POLYDACTYLY, A SUB-LETHAL CHARACTER IN THE PIGEON

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Palmetto Pigeon Plant, Sumter, S. C.

A PIGEON with double hind toes was illustrated in this JOURNAL for 1916 (p. 321). The bird was a domestic pigeon (Racing Homer) found in Australia, and it lived to maturity. Mated with a sister, it produced an offspring which had an extra toe on one foot. According to Fontaine[2], extra toes are found in the Syrian variety of the Spot breed (*le pigeon huerté syrien*), but he gives no further details or illustrations. This variety has apparently never been described elsewhere, and its existence seems questionable.

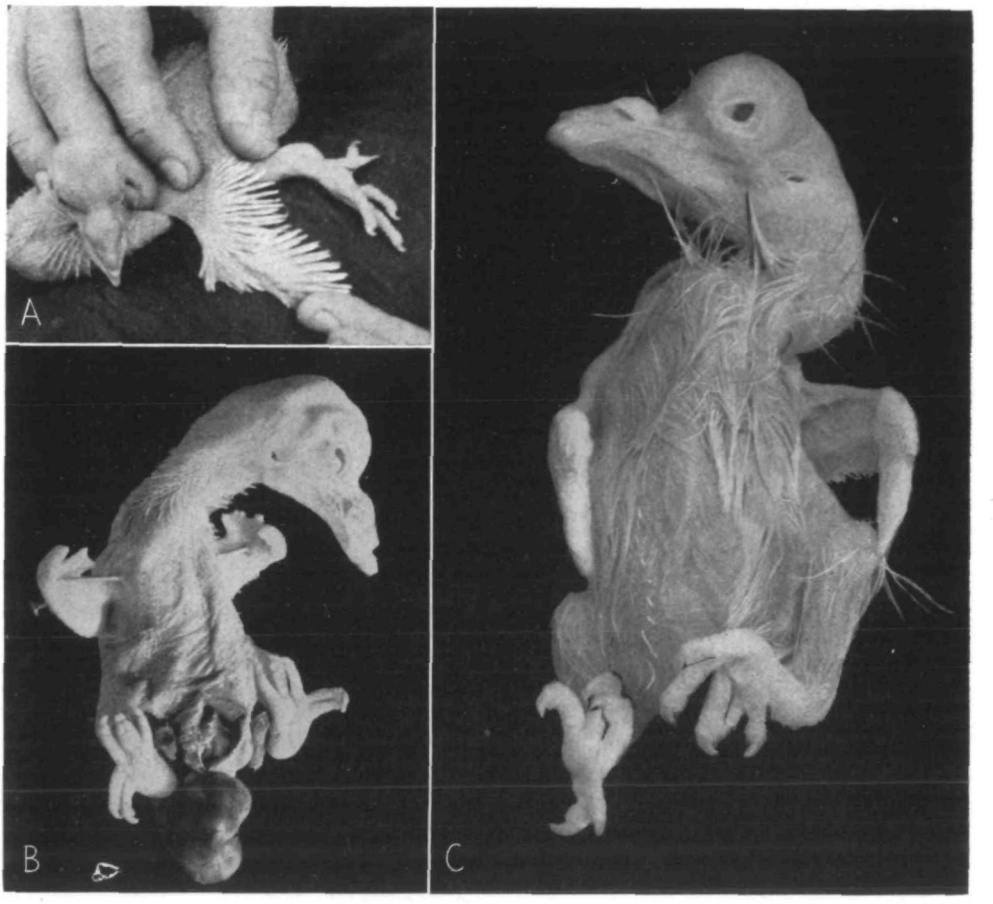
The above references are the only ones, to our knowledge, up to 1941 on the occurrence of polydactyly in pigeons.

In August, 1939, a polydactyl squab appeared at the Palmetto Pigeon Plant of Sumter, S. C. The parents were Silver King pigeons, both perfectly normal (mating K17-531). Each of the squab's feet had an extra hind toe, just as shown in the 1916 illustration; in addition, each wing had an extra thumb (see Figures 5*A* and 4*A*). A photograph of this squab at the age of about five days is given by Levi[3] (p. 240).

