PERSISTENCE OF THE LEFT SYSTEMIC AORTIC ARCH IN THE CHICK

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(With Six Text-figures)

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Introduction

In birds, the aorta is formed from the right-hand member of the fourth pair of embryonic aortic arches, the left one normally disappearing at an early stage of development (Figs. 1, 2). In the chick, this left systemic arch is said to have gone completely by the eighth day of incubation (Lillie, 1952) and it has been recorded only rarely in older embryos (Pohlman, 1920; Bremer, 1928). Fleming (1926) has referred to minor differences between species in the time that the left arch is interrupted. Abnormal developments of the aortic arches, including functional left systemics in first and second week embryos, have been obtained experimentally by cauterization (Bremer, 1928) and by ligaturing the arches on the right-hand side (Stephan, 1949). Vestiges of the fourth left arch in adult birds have been reported by Mackay (1888), Beddard (1898) and Biswas (1946). Glenny (1940), in an account of an anomalous artery in an American kingfisher, concludes that this is a functional left systemic arch, although it has no ventral connexion with the arteries arising from the heart.

Material and methods

During the examination of late embryos from a progeny testing scheme with Rhode Island Red poultry, the left systemic arch was noted, either complete and apparently functional or reduced in size (Fig. 3). These embryos were the 'dead-in-shell' remaining in the incubator after the hatched chicks had been removed. Most of them had died during the last four days of incubation when there is a peak of embryo mortality.

Over a period of three years, 1536 such embryos were dissected, and the left systemic arch could be recognized in 135 of them (8·79 %). In view of the fact that these embryos had failed to hatch, this abnormality might have been attributed to some pathological condition. However, in 1952 the opportunity arose of examining a large number of normal day-old male chicks of the same breed; and 93 out of a total of 1211 of these (7·68 %) also showed some sign of the left systemic arch (Table 1).

The specimens examined each year came from thirteen or fourteen cocks of which ten had not previously been used; and each cock was mated with a different group of ten to fourteen hens. The frequency of the left systemics did not differ significantly in successive years ($P = 0{\cdot}095$), so this condition may be said to have occurred fairly widely and regularly in the breed over this period.

Amongst the embryos, signs of the left systemic were more frequent in females than in males (Table 2), and this difference almost reaches significance at the 5 % level

($P=0{\cdot}055$); so the incidence found in male chicks alone may not be representative of the breed. However, the male chicks formed a more uniform age group than the embryos, and most of the observations reported here were made on them.

The male chicks were obtained from six hatches at weekly intervals during April and early May, and were killed between 24 and 48 hr. after hatching. The arterial system was

