Resumen por el autor, B. M. Patten.

La formación del asa cardiaca del pollo.

Las fases tempranas del establecimiento del corazón del pollo y los estados ulteriores de división en diferentes cámaras han sido cuidadosamente investigados por diversos autores. El presente trabajo se ocupa de los procesos intermedios algo familiares, pero hasta el presente menos completamente descritos, de la formación del asa y la diferenciación regional temprana, basándose en disecciones, reproducidas en modelos plásticos, y en reconstrucciones en cera. Se ocupa de los siguientes puntos: 1. La formación en el tubo cardíaco de un asa en forma de U dirigida hacia el lado derecho, y de algunos de los factores causativos invocados en este proceso. 2. La formación del asa cardiaca y la relación de la torsión y flexión del cuerpo del embrión con el proceso de la formación de dicha asa. 3. La diferenciación regional del corazón en el bulbo cardíaco, ventrículo, atrio y seno venoso, y los cambios tempranos en cada una de estas regiones.

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THE FORMATION OF THE CARDIAC LOOP IN THE CHICK

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TWO TEXT FIGURES AND THREE PLATES

INTRODUCTION

Most of the numerous investigations concerning the development of the heart in birds have dealt either with the very early phases of its establishment or with the relatively late steps of its division into chambers. The intervening process of loop formation, although it is in a general way familiar to embryologists, has received much less attention. When I had occasion to consult the literature for a discussion of the subject, I was unable to find any connected account with adequate figures. It has, therefore, seemed worth while to extend and publish some observations on cardiac-loop formation in the chick which were originally made in the course of other work.

Records of investigations of the development of the chick heart appear in some of the earliest works on embryology. The observations on the heart recorded in such classics as those of Malpighi (1686), Wolff (1759), von Haller (1767), and Pander (1817), though all of them are remarkable for their time, are at present chiefly of historical importance. An interesting summary of the work of these writers appears in the paper of Lindes ('65). The early stages in the establishment of the chick heart have since been dealt with by Afanassiev ('69), Gasser ('77), Duval ('89), His ('00), Rükert and Mollier ('06), Graper ('07), Funccius ('09), Hahn ('09), Miller and McWhorter ('14), and Reagen ('15, '17). Since this work has been summarized from the morphological point of view by Lillie ('08), and from the experimental point of view by Reagen ('17), it seems unnecessary to go over the ground again here. The abundant information available concerning the establishment of the primordial heart tube places us in a position to take up without preliminaries the processes involved in cardiac-loop formation.

The observations recorded here are confined to the period extending from the establishment of the heart as a nearly straight, double-walled tube to the period at which the process of loop formation has been completed and the main regional divisions of the heart have been definitely established.

The later development of the chick heart, involving the formation of the septa and valves which develop during the division of the heart into chambers, is dealt with in papers by Lindes ('65), Tonge ('69), Masius ('89), Langer ('94), Griel ('06), and Hochstetter ('06).

MATERIAL AND METHODS

At the outset of the work it became obvious that there was considerable individual variability as to heart configuration even among embryos having the same number of somites. The first consideration was, therefore, the selection of a series of embryos which would show as nearly as possible the normal sequence of shape changes undergone by the heart. This phase of the work was greatly facilitated by the availability of some 2000 chick whole-mounts in our laboratory collection. By studying the heart in a large group of embryos having the same number of somites, it was not difficult to determine the characteristic heart configuration for a particular stage of development.

Twelve embryos ranging between 29 and 100 hours of incubation were selected as showing the characteristic steps in the formation of the cardiac loop and the early regional differentiation of the heart. Each of the twelve embryos belonging to the initial series was then carefully matched so that three or four embryos of each stage, exactly like one another as far as could be determined, were available for the work. One embryo in each of these sets was reserved for study as a cleared and stained entire mount, the remaining embryos were used for dissection and serial sectioning.

Camera-lucida diagrams of the cephalic and cardiac regions were made from the whole-mount series. In these diagrams the heart and main afferent and efferent vessels, as far as they could be made out, were drawn in directly. Later in the work, the outlines of the heart and main vessels were completed[1] from dissections and reconstructions of embryos of corresponding stages. These diagrams appear as the text figures and serve to show at the same time the stages worked on and the relations of the heart to the neighboring structures in the body of the embryo.

It was found that the configuration of the heart itself could be worked out very successfully from dissections made in alcohol under a binocular microscope. In such preparations the heart shape is beautifully shown by strong reflected light and can be accurately reproduced with the aid of a camera lucida. Employing this method, drawings of the same heart were made from three aspects to the same scale of magnification. By using dividers to keep the dimensions accurate, it was a relatively simple matter to make a preliminary clay model of the heart from the drawings. This model, with its basic dimensions correct, was then finished directly from dissections of the heart, which could be rotated and thus studied under the binocular microscope from all angles.

Although the contours are less likely to be distorted in dissected hearts than in reconstructions, there are certain details that cannot be made out satisfactorily by the dissection method. The chief point of difficulty is the region of the sinus venosus in the older embryos. The manner in which the veins entering the heart are imbedded in the surrounding structures renders it

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[1] Although a consideration of the changes in the aortic arches does not come within the scope of this paper, the condition of the arches at each phase of heart development here dealt with is indicated in the text figures. For discussion of the development of the aortic arches, reference may be made to the works of Boas ('87), Evans ('09), Lillie ('08), and Locy ('06).

The cardinal and umbilical veins are indicated in the figures of the later stages only, because in the earlier stages the position of the embryos is such that these vessels would have to be superimposed on the heart. Moreover, the early stages in the formation of the vessels are shown beautifully in the figures of Evans ('09) and Sabin ('17).

almost impossible to make clean dissections of this region. In the older embryos, therefore, the heart and the main afferent and efferent vessels were reconstructed from serial sections by the wax-plate method of Born. As far as the principal contours of the heart are concerned, these reconstructions were found to conform with the clay models made from dissections. They furnished, moreover, detailed information concerning the sinus region and the entering veins, which it had not been found possible to obtain by means of dissections.

