INHERITANCE OF POLYDACTYLISM IN THE FOWL[1]

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POLYDACTYLISM, where studied in vertebrates, has usually been shown to be a heritable characteristic, although in some instances the mode of inheritance has been somewhat involved.

In the case of the fowl, the usual number of toes is four although five toes constitute a breed characteristic in some instances. The four-toed condition of the fowl is the result of the loss of the fifth digit from the typical pentadactyl foot of higher vertebrates. It has been shown by various workers (KUAFMANN-WOLF 1908; HARMAN and ALSOP 1938) that the additional toe in five-toed breeds does not constitute a restoration of the missing fifth digit but is the result of the development of a new toe on the opposite side of the foot. The work of BOND (1920, 1926) and PUNNETT and PEASE (1929) has indicated that the five-toed condition behaves genetically as a dominant to four toes. Certain irregularities in the expressions of the character including heterodactyly and the occasional lack of penetrance have been noted. A considerable body of data on polydactylism has been accumulated by the writer in connection with other genetic studies on the fowl. Polydactyly, as here studied, cannot be referred to any particular breed, since it was present in crossbred stocks used in various genetic studies, but the original stocks were Silkie Bantam and Houdan. It was the purpose of this study to obtain further information on genetics of polydactylism in the fowl.

INHERITANCE OF FIVE TOES

Several workers (BOND 1926; PUNNETT and PEASE 1929) have studied the inheritance of the five-toed condition as found in some standard breeds of poultry. The conclusions were that polydactylism of this type behaved as an autosomal dominant, with some of the individuals carrying the gene failing to show extra toes. HUTCHINSON (1931) suggests that the occasional normal individual resulting from a mating involving homozygous dominant polydactylous parents may be due to genetic modifiers influencing dominance. The numbers of birds included in previous studies have been somewhat small, and therefore additional data are presented by the writer. The large numbers recorded for heterozygous polydactyls backcrossed to normals are from linkage tests.

Certain facts are evident from the data in table 1. First the earlier evidence of the dominant behavior of polydactylism in confirmed. It is also noted that the ratios show a deficiency of polydactyls. The greatest deficiency is found where the segregating polydactyls are all heterozygotes (backcrosses to normals). The shortage in these crosses is greater than in the F_2 generation, indicating the possibility that the failure of expression of the character is greater

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TABLE 1

Inheritance of polydactyly (five toes).

	FEMALES		MALES		TOTAL	
	POLY-DACTYLS	NOR-MALS	POLY-DACTYLS	NOR-MALS	POLY-DACTYLS	NOR-MALS
Homozygous polydactyl ♂×normal ♀	115	5	107	4	222	9
Homozygous polydactyl ♀×normal ♂	32	0	17	2	49	2
F_2 generation	148	49	143	69	291	118
Backcross of heterozygous polydactyl ♀ to normal ♂	298	359	286	440	584	799
Backcross of heterozygous polydactyl ♂ to normal ♀	818	1247	794	1207	1612	2454
Backcross of heterozygous polydactyl ♀ to homozygous polydactyl ♂	87	4	87	3	174	7
Backcross of heterozygous polydactyl ♂ to homozygous polydactyl ♀	10	1	13	0	23	1

in heterozygotes than in homozygotes. There seems to be a slightly weaker penetrance of the character in males than in females, but the difference is so slight as to be of questionable significance.

The shortage of polydactyls might be due to a number of conditions such as the action of genetic suppressors or inhibitors, to poor penetrance of the factor, or to low viability of birds showing the character. General observations would lend little support to the view that the last mentioned possibility will account for the shortage. As to the existence of genetic inhibitors, the data in table 1 indicate the possible presence of such inhibitors. If the polydactylous stock carried genetic inhibitors, the greater shortage should occur in the F_2 generation or in backcrosses to polydactyls, unless the action of the inhibitor is limited to heterozygous polydactylism. Table 1 shows the greatest deficiency of polydactyls in the backcrosses to normal. Most of the backcrosses of heterozygotes to normals involved purebreds on the normal side of the cross, and these purebreds would ordinarily not be expected to carry inhibitors for polydactylism which they themselves did not carry. The fact that a breed does not carry a factor, however, is no assurance that it does not carry modifying factors or inhibitors for the same. If the deficiency of polydactyls in backcrosses to normals is due to genetic inhibitors, the action must be due to either the normal stocks carrying the same recessive inhibitor found in the polydactyls or to a dominant found in the purebreds. Any dominant inhibitor in the polydactylous stock would tend to suppress polydactylism in the heterozygotes. It remains doubtful, therefore, as to how to account for the observed shortage of polydactyls. The shortage in the offspring of 22 males heterozygous for polydactylism when backcrossed to normals ranged from 0 to 60 percent.

