



6. THE ORIGIN OF A POLYDACTYLOUS RACE OF
GUINEA-PIGS

BY

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6. THE ORIGIN OF A POLYDACTYLOUS RACE OF GUINEA-PIGS.

BY W. E. CASTLE.

1. FIRST APPEARANCE OF THE POLYDACTYL CHARACTER.

Normal guinea-pigs have four toes on each front foot but only three on each hind foot. The race of guinea-pigs whose origin is to be described differs from ordinary guinea-pigs in possessing four digits on each hind foot instead of three. The four digits of the front foot apparently correspond with digits 2-5 of the typical five-fingered appendage, while the three digits of the hind foot correspond with digits 2-4 of the typical appendage. In other words, all guinea-pigs have lost from the front foot the digit which corresponds with our thumb, and normal guinea-pigs have lost from the hind foot two digits, which correspond respectively with our "great" and "small" toes. In the race to be described the "small toe" is present on the hind foot as well as on the front.

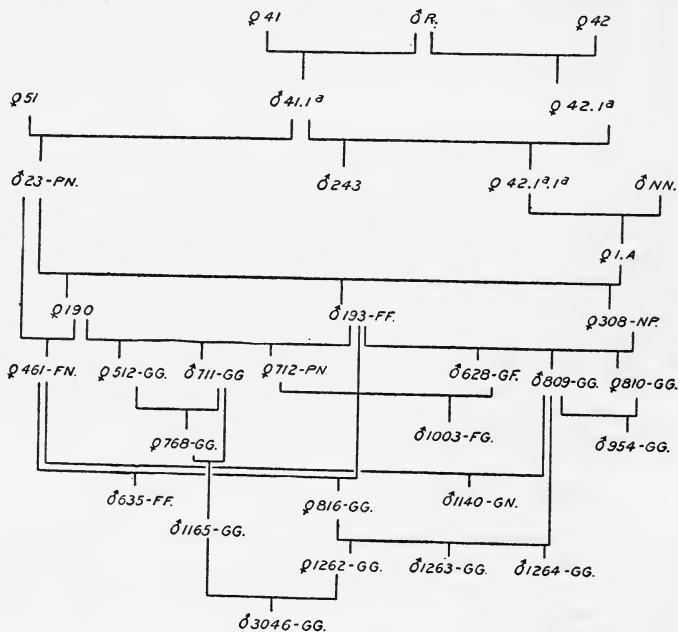
In October, 1900, several ordinary guinea-pigs were obtained from a nearby breeder, one pair of which produced in the following June three male young. The largest of these young bore an imperfectly developed digit on its left hind foot, in the position of a "small toe." This toe bore a well-developed claw and apparently contained the bony phalanges, but these evidently were not joined with the foot by appropriate muscular and tendinous connections, for the toe hung limply down from the side of the foot like a bag of skin. It remained attached to the foot until the animal was fully grown, but was then lost, probably having been accidentally pulled off.

Previous to the birth of this polydactylous guinea-pig, I had never seen a fourth digit on the hind foot of a guinea-pig, nor heard of its occurrence either among wild or domesticated Caviidæ, and I am unable to find any reference to such a character in the literature of the group. But I have since found that the "extra-toe" does occur not infrequently among guinea-pigs in an imperfectly developed condition, and I have twice since obtained animals of this sort from breeders. From the progeny of the single polydactylous individual born in June, 1901, a well-established race of four-toed guinea-pigs has now been formed. An account of how this was done, it is hoped, may be of value as bearing on the origin of breeds.

The original polydactylous guinea-pig (σ^7 23, table 1, p. 18), was born to parents of almost unknown ancestry, but certainly not closely related to each other. The mother, a spotted animal (q 51) produced no other polydactylous offspring, though she bore in all thirty young. But the father (σ^7 41.1^a), who sired in all one hundred and forty-seven young, had five other polydactylous offspring. These were all, except one,* borne by females descended from himself, and that one was borne by his half-sister (q 42.1^a), so that it seems certain that the polydactylous character came in every case from the same individual, σ^7 41.1^a. A son of σ^7 41.1^a—viz, σ^7 243 (table 1)—whose mother was half-sister to σ^7 41.1^a, produced, like his father, a certain number (five) of polydactylous offspring, which were used in building up the polydactylous race.