The drawings of the heart shown in the plates were made for the most part directly from dissections. They contain some details, however, that were added from the wax-plate reconstructions. The orientation of the heart in the body of the embryo, and the relations of the vessels are shown in the text figures, which are lettered in correspondence with the plates.

THE FORMATION OF THE CARDIAC LOOP

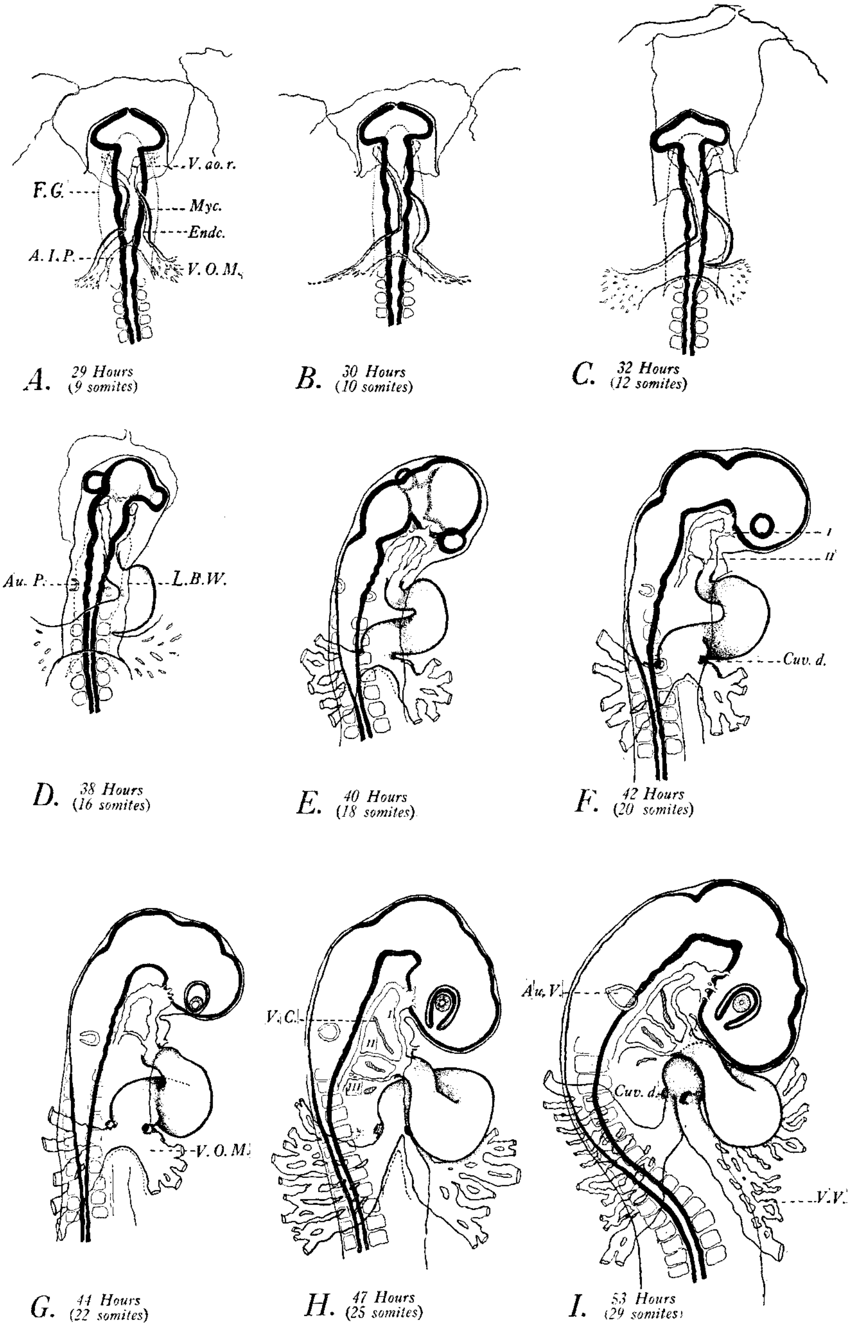
The youngest stage studied is represented by embryos of 9 somites (approximately twenty-nine hours' incubation), in which the heart is a nearly straight tube (fig. 1, A, and pls. 1, 2, and 3, A). Even when the myo-epicardial folds are first approximated to each other to form the outer wall of the heart tube, there is already a tendency for the right lateral margin of the heart to show a greater convexity than that of the left. This asymmetry is due, at first, more to unequal dilation of the heart wall than to actual bending of the entire tube, as is indicated by the fact that the line of attachment of the dorsal mesocardium lies very nearly in the sagittal plane of the body.

The dorsal mesocardium at this stage forms an unbroken supporting membrane throughout the entire length of the heart. In contrast to the condition in mammals described by Yoshinaga ('21), the ventral mesocardium in the chick is complete, or nearly so, when it is first formed by the approximation of the two folds of splanchnic mesoderm which constitute the medial wall of the cephalic portion of the right and left coelomic chambers. The ventral mesocardium is, however, a more transitory structure than the dorsal, and even at the 9-somite stage its rupture has begun in the midcardiac region, although its line of attachment to the heart can still be discerned (pl. 1, A).

In the chick heart the endocardial tubes are less irregular in contour and are more completely fused with each other at this stage than in the mammalian heart of corresponding age. Furthermore, the chick endocardium shows no such early foreshadowing of the atrioventricular and the sino-atrial constriction as has been observed in mammals (Murray, '19; Schulte, '16; Yoshinaga, '21). In the later stages studied the endocardium is of secondary interest, its configuration being determined largely by the limitations imposed upon it by the myoepicardium. Although the endocardium has been shown in the figures of our earliest stages by way of bringing this work into continuity with that of other investigators, the later changes in its configuration have not been followed in detail.

