the differing residual heredities ($\Sigma-$, $\Sigma+$) of different strains. The wild cavies ($rrMM\Sigma-$) and the extreme rough

type (RRmmΣ+) must thus differ by at least 3 independent sets of factors. The occasional asymmetry of the pattern was taken to indicate a slight influence of non-hereditary developmental factors. Finally, it was found that not all irregularities of hair direction require gene R. In one inbred strain which lacked this factor, many of the animals showed irregularities on the chest and belly but never reversal on the toes. There was evidence of heredity but no simple Mendelian mechanism was apparent. In other strains single dorsal crests or even rosettes occurred sporadically. The only indication of heredity was a higher percentage incidence in particular strains.

I have made no intensive study of the variations in roughness since the above paper. Rough fur has, however, been common in my stocks and the major variations have behaved in accordance with the above two factor hypothesis.

The character has been used in tests for linkage and summaries of the results in this respect illustrate well the theory. Some 12 years ago a strain (A)¹ was started which was designed to carry a large number of dominant genes. It has been made homozygous in the 2 dominant rosette factors and 7 dominant color factors (RMSEACFPB). There have been 36 matings of Rough E × Rough E or D with young recorded since 1926. Most of these were certainly RRMM × RRMM. These produced 18 smooth, 294 grade E, 12 grade D and 3 doubtful grade C. Some of the smooths may have been segregants (rr) from matings RrMM × RrMM but some at least have been shown by outcrosses to transmit gene R. Tests have also shown that animals with a slight crest (grade D) are occasionally RRMM. It appears that at least 90% of the animals of constitution RRMM are of grade E with the remainder probably about equally divided between smooth and grade D.

This multiple dominant stock was mated with a strain (B) which had been made recessive in 8 respects including the two factors affecting hair direction. In the development of this strain (rmse^pac^kFpb), most matings were made between full roughs and smooths. In the end, the entire stock was derived from smooth segregants from matings between full roughs (Rrmm × Rrmm), thus insuring the absence of gene M.

¹) These strain designations A, B, C, D must not be confused with the grades of roughness.

At the time the first cross was made, the multiple dominant stock was far from homozygous and F_1 included many smooths and full roughs in addition to the desired partial roughs of grades C and D. The latter were chosen for backcrossing to the multiple recessive strain and gave the following results.

Parents	Percentage						Total No.
	Sm	E	D	C	B	A	
RrMm \times rrrmm . .	50.3	0.5	8.1	15.0	3.9	22.2	469

The results are evidently in good agreement with the expected ratio of 50% rr, 25% RrMm and 25% Rrrmm, assuming that RrMm is usually of grades C and D, rarely E or B, while Rrrmm is usually A but also includes most of those graded B. A few of the B's closest to grade C were called RrMm in the analysis of the data for linkage (WRIGHT 1928).

The multiple dominant strain has been mated with other strains in linkage studies since it has become homozygous. One of these was strain D of constitution r m S e^p a CFPB and characterized by perfect development of the little toe (always absent in strain A). This strain traces without out-cross to a polydactyl strain developed by CASTLE (1906). It was used extensively in my earlier experiments with rough fur and in my 1916 paper was called (4 toe). The formula rrrmm was assigned to it then on the basis of adequate data and the recent tests, made 15 years later confirm this conclusion. The results were as follows:

Parents	Percentage						Total No.
	Sm	E	D	C	B	A	
Strain D (rrmm) . .	100	0	0	0	0	0	
Strain A (RRMM) .	5	90	5	0	0	0	
F_1 (RRMM \times rrrmm)	0	0	31.7	68.3	0	0	82
BX (RrMm \times rrrmm)	47.9	2.5	9.5	15.9	2.2	22.0	359

These results are close to those obtained from strains A and B and sufficiently in harmony with expectation. The appearance of 100% obviously rough animals in F_1 from a cross between two pure strains both of which would be considered smooth furred (with a few

exceptions in one case) if one disregarded hair direction on the toes, and the appearance of a large proportion of full roughs on backcrossing F_1 to the wholly smooth parent strain are at variance with any hypothesis involving more than 2 major factors.