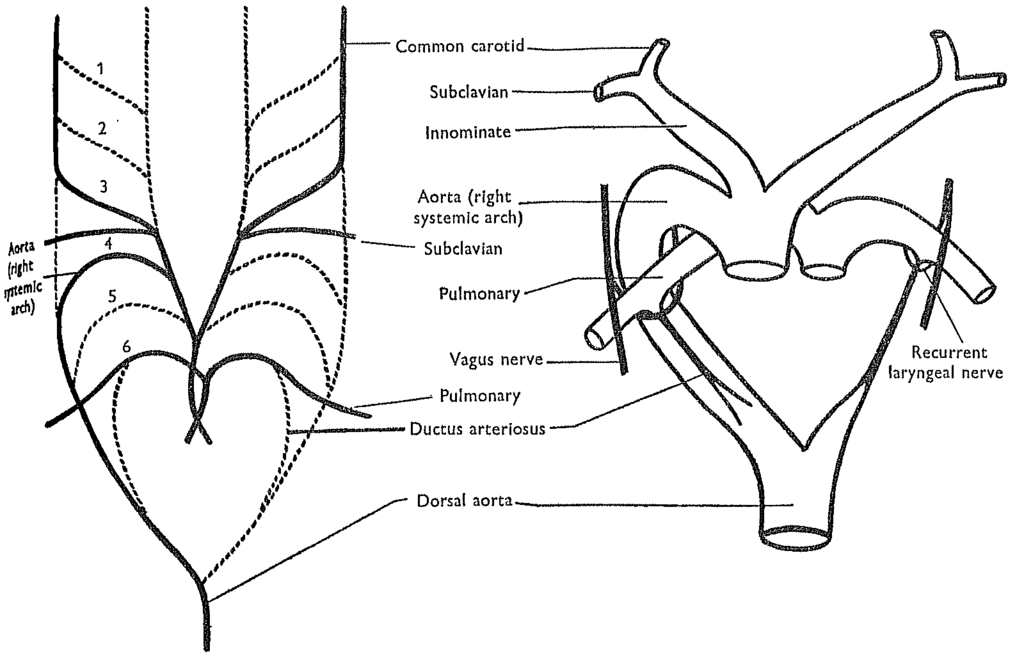

Fig. 1. Fig. 2.

Fig. 1. Diagram of the six pairs of embryonic aortic arches in birds and the definitive arteries derived from them (ventral view). Dotted lines indicate vessels which normally disappear before the end of the eighth day of incubation in the chick except for the ductus arteriosus which functions up to the time of hatching.

Fig. 2. Ventral view of the arteries arising from the heart in a normal day-old chick (no. 7763); slightly diagrammatic.

Table 1. *Incidence of the left systemic arch in the Rhode Island Red breed*

	Normal	Abnormal	Total	Abnormal (%)
		Embryos of 18–21 days' incubation		
1949	288	19	307	6·18
1950	602	70	672	10·42
1951	511	46	557	8·26
Total embryos	1401	135	1536	8·79
		Day-old male chicks		
1952	1118	93	1211	7·68

$\chi^2=6{\cdot}363$; $n=3$; $P=0{\cdot}095$.

injected through the heart with a coloured solution of rubber latex, and abnormal specimens were classified according to the size of the persistent left systemic arch. Examples of these were drawn, and the specimens then cleared in methyl salicylate which enabled the injection medium to be seen in the vessels. Occasionally a fine thread of tissue was found attached to the aortic trunk which was probably the last stage in the reduction of the left arch. These, however, were ignored; and only cases where the remains