STURKIE (1942) has made a preliminary report on the effect of low temperatures during the early embryonic development upon polydactylism. He reported shortages (normals) of from 18 to 78 percent among heterozygous polydactyls. This is good evidence that the expression (penetrance) of polydactylism is dependent upon environmental factors during chick development. Factors such as this may be the cause of the shortage of polydactyls shown in table 1. That this can be entirely due to temperature fluctuations seems questionable, since the individuals reported here were produced over a period of

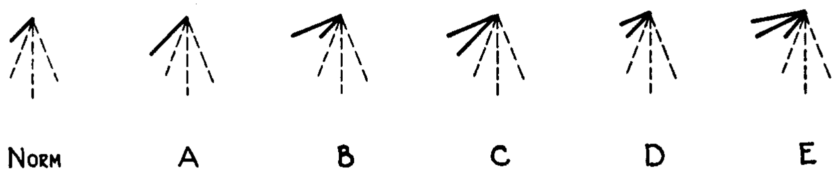

FIG. 1. Diagrammatic representation of the arbitrary classification of polydactylism used in this study. Type A, polyphalangy; type B, the usual type of polydactylism in five-toed breeds; type C, most common type of duplicate; type D, common in the usual type of polydactylism; type E, another common type in duplicate. The diagram listed as normal represents the non-polydactylous four-toed foot.

years under what were believed to be optimum incubation temperatures. In one hatching season two heterozygous polydactylous males were backcrossed to normal females, whose eggs were set weekly and hatched in the same incubator over a period of several weeks with the following results: male 1289, 34 normals to 169 polydactyls and male 1290, 131 normals to 121 polydactyls. It would appear that these divergent ratios could not be due to temperature fluctuations alone. It seems probable that the variation in the expression of polydactyly is due to both genetic and environmental factors.

DUPLICATE

The writer (1941) described a new type of polydactylism which varied somewhat from the usual expression. It frequently showed conspicuous abnormality of the wing as well as the foot digits. BARFURTH (1911) has described minor wing deformities in usual type of polydactylism. This new factor showed other differences in the expression of polydactylism of the feet. Duplicate behaved as a dominant toward normal and its relation to usual five-toed polydactylism will be discussed later.

POLYPHALANGY

In studies of the usual type of polydactyly, another variant has been observed, which has been called polyphalangy. It appears only in polydactylous stocks and constitutes a reversion to the four-toed condition but is characterized by the inner toe (No. 1) having an extra phalanx and being relatively long (fig. 2A). The usual polydactylism (fig. 2B) is the result of what seems to be the addition of a long toe at the inside base of the No. 1 toe. This additional toe has one more phalanx than does the No. 1 toe, and polyphalangy has the appearance of a five-toed polydactyl with the No. 1 toe missing. Since polyphalangy appears only in polydactylous stock, it seems to be a modified polydactyl. The evidence early indicated that this variant of polydactylism was inherited, but several generations of selection failed to produce a stock of polydactylous birds breeding true for polyphalangy.

The mode of inheritance of the modified polydactylism referred to as polyphalangy appears to be complicated. Data from matings of polyphalangy are given in table 2. That this character is inherited is well demonstrated by comparing the F_2 generation results of the polyphalangy and the polydactyly matings. In the polyphalangy F_2 generation where both parents were polydactyls of the polyphalangeal type (matings 12 to 15) the ratio of polydactyls to polyphalangyls was 241 to 280 while in polydactyly F_2 where both parents were polydactyls not showing the polyphalangeal type (mating 17) the ratio

TABLE 2

Inheritance of Polyphalangy.