Another smooth strain (F) with which the multiple dominant strain (A) was crossed had the constitution (rmse^aac^fp^b). The results in F_1 and the backcross of F_1 to strain F were as follows:

Parents	Percentage						Total No.
	Sm	E	D	C	B	A	
F_1 (RRMM \times rrrmm)	0	3.7	48.2	44.4	3.7	0	27
BX (RrMm \times rrrmm)	52.3	0.0	6.4	18.0	1.8	21.5	172

In this case there is a wider range of variability in F_1 due to one individual of grade E and one of grade B. The results in the backcross are, however, very similar to the preceding ones.

In a fourth series of tests, strain A was crossed with smooth strain C (constitution rmSe^aac^fp^b). In this case it is desirable to present the data from reciprocal crosses separately. The proportions in sons and daughters were not appreciably different in either case and are not separated.

Female \times Male	Percentage						Total No.
	Sm	E	D	C	B	A	
F_1 (RRMM \times rrrmm)	0	0	17.9	82.1	0	0	28
BX (RrMm \times rrrmm)	54.8	0	0	19.0	0	26.2	42

The results are sufficiently in accord with expectation, making allowance for the small numbers. The reciprocal cross on the other hand, gave the most aberrant results which I have observed.

Female \times Male	Percentage						Total No.
	Sm	E	D	C	B	A	
F_1 (rrmm \times RRMM)	0	0	2.2	73.3	24.4	0	45
BX (rrmm \times RrMm)	37.5	0	0	12.5	12.5	37.5	64

Here F_1 included 11 animals (5 ♂, 6 ♀) of grade B. Four of these were very close to grade A (4 good dorsal rosettes, fair head rosettes).

These were all undoubtedly of constitution $RrMm$ (3 tested in next generation). In the backcross generation, there were 3 males and 5 females of grade B, and the excess of grade A over 25% suggests the likelihood that some of this grade were $RrMm$. Apparently some of the females of strain C introduced a modifying factor (or factors) which substantially raised the level of development of rosettes in heterozygotes ($R-Mm$). The apparent transmission of this tendency by females only is probably accidental, but requires investigation. Strain C, it may be said, was not closely inbred.

Two matings between backcross animals of grade B produced the entire range of grades of roughness (2E, 1D, 8C, 4B, 3A) in addition to 3 smooth. The results show that grade B in this case was of constitution $RrMm$. Ordinary matings of $B \times B$ (as of $A \times A$) produce only high grades (A, rarely B) irrespective of ancestry.

We will turn now to the results obtained by PICTET and FERRERO. In their first paper (1922) they described a cross between a smooth strain and one characterized by at least 4 well developed rosettes on the trunk. This was probably a mating of smooth and rough A in my terminology. F_1 had the four dorsal rosettes and thus was also probably of grade A. In F_2 they obtained the following:

Trunk rosettes	No.
2 pairs	56
Anterior pairs only	10
Posterior pairs only	16
Smooth	22
	104

They interpreted this as indicating two independent pairs of genes, one dominant gene for the anterior rosette, the other dominant gene for the posterior rosettes. This was supported by evidence from later generations. For example matings between the type with anterior rosettes only ($T-t't'$) and that with posterior ones only ($ttT'—$) is stated to have produced some young with both pairs ($T—T'—$) although each type bred inter se produced only its own type (apart from smooth).

The above ratio deviates very seriously from the expected $9 : 3 : 3 : 1$ (probability of worse fit less than .000001 under random

sampling). This was pointed out by GUYÉNOT and, in later papers, the authors have accepted CASTLE's conclusion that rough fur, taken collectively, differs from smooth by only one gene.

The occurrence of the type with only one pair of dorsal rosettes, whether anterior or posterior, suggests the presence of gene M. This, however, requires the original mating to have been $rrMM \times RRmm$ which should produce partial roughs in F_1 instead of the full roughs described. Moreover the F_2 ratio is incompatible with this assumption. The mating $RrMm \times RrMm$ produces about $\frac{3}{16}$ full rough $\frac{6}{16}$ partial rough to $\frac{7}{16}$ smooth if R-MM is included with smooth as would usually be the case if hair direction on the toes is ignored. This is wholly at variance with the observed result. It may be concluded that the original cross was of the type $rrmm \times RRmm$ and that the partial rough types in F_2 correspond to the grade B of most of my experiments. The head rosettes are not described. If not present in these animals, it indicates that $rrmm$ ranged somewhat lower than in my data.

