TRICOLOR INHERITANCE. IV. THE TRIPLE ALLELOMORPHIC SERIES IN GUINEA-PIGS[1]

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In a previous paper (IBSEN 1916) mention was made of a fact, at that time fairly well established by the author, that complete extension (E) of black or chocolate pigment, partial extension (e^p) of the same pigments, and non-extension (e) of these pigments, form an allelomorphic series in guinea-pigs. No evidence for this was given at that time because the complete data were to be reserved for a later paper.

Several authors, among others notably LITTLE (1913), had given a different view as to the inheritance of these characters, and it therefore seemed advisable to obtain very complete evidence before presenting it for publication. This has now been obtained, and will be given as briefly as possible in the following pages. Since LITTLE's theory has already been discussed fully in the paper previously mentioned, it will not be taken up again here.

Before proceeding it may be well to mention that the experimental results entirely corroborate the multiple allelomorphic conception. This would of itself exclude every other conception except that of complete linkage, and while these two differ from each other theoretically, they are exactly alike so far as practical results are concerned. In no single instance has a genotype been obtained which was not expected according to theory. The same, however, cannot be said with respect to phenotypes. A few animals have been born which closely resembled an unexpected phenotype, but which when tested proved to be of the expected genotype. This will be taken up later in the discussion.

The one disturbing factor is that the *proportionate numbers of individuals* in a phenotype have not always been according to expectation. This disproportion of individuals in the phenotypes, which does not in

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any way invalidate the allelomorphic relations of the three factors, will also be discussed more fully later.

All of the data have been placed in one large table (table 1). In a triple allelomorphic series 21 different types of mating are possible. These have all been indicated in the table, although in two cases (matings 1 and 2) no matings were actually made.

The offspring have been classified in two ways, (1) the number under each phenotype is given, and (2) those which have been tested are classified according to their genotype. Almost invariably this testing has been done by mating the animal to be tested to a self red (*ee*), this being the lowest in the allelomorphic series.

In each case after the recorded number of offspring a figure is placed in parentheses to indicate the expected number. The method employed in the working out of the theoretical expectation, especially in the case of the genotypes, should be explained. Mating 10 may serve as an example. Of the 87 self black offspring, 14 were tested by being mated to self reds. Of these, 12 proved to be Ee^p, while 2 were Ee. According to expectation there should have been equal numbers of each genotype, or 7 and 7. In a similar manner, of the 11 tortoises tested, 3 were homozygous (e^pe^p) and 8 heterozygous (e^pe). Since equality was expected, the number here should theoretically have been 5 of each.

We are now in a position to discuss the matings in table 1. Through mating 6 there is only one kind of phenotype, and the genotypes are close to expectation. In mating 7 we find the first example of genotypic as well as phenotypic disproportion. Instead of 3 blacks to 1 tortoise, the proportion is almost exactly 4:1 (129 self blacks: 32 tortoises, and of the tested self blacks the ratio of $Ee^p : EE$ is again almost exactly 4:1, instead of the expected 2:1 (21 Ee^p: 5 EE).

A further inspection of the matings shows other disproportions. In mating 8 we have an excess of tortoises instead of self blacks as in mating 7; in mating 9, a deficiency of tortoises, and in mating 13, a surplus of tortoises again. In the other matings the obtained results are fairly, and sometimes quite, close to expectation.[2]

What is the cause of these discrepancies? As yet none has been

[2]It is worthy of mention that in a previous paper (IBSEN 1916) attention was called to the fact that in $e^pe \times e^pe$ and $e^pe \times ee$ matings an excess of self reds occurred in the offspring. In the present paper, with much larger numbers of offspring in these matings, this excess has been cut down till the actual numbers are quite close to expectation. It may possibly be that with larger numbers the discrepancies in some of the crosses reported in this paper may rectify themselves.