Between thirty and forty hours of incubation (10 to 18 somites), there is a marked dilation of the heart, but its most conspicuous change in shape is due to the bending of the entire middle portion of the heart tube to the right (pls. 1 and 3, A to E). In this process of bending, as indeed in the entire series of changes involved in loop formation, there is undoubtedly a considerable factor of mechanical compulsion. The accompanying graph shows how much greater the elongation is in the heart tube itself than is the increase, during the same period of time, in the distance between the attached cephalic and caudal ends of the heart. Under such growth conditions, bending of the heart is inevitable. It is quite logical, furthermore, that this bending should be lateral because of the impediment offered dorsally by the body of the embryo and ventrally by the yolk. Why it should take place to the right rather than to the left is not so clear.

It has been suggested that the bending of the heart to the right might be due to the entry of a stronger current of blood from the left omphalomesenteric vein than from the right, the left vein being conspicuously larger at this stage of development. Sabin ('17) has shown, that while heart contractions begin in the chick as early as the 10-somite stage, the actual circulation



A. 29 Hours (9 somites)

B. 30 Hours (10 somites)

C. 32 Hours (12 somites)

D. 38 Hours (16 somites)

E. 40 Hours (18 somites)

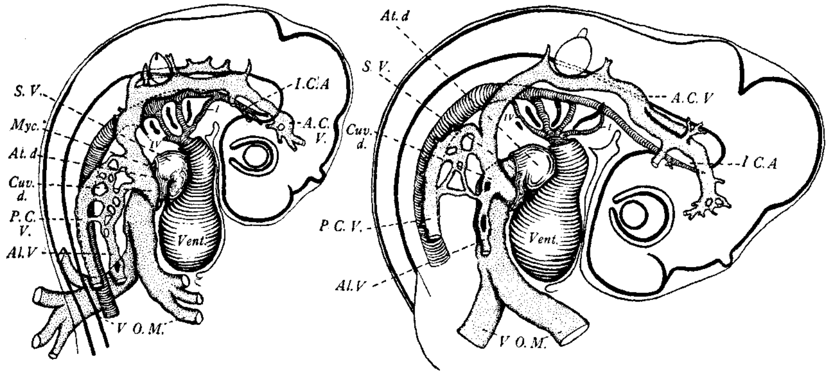
F. 42 Hours (20 somites)

G. 44 Hours (22 somites)

H. 47 Hours (25 somites)

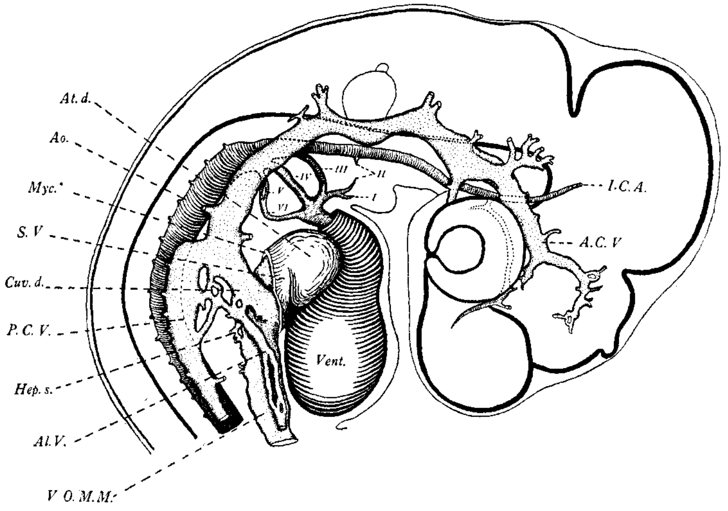
I. 53 Hours (29 somites)

Fig. 1, A to L Camera outlines (× 15) of cephalic and cardiac regions of chick embryos, showing for each stage studied the relations of the heart to neighboring



J. 65 Hours (33 somites)

K. 76 Hours (38 somites)



L. 100 Hours (45 somites)

structures in the embryo. These figures are arranged and lettered to correspond with the detailed drawings of the hearts shown in the plates. *I* to *VI*, aortic arches I to VI, respectively; *A.C.V.*, anterior cardinal vein; *A.I.P.*, anterior intestinal portal; *Al.V.*, allantoic vein; *Ao.*, aorta; *At.*, atrium (*d.*, right), (*s.*, left); *Au.P.*, auditory pit; *Au.V.*, auditory vesicle; *Bul.*, bulbus cordis; *Cuv. d.*, duct of Cuvier; *Endc.*, endocardium; *F.G.*, foregut; *Hep.s.*, stubs of some of the larger hepatic sinusoids; *I.C.A.*, internal carotid artery; *L.B.W.*, lateral body wall; *Myc.*, myoepicardium; *Myc**., cut edge of myoepicardium; *P.C.V.*, posterior cardinal vein; *Sin.-at.*, sino-artrial region of heart before its definite division; *S. V.*, sinus venosus; *Vent.*, ventricle; *V.ao.r.*, ventral aortic roots; *V.C.*, visceral cleft; *V.G.M.*, omphalomesenteric veins; *V.O.M.M.*, fused omphalomesenteric veins; *V.V.*, vitelline veins.

of blood is not established until the 16-somite stage. The fact that circulation does not begin until after the bending of the heart is well advanced excludes inequality of blood-flow from consideration as causative factor ontogenetically. There is still the possibility that the bending of the heart to the right is a recapitulation of development in some ancestral form where lateral inequality of the circulation had become established prior to the bending of the heart, but it would be equally plausible to urge that the bending of the heart to the right was primary, and that the left omphalomesenteric vein became secondarily enlarged owing to the opposition of less resistance to the discharge of its blood.