TABLE I. — *Ancestry of the various males used in building up the polydactylous race.*

The character of the extra-toe is indicated by letters following the numeral which designates each individual. These letters signify: *G*, good; *F*, fair; *P*, poor; *N*, normal, *i. e.*, three-toed. Read downward.



* In an earlier paper (Castle, :05) this exception was inadvertently overlooked, and the total number of young sired by σ^7 41.1^a was given as 139 instead of 147.

2. PROGENY OF THE ORIGINAL POLYDACTYLOUS INDIVIDUAL.

The polydactylous male (σ^23), in a total of seventy-seven young, produced fifteen polydactylous ones. The proportion of polydactylous individuals varied much among the offspring by different mothers. (See table 2.) Unrelated mothers, from families in which polydactylism had not been observed, gave only two polydactylous young to thirty normal ones, or 6.25 per cent. polydactylous. *Related* normal mothers—that is, mothers descended from $\sigma^41.1^a$ —gave nine polydactylous to twenty-seven normal, or 25 per cent. polydactylous, while polydactylous mothers gave four polydactylous to five normal young, or 44 per cent. polydactylous young.

Many of the young of σ^23 had the extra digit present on both the right and the left hind feet, and in several of these the digits were better developed than in the father, evidently with all the appropriate muscles necessary for functional toes. One of the best of these young was σ^193 (table 1). His mother was a normal individual descended from $\sigma^41.1^a$, but gave a larger proportion of polydactylous young than any other mother had done up to that time. By σ^23 she had five polydactylous and six normal young.

To express the degree of development of the extra digit a series of three grades was now established, *good*, *fair* and *poor*, which will be abbreviated to *G*, *F* and *P* respectively. *Good* means a fully developed and functional fourth toe; *fair* means a fourth toe rather smaller than the others, often turned upward a little in walking, as if its muscular equipment were imperfect; *poor* means a loosely hanging toe, either with or without a nail; sometimes the toe described as *poor* is represented by only a soft fleshy bag of skin attached to the side of the foot, without either nail or hair, destined to shrivel up and drop off within a few days after birth. In distinction from these three classes, the term *normal* (*N*) will be used to describe a three-toed foot. In describing the condition of the toes of an individual, the left foot will always be named first; thus *GP* will mean an individual having a good fourth toe on the *left* foot, a poor one on the *right* foot.

3. PROGENY OF THE SECOND POLYDACTYLOUS GENERATION.

Male 193, as regards the extra-toe, was classed as *FF*, but he produced about fifteen young with well-developed extra-toes, which placed them in class *G*. About one-fourth of all his polydactylous young were of this sort, the polydactylous including more than half his young (forty-eight out of eighty-six).

METHOD OF GRADING THE PROGENY.

Of course the female mates of ♂ 193 were in many cases superior in toe development to the mates of his father, ♂ 23, though in many cases they were identical. Accordingly it is necessary, in estimating the respective potency of the two animals, to separate the mothers into groups of similar toe development, or of similar pedigree when no extra-toes were present. Consequently, five groups of mothers have been made (see tables 2-14), viz, *G*, *F*, *P*, *N* and *N'*. Group *G* includes only mothers having well-developed extra-toes on both feet (*GG*); *F* includes mothers having fairly well-developed toes, or with one good toe only (*FF*, *FG*, or *GF*); *P* includes mothers with at least one toe poorly developed (*P*); the other toe may be fair or poor, or the foot may be normal. *N* includes normal (*NN*) mothers descended from ♂ 41.1^a or nearly related to him; *N'* includes normal mothers not descended from ♂ 41.1^a, but belonging to families in which, when inbred, polydactylism does not occur.