The authors presented a much larger body of data in papers in 1928 and 1929. They describe the localization of the rosettes in considerable detail and compare with that described by CASTLE and me. The principal differences seem to be the following. The forehead rosette which has been one of the necessary criteria for the common grade A in my stocks, seems to have been poorly developed in their stocks. I do not find any mention of reversal of hair direction on the toes although this has been the most consistent indicator in my stocks for gene R and the sole criterion for grade E. From their photographs it appears that this character was present at least in some cases but was not treated as a criterion. They also do not mention the ventral rosettes. On the other hand the dorsal trunk rosettes seem to have been better developed in their more extreme types than in my stocks. They locate the rosettes in 5 transverse zones: (1) coccygial, (2) posterior lumbar, (3) mid lumbar, (4) anterior lumbar, (5) post cervical. They distinguish two primary types of patterns:

(1) Generalized Type. Rosettes either in Zone 1 or in Zone 5 or in both as well as in one or more of the intermediate zones. Total number of dorsal trunk rosettes 4—16, the larger number depending on the occurrence of multiple centers in zones 2, 3 or 4.

(2) Localized Type. No rosettes in either zone 1 or 2. Total number from 1 to 8.

They state that each of these types may occur either with well developed or with rudimentary head rosettes.

It is difficult to make direct comparison between their classification and that which I have used. Rosettes as far back as their zone 1 are certainly rare in my stock and perhaps never occur. Rosettes of their zones 2, 3 and 4 are common enough in my higher grades. I have noted small whorls close to the midline in the post cervical region (zone 5) but have not used the presence or absence of these as a criterion. Some of my animals of grade A have from 8 to 12 or even 14 distinct dorsal rosettes. Most of these would probably come under PICTET and FERRERO's generalized type with well developed head rosettes. Their generalized type with poorly developed head rosettes seems to be absent from my colony. Many of my animals of grades A and B would undoubtedly come under the localized type with strong head rosettes. Others of grade B and all of grades C and D would come under the localized type with rudimentary (or no) head rosettes. Grades C and D while present in their stocks („monorosettes", „lisses à crête" etc.) seem to have been decidedly uncommon and grade E (smooth except for toes) is not described at all. Thus their studies have been concerned primarily with what I call grades B and A and types rougher than typical A, the differences among which I attributed to multiple factors ($\Sigma+$, $\Sigma-$) in my 1916 paper but which they attribute to two pairs of unit factors G, g distinguishing their generalized and localized patterns of trunk rosettes and D, d distinguishing well developed and rudimentary head rosettes. On the other hand, gene M could clearly not have been as common in their stocks as in mine and if present, as I suspect, in their monorosettes and crested smooths, was not recognized. There is no necessary conflict in our principal results. It is, however, desirable to examine the data critically to determine how conclusively the postulated new genes G, g and D, d are established. PICTET and FERRERO's hypotheses are as follows:

Trunk Rosettes

Generalized type	RRGG, RrGG, RRGg, RrGg
Localized type	RRgg, Rrgg
Smooth	rrGG, rrGg, rrgg

Head Rosettes

Well developed	RRDD, RrDD, RRdD, RrDd
Rudimentary	RRdd, Rrdd
Smooth	rrDD, rrDd, rrdd

The results given in the 1928 and 1929 papers at first appear to give an agreement with expectation which is all that could be desired. From their 1929 summary relative to trunk rosettes, I calculate a value of χ^2 of 2.8 with 15 degrees of freedom giving a probability greater than .9999 that random sampling would give a worse result. Similarly the summary for head rosettes yields χ^2 of 0.40 with 11 degrees of freedom and a probability of a worse fit by random sampling of about .99995. It would require several hundred million repetitions to have a reasonable chance of getting as good agreement again in both respects if G and D are independent.

There are, however, difficulties. Matings of a given sort phenotypically should obviously include many types genotypically, especially in the later generations. Yet several types of mating are not reported at all. Apparently the genotypic formulae of the parents were assigned almost wholly on the basis of the ratios observed among the young, a procedure which involves a dangerous amount of circular reasoning in the case of an animal which produces such small numbers as the guinea pig, and especially with a character which shows continuous intergradation and variation in more than one direction.