It has also been suggested that, owing to the direction of the torsion of the embryo's body, the heart tube is free to expand to the right, while it would be obstructed on the left by the swinging of the left side of the body wall toward the yolk. Again we encounter a disregarded time factor. The heart bending is initiated before there is any indication of torsion in the embryo. There is undoubtedly correlation between the two processes in the sense that the development of the heart would be mechanically impeded, if not stopped, by torsion of the embryo in the opposite direction. Here also it might be maintained that the heart bend itself is the primary factor and that the direction of embryonic torsion follows it as a necessary consequence. Certain it is that the bending of the embryonic heart to the right is not peculiar to forms in which torsion is conspicuous. The heart bend is the more deep seated phylogenetically. It occurs in the vertebrate stock as far back as the elasmobranchs (Hochstetter, '06) and Dipnoi (Robertson, '13), and is a characteristic feature of heart development in Amphibia (Rabl, '87). One would scarcely expect to work out the primary causative factors of such a long-established process entirely from the ontogeny of forms as far up the scale as birds.

As has already been stated, the ventral mesocardium has disappeared by the time the bending of the heart becomes apparent. The dorsal mesocardium, which is complete when the bending process begins, soon ruptures in the midheart region (pl. 3, C, D), and is rapidly obliterated except at the caudal end of the heart (pl. 3, E). Thus the heart tube, being attached only at its two ends, is more free to undergo extensive and rapid changes in shape and position.

Even before the bending of the heart to the right has reached its maximum, torsion of the embryo's body begins to change the mechanical limitations in the cardiac region. As the cephalic part of the embryo comes to lie on the yolk on its left side (fig. 1, D, E, F) the heart, no longer closely confined between the body of the embryo and the yolk, begins to swing somewhat ventrad and lies less closely against the dorsal body wall of the embryo (pl. 2; cf. C and D with E and F).

The initiation of torsion has another very definite influence on the heart. Since torsion involves the cephalic region of the embryo first and progresses caudad, the body of the embryo becomes more inclined toward the yolk at the level of the cephalic attachment of the heart than at the level of its caudal attachment. As a result, the truncus arteriosus is twisted by the carrying of its attached end away from the yolk before a similar twisting effect is exerted upon the sino-atrial region of the heart (fig. 1, E, F, G). This is, I believe, the primary mechanical factor in starting the transformation of the U-shaped bend into the cardiac loop. Once the initial twist is imparted, loop formation progresses extremely rapidly, for the rate at which the heart tube is outgrowing the pericardial chamber in length is exaggerated at this time. The distance between the attached cephalic and caudal ends of the heart is actually being shortened by the progress of flexion in the embryo at just the time when the heart tube is elongating most rapidly (fig. 1, G, H, I, and fig. 2). The attached truncus and sinus ends of the heart are thus brought closer together, tightening the loop as it is formed. In the formation of the loop the truncus and bulbus swing away from the yolk (i.e., toward the embryo's right), and come to lie across the caudal part of the heart, at the atrio-ventricular constriction (pl. 2, G, H, I). The sino-atrial region being anchored to the body walls by the remaining part of the dorsal mesocardium, the ducts of Cuvier, and the omphalomesenteric veins, undergoes little change in position.

It is during this stage that the individual variability previously alluded to is most conspicuous. The more usual configuration of the heart is indicated in the figures referred to in the preceding paragraph where the loop is shown as rather closely twisted. There were not a few embryos, however, in which the heart stood out from the body, and was more loosely twisted than in the

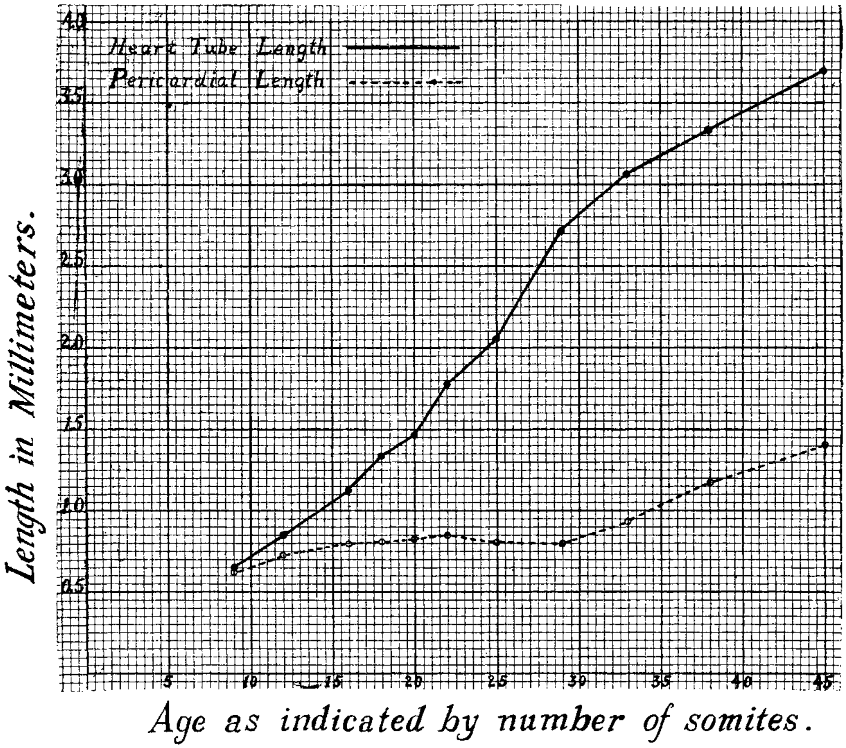


Fig. 2 Graph to show the rate of heart-tube elongation as compared with the rate of elongation of pericardial region. The heart length was measured along the original middorsal line of the heart tube from the point of bifurcation of the aortic roots to the point of convergence of the omphalomesenteric veins. (In the older embryos the omphalomesenteric veins have begun to fuse with each other. The caudal point for the measurements had, therefore, to be approximated by taking it in a given relation to the point of entrance of the ducts of Cuvier.) As an index of the length of the pericardial cavity, the distance between these same two points was measured along the middorsal line of the embryo. All of the measurements were taken on models made to the same scale of magnification, and then converted to actual size.

embryos represented in figure 1, G and H. In the embryos I have studied this condition seems to be correlated with delayed flexion rather than with any abnormality of the heart tube. It is probably to be regarded as within the limits of normal variability.