When the mothers are grouped in this way, we find, first, that the proportion of polydactylous young produced by a male decreases in the successive classes from *G* to *N'*; and secondly, that the degree of development of the toes produced on those polydactylous young diminishes in the same order.

It would manifestly be unfair in estimating the potency of transmission in a given case to omit either of these considerations—the proportion of polydactylous young, or the degree of development of their extra-toes. So an attempt has been made to combine the two into a numerical grade for the young by each group of mothers. This grade is given in the last column of tables 2 to 14. In making up the grade each *G* toe counts 100, each *F* toe 80, and each *P* toe 50, while *N* counts 0. The total thus obtained for a group of young is divided by twice the total number of young in that group, that is, by the whole number of feet which *might* bear the extra-toe. Measured by this standard, a group of young, *all* of which had the extra-toe well developed on both hind feet, would be graded 100; a group of young with no extra-toes would be graded 0, while mixed groups would come in between 0 and 100. A group of young averaging *P* would be graded 50, and a group averaging *F* would be graded 80.

Comparing the young of ♂ 193 (table 3) with those of his father, ♂ 23 (table 2), we see a marked increase in the potency of transmission of the extra-toe within the same group of mothers. The grades of the young produced by the last four groups of mothers (*F* to *N'*) in the case of ♂ 23 are 29, 19, 17, and 1.5, respectively, while in the case of ♂ 193 they are 58, 57.5, 22 and 18.5.

4. PROGENY OF THE THIRD POLYDACTYLOUS GENERATION.

Continuing to trace the history of the polydactylous race in the male line, we may notice that the sires of the next generation of young consisted of four sons of ♂ 193. Two of these were own brothers, viz, ♂ 628 and ♂ 809 (see table 1). The other two were half-brothers to these two and to each other. They were ♂ 635 and ♂ 711. The young of these four males are classified as regards the extra-toe character in tables 4 to 7 (see pages 25 and 26). An examination of these tables shows for ♂ 809 an increase of potency over that of his father, ♂ 193; ♂ 711 shows a potency very similar to that of his father, but the other two males, ♂ 628 and ♂ 635, are clearly inferior to their father in potency, their average grades being about 34 and 38 respectively, while that of their father was 46.

5. PROGENY OF THE FOURTH POLYDACTYLOUS GENERATION.

The sires of the next generation consisted of six males, four of which were sons of the best male (809) of the previous generation, while one was a son of ♂ 628, and one a son of ♂ 711. Considering first the four sons of ♂ 809 (table 7), we notice that three of them, ♂ 954 (table 8), ♂ 1140 (table 10) and ♂ 1264 (table 13), are clearly inferior to their father in potency. The fourth male, ♂ 1263 (table 12), makes a somewhat better showing than his father, though two of the possible groups of mothers (*F* and *N*) are wholly unrepresented among his mates and their values can only be roughly estimated by interpolating values, while two other groups are very inadequately represented. Yet all the data available agree in showing high potency on the part of this male. Out of a total of eighty-three young which he has sired, only one has been three-toed.

Male 1003 (table 9) has a record similar to that of his father, ♂ 628 (table 4), but on the whole better. It is noteworthy that neither of these animals gave polydactylous offspring when mated to unrelated normal females, though by polydactylous mothers they had a good proportion of polydactylous young.

Male 1165 (table 11), also, has a record like that of his father, ♂ 711 (table 6). By unrelated normal (*N'*) females he produced offspring grading 10 as regards the extra-toe character, his father's offspring by the same group of mothers grading 8. By matings with polydactylous mothers, both father and son have produced offspring grading below those of ♂ 809 and of ♂ 1263.

The attempt has twice been made to increase by selection the asymmetry of the two sides of the body with reference to the extra-toe, but without success. The slightly superior development of the extra-toe on the left side of the body apparently remains unaffected. The cause of the asymmetry is unknown. The case doubtless belongs in the same category as the unequally developed right and left sex-glands of certain birds and mammals.