The authors state that in starting their new experiments (after 1922) they found it impossible to produce homozygous types and thus had to make their matings between individuals of uncertain constitution, trusting to segregation among the offspring for analysis. It happened that of the 20 original matings made between generalized rough and smooth *all* produced young of both the generalized and localized types but no smooths and were therefore interpreted as $RRGg \times rrgg$. The ratio, 100 generalized to 98 localized certainly agrees with expectation, but it is surprising on the Two factor hypothesis that among parents of uncertain constitution all matings should happen to be of the same type. No tests seem to have been made of the supposed segregants to determine whether they transmitted different heredities. Instead 22 matings were made between F_1

generalized and F_1 localized. These gave exactly the expected 3 : 3 : 2 ratio — 159 generalized, 159 localized, 106 smooth. The segregation of 25% smooths confirms the existence of CASTLE's gene pair R, r and the later data are in agreement with a few apparent exceptions to be discussed later. As to the types of rosette pattern one would expect approximately the same ratio as in F_1 whether one or many factors are involved, from a cross between the two types. The first crucial test of the one factor hypothesis comes in F_3 . Unfortunately the F_3 and F_4 data are not kept wholly separate.

However, their table 3 (1929 paper) gives 17 matings between generalized F_2 animals whose record is important in this connection. These produced 148 young, all of the generalized type. These 17 matings are listed as $RRGG \times RRGG$ in spite of the fact that these animals should have been heterozygous (Gg), as coming from generalized F_1 (Gg) \times localized F_1 (gg). The failure of recessives to appear can not be explained satisfactorily as due to small numbers since 2 of these matings produced 23 young each (chance of occurrence of no recessives .0013 each), two others produced 16 each (chance of no recessives .010 each) and another 14 young (chance of no recessives .024). That the parents of this progeny were actually from F_2 is stated not only in table 3 but in the text (p. 255) and in the summary table (p. 254) and in the 1928 paper (p. 81). This result would seem to eliminate the hypothesis that the localized and generalized types as defined are differentiated by a single pair of genes.

On the other hand, the combined F_3 and F_4 data show that the two types, each bred inter se, gave progenies which differed much more than would be expected on a multiple factor basis. Following is a combination of all matings between F_2 or F_3 rough furred animals.

	Gen.	Loc.	Sm.
Gen. \times Gen.	586	161	(140)
Gen. \times Loc.	56	60	(0)
Loc. \times Loc.	0	209	(37)

The frequency of the smooth young is not important since some of these matings are expected to be $RR \times R-$ and others $Rr \times Rr$. Clearly the generalized and localized types from the same source,

transmit widely different heredities. This argues for a single major gene difference, rather than 2 or more. These conflicting results can perhaps be reconciled best by postulating a single major gene pair G, g , but one which causes a less clear cut distinction of types than held by the authors. In this connection it is to be noted that in their preceding paper (1922) and also in their most recent one (1934) cases are given of localized \times localized giving generalized. Clearly there are several points which must be cleared up before the pair G, g can be listed among the genes which have been conclusively demonstrated.

The authors treat the inheritance of head rosettes as a wholly independent matter. They justify this by citing cases in which the head rosettes were rudimentary in spite of the presence of the generalized pattern on the trunk. But imperfect correlation does not necessarily mean no correlation. In my stocks there is a high correlation.

There were 11 foundation matings between animals with well developed head rosettes and smooths. All of these gave both types of head rosettes (ratio 48 : 48) but no smooths and all are therefore interpreted as having been $RRDd \times rrrd$. Again no separate tests were made of the supposed segregants. 13 matings between developed and rudimentary were made and produced a nearly perfect 3 : 3 : 2 ratio (108 developed : 107 rudimentary : 72 smooth). Matings were made between F_2 's of the developed type and it turned out that in 8 cases only dominants were produced. The parents are listed as $RRDD \times RRDD$ in spite of the fact that they are reported as coming from matings of $RrDd \times Rrdd$. As in the exactly parallel case of the trunk rosettes the one factor hypothesis for grade of development of head rosettes is flatly contradicted by the data. However, the evidence that these parents really were homozygous is not as secure as in the other case since no mating produced more than 13 young.

As before, the F_3 data which are most critical for the hypothesis are not kept distinct from the less critical F_4 data in all cases. Combining F_3 and F_4 , matings of rough \times rough are reported as giving the following results:

	Developed	Rudimentary	Smooth
Developed \times Developed	250	65	(43)
Rudimentary \times Rudimentary . .	0	123	(18)

The great difference again indicates a single major gene difference. Whether this is a different factor from that involved in the trunk rosettes, it is impossible to judge from the data as presented. More critical data on this and other points would seem necessary before genes *D*, *d* can be accepted as demonstrated.