This squab was given careful attention. It was very plump and fat, but was retarded in growth and had a chronic wheeze or rattle in breathing. At weaning age (about one month) it was removed from the adult pigeons and placed in an individual coop. It showed no ability to feed itself and had to be hand-fed. At this time it was considerably smaller than normal Silver Kings of the same age, and was abnormal in several other respects. The lower beak projected nearly an eighth of an inch beyond the upper; the legs were short, particularly the tarsi, giving a squatty, duck-like appearance; and the plumage was somewhat defective. The main tail and wing feathers were somewhat frayed and twisted, and there were only six rectrices instead of the normal twelve. The bird could not fly, and had some difficulty even in walking. In spite of good care and superficial healthiness—no emaciation—it died at the age of 35 days. Autopsy failed to reveal the cause of death; the internal organs appeared normal. The sex was female.

In the following year (1940) more polydactyl squabs appeared, not only from the same parents but from three other pairs of Silver Kings (matings K17-534, K15-453, and K7-365). Two more pairs of Silver Kings produced polydactyls in 1941 (K15-457 and K3-422). From these six pairs a total of 24 polydactyl squabs has been obtained. An additional specimen of unknown parentage was found under foster parents in 1940; its color indicated that it, too, was of Silver King origin. None of the polydactyls lived to maturity in spite of better than ordinary care. Though often placed under the best foster-parents, the majority died at less than three weeks of age from no definite ailment.

Although these polydactyls all resembled each other to some extent, there was nevertheless a wide variation. An exhaustive study of the anatomical differences has not been attempted, but a brief survey of the range is desirable. Of the 25 specimens, 18 were preserved for study, and these are probably a fair sample. The feet varied from having only a single, broad, flat hind toe with two claws to fantastic hand-like extremities with six digits and up to seven claws. Leg length varied from slightly below normal to very much shorter. Extra thumbs on the wings were absent in several cases. At the other extreme, two young which died before hatching



POLYDACTYL SQUABS

Figure 4

A—the first polydactyl discovered at an age of about one week. Note the extra hind toe, the extra thumb on the wing, and the undershot beak. The bird is a female and is classified as Group II. *B*—An extreme (Group IV) polydactyl female which failed to hatch. Note the multiple thumbs on the wings and their paw-like appearance. On the feet the extra toes are markedly distorted. The undershot beak and the short down are also characteristic. *C*—The female polydactyl from the White family,—not closely related to the others shown here. The extra toe and the undershot beak resemble the Silver King polydactyl, but the wings and the down are normal.

had wings so extremely polydactylous that they resembled embryonic mammalian fore-paws. All the polydactyls except one had undershot beaks; and that one, which lived to 45 days, had upper and lower beaks of equal length, without the normal tendency for the upper to hook over the lower. The tail feathers were of sufficient length to be counted accurately in only six cases. Only one bird in addition to the first had a subnormal number; two others were normal, and the remaining two had one more than normal. The plumage was slow-growing in all specimens, and somewhat defective in the two older specimens which had fully developed feathers (see Figure 7). Another peculiarity observed in all cases which were examined early enough was shortness of the nestling down, similar to the condition found in young of "dilute"

POLYDACTYL FOOT AND "HAND"

Figure 5

At left, the "hand" region of the right wing of a Group III polydactyl male, which survived 15 days. Some feathers have been removed to show the extra thumb (indicated by arrow). At right, is the right foot of a Group II polydactyl dead at 35 days.

coloration. Normal Silver Kings are not of this type (Levi,[3] p. 222).

Correlated Variation

All the above abnormalities were clearly correlated in their variation. That is, the more abnormal a squab was in regard to one feature, the more abnormal it tended to be in regard to the others. This correlation was not perfect, but it should be noted that a small degree of asymmetry or difference between right and left sides in regard to any one feature was found in many of the specimens (Figure 6). Because of the correlation it was rather easy to classify the polydactyls into four grades or groups. as follows:

Group I. No extra thumb or only on one wing; single extra hind toe, generally more or less joined with other toe.

Group II. Single extra thumb on both wings; single extra hind toe on each foot, usually not joined with other toes.

Group III. Single, usually large, extra thumb on each wing; two extra toes or claws on one or both of the feet.

Group IV. More than one extra thumb on each wing; two or more extra toes or claws on one or both feet; feet distorted.

Only one specimen, a 24-day-old male, did not fit into this grouping. This squab had two extra toes or claws on each foot, but an extra thumb on only one wing. It seemed to be a compromise between groups III and I, and hence was placed in group II. The frequencies in the four groups are roughly equal except for group IV, which has only two representatives.

