THE REPTILIAN HEART

by H. V. Kashyap, *Department of Zoology, College of Science, Nagpur*

(Communicated by B. S. Bhimachar, F.N.I.)

(*Received February 9; after revision July 22; read October 2, 1959*)

Abstract

Hearts of twenty nine species of reptiles are studied here with a view to understanding the relation between the incomplete inter-ventricular septum of the non-crocodilian reptiles and the complete inter-ventricular septum of the crocodiles. The pars muscularis of the crocodilian inter-ventricular septum has been shown to correspond to the incomplete inter-ventricular septum of the lower reptiles. The pars endocardialis has no counterpart within the ventricle of the lower reptiles. It is a new formation and has probably developed as a ventricular continuation of the left endocardial ridge of the embroynic bulbus. The 'secondary or vertical' septum of some authors is merely the most medial and prominent of the many vertical ridges present in the wall of the ventricle. It is unlikely that it plays any role in the completion of the inter-ventricular septum. It has been shown, on circumstantial grounds, that the incomplete inter-ventricular septum lies between the pulmonary arch and the systemic arches. The present study records the salient features of the morphology of the reptilian heart also.

Introduction

Reptiles are the first truly terrestrial vertebrates in so far as their respiration and reproduction are concerned, but in other respects they are still in the process of evolution and hence are imperfect. This is particularly so in regard to the circulatory organs. The heart of the reptile is, in most cases, imperfectly four-chambered. There are two auricles separated from one another by a complete interauricular septum while the single ventricle is divided imperfectly into two parts by means of a muscular partition which is still incomplete. It is only in the crocodiles that the heart becomes completely four-chambered. How this change from a three-chambered heart of the lower reptiles to a four-chambered one of the crocodile is brought about is a question that has been troubling the minds of the anatomists for a long time.

A scrutiny of the literature on the reptilian heart reveals that there has been some misunderstanding regarding the nature of the ventricular cavity and the septa therein.

Goodrich (1916) declared that "in the reptilia the interventricular septum tends to divide the chamber into a left cavity leading to the base of the right systemic arch and a right cavity leading to the base not only of the pulmonary but also of the left systemic arch". He also believed that the separation of the left and right cavities may have been brought about not by mere fusion of the incomplete muscular septum with the opposite wall, but by the growth from behind forwards of a new muscular septum differentiated from the muscular strands which unite the base of the old septum with the dorsal wall of the ventricle.

O'Donoghue (1918) opined that regarding Ophidia and Lacertilia the above conclusion needed modification and said that in these reptiles the ventricle is "partially divided into a right and left chamber but the two systemic arches come off from the right side and the pulmonary arch comes of from the left". With regard to the flow of blood within the heart he has caused some confusion by saying that "whereas in the Crocodilia and Chelonia as in birds and mammals the aerated blood is poured into the left side of the ventricle, in Ophidia and Lacertilia the reverse is the case and the aerated blood passes into the right ventricular chamber".

Rau (1924) described, in addition to the incomplete interventricular septum, a median vertical muscular ridge dividing the caudal portion of the large dorsal cavity into right and left halves. This vertical ridge is also incomplete anteriorly.

Leene and Vorstman (1930) called this vertical muscular ridge as the "vertical septum" and attributed to it great phylogenetic significance. They believed that it helped in the formation of the complete interventricular septum of the crocodilian heart.

Mathur (1944) mentioned incomplete dorsal and ventral "septoid processes" occuring as the anterior remnants of the median vertical ridge. He, however, named the interventricular septum "muscular ridge" and homologised it with the median vertical muscular ridge described by Rau (1924).

Foxon (1955) emphasising the role of the median vertical muscular ridge said that "it is this secondary septum which in crocodiles and birds becomes the definitive interventricular septum". He has also stated that in mammals the interventricular septum is derived from the primary septum.