	FEMALES			MALES			TOTAL	
	NORMAL	POLYDACTYL	POLYPHALANGYL	NORMAL	POLYDACTYL	POLYPHALANGYL	POLYDACTYL	POLYPHALANGYL
Heterozygous polyphalangy ♂ by normal ♀								
Mating 1—Male 1526	19	5	7	20	1	3	6	10
Mating 2—Male 1528	2	12	9	2	9	1	21	10
Mating 3—Male 1546	4	36	9	1	33	9	69	18
Mating 4—Male 1562	47	13	26	43	13	20	26	46
Mating 5—Male 1579	14	12	0	10	15	0	27	0
Mating 6—Male 1606	17	15	1	23	18	1	33	2
Mating 7—Male 1606	17	13	10	27	17	5	30	15
Mating 8—Male 1610	51	23	4	52	20	1	43	5
Total	171	129	66	178	126	40	255	106
Normal ♂ by heterozygous polyphalangy ♀								
Mating 9—Male 1592	88	36	22	85	45	14	81	36
Mating 10—Male 1634	22	18	8	17	11	7	29	15
Mating 11—Male 1555	17	32	4	29	36	0	68	4
Total	127	86	34	131	92	21	178	55
Polyphalangy F_2								
Mating 12—Male 1546	4	53	34	3	67	20	120	54
Mating 13—Male 1606	12	14	30	16	19	30	33	60
Mating 14—Male 1610	22	16	34	30	15	28	31	62
Mating 15—Male 1637	22	27	51	25	30	53	57	104
Total	60	110	149	74	131	131	241	280
Polydactylous matings								
Mating 16—Polydactyl by normal	331	266	11	296	278	15	544	26
Mating 17—Polydactyly F_2	10	46	4	21	61	2	107	6

was 107 polydactyls to six polyphalangyls. Since polyphalangy appears to be a modification of polydactyly, the normals in the table may be disregarded. In some matings one of the parents may have been homozygous for the factor for the usual type of polydactyly, but the data of significance here are those showing the ratio of a polyphalangyls to non-polyphalangyls among the polydactyls. It is true that only four-toed polydactyls having a long inside toe (fig. 1, Type A) were classed as polyphalangeals in table 2. Later analyses in this study seem to show that types C and E (fig. 1) may also carry the polyphalangeal factor. However, the numbers of these two types were not large and if accounted for would not greatly change the ratios in table 2.

Reciprocal F_1 matings between normal and polyphalangy show no evidence of sex-linked factors being involved. The F_1 generation shows wide variability as to the incidence of polyphalangy ranging from zero to 64 percent of the polydactyls exhibiting the modification. The variability might be due either to differences in the genetic constitution of the parents or to the influence of some environmental factor. The two matings (matings 6 and 7) listed for male 1606 involve two different groups of normal female mates. The term normal as used in table 2 indicates the absence of any type of polydactyly. The White Leghorn female mates in mating 7 produced a much larger proportion of the polyphalangeal type than did the Rhode Island Reds in mating 6. The same Rhode Island Red females were mated with males 1579 and 1610 in matings 6 and 8, and in each case gave a low incidence of polyphalangy in the F_1 generations. These results might be taken to indicate genetic differences among the purebred non-polydactylous stocks as to the presence of the modifier converting polydactyly into polyphalangy. In view of the evidence, however, that the expression of other forms of polydactyly in the fowl is influenced by environmental factors, it is possible that such factors are also acting here.

The F_2 generation ratio is also probably influenced by the factors causing variability in the F_1 generation. It would seem then that polyphalangy is a factor which behaves as an autosomal dominant with some unknown factors causing variability in dominance.

EXPRESSION OF POLYDACTYLY IN THE DIFFERENT GENETIC STOCKS

In studies of polydactyly it was evident that most of the variants fell into five major types which are illustrated diagramatically in figure 1. Photographic examples of the types are found in figure 2. In the polydactylous fowl the digits 2, 3, and 4 seem to be unaffected, and in some types even digit 1 remains normal. The classification in figure 1 is based upon the relative lengths of extra toes in comparison to digit 1. In the normal four-toed foot the No. 1 digit is relatively short, possessing one phalanx and the nail. The ordinary type of polydactyly (type B, fig. 1) seems to possess an unaffected No. 1 digit with an extra digit added to the outside of this digit (on inside of foot). The extra digit has an additional phalanx making it longer than the No. 1. Polyphalangy (type A) has the appearance of type B with the No. 1 digit missing. Type C has two long extra digits and might be considered to be type A with the long inside toe split. Type D possesses an extra toe which is short. Type E has six toes with the appearance of being a combination of the normal and type C. Variants of polydactyly occur which do not fit the foregoing classifications, but in general the suggested groupings are quite satisfactory for a large majority of the expressions.