When the ages at death in the different groups are compared (see Figure 9), it is seen that there is a definite correlation between the grouping and life expectancy. The more abnormal a squab is, the poorer are its chances to live to a given age. Sex, however, appears to have little or nothing to do with the grouping or with age at death, although the three oldest specimens were all females. As the female in pigeons is the heterogametic sex, and generally the weaker under adverse conditions, it is

MULTIPLE TOES
Figure 6

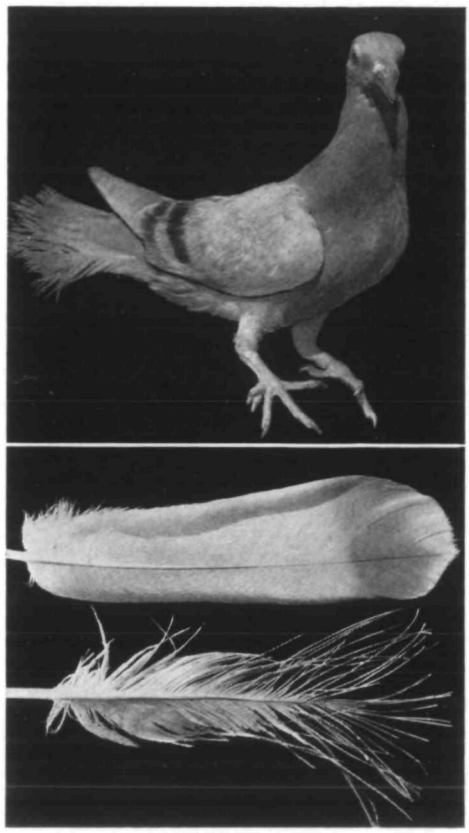
Feet of a Group III polydactyl dead at 20 days. Note the joined extra hind toes on the right foot and the broad extra toe with two fused claws on the left foot. Note also the short thick tarsi.

interesting that the female polydactyls were at least equal to the males in vigor.

Inheritance

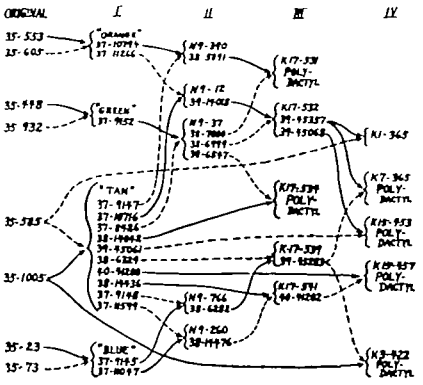
The stock of Silver Kings here involved originated from a few pairs of 1935-bred birds obtained from the pigeon farm of G. W. Middleton and Sons, in Norristown, Pa. In answer to an inquiry about the polydactyls, they stated that they "occasionally get a squab like this" (pers. com., 1940). Evidently then this stock can be expected to produce the condition regardless of environment. However, it must be noted that not one of the very numerous offspring of the original pairs was polydactyl, nor were any of the far more numerous second generation descendants of that type. Polydactyls appeared only in the third and fourth generations.

An investigation of the pedigrees reveals two very significant facts. In the first place, no inbreeding occurred before the production of the third generation (because it has been a breeding policy here to discourage brother × sister matings). In the second place, all the polydactyls trace back on both maternal and paternal sides to one of the original pairs—the parents of the "Tan" family. In other words, the polydactyls were produced by inbreeding, from matings of birds related to each other only through that particular pair of original Silver Kings. These facts all suggested the following explanation: that the polydactyls are homozygous for a simple Mendelian



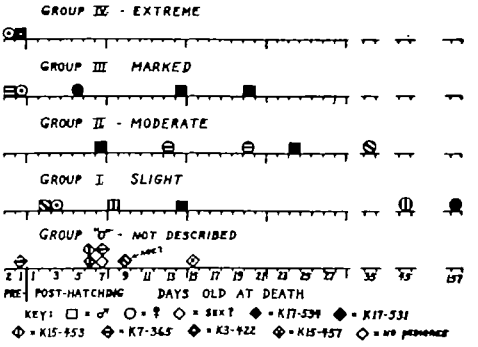
POLYDACTYL METHUSELAH
Figure 7

This female lived to the age of 157 days, which far exceeded the life-span of any other extra-toe bird. She was classified as a squab in Group I, the least abnormal type. Below is shown a tail-feather from this bird compared with a normal tail feather, to show the defective structure.