TABLE 1

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	ee Self red	EE	Ee^p	Ee	e^pe^p	e^pe	ee
1	$EE \times EE$									
	Ee^p♀ $\times$ EE♂ EE♀ $\times$ Ee^p♂									
2	Total									
	Ee♀ $\times$ EE♂ EE♀ $\times$ Ee♂	6 49			0 (1.5)		3 (1.5)			
3	Total	55			0 (1.5)		3 (1.5)			
	e^pe^p♀ $\times$ EE♂ EE♀ $\times$ e^pe^p♂	19 0				5 (5)				
4	Total	19				5 (5)				
	e^pe♀ $\times$ EE♂ EE♀ $\times$ e^pe♂	30 6				6 (7)	8 (7)			
5	Total	36				6 (7)	8 (7)			

TABLE I (continued)

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	ee Self red	EE	Ee^p	Ee	e^pe^p	e^pe	ee
	ee ♀ × EE ♂ EE ♀ × ee ♂	43 71					8 (8) 2 (2)			
6	Total	114					10 (10)			
7	Ee^p × Ee^p	129 (120.75)	32 (40.25)		5 (8.67)	21 (17.33)		1 (1)		
	Ee ♀ × Ee^p ♂ Ee^p ♀ × Ee ♂	129 (140.25) 37 (38.25)	58 (46.75) 14 (12.75)		2 (3.3) 0 (0.7)	2 (3.3) 1 (0.7)	6 (3.3) 1 (0.7)		3 (3) 3 (3)	
8	Total	166 (178.5)	72 (59.5)		2 (4)	3 (4)	7 (4)		6 (6)	
	e^pe^p ♀ × Ee^p ♂ Ee^p ♀ × e^pe^p ♂	18 (12) 51 (41.5)	6 (12) 32 (41.5)			1 (1) 7 (7)				
9	Total	69 (53.5)	38 (53.5)			8(8)				
	e^pe ♀ × Ee^p ♂ Ee^p ♀ × e^pe ♂	87 (86)	85 (86)			12 (7)	2 (7)	3 (5.5)	8 (5.5)	
10	Total	87 (86)	85 (86)			12 (7)	2 (7)	3 (5.5)	8 (5.5)	

TABLE I (continued)

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	ee Self red	EE	Ee^p	Ee	e^pe^p	e^pe	ee
	ee♀ × Ee^p♂ ee♀ × Ee^p♂	55 (50.5) 97 (106.5)	46 (50.5) 116 (106.5)				5 (5) 7 (7)		4 (4) 3 (3)	
11	Total	152 (157)	162 (157)				12 (12)		7 (7)	
12	Ee × Ee	74 (73.5)		24 (24.5)	3 (4.33)		10 (8.67)			
	e^pe^p♀ × Ee♂ Ee♀ × e^pe^p♂	17 (23.5) 35 (53)	30 (23.5) 71 (53)			3 (3) 2 (2)			2 (2) 9 (9)	
13	Total	52 (76.5)	101 (76.5)			5 (5)			11 (11)	
	e^pe♀ × Ee♂ Ee♀ × e^pe♂	83 (85) 17 (17.5)	41 (42.5) 11 (8.75)	46 (42.5) 7 (8.75)		7 (7) 3 (3.5)	7 (7) 4 (3.5)		3 (3) 4 (4)	
14	Total	100 (102.5)	52 (51.25)	53 (51.25)		10 (10.5)	11 (10.5)		7 (7)	
	ee♀ × Ee♂ Ee♀ × ee♂	71 (70.5) 111 (111.5)		70 (70.5) 112 (111.5)			5 (5) 11 (11)			
15	Total	182 (182)		182 (182)			16 (16)			
16	e^pe^p × e^pe^p		36					1		

TABLE I (continued)