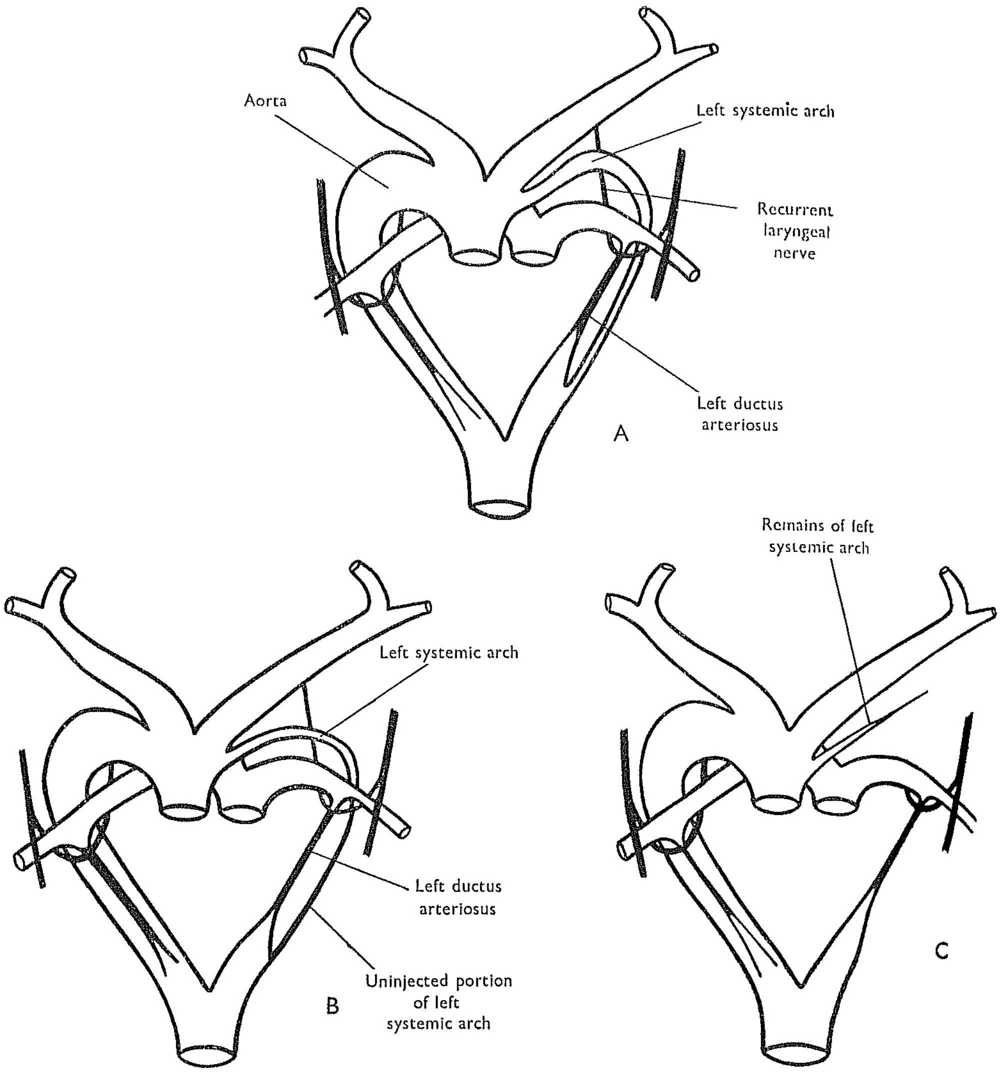

Fig. 3. Three forms of the persistent left systemic arch in day-old chicks: slightly diagrammatic. A, specimen no. 3222. B, specimen no. 1810. C, specimen no. 1813.

Table 2. *Incidence of the left systemic arch in each sex amongst embryos* (1949–51)

	Normal	Abnormal	Total	Abnormal (%)
Males	693	55	748	7·35
Females	708	80	788	10·15

$\chi^2 = 3{\cdot}751$; $n = 1$; $P = 0{\cdot}055$.

of the vessel were large enough for the injection medium to have entered it, even if only for a short distance, were classed as abnormal.

OBSERVATIONS

The examples of the left systemic arch form a series showing its gradual reduction in size, but they can be grouped into the following three categories:

A. The complete left arch present and injected throughout. It arises from the aortic trunk or from the innominate, and curves backwards, dorsal to the pulmonary artery, joining the base of the ductus arteriosus and leading into the dorsal aorta (Figs. 3 A, 4).

B. The left arch still reaches round to the dorsal aorta, but it is reduced distally to a solid thread and so is only injected for part of its length (Fig. 3 B).

C. Only a short stump of the left arch remains, and it ends as a fine thread in the connective tissue between the innominate and pulmonary arteries (Fig. 3 C).

The distinction between the smaller A and the B types was sometimes difficult to make out by dissection alone; but after clearing, any specimen with the injection medium in the left systemic arch interrupted was classed as B. The proportion of these three forms amongst the abnormal day-old chicks was A, 13 (14·0 %); B, 23 (24·7 %); C, 54 (58·1 %).

In three specimens there is a vessel in the position of the left systemic arch which runs forwards dorsal to the innominate and joins the common carotid opposite the origin of the vertebral artery (Fig. 6 C). In the specimen figured, this vessel is injected the whole way along; in the other two it is reduced to a solid thread where it joins the common carotid.

Approximately 1 % of the chicks examined (13 out of 1211) showed the A condition, that is, a complete left systemic arch injected throughout. These additional vessels vary in size, the largest being almost as large as the normal aorta and showing no sign of becoming reduced (Fig. 4). Especially in the case of the smaller ones, the presence of the injection medium does not necessarily prove that the vessel was functioning in the living chick, since the injection pressure was greater than the normal blood pressure. In addition, the medium might be forced forwards from the dorsal aorta, as is clear from the fact that the base of the ductus arteriosus is often injected even when the rest of it is occluded. However, there can be little doubt that in many cases the persistent left systemic arch was functioning as an additional aorta at the time of hatching (Figs. 4, 5).

It is quite possible that such vessels might continue to grow and remain functional in the adult. There seem to be no records of this in birds; but in mammals, where the normal aorta is formed from the left systemic arch, cases are known of bilateral aortic arches, due to the persistence of the right-hand arch which normally disappears in the embryo (Sawin & Edmonds, 1949). The B and C conditions of the left systemic in these chicks could not of course have been functional, and they would almost certainly have disappeared during later growth.