In the ventral views of the heart it can be seen that as the process of loop formation progresses, the extension of the heart to the right is diminished, and that the loop as it is formed swings not only ventrad, as has been mentioned above, but also distinctly toward the sagittal plane (pl. 1, G, H, and I). This change in position may well be due to the fact that by this stage the body at the cardiac level has completed its torsion and lies on its left side, so that the heart is no longer prevented by the yolk from expanding midventralward.

The heart in the stage when the cardiac loop is first definitely formed (i.e., in embryos of about 25 somites) has been described by many investigators as 'S-shaped.' Neither the dorsal (pl. 3, H) nor the lateral (pl. 2, H) nor the dextrodorsal view of the heart as seen in the ordinary whole-mount (fig. 1, H) can be characterized as 'S-shaped.' Only when a heart model or a heart freed by dissection is rotated, so that a direct ventral view is obtained, does the 'S-shaped' configuration become recognizable (pl. 1, H).

At the close of the second day of incubation, the cranial flexure of the embryo is developing extremely rapidly (fig. 1, G, H, I). As the anterior part of the head is bent caudad, it begins to crowd the heart loop. As a result the ventricular bend of the loop moves at first caudad and then dorsad (fig. 1, H to L). Prior to the formation of the cardiac loop and its dorsocaudal bending, the ventricular portion of the heart is cephalic to the atrium, in the primitive vertebrate position. The bending of the loop brings the ventricle caudal to the atrium in approximately the definitive relationship characteristic for adult sauropsida.

THE REGIONAL DIFFERENTIATION OF THE HEART

Certain text-book diagrams of the chick heart show bulbar, ventricular, and atrial regions, separated by conspicuous constrictions while the heart is still in the straight tubular stage. Although perhaps suggestions of such constrictions are to be detected at this early stage of development, I have not been able to satisfy myself as to their definite appearance until the heart is well bent to the right, and they do not appear at all conspicuously until nearly forty hours of incubation (16 to 18 somites). In the heart of a chick of 20 somites, the bulboventricular constriction, previously but vaguely discernible, has become quite definite (pl. 1, F). The atrioventricular constriction is also well marked by this time (pl. 2, F). The sinus venosus exists rather as the place of confluence of the omphalomesenteric veins with each other and with the atrium than as a definite division of the heart. Nevertheless, the sino-atrial boundary may be said to be foreshadowed by an increased conspicuousness of the grooves formed on either side where the omphalomesenteric veins enter the heart at an obtuse angle to it (pl. 3, F). The apparent deepening of these lateral grooves is, however, due rather to expansion of the atrium than to any actual constriction in this region. There is as yet no demarcation between sinus and atrium dorsally, and no caudal line of demarcation between the sinus and the omphalomesenteric veins.

For convenience in description, the heart at this stage can best be compared to a U with its upright limbs attached to the body of the embryo (fig. 1, F). The ventricle, definitely marked off both cephalically and caudally by constrictions, constitutes the bend of the U. The bulbotruncus portion of the heart tube constitutes the cephalic limb of the U, which is attached to the body by the aortic roots. The sino-atrial region constitutes the caudal limb of the U, which is attached by the omphalomesenteric veins, the ducts of Cuvier, and the remaining part of the dorsal mesocardium.

The early changes in the bulboventricular portion of the heart are already so well known that they require but a brief summary.

In the formation of the cardiac loop, the U-shaped ventricular bend becomes compressed (pl. 1, F, G, H). Coincidently, the apex of the bend is dilated so that the ventricle loses its U shape and becomes more saccular. The same process of dilation shortens, almost to obliteration the ventricular portion of the limbs of the U, so that the atrioventricular canal and bulbus cordis appear to lead off side by side, from a common ventricular sac (pl. 1, I). Meanwhile, as has already been described in connection with the formation of the loop, the entire ventricle has shifted more toward the sagittal plane (pl. 1, F to J). It has at the same time been bent caudad and then dorsad (fig. 1, H to L). In this manner the apex of the ventricle, which was originally the most right-hand portion of the U-shaped heart tube, becomes the most caudal part.

The first external manifestation of the impending division of the ventricle into right and left chambers shows in the oldest stages here studied. During the fourth day, a slight groove appears on the ventral surface of the ventricle, which extends caudad from the angle between the bulboventricular constriction and the atrioventricular constriction (pl. 1, K, L). This groove in later stages extends still farther caudad and marks externally the position at which the septum interventriculorum develops.

In the bulbotruncus region the early changes are shown so definitely by the figures that little can be added by description. The most interesting phases of the development of the bulbus occur in stages of development more advanced than those with which this study is concerned. They have been described in detail by Lindes ('65), Langer ('94), Masius ('89), Hochstetter ('06), and Lillie ('08).

The early differentiation of the sinus venosus has been less fully described and calls for more detailed attention. A definite dorsal line of demarcation between the sinus venosus and the atrium, can first be made out at the close of the second day of incubation (chicks of 25 somites). At this time the middorsal portion of the sino-atrial region of the heart becomes dilated. This dilation is situated just where the persistent caudal portion of the dorsal mesocardium is attached to the heart. On either side it is marked off by a groove extending from the lateral constriction at the point of entrance of the omphalomesenteric vein, onto the dorsal surface of the heart (pl. 3, H and I, *S-A. c.*). The dorsal dilation thus bounded may now be differentiated definitely from the atrium as the sinus venosus.

The differentiation of the sinus venosus takes place at the same time as the caudal bending of the cardiac loop. It is possible that their appearance may be more than casually coincident. The caudal bending of the loop causes the blood from the omphalomesenteric veins to be directed against the dorsal and cephalic wall of the sino-atrial chamber, rather than toward the atrioventricular ostium, as in earlier stages of development (pl. 2, H, I, and J). It will be noted that the sinus dilation occurs at precisely the point at which the blood current impinges against the heart wall. A deduction that the blood current is a causal factor in the dilation is alluring, but in default of experimental evidence, any suggestion to this effect must be considered as purely tentative.