Table 3 presents data showing the incidence of these variants of polydactyly as found in the polydactylous (usual) matings, polyphalangy matings, and duplicate matings. Heterodactyls have not been included in this table

TABLE 3

Incidence of types of polydactyly in different stocks.

TYPE OF OFFSPRING	STOCKS MATED					
	USUAL POLYDACTYLY		POLYPHALANGY		DUPLICATE	
	NO.	PERCENTAGE	NO.	PERCENTAGE	NO.	PERCENTAGE
A	13	2	222	39	25	3
B	527	85	248	44	152	16
C	3	0	51	9	337	36
D	70	11	42	7	24	3
E	4	1	6	1	397	42
Total	617		569		935	

because of difficulty of classification. Polyphalangy differs from the usual five-toed type in the distribution of its variants only by showing an increase of types A and C. Agreement in the other classes might be expected, since polyphalangy appears to be a modification of the five-toed type. Duplicate, which differs considerably from the usual polydactyly, shows a high incidence of the six-toed, type E which is rarely found in the other two stocks. It also shows a large proportion of type C. The differences found in the proportion of types of polydactyls appearing in the stocks is evidence of genetic diversity. Similarity of types as found in the three different stocks makes it impossible to determine origin of some individuals without reference to their pedigree, but breeding tests reveal differences. The type E (fig. 1) is found commonly in duplicate, but virtually never in polydactylous and seldom in polyphalangeal stocks. An example of the difference in breeding behavior of types E from duplicate and polyphalangeal stocks is found in table 4. The data in table 4 were presented for another purpose, but a comparison of data obtained under normal temperature conditions affords a striking contrast of the expression of polydactylism among offspring of males identical in appearance but originating in duplicate and polyphalangeal stocks. The four males used for matings reported in table 4 were virtually indistinguishable but those from the duplicate and polyphalangeal stocks differ widely with respect to the relative incidence of the various types of polydactyly.

Following the suggestion of STURKIE (1942) that low incubation temperatures influenced the expression of polydactyly, an experiment was planned to test the effect of this factor on the types of polydactylism obtained. STURKIE considered primarily the tendency of subnormal incubation temperatures to suppress polydactylism. Since there was reported in the present study considerable variation in the types of polydactyly obtained in the different stocks, it is of interest to determine whether incubation temperatures were influencing factors. DR. STURKIE kindly advised the writer as to what temperature changes

TABLE 4

Effect of lowered incubation temperatures on expression of polydactyly.

MALE NO.	TREATMENT	NO. OFF-SPRING	PERCENTAGE OFFSPRING DESCRIBED AS—						
			NOR-MAL	TYPE A	TYPE B	TYPE C	TYPE D	TYPE E	HETERO-DACTYL
Duplicate	Normal	302	42		1	9		39	9
2407	Cold	33	46	3	12	18		9	12
Duplicate	Normal	442	52	2	5	16		8	17
5372	Cold	52	48	15	6	12		4	15
Polyphalangy	Normal	127	1	14	32	2	12	2	39
4987	Cold	69	12	32	17	1	10		28
Polyphalangy	Normal	108	1	47	10	7	3	3	29
1729	Cold	17	11	77	6				6

he was finding most effective in suppressing polydactylism. The procedure here followed was to carry the eggs at normal incubation temperatures (100°F) for the first 48 hours. Then the eggs were placed in a large refrigerator for 16 hours where temperatures varied from 37 to 40°F. For the next 72 hours the incubation temperature was 93°F, following which normal incubation temperatures were maintained for the remaining incubation period. The embryonic mortality was somewhat high, but all late stage embryos and hatched chicks were classified as to the type of polydactyly. Those individuals listed in table 4 as being subjected to normal incubation temperatures were produced by the same parent stock before and after the period of low incubation temperature conditions. Males 2407 and 5372 were type E duplicates, and males 4987 and 1729 were type E polyphalangyls. The first three named males were mated with White Leghorn females, and male 1729 was mated with polyphalangeal females. STURKIE (1942) found polydactyly to be suppressed in Houdans (mostly of type B) by the cold treatment here used. The results in table 4 indicate only a slight increase in the number of normals (no type of polydactyly) due to cold treatment in the polyphalangyls and virtually no influence on the duplicates. In the matings of polyphalangyls there was a definite increase in the percentage of type A (14 to 32 percent and 47 to 77 percent) and a corresponding reduction in the percentage of type B. In the duplicate matings cold treatment resulted in reductions in the incidence of the type E with increases in the types A and B. It would seem, therefore, that the incidence of the various types of polydactyly in the different stock may be the result of environmental as well as inherent factors. Extremely low temperatures such as here provided would seldom be encountered in the incubation period, but it is of interest to record that the expression of polydactyly is influenced by environmental factors. The writer failed to obtain the degree of suppression of polydactyly such as reported by STURKIE, but this may be due to differences in the stocks utilized in the test.