The anomalous artery running forwards to the common carotid (Fig. 6 C) should most probably be regarded as a variation of the persistent left systemic. Such a vessel might be formed if the lateral dorsal aorta between the third and fourth arches (the ductus caroticus) persisted on the left side in addition to the fourth arch, whilst the more posterior connexion between the fourth arch and the ductus arteriosus disappeared, as it usually does. If this explanation is correct, then the point where this anomalous vessel joins the common carotid probably marks the dorsal end of the third arch.

Seven more cases of such an anterior prolongation of the left systemic arch had been found amongst the late embryos examined in previous years. These, however, showed some differences; in four of them the extra vessel runs parallel with the common carotid artery for some distance, joining with it between one-third and one-half of the way along the neck (Fig. 6A). In the other three specimens, this vessel passes more laterally and forms the artery which runs up the neck alongside the vagus nerve (the comes nervi vagi of Hafferl, 1933), in one case also giving rise to the vertebral artery (Fig. 6B). Both these vessels normally arise from the carotid by means of a common stem. Abnormal developments of the aortic arches resembling these conditions were obtained experimentally by Bremer (1928).

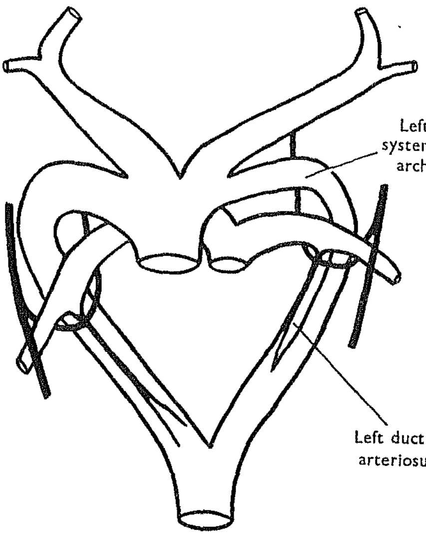

Fig. 4.

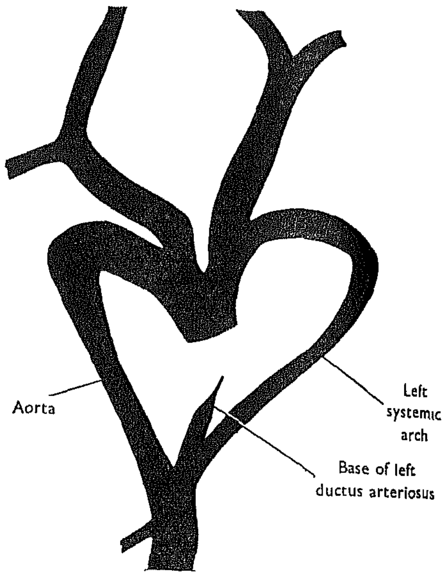

Fig. 5.

Fig. 4. Ventral view of the arteries arising from the heart in day-old chick no. 2745 showing a complete and well-developed left systemic arch. The left ductus arteriosus originally ran along the ventral surface of the left systemic arch; it has been displaced slightly towards the mid-line.

Fig. 5. Camera lucida drawing of the injection medium in day-old chick no. 7191 showing injection of the persistent left systemic arch. The slight constriction along both systemic arches indicates where they are crossed by the pulmonary arteries.

Genetics

The parentage of the day-old chicks was known, and there is some evidence of genetic influence in the persistence of this embryonic vessel. Chicks with some sign of the left systemic occurred amongst the progeny of all the cocks, but there seemed to be differences in the percentage of abnormal offspring from each cock (Table 3). Ten of the cocks used

Table 3. *Incidence of left systemics amongst offspring from each cock. Day-old male chicks (Rhode Island Red), 1952*

Cock no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Normal	99	70	92	118	68	105	99	79	117	124	28	22	37	60	1118
Abnormal	10	1	8	19	4	12	7	11	7	4	2	2	1	5	93
Total	109	71	100	137	72	117	106	90	124	128	30	24	38	65	1211
Abnormal (%)	9·17	1·41	8·00	13·86	5·55	10·27	6·60	12·22	5·64	3·16	6·60	8·33	2·61	7·71	7·68

χ^2 (for cocks 1–10) = 19·998; $n=9$; $P=0{\cdot}0175$.