9. RESULT OF MATING NORMAL WITH POLYDACTYLOUS INDIVIDUALS.

Matings between normal females and polydactylous males have repeatedly been made, as will appear from tables 2 to 14. Crosses reciprocal to these have yielded the results indicated in table 17. The results, it will be seen, are not uniform. The offspring have, in some cases, a greatly weakened condition of the extra-toe, in other cases no extra-toe at all; in still other cases, the extra-toe may be present in a fairly well-developed condition. The inheritance is evidently neither sharply alternative (*i. e.*, Mendelian) nor completely blending. The result of a cross involving the extra-toe character is influenced by the individual potency of the respective parents. Fewer polydactylous young are produced if the normal parent comes of a stock in which the polydactylous character does not occur.

10. INHERITANCE NEITHER ALTERNATIVE NOR BLENDING.

It is very evident that in the inheritance of the extra-toe we are not dealing with a case of simple Mendelian dominance. An occasional case, like the matings of ♂ 628 with normal females (see table 4), would indicate that the extra-toe is a recessive character, but most polydactylous parents, in matings with normal individuals, give a mixture of normal with polydactylous offspring. Further, in these mixed lots of offspring, the polydactylous and normal individuals are rarely equal to each other in number, as we should expect if one parent were a Mendelian heterozygote, the other pure.

On the other hand, when two of the offspring produced by a cross between polydactylous and normal parents are mated together, we do get some evidence of Mendelian segregation. The offspring are highly variable as regards the character, extra-toe. Some are normal, some have poorly developed toes, and some have very well developed toes. The experiments are still incomplete as regards this matter, but so far do not indicate the formation of sharply separated Mendelian classes.

On the whole, it seems probable that the extra-toe is inherited in a manner intermediate between blending and alternative inheritance. The gametes only *partially* blend in the zygote, producing a variable result, most

often an intermediate condition. The gametes formed by the cross-breds are not homogeneous, as would be the case if complete blending occurred in the zygote, but are highly variable as regards the extra-toe. If the inheritance were sharply alternative, we should expect to get, not a series of graduated forms, but two or at most three sharply distinct groups, but this is not the observed result. If, on the other hand, inheritance were fully *blending*, all the offspring of two pure parents, or of two cross-bred parents, should be alike, but this is not the observed result. We are forced to conclude, therefore, that there occurs a *partial* blending of gametes in the zygote, and a *partial* segregation as the zygote gives off gametes.

Not improbably more characters fall in this category than in any other. Sharp alternative inheritance is comparatively rare, so is fully blending inheritance; most characters appear from generation to generation in a more or less well developed condition, not always strictly intermediate between the conditions found in the respective parents, nor always corresponding closely either with the condition found in one parent or with that found in the other. In dealing with such characters, selection must be the breeder's method of working. If he wishes either to eliminate or to "fix" a partially blending character he must make an appropriate choice of parents, not once nor twice, but many times over until the undesired condition ceases wholly to reappear.

It would be interesting to know in what condition characters like the extra-toe exist in the germ. It can not be in a state of simple recessiveness, for in that case the character should reappear in a Mendelian proportion of the offspring formed, but this, as we have seen, is not the case. More probably the character is present, active or inactive, in *every* gamete, but the conditions under which it may become active are too complex for present analysis. On the other hand, it is possible that *nothing* in the germ of a normal guinea-pig stands for the character, extra-toe, and that when this character is formed, it is formed *de novo*. But if so, we must account for the appearance of a new digit in the precise position of a lost one, and with all the appropriate nervous and muscular connections. This it seems quite as hard to do as to suppose an antecedent state of latency or inactivity of the character throughout certain generations of ancestors. Moreover, we have strong reasons for believing that, in color inheritance, specific pigments and specific color patterns may be transmitted unseen in a latent condition, often through long series of generations. If color characters are subject to transmission in a latent condition, it seems reasonable to suppose that other characters also may be transmitted in the same way.