Because of the limited numbers and irregular distribution of data in table 4, the data are not very satisfactory for statistical analysis. The χ^2 test is probably the best one for material of this type. This test[2] showed statistically significant differences in expression of the polydactyly due to subjecting eggs to cold treatment during the early incubation period. In all the males, except the last one listed, the differences are statistically significant, and for the last one the numbers of treated chicks are small. The results of the test are as follows:

Male 2407—$\chi^2=31.15$, 3 degrees of freedom, P less than .001
Male 5372—$\chi^2=26.05$, 4 degrees of freedom, P less than .001
Male 4987—$\chi^2=20.65$, 5 degrees of freedom, P=.001
Male 1729—$\chi^2=8.75$, 5 degrees of freedom, P=.12

HETERODACTYLY

The phenomenon of heterodactyly in toe numbers has been observed by earlier workers (BOND 1920, 1926; PUNNETT and PEASE 1929). It has been noted that in heterodactylous birds the extra digit more often appears on the left foot. Although other types of heterodactyly occur in polydactyls, the usual reference to heterodactyly in the fowl has been applied to individuals possessing one normal and one polydactylous foot.

In table 5 are shown the types of heterodactyls observed in both the usual polydactylous stocks and in stocks of duplicates. The table is arranged to record the type of polydactyly found in each foot and brings out a number of interesting facts. The homodactyls found in the same matings are not here recorded. Considering first the data for the polydactyls (usual form), it is seen that we have confirmation for the findings of earlier workers that in polydactylous birds if one foot is normal (four-toed), it is more likely to be the right foot. Of the 177 individuals with one normal foot, only 35 showed polydactyly on the right foot, while 142 had the extra toe on the left foot. In the foregoing statement no consideration was given to the type of polydactyly found on the polydactylous foot. No statistical treatment is here necessary to prove that when polydactyly occurs on one foot only, the left foot is more usually affected. It is also evident that the incidence of the type D (fig. 1) polydactyly is high among heterodactyls with one normal foot. Of the 177 heterodactyls

[2] The statistical treatments given in this paper were made by DR. H. C. FRYER, statistician of the KANSAS AGRICULTURAL EXPERIMENT STATION.

of this type, 98 had the type-D polydactyly. Among the homodactyls reported in table 3 only 70 of type D were found in a total of 617. The high incidence of type D among heterodactyls having one normal foot may be taken to indicate that the factors which cause the development of a normal foot also suppress polydactylism in the other foot so that the expression is not normal. Thus type D may be considered as an aberrant or partially suppressed type B.

TABLE 5

Types of heterodactyly.

CONDITION OF RIGHT FOOT	CONDITION OF LEFT FOOT						
	NORMAL	TYPE A	TYPE B	TYPE C	TYPE D	TYPE E	TOTAL
Polydactylous stocks:							
Normal		11	59		72		142
Type A	1		49	20	3	1	74
Type B	8	76		3	25	11	123
Type C		4	3				7
Type D	26	17	57				100
Type E			5	2			7
Total	35	108	173	25	100	12	453
Duplicate stocks:							
Normal		4	11		33	3	51
Type A			19	7	4	11	41
Type B	3	19		19	6	75	122
Type C		4	11		1	83	99
Type D	12	1	25			5	43
Type E	1	3	31	112	1		148
Total	16	31	97	138	45	177	594

The tendency of polydactylism to be more readily suppressed on the right foot is also seen in the portion of table 5 presenting data on duplicate stocks. Of those having one normal foot, 16 showed normalcy on the left foot and 51 on the right foot, which would indicate that when polydactylism is expressed on one foot only, it occurs more frequently on the left foot. Of the duplicate heterodactyls possessing one normal foot, four were of type A, 14 of type B, none of type C, 45 of type D, and four of type E. The proportion of the various types of polydactyly among heterodactyls is very different from those found in table 3 for duplicate homodactyls. In table 3 the types C and E were far more numerous than any others, while they are rare among the heterodactyls. These results may be taken to indicate that the factor which produces one normal foot in a duplicate individual also tends to cause an abnormality in the expression of duplicate on the other foot. The existing combination of the various types of polydactyly in heterodactyls as shown in table 5 should throw further light on their relationships which are discussed later.