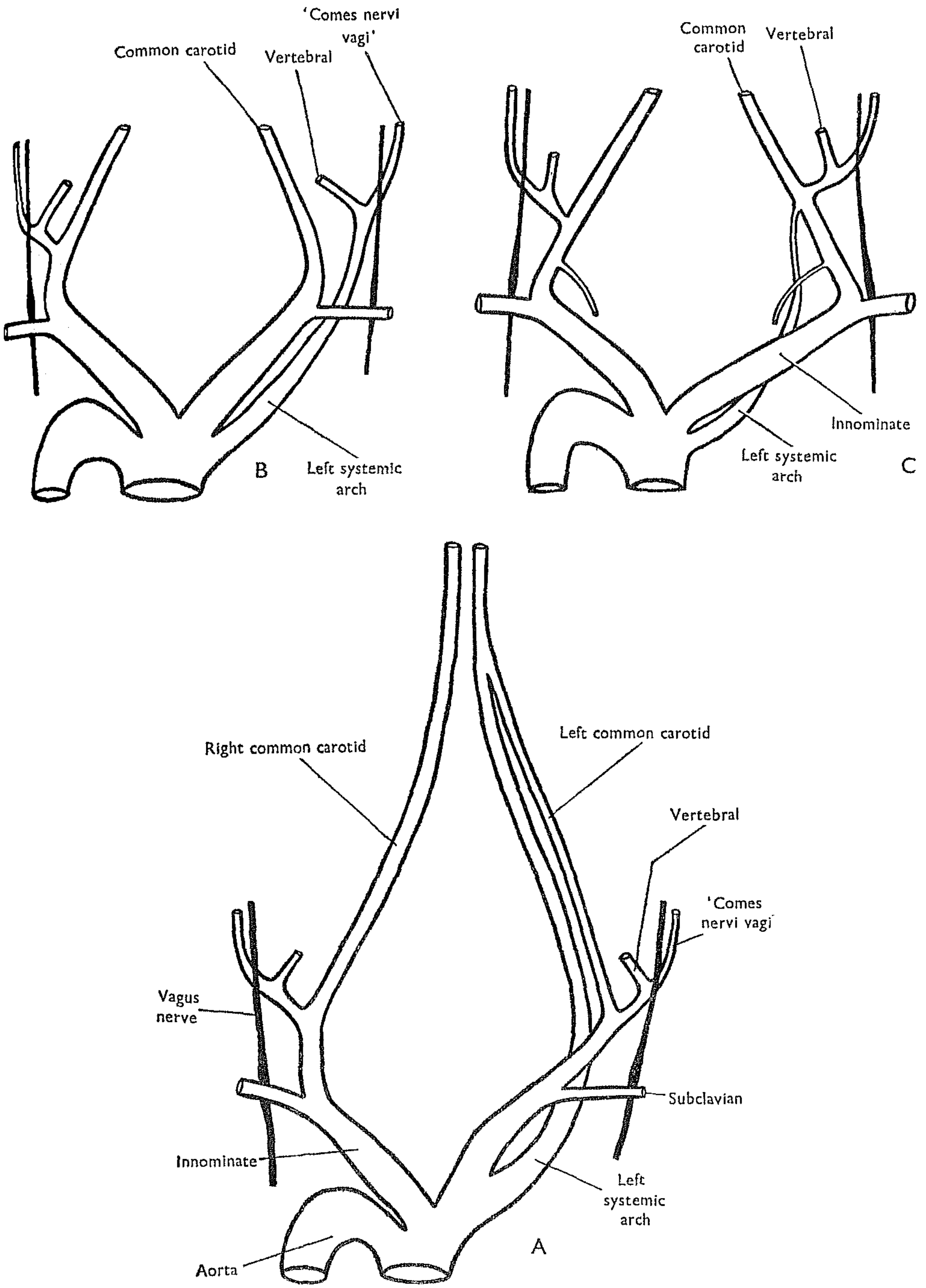

Fig. 6. Three forms of the anterior prolongation of the persistent left systemic arch; slightly diagrammatic. A, an 18-day embryo no. 1186 (1951). B, an 18-day embryo no. 71/933 (1949). C, a day-old chick no. 4386 (1952).