Whatever molding effect the blood stream may exert in the process, the demarcation of the sinus venosus becomes more and more distinct as the caudal bend in the heart becomes more pronounced (pls. 2 and 3, J to L). The caudal bending of the loop, too, results in the shifting of the sinus from its original position, caudal to the atrium, to the dorsal position it occupies at the end of the fourth day of incubation (pls. 2 and 3). At this stage the sinus venosus is a pouch-like dilation which receives the ducts of Cuvier laterally and the fused omphalomesenteric veins caudally. It is marked off from the atrium by a groove, which is especially strongly developed caudally and dextrally. Already it opens into the atrial chamber somewhat to the right of the midline, foreshadowing its later association with the right atrium.[2]

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[2] At this stage the two layers of splanchnic mesoderm which constitute the dorsal mesocardium flare out on either side and are reflected over the ducts of Cuvier at their points of entrance into the sinus venosus (pl. 3, I). These transverse folds of the mesocardium have been designated (Lillie) as the mesocardia lateralia.

The most conspicuous change in the atrial region is its lateral expansion. As early as forty hours the future atrial region is dilated so that its transverse diameter is greater than that of any other part of the heart tube. From the first the dilation to the left is more marked (pl. 3, E, F). When the bulbus is thrown against the right side of the atrium in the formation of the cardiac loop (pls. 2 and 3, H), it seems to crowd the less developed right atrium and retard its development still more. After the configuration of the loop has changed so that the bulbus slips by the atrium, and crosses the heart at the atrioventricular constriction (pls. 2 and 3, I), the right atrium begins to expand more rapidly, but the size of the two atria does not become equalized until after the stages here under consideration.

The first indication of the separation of the atrium into two chambers appears in chicks of 29 to 30 somites (53 to 55 hours). A longitudinal sulcus develops at this time on the ventrocephalic face of the atrium. In a ventral view of the heart this sulcus is at first concealed by the truncus and bulbus; but as it becomes more clearly marked, its caudal portion can be seen extending toward the atrioventricular constriction (pl. 1, J. K. L, *i-a.g.*).

This interatrial groove is an external manifestation of the formation of the septum superius. (The septum superius or atriorum of the chick heart corresponds to the septum primum of the mammalian heart. In the chick no septum secundum is formed.) The formation of the interatrial groove does not appear to be dependent on pressure exerted on the atrium by the truncus arteriosus. When the groove first appears, an appreciable space separates the truncus from the atrium. With further growth, however, the truncus appears to sink into the cephalic portion of the interatrial groove, and the auricles expand rapidly on either side of it. Under these later conditions, the truncus probably does play a secondary part in the division of the atrium in the sense that it acts as a constricting band on either side of which the auricles expand.

SUMMARY

The early phases in the establishment of the chick heart and the later stages of its division into chambers have already been carefully investigated by many workers. This paper covers the somewhat familiar, but heretofore less completely described, intermediate processes of loop formation and early regional differentiation.

The work is based on dissections from which plastic models were made and on wax-plate reconstructions from serial sections. It deals with:

1. The formation in the heart tube of the U-shaped bend to the right and some of the alleged causative factors in this process.
2. The formation of the cardiac loop and the relation of torsion and flexion of the body of the embryo to loop formation in the heart.
3. The regional differentiation of the heart into bulbus cordis, ventricle, atrium, and sinus venosus, and the early changes in each of these regions.

Since these phases of heart development all involve complex changes in configuration and relations, the figures constitute a graphic summary much more satisfactory than a written résumé. The shortness of the intervals between the phases of development figured allows the continuity of the processes to be followed readily.

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EXPLANATION OF PLATES

Series of chick hearts, showing the formation of the cardiac loop and the progress of regional differentiation. The heart contours were drawn directly from dissections with the aid of the camera-lucida outlines. In drawing the older stages, wax-plate reconstructions were used for working out the relations of afferent and efferent vessels and as a check on the configuration of the heart shown by the dissections.

In the stages represented in figures E to I torsion has involved the cardiac region of the embryo. Since torsion affects the more cephalic regions first and progresses caudad, the transverse axis of the body of the embryo is at different inclinations to the yolk at the cephalic, and at the caudal end of the heart. The drawings of the ventral and dorsal views are oriented from the frontal plane, and those of the dextral views from the sagittal plane of the body, at the level of the aortic arches. For this reason the sinus region of the heart appears inclined.

The relation of the heart to neighboring structures in the embryo is shown in the text figures. The lettering of the text figures and plates corresponds throughout.

ABBREVIATIONS

I-VI, aortic arches I to VI
At., atrium (*d.* right), (*s.* left)
A-V.c., atrioventricular constriction
Bul., bulbus cordis
B-V.c., bulboventricular constriction
Cuv.d., duct of Cuvier
Endc., endocardium
Hep.s., stubs of some of the larger hepatic sinusoids
i-a.g., interatrial groove
i.v.g., interventricular groove
Mes.d., dorsal mesocardium
Mes.v., ventral mesocardium
Myc., cut edge of myoepicardium
Myc.F., myoepicardial fusion[3]
S-A.c., sino-atrial constriction
Sin-at., sino-atrial region (before its definite division)
S.V., sinus venosus
V.ao.r., ventral aortic roots
Vent., ventricle
V.O.M., omphalomesenteric veins
V.O.M.M., fused omphalomesenteric veins