RELATIONSHIP OF POLYDACTYLS
Figure 8

Pedigree chart of the Silver King polydactyls. The generations progress from left to right. The male line is drawn solid and the female dotted. Sibs are enclosed in a bracket and headed by the mating number or name of the parents.



VITAL STATISTICS OF POLYDACTYLS
Figure 9

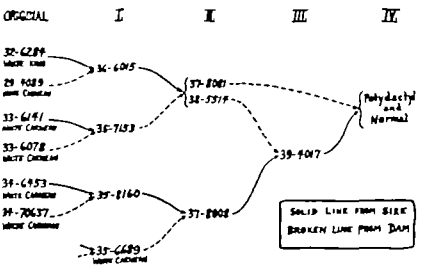
A tabulation to show the relationships between the degree of polydactyly (group classification), sex, family, and age at death.

recessive factor, which was introduced by one of the parents of the "Tan" family. To test these original birds, each was mated with a descendant which had produced polydactyls. The new mating involving the old male (K3-422) supported the theory by producing a polydactyl, and the new mating involving the old female (K1-365) also supported it by not producing any. It appears therefore that the original male, 35-1005, was the sole source of the trait. (See pedigree chart of the polydactyls—Figure 8).

The theory that polydactyly is a simple Mendelian recessive in inheritance is further supported by the ratio of 91 normal to 24 polydactyls produced by the six matings (Table I). This ratio is not significantly different from 3:1 (expectation 86:29).

A final test was made to ascertain whether polydactyly could be produced without inbreeding—whether some chromosome aberration, rather than a recessive factor, might be responsible. Matings K17-534 and K15-453, which had produced polydactyls, were broken up. The male parents were mated with ordinary females of the White Carneau breed (matings K11-330 and K11-349), and the female Silver King parents were mated with White Carneau males (matings K12-353 and K12-359). These four new matings produced a total of 42 squabs from 43 eggs, and all young were normal. Adding mating K1-365, we have five matings of polydactyl-producers to pure normal pigeons. These laid a total of 54 eggs and raised 50 young, all normal. With such a low proportion of losses, there is certainly no indication of chromosome aberration here. Accordingly it appears unquestionable that the polydactyly and associated abnormalities are the effect of a simple Mendelian recessive factor, not sex-linked. We have given it the factor symbol *py*.

Since not one of the 25 polydactyls survived to maturity, in spite of our efforts to maintain them, we consider the *py* factor sub-lethal. The immediate cause of death has not been found, and most of the specimens seemed to be thriving the day before death. The respiratory trouble noted in the first polydactyl was also present in most of the others which lived to the second week or beyond, and might have caused death by suffocation, but ordinarily this ailment is not serious, and none of the specimens showed internal lesions severe enough to be fatal. The polydactyls in group IV (extreme) were so abnormal that they were unable to hatch. The fe-



WHITE POLYDACTYL PEDIGREE
Figure 10

This shows some remote relationship to the Silver King breed wherein the other polydactyls appeared.

male which lived to the age of 157 days would have died much younger under ordinary conditions, for the undershot beak made it difficult for the bird to pick up grain. It had to be hand-fed for some time after weaning, and would have starved to death later if feed and water had not been placed in the most obvious positions. Its eyes appeared to be normal but they did not focus forward properly, and the mental development seemed poor. The bird could not fly, and walked awkwardly. In short, whether extreme or slight, the expression of this factor makes for early death.

A Separate Occurrence of Polydactyly

By a remarkable coincidence polydactyly has also been discovered in an entirely unrelated family of pigeons at the Palmetto Pigeon Plant. This is a family of "Show White Carneaux," but not purebred, as a White King male figures in the immediate ancestry. The first polydactyl from this family appeared in 1940. The bird seemed fairly vigorous but died at the age of one day. There was a distinct extra hind toe on each foot, and the lower beak was somewhat undershot, but there were no extra thumbs on the wings and the nestling down was normal. The legs and tarsi seemed normally proportioned, not shortened (Figure 4*C*). This specimen was female.