(nos. 1–10) were one-year-old birds, and their offspring were represented in each hatch group in about equal numbers. Cocks 11–14 formed a separate group of two-year-old birds, and their contribution to each hatch group was very unequal, two-thirds of their offspring coming in the last two hatches. If these four cock groups are omitted, the expected number of abnormal offspring in the remaining groups is greater than five in each case, so the χ^2 method can be used to test the significance of these differences in the frequency of left systemics amongst the progeny of each cock. This shows that the probability of getting differences between cocks as great or greater than those observed, by chance alone is less than 2% ($P = 0{\cdot}0175$). This indicates that the likelihood of the left systemic arch persisting in any chick is partly determined by the genetic influence of the cock.

Table 4. *Distribution of normal and abnormal chicks from all matings of cocks 1–10*

Cock no.		Hen no. 1	2	3	4	5	6	7	8	9	10	11	12	13	Total	P value by Smith's method
1	Normal	10	12	11	7	10	7	1	9	3	7	9	13	.	99	0·376
	Abnormal	0	1	0	1	0	1	0	1	0	1	1	4	.	10	
2	Normal	17	9	11	7	1	7	8	6	2	2	.	.	.	70	0·477
	Abnormal	0	1	0	0	0	0	0	0	0	0	.	.	.	1	
3	Normal	6	12	7	9	11	8	3	10	4	7	11	2	2	92	0·058
	Abnormal	0	1	0	1	0	0	0	4	0	0	2	0	0	8	
4	Normal	16	6	6	9	16	12	12	7	11	10	6	7	.	118	0·089
	Abnormal	1	0	2	2	1	1	0	2	2	3	5	0	.	19	
5	Normal	3	5	5	9	11	7	8	10	5	5	.	.	.	68	0·298
	Abnormal	1	0	0	1	0	0	2	0	0	0	.	.	.	4	
6	Normal	5	4	15	13	12	8	14	4	5	14	11	.	.	105	0·303
	Abnormal	0	0	2	2	2	1	0	0	1	0	4	.	.	12	
7	Normal	11	9	8	6	6	11	7	2	13	9	11	6	.	99	0·080
	Abnormal	0	3	0	1	1	0	0	1	0	0	0	1	.	7	
8	Normal	13	11	7	13	4	5	11	5	4	6	.	.	.	79	0·047
	Abnormal	0	1	0	1	1	4	0	1	2	1	.	.	.	11	
9	Normal	11	13	11	7	11	12	3	8	12	13	16	.	.	117	0·0025
	Abnormal	2	0	4	0	1	0	0	0	0	0	0	.	.	7	
10	Normal	7	12	17	10	11	16	11	8	9	5	8	10	.	124	0·184
	Abnormal	0	0	0	0	1	0	2	0	0	1	0	0	.	4	

Combined probability value for all cock groups $P = 0{\cdot}0003$.

N.B. There is a different group of hens mated with each cock, but for convenience the same numbers 1–13 have been used in each group.

Table 4 shows the distribution of abnormal chicks amongst all the hens mated with cocks 1–10. The χ^2 method cannot be used to test the significance of these 'between-hen' differences within each cock group because the expected number of abnormals from each hen is often much less than five. However, the heterogeneity test devised by Smith (1952) is applicable to these data and it shows that in the case of cock 9 the 'between-hen' differences are significant at the 1% level ($P = 0{\cdot}0025$) and for cock 8 at the 5% level ($P = 0{\cdot}047$). Combining the probability value for each cock group according to Fisher's method gives an overall value for the 'between-hen' differences which is significant at the 0·1% level ($P = 0{\cdot}0003$). These differences, however, are not necessarily all genetic in origin, since, in the case of the female, there is the possibility of non-genetic influences acting on the embryo through the egg.

The strongest evidence for the existence of genetic control of this phenomenon comes from a comparison between two different breeds. In the last three hatch groups a number of Light Sussex day-old males were examined. The parents of these had been housed and fed in the same way as the Rhode Island Red birds, and the eggs were hatched at the same time and in the same incubator. Table 5 shows that persistent left systemics were much more frequent in the Light Sussex chicks and this difference is highly significant.