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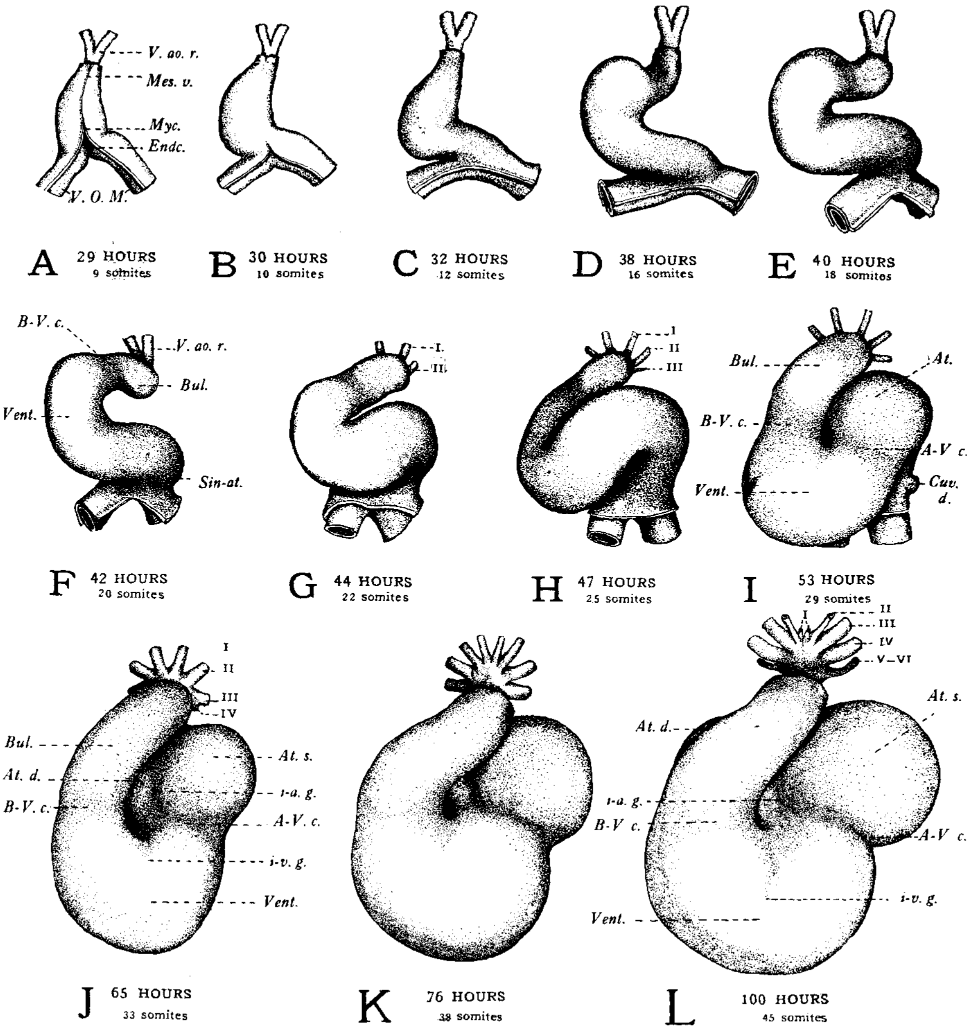
[3] During the fourth day there is formed a curious attachment between the myoepicardium of the ventral wall of the sinus venosus and the myoepicardium of the ventricle (pl. 2, K, L). I have not seen it described elsewhere. From work now in progress on later stages of development, I believe this strand becomes a broad fusion and serves as a pathway over which one of the main coronary veins from the ventricle reaches the coronary sinus.

PLATE 1

Ventral views (× 25) of chick heart in various stages of loop formation. The somite number and the approximate incubation age of each embryo are indicated on the plate.