INHERITANCE OF VARIANTS OF POLYDACTYLISM

In table 3 are shown the various expressions of polydactylisms in the different stocks. It is seen that the proportion of the various types differs in the three stocks, thus indicating genetic differences among them. Convincing evidence has been presented showing that the polyphalangeal type of polydactyly is due to genetic modifiers. The only other variant occurring frequently in ordinary polydactylous stock is the type D which is somewhat variable in its expression, with the extra toe ranging in length from an atrophied single

TABLE 6

Types of duplicate offspring obtained from different parental types when mated with normals. (Normal and heterodactylous offspring not included.)

TYPE OF OFFSPRING	PARENT OF THE TYPE—					
	B		C		E	
	NO.	PERCENTAGE	NO.	PERCENTAGE	NO.	PERCENTAGE
A	2	3	2	2	4	3
B	32	53	25	28	35	29
C	8	13	43	48	31	26
D	12	20	4	4	2	2
E	6	10	16	18	49	40

phalanx to one of the same approximate length as the No. 1 toe. There were only a few matings involving the type D parents, and these produced a shortage of polydactylous offspring and a high percentage of heterodactyls. This might be taken as evidence for a genetic suppressor which either completely inhibits polydactylism or causes an abnormal type of polydactylism such as the type D. It was earlier found that these two conditions were frequently associated in heterodactyls. However, the data are not adequate to demonstrate existence of such a modifier.

From the data on duplicate stock matings (table 6) there is evidence for genetic factors influencing the type of duplicates obtained. The three most common types of duplicates—B, C, and E (see table 3)—were each mated with normals. Although all five types of duplicates were obtained from each of the parent types, there was a definite tendency for each to produce a high percentage of offspring of its own kind. To obtain such results in matings with normals would mean that any genetic modifiers differentiating duplicate into the three types must be at least partially dominant. The fact that the B and D types of duplicate are identical with the more common expression of the ordinary type of polydactyly might be interpreted as evidence for contamination of the duplicate stock by the polydactylous stock. Such a possibility was early recognized in view of the similarity of expressions, and it is believed that the precautions taken prevented such being the case.

The χ^2 test showed the association between parent and offspring types of polydactyly to be statistically highly significant. The χ^2 value of 63.57 with eight degrees of freedom gave a P much less than .001.

ANATOMY OF POLYDACTYLOUS FEET

In the classification of the variants found in the three stocks of polydactyly—usual type, duplicate and polyphalangy—the individuals fell fairly definitely in the arbitrarily established classes (fig. 1). A few questionable ones were included in type D, since these appeared to be modified type B in which the extra digit failed to develop completely. In such cases the extra toe might vary from a mere suggestion of a nail to a toe approximately as long as the first digit. The data presented earlier seem to indicate that the type D is the expression of the usual type of polydactyly (type B) under the influence of an inhibitor. The careful studies of HARMAN and ALSOP (1938) and HARMAN and NELSON (1941) on the anatomy of polydactylous feet through the use of alizarin preparations showed considerable variation in the number of phalanges and metatarsals. There was evidence of fusion or perhaps failure in separation of the phalanges. Thus the relative length of the digits is not always an accurate measure of the number of bones they carry.

The survey of the various types of polydactyls observed in this study suggests the action of three rather distinct developmental procedures. These steps are not always perfectly executed, thus giving a rather wide range of types of polydactylism. The three steps are: first, the addition of a longer digit outside of the halux or number one digit; second, the splitting of the added digit; and third, the loss of the normal halux or number one digit. It is true that other explanations might be found for the observed types of polydactyls, but the following facts seem to lend support to the hypothesis. First the type B (fig. 1) polydactyl, which is the usual expression found in five-toed breeds, seems to be the result of an addition rather than a splitting of the halux of a normal (four-toed) foot. In the large number of polydactyls observed in this study, there was virtually no evidence of splitting of the halux, although the phenomenon was of common occurrence in the extra digit. Furthermore the studies of HARMAN and NELSON (1941) revealed the fact that the halux and the extra digit usually had separate metatarsals. The fact that the extra toe has one more phalanx than the halux is further evidence that it is not being split off from the halux.