Regarding the relationship between the openings of the aortic trunks and the incomplete interventricular septum of the lower reptiles there is a tendency to separate Crocodilia and Chelonia from Ophidia and Lacertilia. Thus O'Donoghue (1918) states that the interventricular septum lies between the pulmonary and left systemic trunks in Ophidia and Lacertilia while it lies between the pulmonary and the right systemico-carotid trunks in Crocodilia and Chelonia. Goodrich (1919) describes the opening of the right systemic trunk as being dorsal to the interventricular septum and that of the pulmonary trunk ventral to it, the opening of the left systemic trunk being situated almost opposite to the free edge of the interventricular septum, nearer to the opening of the right systemic trunk in Ophidia and of the pulmonary trunk in Chelonia. von Hofsten (1941) also considers that the position of the left systemic trunk in relation to the ventricular septum cannot be ignored and observes that in Lepidosauria it is dorsal to the septum while in Chelonia and Crocodilia it is ventral to it.

Thus a review of the literature on the reptilian heart will bring to light the fact that our understanding of its internal structure, particularly of the ventricle, is far from being conclusive. It also shows that there is still no correct evaluation of the role that the incomplete interventricular septum and other structures within the ventricle play in the formation of the complete interventricular septum of the crocodilian heart.

It is this fact that induced the present writer to study this problem afresh from a comparative point of view and find out the true nature of the ventricular cavity and of the interventricular septum. For this study, hearts of twenty-nine species of reptiles were used. Most of these species belong to Ophidia and Lacertilia, those of Chelonia and Crocodilia being relatively few. A list of the names of reptiles studied is given at the end. Most of the specimens were collected at Dharwar and neighbouring areas in North Karnatak. A few specimens were procured from Bangalore, Annamalainagar, Waltair and Visnagar through the kind co-operation of friends to whom the author is greatly indebted.

The hearts were dissected under a stereoscopic binocular dissection microscope. Hearts for serial sectioning were fixed in Bouin's fluid and the sections were stained with Ehrlich's or Delafield's Haematoxylin. In some cases sections were counterstained with eosin or Congo-red. Wax model reconstructions of some hearts were also made. Hearts of *Geomyda trijuga*, *Calotes versicolor* and *Naja naja* have been treated as representing Chelonia, Lacertilia and Ophidia for purposes of illustration. All the figures have been drawn by the author.

Shape and size of the heart

A detailed account of the external morphology of the heart of reptiles has been sent to press. Only pertinent features are herein recorded.

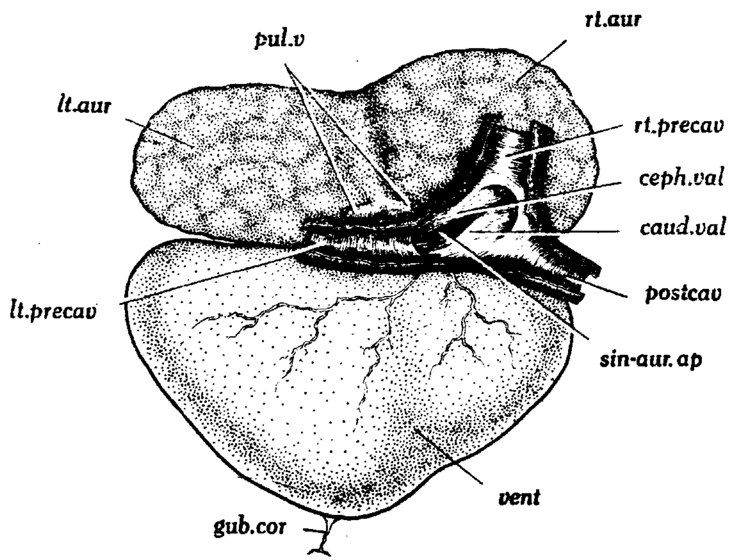
The shape of the heart seems to depend upon the external form of the animal to which it belongs. Thus in Chelonia the heart is generally broader than long, in conformity with the characteristic flat and laterally expanded body.