The persistence of this vessel is evidently also influenced by the environmental conditions before or during incubation. The differences in frequency of left systemics occurring in the six-weekly hatch groups shown in Table 6 are significant at the 1 % level ($P=0{\cdot}002$), and this significance remains after allowance has been made for the small differences in the contribution which each cock makes to the different hatch totals. Nothing is known about these environmental factors; all that can be said is that the hatch differences show no seasonal trend.

Table 5. *Incidence of left systemics amongst day-old male chicks from two breeds hatched at the same time*

	Rhode Island Red	Light Sussex	Total
Normal	647	86	733
Abnormal	47	26	73
Total	694	112	806
Abnormal (%)	6·77	23·21	

$\chi^2=31{\cdot}651$; $n=1$; $P\sim10^{-8}$.

Table 6. *Incidence of left systemics in each hatch group amongst chicks from cocks* 1–10

	Hatch date (1952)						
	1. iv	8. iv	15. iv	22. iv	29. iv	6. v	Total
Normal	114	157	172	196	157	175	971
Abnormal	12	25	8	14	18	6	83
Total	126	182	180	210	175	181	1054
Abnormal (%)	9·52	13·74	4·44	6·66	10·29	3·31	7·87

$\chi^2=19{\cdot}033$; $n=5$; $P=0{\cdot}002$.

Discussion

There seem to be no records of the whole of the left systemic arch persisting in birds as a functional vessel beyond the embryonic stage, and its presence, even in a reduced condition, has usually been regarded as a rare abnormality. The data presented here, consisting of late third week embryos and newly hatched chicks from 44 different cocks and approximately 500 hens examined over a period of four years, indicate that in this breed a certain proportion of specimens regularly show some signs of the left systemic arch at this stage. Since the same condition has been found in a second breed it is possible that it is a feature of this species. This may be an example of the greater variation which is often found in domestic as compared with wild animals. On the other hand, variation in the rate at which these embryonic vessels disappear may be more widespread than is generally recognized, its discovery in this case being due to the unusual opportunity of examining large numbers of specimens of the same age and of known pedigree.

The cause of the persistence of the left systemic arch is probably to be looked for in variation in growth movements in the neck region. Bremer (1928) has argued that the different developmental fate of the right and left arches is due to a functional disadvantage which the left one suffers as a result of the backward movement of the aortic arches and heart associated with the elongation of the neck in the early embryo. Hughes (1934) has shown that this movement is brought about by differential growth of the aortic arches in relation to the axial structures in the neck, so that, for instance, the third pair of arches which at first lie in front of the first spinal ganglion finish up opposite the fifteenth, having moved backwards through twenty segments. After this 'the anterior region of the body grows as a whole, the aortic arches maintaining their position relative to the spinal cord'. Hughes has also shown that this movement of the aortic arches begins on the fourth day of incubation and is completed by the eighth. This is just the period during which the left systemic is normally reduced in size, at first being as large as the right-hand arch but finally disappearing altogether.

The regular occurrence of the left systemic in a certain proportion of late embryos and newly hatched chicks indicates that these growth movements are subject to variation, and the data show that some of this variation is genetic in origin. Vascular variations are of course found very frequently during dissection in animals and man. The only cases in which their genetic control has been demonstrated are in the rabbit (McNutt & Sawin, 1943; Sawin & Nace, 1948; Sawin & Edmonds, 1949) and in the mouse; in the latter animal, a vascular variant has been identified by the presence, in one inbred strain, of an anomalous canal through the pelvis (Grüneberg, 1952), and a variation of the tail veins is brought about by the gene for undulated (Grüneberg, 1954). Quite recently, extensive variations of the embryonic vascular system due to the gene for luxate have been described by Carter (1954).

Summary

Persistence of the left systemic aortic arch occurs frequently in Light Sussex and less commonly in Rhode Island Red chickens as classified on hatching. Some degree of genetic control of this variant within the Rhode Island Red breed is indicated by differences in the incidence of the anomaly in the offspring of individual cocks and hens. Significant differences between hatches indicate the existence of environmental influences of unknown origin.

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