As already noted, most of the variations of rosette pattern which PICTET and FERRERO discuss are clearly within the genotype *R-mm*. In their 1929 paper, however, they discuss a few cases of extreme reduction of rosettes (monorosettes), smooths with a slight medio-dorsal crest, etc.) which suggest the action of gene *M*. Confirming this is their statement that matings between such animals may produce relatively high grade types with 4 to 6 good pairs of dorsal rosettes. In my stock, matings of grades *C* or *D* inter se (*R-Mm* × *R-Mm*) regularly produce many young of grades *A* or *B* (*R-mm*). PICTET and FERRERO consider the reduced condition as due to nongenetic developmental irregularities. But the few family histories published in their 1929 paper clearly indicate heredity of some sort and indeed are fully in harmony with my results with genes *M* and *m*.

Their recent paper (1934) presents additional data on reduced types, in this case derived from 6 pairs of smooth parents. They put these cases in two categories. In 4 of them, only a few sporadic animals with rosettes appeared and the ancestral stock had given no indication of transmitting roughness. They interpret these as mutations from *r* to *R*. This is possible, but no data are presented to show that the mode of transmission was like that of *R* in later generations. It is possible that these were of the sporadic type of roughness which shows no heredity except for differences in percentage incidence in different strains.

In the other two cases, one at least of the smooth parents came from animals of the extreme reduced type. In these cases transmission of gene *R* in later generations was clear. The authors interpret these as cases of diminution in the intensity of action of the rosette factor in the course of generations, leading in extreme cases to apparent smooth. The data are, however, in full harmony with the hypothesis that these lines carried gene *M*, recalling that *R-MM* is completely smooth except for the toes (apparently not used by PICTET and FERRERO as a criterion for roughness). A mating of such a smooth with ordinary smooth (*R-MM* × *rrmm*) produces young of

grades C or D, never A and rarely B. This agrees with their statement (p. 81) „Un premier point qu'il convient de préciser maintenant c'est que tous les Cobayes à rosettes issus de lisses étaient des Cobayes à rosettes croupe ou à simple crête, c'est à dire des animaux chez les quels le réduction des verticelles avait acquis un degré avancé.”

The ancestry of one of these smooth carriers of rough is presented. A pair of monorosettes produced the following progeny and descendants in later generations.

NO. OF ROSETTES						
Generation	6	4	2	1	Crest	Smooth
1st	6	4	6	1	4	12
2nd	1	2	8	0	2	10
3rd	0	2	7	2	4	7
4th	0	0	4	0	1	1
Total	7	8	25	3	11	30

These results are readily explicable if these matings (except probably the last) were of the type $RrMm \times RrMm$, producing $\frac{3}{16}$ R-mm (grades A or B with 4 or more rosettes), $\frac{6}{16}$ R-Mm (grade C or D with 1 or 2 rosettes or mere crest) $\frac{3}{16}$ R-MM (grade E, smooth except toes and occasionally a slight crest) and $\frac{4}{16}$ rr (smooth). The single smooth in the last generation was the carrier of rough, here interpreted as R-MM.

SUMMARY

New data on the heredity of rosette pattern in guinea pigs and a critical review of the data of PICTET and FERRERO support the conclusions reached in 1916 on the genetics of the major variations of this character.

The results of PICTET and FERRERO fully confirm the existence of the primary pair of alleles R, r and are so treated by them in their more recent papers. There is strong evidence that the rough inhibiting factor M (of wild species of *Cavia* and of many guinea pigs) was present in their stock, in certain smooths which transmitted roughness

(R-MM) and in the types described as „lisses à crête” and „monorosettes” (R-Mm) but was not recognized. This gene was clearly much less common than in my stocks.

Their stocks on the other hand seem to have exhibited more variability in the high grades of roughness and to have reached somewhat higher grades than I have observed. They attribute these variations to two new pairs of genes G, g and D, d, the former said to distinguish two patterns on the trunk, the latter, grades of roughness of the head. The data as presented, contain contradictions in both cases. Nevertheless they indicate segregation in their stock of a pair of alleles distinguishing the highest grade of fancier's rough (RRmmGG), from ordinary high grades (RRmmgg). The contradictions may perhaps be due to overlap. No judgment of the validity of genes D, d can be reached without presentation of data showing the breeding results for trunk and head rosettes simultaneously.

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