The view that types C and E (fig. 1) are the result of splitting of the extra digit is sustained by the large number of variants of these groups. They show evidence of splitting originating distally and varying from merely a double nail to two distinct toes of equal length. HARMAN and NELSON (1941) found the split toes frequently to have one or more phalanges in common and usually to possess a single metatarsal.

Evidence that types A and C are the result of the loss of the normal halux from a foot carrying one extra digit, split in type C and unsplit in type A, is found in variants of these two types. Frequently the types A and C showed a

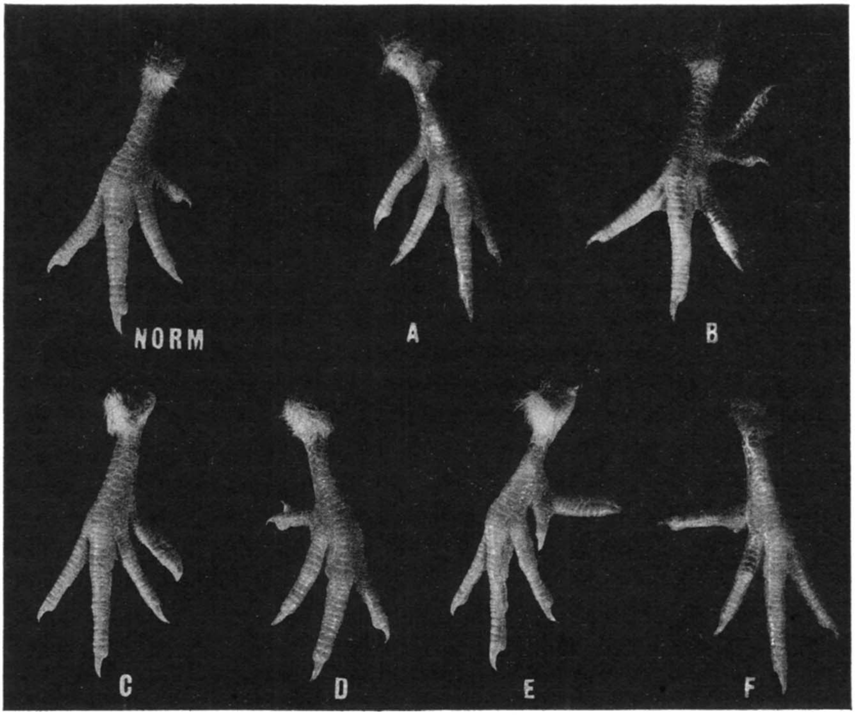

FIG. 2. Illustrating the normal four-toed foot, the five types of polydactylism and (F) an expression of polyphalangy showing a vestige of the missing halux.

vestige (see fig. 2, type F) of the halux in the positions where the digit occurs in types B and E. The vestige of the halux may carry a nail or show only as a thickening at the inside base of the extra toe. If the hypothesis of the loss of the halux is accepted, types A and C may be interpreted as being the result of this action in types B and E, respectively.

Thus far all observed types have been accounted for except type D. As mentioned before, those variants placed in this class are somewhat divergent. It is proposed that those classed as type D are imperfectly expressed type B polydactyls. Support for this view is found in the fact that type D was most commonly observed in stocks carrying the type B polydactylism (see table 3). Furthermore, in table 5 it is seen that in heterodactylous individuals (complete suppression of polydactyly in one foot) there is a high incidence of type D polydactyls. This seems to suggest that type D is an imperfectly developed type B and would thus account for the wide variation in those polydactyls of the type D group.

The data on heterodactyls in table 5 also lend support to the earlier proposal that type A is a modified B, and C a modified E. It is seen that in the heterodactylous foot, types A and B and types C and E are most commonly associated, indicating that developmentally they are related. Likewise the data in table 3 on incidence of the various types in the different stocks show association of the above mentioned classes of polydactyly.