A 29 HOURS 9 somites

B 30 HOURS 10 somites

C 32 HOURS 12 somites

D 38 HOURS 16 somites

E 40 HOURS 18 somites

F 42 HOURS 20 somites

G 44 HOURS 22 somites

H 47 HOURS 25 somites

I 53 HOURS 29 somites

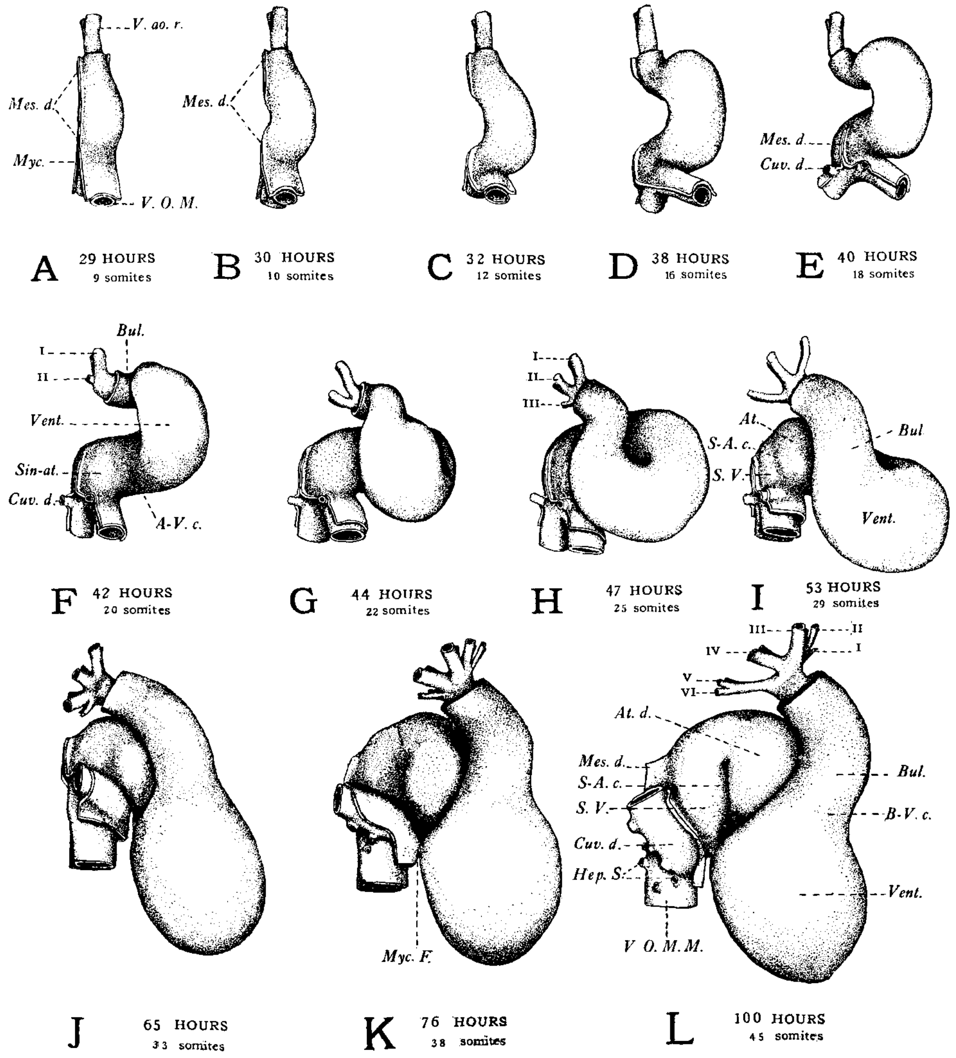
J 65 HOURS 33 somites

K 76 HOURS 38 somites

L 100 HOURS 45 somites

PLATE 2

Dextral views (× 25) of same series of hearts shown in plate 1.



A 29 HOURS 9 somites

B 30 HOURS 10 somites

C 32 HOURS 12 somites

D 38 HOURS 16 somites

E 40 HOURS 18 somites

F 42 HOURS 20 somites

G 44 HOURS 22 somites

H 47 HOURS 25 somites

I 53 HOURS 29 somites

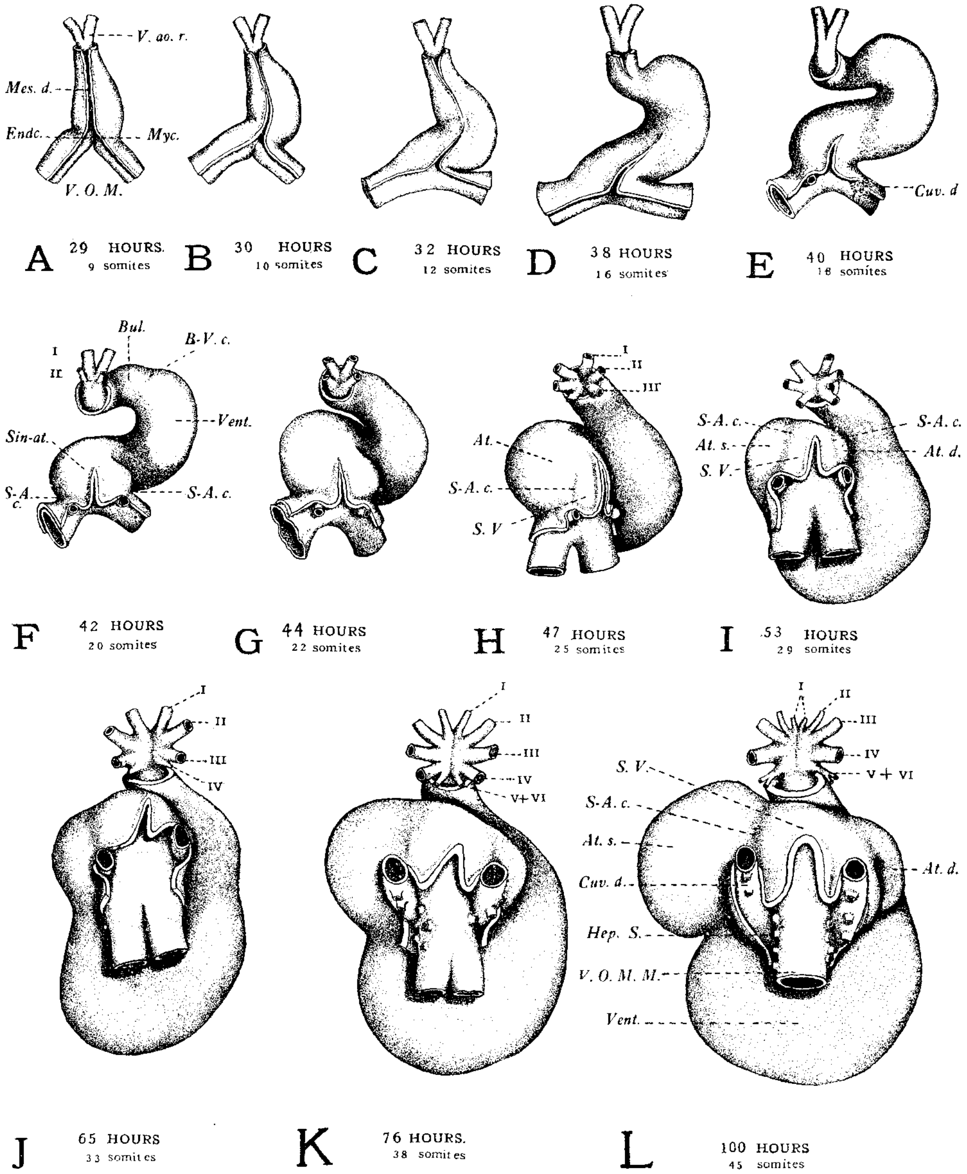
J 65 HOURS 33 somites

K 76 HOURS 38 somites

L 100 HOURS 45 somites

PLATE 3

Dorsal views (× 25) of same series of hearts shown in plates 1 and 2.



A 29 HOURS. 9 somites

B 30 HOURS 10 somites

C 32 HOURS 12 somites

D 38 HOURS 16 somites

E 40 HOURS 18 somites

F 42 HOURS 20 somites

G 44 HOURS 22 somites

H 47 HOURS 25 somites

I 53 HOURS 29 somites

J 65 HOURS 33 somites

K 76 HOURS. 38 somites

L 100 HOURS 45 somites