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	ee Self red	EE	Ee^p	Ee	e^pe^p	e^pe	ee
	e^pe ♀ × e^pe^p ♂ e^pe^p ♀ × e^pe ♂		30 (30) 21 (21)					0 (0.5) 1 (1.5)	1 (0.5) 2 (1.5)	
17	Total		51 (51)					1 (2)	3 (2)	
	e^pe^p or e^pe ♀ × e^pe^p ♂ e^pe^p ♀ × e^pe^p or e^pe ♂	"3"	112 (115) 7 (7)					1		
17a	Total		122 (122)					1		
	ee ♀ × e^pe^p ♂ e^pe^p ♀ × ee ♂		128 (128) 127 (127)						6 (6) 12 (12)	
18	Total		255 (255)						18(18)	
19	e^pe × e^pe	"5"	133 (138)	46 (46)				6 (4.33)	7 (8.67)	
	ee ♀ × e^pe ♂ e^pe ♀ × ee ♂		84 (85) 181 (179.5)	86 (85) 178 (179.5)					6 (6) 7 (7)	
20	Total		265 (264.5)	264 (264.5)					13 (13)	
21	ee × ee		"1"	887 (888)						
	Total	1246	1405	1456						

found, but a certain relation has been noticed. This relation may be stated as follows: In those matings in which both parents are self blacks or else one parent is a self black and the other a tortoise, and in which both self blacks and tortoises occur in the offspring, there is a deficiency of tortoises among the offspring when these are all homozygous (matings 7 and 9) and a surplus when they are all heterozygous (matings 8 and 13). When both classes of tortoises occur in the offspring the excess of one class (the heterozygous) tends to be offset by the deficiency of the other (the homozygous), and as a result the total number is close to expectation (mating 10).

COLE (1914, p. 350) has suggested four possible explanations for modifications of monohybrid ratios. "They might be attributed (1) to the non-viability of a particular class of the F_2 zygotes (as is the explanation offered for both the yellow mice and Antirrhinum); (2) to selective fertilization, i.e., to a selective union of the gametes; (3) to a disproportionate production of the two kinds of gametes; or (4) to a differential viability of the zygotes, but without the complete disappearance of any one class."

No one of these explanations can be made to fit all the aberrant cases just described. The first one, of course, does not apply at all because in none of the matings is one expected class entirely missing. The second explanation, selective fertilization, looks as if it might fit some of the matings, as for instance mating 7. Here one might say that the e^p-bearing gametes tended to unite with those carrying E. The fact that 21 of the 26 tested black offspring were Ee^p would tend to bear this out. On the other hand, if we turn to mating 9, where one of the parents is homozygous for partial extension (e^p), there is still an aberrant ratio in spite of the fact that there is no opportunity here for selective fertilization.

The third explanation, a disproportionate production of the two kinds of gametes, does not apply either, because heterozygous animals of whatever gametic composition when mated to recessive reds (ee) always produce equal numbers of the two expected classes of offspring (matings 11, 15 and 20).

The fourth explanation, the partial viability of some one class, seems to have more in its favor than either of the other three. By referring to table 2 it will be seen that in matings 7 and 9 (in which occur the homozygous tortoises) the average size of litter is comparatively high, while in matings 8 and 13 (which have the heterozygous tortoises) the aver-

TABLE 2
Average litter size for various matings.

Matings		Total number of offspring	Number of litters	Average litter size
No. 7	$Ee^p \times Ee^p$	161	52	3.10
No. 9	$Ee^p \times e^pe^p$	107	37	2.89
No. 8	$Ee^p \times Ee$	238	91	2.62
No. 13	$Ee \times e^pe^p$	153	56	2.73
No. 10	$Ee^p \times e^pe$	172	62	2.77
No. 11	$Ee^p \times ee$	314	110	2.85
No. 12	$Ee \times Ee$	98	39	2.51
No. 14	$Ee \times e^pe$	205	77	2.66
No. 15	$Ee \times ee$	364	143	2.55
No. 20	$e^pe \times ee$	529	196	2.70
Total		2341	863	2.71

age size of litter is comparatively low. From this one might infer that in the case of the last two matings there is an incomplete viability of the self blacks to account for the excess of tortoises in this mating. But even if this were the true explanation it does not account in the first two matings for the excess of self blacks and consequently the deficiency of tortoises.