Inasmuch as it has been shown that some, and perhaps several others of the variants of polydactylism have genetic bases, it is somewhat difficult to see how they are associated developmentally. The distribution of the different types suggests the interaction of the addition of a digit, the splitting of the added one, and finally the suppression of the number one digit of the normal foot. In the usual polydactylous breeds, the development of the extra toe seems to be the only change. In the polyphalangeal stock, the usual type of polydactyly is further modified by the suppression of the normal halux. Polyphalangy also occasionally shows splitting of the additional digit. In the case of the duplicate stock, most individuals show the splitting of the extra digit, and suppression of the normal halux is common.

GENETIC RELATIONSHIPS OF DUPLICATE

Although duplicate has many characteristics in common with the polydactyly found as a standard trait in several breeds of poultry, it also differs sufficiently to demonstrate an independent genetic origin. An earlier publication by the writer (1941) contained the suggestion that duplicate and polydactyly constitute a multiple allelic series since the segregation ratios from crossing the two kinds of polydactylism favored this interpretation. Fortunately the recent studies of HUTT and MUELLER (1943) supplied information which made possible a crucial test of theory of the existence of multiple allelic series for polydactylism. HUTT and MUELLER found that ordinary polydactylism belonged to the same linkage group as did duplex comb and multiple spurs. If duplicate is a mutation of the same gene as is polydactyly, then the former should show linkage relations with duplex comb and multiple spurs similar to those of polydactyly. A mating was set up to test the linkage of duplicate with multiple spurs (repulsion series), since data were already at hand testing linkage of duplicate with duplex comb. The test of two males heterozygous for duplicate and multiple spurs gave the following linkage results: duplicate, non-multiple spurs 187 and 119; non-duplicate, multiple spur, 149 and 104; duplicate, multiple spurs 46 and 67; nonduplicate, non-multiple spurs 89 and 37 where the first two groups constitute the parental combinations and the latter two the new combinations. The combined results of the two tests gave a crossing over percentage of 30. A total of 191 individuals gave a crossover percentage of 43 percent between duplicate and duplex comb.

In table 7 is given a comparison of the linkage relations of duplicate and polydactyly with duplex comb and multiple spur. The table carries data of both the writer and HUTT and MUELLER (1943). It is seen that duplicate gives crossing over data with duplex and multiple spur similar to that obtained from polydactyly with the same characters. The crossover percentages for duplex with polydactyly and with duplicate were 46 and 43, respectively, and for multiple spurs were 34 and 30. Some of the difference in percentage crossing over is probably due to variation in the degree of expression of polydactyly

TABLE 7

Comparison of linkage relations of polydactyly and of duplicate.

CHARACTERS TESTED	PERCENTAGE CROSSING OVER REPORTED BY	
	HUTT AND MUELLER	WARREN
Polydactyly—duplex	42	46
Duplicate—duplex	—	43
Polydactyly—multiple spur	34	—
Duplicate—multiple spur	—	30
Duplex—multiple spur	28	28

noted by numerous workers and its effect on linkage data reported by HUTT and MUELLER (1943). The writer's data on the linkage relation of polydactyly and duplex involved 1079 individuals; however, the elimination of matings showing striking shortages of polydactyls failed to significantly change the crossover value of 46. In the case of matings involving duplicate and multiple spurs there was probably some error due to the duplicate character so extremely deforming the leg that multiple spurs were not easily identified. The shortage of polydactyls in the duplicate stock was not so great as that observed in the usual form of polydactylism.

The linkage data in table 7 fairly definitely substantiate the earlier proposal that duplicate and the usual type of polydactyly are probably mutations at the same locus, thus constituting a multiple allelic series.

SUMMARY

Three strains of polydactylous fowl, the usual five-toed type, a polydactylous stock selected for polyphalangy, and the duplicate type of polydactylism, were investigated. Each of the three stocks showed a distinctive incidence of the various expressions of polydactylism.

An analysis of data on heterodactyly indicated that some of the variations in expression of polydactylism were the result of partial suppression of this character. The suppression appeared to be due to both environmental and inherent factors. Low temperatures during the early incubation period influenced the expression of polydactylism.

It is proposed that expression of polydactylism is accomplished by varying combinations of three processes—the addition of a digit beside the No. 1 digit; the splitting of the added digit; and the loss of the normal No. 1 digit.

Polyphalangy appeared to be due to an incompletely dominant modifier of the usual five-toed type of polydactylism. That the usual type of polydactylism and duplicate are each dominant mutations at the same locus is indicated by segregation ratios and by linkage relations. There is also evidence that the expression of polydactylism in three stocks studied is influenced by minor genetic factors.

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