TABLE 2.—Character of the extra-toe in young of ♂ 23 (PN), of polydactylous generation I.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G												
F			2—1		—1				2	3	40	29
P					2—1		—1		2	2	50	19
N			4—5		2—2		3—2		9	27	25	17
N'					2—		—2		2	30	6	1.5
			6—6		6—4		3—5		15	62	19.5	22(?)

TABLE 3.*—Character of the extra-toe in young of ♂ 193 (FF), generation II.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	1—1		1—		—1				2	1	[67]	[55]
F	3—3		5—4				—1		8	2	80	58
P	6—5		10—7		2—4		1—3		19	5	79	51.5
N	5—4		3—2		4—7		4—3		16	26	38	22
N'			1—1		1—1		1—1		3	4	43	18.5
	15—13		20—14		7—13		6—8		48	38	56	46

TABLE 4.—Character of the extra-toe in young of ♂ 628 (GF), generation III.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	1—1		1—1						2		[100]	[90]
F					1—1				1	2	[33]	[17]
P	7—5		1—3		4—3		1—2		13	2	87	62
N										4	0	0
N'										8	0	0
	8—6		2—4		5—4		1—2		26	16	62	31

TABLE 5.—Character of the extra-toe in young of ♂ 635 (FF), generation III.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G					2—1		—1		2	1	[67]	[25]
F	1—1		2—2						3		[100]	[87]
P	3—1		4—4		4—4		—2		11	7	78	40
N	3—2		8—8		11—7		1—6		23	32	42	21
N'			3—3		7—3		—4		10	24	29	14
	7—4		17—17		24—15		1—13		49	64	43	38

* In the last two columns of tables 3 to 13, per cent. or grades of the young, when based on a smaller number of individuals than four, are placed within brackets.

TABLE 6.—Character of the extra-toe in young of ♂ 711 (GG), generation III.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	7	7	1	1					8		100	97.5
F	2	3	2	2	3	2			7	2	78	60
P	1	1	2	1	1	2			4	3	57	42
N	1	4	3	1	3	2	1	1	8	8	50	33
N'			1	1	4	3		—1	5	27	12.5	8
	11	15	9	6	11	9	1	2	32	40	44	48

TABLE 7.—Character of the extra-toe in young of ♂ 809 (GG), generation III.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	28	24	4	7	1	3	1	—	34	1	97	90
F	4	4							4	1	80	80
P	4	3	3	3	2	1		—2	9		100	74
N	1	—		—1					1	1	[50]	[45]
N'	1	—	1	2	5	4	1	—2	8	6	57	28
	38	31	8	13	8	8	8	8	56	9	86	63

TABLE 8.—Character of the extra-toe in young of ♂ 954 (GG), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	9	9	3	3	6	5	1	—2	19	2	90	67
F	3	2	3	4	1	1			7	1	87.5	73
P	7	5	7	9	10	10	2	—2	26	3	90	60
N	1	—3	2	—	4	5	1	—	8	1	89	56
N'					1	—		—1	1	1	[50]	[12.5]
	20	19	15	16	22	21	4	5	61	8	88	54

TABLE 9.—Character of the extra-toe in young of ♂ 1003 (FG), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	6	6							6		100	100
F												
P	3	3	2	1	—	—2	1	—	6	3	67	52
N												
N'										20	0	0
	9	9	2	1	—	—2	1	—	12	23	34	51

TABLE 10.—Character of the extra-toe in young of ♂ 1140 (GN), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G												
F	3	2	2	3	4	1		3	9	2	82	48
P	4	2	3	3	4	4	1	3	12	3	80	49
N	3	2	2	2		1			5	1	83	72.5
N'												
	10	6	7	8	8	6	1	6	26	6	81	56.5