When the sex ratios are examined certain aberrancies are found here also. In table 3, which has the matings arranged in the same order as in table 2, it will be found that for matings 7 and 9 the sex ratios are quite close to normal expectation,[3] while in matings 8 and 13 there are marked disproportions. Disproportions occur also in some of the other matings, particularly matings 10 and 14. Why these disproportions should occur it is hard to see since the factors in this allelomorphic series are not sex-linked. Further carefully controlled experimental work is necessary in order to help clear up some of this apparent confusion.

As previously stated, some animals were born that were phenotypically contrary to expectation. This is true of matings 17 a, 19 and 21. The numbers enclosed in quotation marks in table 1 refer to these animals. In the first two of the above-mentioned matings some apparently self-black animals were born from tortoise parents. It had been noticed in a number of cases that animals which were apparently self black at birth later showed a few red hairs and so were undoubtedly tortoises and

[3] The ratio for the total 2341 animals in the table is 105.93 males to 100 females. This approximates that found in many other animals.

TABLE 3
Sex ratios for various matings.

Matings	Sexes of offspring						Unclassified offspring			Total offspring
	E		e^p		*ee*					
	♂	♀	♂	♀	♂	♀	*E*	e^p	*ee*	
No. 7 $Ee^p \times Ee^p$	67	62	19	13						161
No. 9 $Ee^p \times e^pe^p$	36	33	18	20						107
No. 8 $Ee^p \times Ee$	91	74	29	43			1			238
No. 13 $Ee \times e^pe^p$	38	14	49	49				3		153
No. 10 $Ee^p \times e^pe$	42	45	34	50				1		172
No. 11 $Ee^p \times ee$	77	73	77	82			2	3		314
No. 12 $Ee \times Ee$	38	34			11	11	2		2	98
No. 14 $Ee \times e^pe$	41	54	25	25	31	20	5	2	2	205
No. 15 $Ee \times ee$	93	81			94	79	8		9	364
No. 20 $e^pe \times ee$			137	120	131	130		8	3	529
Total	523	470	388	402	267	240	18	17	16	2341

were classified as such. Some of the animals listed as self blacks were born dead and hence had to stay classified as such. The few, however, that remained self black in appearance when adult, behaved as tortoises when mated to self reds (*ee*) or tortoises. It is probable that few if any "selfs" or almost selfs would have been produced were it not for the fact that selection was being practiced in a plus direction in a definite attempt to produce actual *E* selfs in this manner. So far, as above indicated, the attempt has been entirely unsuccessful.

In mating 21 we have another example of an apparent dominant being produced from two recessives. Here, what looked like a tortoise was born from self red parents. The animal in question, A 85.1, was entirely red except for a very small chocolate patch back of the left ear. It was one of a litter of five all of which unfortunately died shortly after birth. The parents have had 14 offspring altogether, and of these 13 were self reds.

The aberrant "tortoise" might be looked upon as a mutation, but evidence based on another animal indicates that it was genetically a self red (*ee*) in which the non-extension factor (*ee*) was "accidentally" over-expressed. The other animal referred to is 665.2, which was red with a few small white patches on the head and a very small black area in front of the right ear. She came from an $e^pe \times ee$ mating and was originally classified as a tortoise (e^pe) (IBSEN 1916, p. 302). However, when mated to self reds she had 15 offspring, all self reds. Tortoises as a rule have at least half of the body surface covered with black patches. The two animals, A 85.1 and 665.2, referred to above, had far less black (or chocolate) pigmentation than any genotypic tortoise so far born in our laboratory, and therefore in spite of the black patches on their bodies must be looked upon as genetically self reds.

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