The second polydactyl from this family failed to hatch. It closely resembled the first except that the extra toe on the left foot had two claws, and the sex was male. The parent pair produced in all 18 eggs, of which four were broken or lost, three had dead young embryos, and eleven produced describable squabs. Except for the two polydactyls, all young were quite normal.

An examination of the pedigree (Figure 10) shows that inbreeding is again involved. As purebred Carneaux have never been known to produce polydactyly, it is logical to place most suspicion on the King ancestor as the source of the trait, but in this case the original bird was dead and could not be tested.

To test whether the same factor was involved here as with the Silver Kings, this white pair and mating K17-531 were broken up and the mates interchanged. The White male with the female Silver King produced 22 eggs, from which 16 young were examined, all normal. Three of the remaining eggs were infertile and three had embryos dead at an early stage. The White female with the Silver King male produced 19 eggs, from which 13 young were described, all normal; one of the remaining eggs was lost, another infertile, three had young dead embryos.

TABLE I. Matings of polydactyl-producers with each other (above), and with non-polydactyl-producers (below).

MATING	EGGS				SQUABS		
	NUMBER LAID	INFERTILE	DEAD YOUNG EMBRYO	LOST OR BROKEN	NORMAL	POLY-DACTYL	NO RECORD
K17-531	30				26	3	1
K17-534	40		4	3	22	7	4
K15-453	18		1		13	4	
K7-365	16	2	1		8	5	
K15-457	12				8	4	
K3-422	16		1		14	1	
TOTAL	132	2	7	3	91	24	5
K1-365	11			3	8		
K11-330	12				12		
K11-349	11			1	10		
K12-353	10				10		
K12-359	10				10		
TOTAL	54	0	0	4	50	0	0

and one produced a squab which was not examined. Although the number of dead embryos from these matings is rather high, it is no higher than in the original white mating, and it probably has nothing to do with polydactyly. If we judge from the young described, it appears unlikely that the two types of polydactyly are produced by the same factor, or even by different alleles. In any case it appears that the second type is similar to the first in being simple recessive, autosomal, and sub-lethal.

Discussion

At present only speculation is possible as to the causes of the wide variation of expression of the *py* factor. Modifying factors could be postulated, but the existence of some asymmetry suggests that the factor may be sensitive to slight differences in environmental conditions during incubation. Two types of polydactyly are now known in the chicken, and both of these are considerably variable also. Sturkie[5] has studied the effect of temporary chilling of young polydactyl embryos; this treatment appears to inhibit the development of extra toes in many cases. Perhaps variation in incubation temperature or other conditions has influenced the course of growth in the pigeons also; but it is interesting that no correlation of the grouping with season of the year could be found.

The two types of polydactyly in the chicken are not recessive as in the pigeon, but dominant to normal, and apparently allelic to one another. Further, their effects seem limited to the feet and wings, and viability is normal except in extreme variants.[6] The more common type of polydactyly in the chicken shows no extra thumbs on the adult wings, though the embryos are said to have them temporarily.[4] It is curious that polydactyly in the pigeon, while superficially similar to that in the chicken, should be so fundamentally different. It is possible that the cases reported from Australia[1] are a dominant type as in the fowl, as well as not being sub-lethal.

Our first impression of the pigeon polydactyls was that they suggested some grotesque prehistoric creature come to life. Probably they have little evolutionary significance, but they are of interest to the student of teratology. Dr. Walter Landauer has suggested (pers. com., 1940) that the condition may be analogous to the Laurence-Moon-Biedl syndrome found in certain human families. This syndrome is characterized not only by polydactyly and syndactyly but also by such features as obesity, hypogenitalism, and mental retardation.

Summary

A variable syndrome including polydactyly of feet and wings, shortened legs, undershot beak, short nestling down, and defective plumage was found in a family of Silver King pigeons. Of 25 specimens, none survived to maturity. Breeding data show that a simple recessive pleiotropic factor is responsible, which is symbolized *py*. A somewhat similar condition was also found in an unrelated family, and appears to be similar in inheritance but not allelic with the previous type.

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Population Growth in India

Preliminary returns of the Census of India of March 1, 1941, indicate a population of 388.8 millions, an increase of 50.7 millions since 1931. This increase of fifteen per cent is the largest in Indian census history, both relatively and absolutely. India now has a population which is not much smaller than that of all Europe outside of Russia. In the past decade its population increase alone amounted to more than the total population of the British Isles. The trend of growth of the Indian population has been almost cyclical.