TABLE 11.—Character of the extra-toe in young of ♂ 1165 (GG), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	32	30	5	7	2	2			39	2	95	90
F	4	4	5	5	1	1			10		100	85
P	2	1			1	2			3	2	60	45
N							1	3	3	7	30	10
N'							2					
	38	35	10	12	5	8	2		55	11	83	50

TABLE 12.—Character of the extra-toe in young of ♂ 1263 (GG), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	66	61	6	6	5	9		1	77		100	93
F												
P	2	2							2	1	[67]	[67]
N												
N'	1		3	4					4		100	82.5
	69	63	9	10	5	9		1	83	1	99	81

TABLE 13.—Character of the extra-toe in young of ♂ 1264 (GG), generation IV.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	21	22	12	9	2	4	1	1	36	1	97.5	85
F	1	1	1						2		[100]	[82.5]
P	6	5	3	2	3	4		1	12	2	86	66
N					2	2			2	4	33	17
N'										3	[0]	[0]
	28	28	16	11	7	11	1	2	52	10	84	50

TABLE 14.—Character of the young of ♂ 3046 (GG), generation V.

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G N	79—77		8—8		1—2 1—		—1 —1		88 1	0 3	100 25	97 8
	79—77		8—8		2—2		—1		89	3	97	

TABLE 15.—Sires grouped by generations of polydactylous ancestry.

[The numerals in parenthesis indicate rank in potency of transmission of the polydactylous character. Descent is shown in the male line only.]

Polydactylous generations in ancestry.	0	½	1	1½	2	2½	3
	23(5)	193(3)	711(3)	628(1) 635(1)	1003(3)	1165(3)	3046(1)
				809(2)	1140(3) 1263(1) 1264(3)	954(3)	
Generation (in male line)	I.	II.	III.		IV.		V.

TABLE 16.—Frequency of occurrence of the extra-toe in its several degrees of development on the two sides of the body.

	Left side.	Right side.	Per cent. left.
G	335	310	51.9
F	148	133	52.6
P	147	146	50.2
	630	589	51.6

TABLE 17.—Character of the young produced by a mating between a normal (N) male and females either polydactylous or of polydactylous ancestry.

Father.	Character of mother.	F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
		L	R	L	R	L	R				
♂ 482	P	1—		1—		—2		2	0	[100]	[32.5]
♂ 981	F			2—1		1—2		3	2	60	15
	P			2—3		1—		3	0	[100]	[25]
♂ 2054	P							0	4	0	0
	N			—1		1—		1	5	17	4
♂ 2060	G	2—1		4—5				6	10	37.5	22
♂ 3609	G			2—1		—1		2	6	25	9

POSTSCRIPT.

A critical examination of the results obtained by Bateson, Punnett and Hurst (see Bateson, Saunders, Punnett and Hurst, :05) in poultry indicates that there too the inheritance of extra-toe is not strictly Mendelian, but corresponds with what I have found to be the condition in the *most potent* polydactylous sires. In poultry the extra-toe has been for a long time an established character of certain breeds. During all that time selection has undoubtedly been exercised in its favor, so that it is not surprising to find the character more strongly dominant than in my four-toed race of guinea-pigs. Nevertheless both Bateson and Hurst record cases in which polydactylous chicks are produced by normal parents of polydactylous ancestry.

Similar observations have repeatedly been made concerning the inheritance of polydactylism in man. See Ballowitz (:04) and Davenport (:04). Polydactylism usually makes its (recorded) appearance in some note-worthy form, is transmitted more or less strongly through two to five generations and then disappears, doubtless so weakened by repeated out-crosses that its manifestations, if any occur, are no longer observed.

Apparently it is only when selection is exercised for the polydactyl character and like individuals are mated to each other that a polydactylous race can be established. In its origin, polydactylism is a discontinuous variation or mutation, but without the aid of selection it would probably never become a racial character. Is not the same thing true of a great many of the characters which serve to distinguish the various races of domesticated animals and plants?

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