In Rhynchocephalia and Lacertilia, the heart is slightly broader than long and bears some resemblance to the chelonian heart in typically lizard-like forms such as *Sphenodon punctatus* (O'Donoghue, 1920), *Hemidactylus leschenaulti*, H. *flaviviridis* (Mahendra, 1942), *Calotes versicolor*, *Teratolepis fasciata*, *Ophisops beddomei*, *Mabuya carinata* and *Varanus monitor* (Mathur, 1944). Unlike the chelonian heart the apex of the lacertilian heart is nearly always pointed. In lizards in which the shape of the body is altered as in *Chamaeleon Zeylanicus*, *Riopa guentheri* (Kashyap, 1951) and *Barkudia insularis* the heart tends to become elongated. In *Barkudia insularis* in which the body is elongated and devoid of limbs. the heart is extremely modified and shows highly unequal auricles, a deep interauricular fissure, oblique coronary sulcus and even a left anterior shoulder-like extension of the base of the ventricle as in the heart ofsnakes.

In Ophidia the heart is highly elongated and exhibits all the characters referred to in connection with the heart of *Barkudia insularis*, but in a more marked and typical manner. The heart of *Acrochordus granulatus*, the marine Colubrid snake is, however, unique in being highly truncated in appearance and in being situated almost in the middle of the body as in no other snake so far studied.

The heart of crocodiles, like those of lizards and Rhynchocephalia, is only slightly elongated.

Regarding the size of the heart relative to the size of the body it is found that the chelonian and lacertilian hearts are generally bigger than those of other reptiles. Among the snakes, which generally show a small heart relative to the size of the body, *Eryx johni* seems to be an exception in possessing a comparatively large heart.



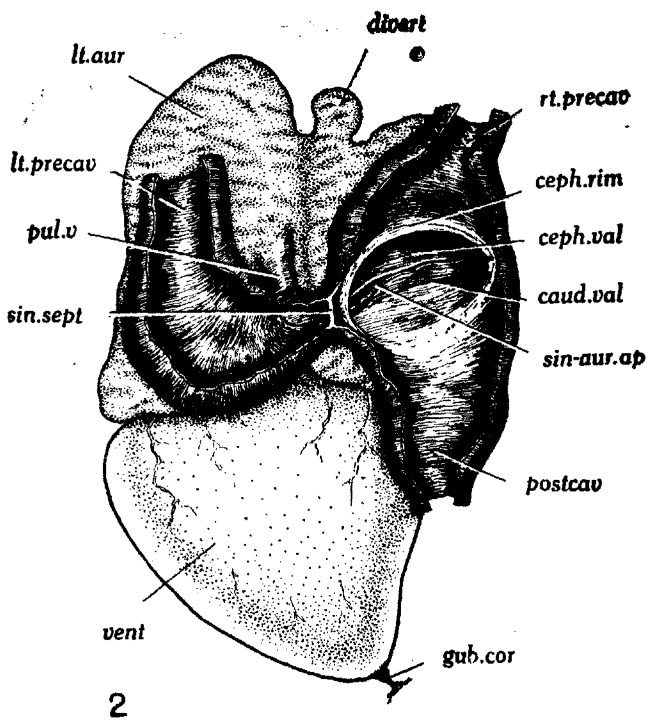
TEXT-FIG. 1.

Dissection of the sinus venosus of *Geomyda trijuga* showing the oblique sinu-auricular aperture with the cephalic and caudal valves.

A gubernaculum cordis is generally present in the hearts of Chelonia, Lacertilia and Crocodilia.

Venous trunks and Sinus Venosus

The base of the venous trunks and the sinus venosus are usually of large size in Chelonia and Lacertilia. The internal structure of the sinus venosus is at its simplest in the chelonian heart, there being no sinus septum (Text-fig. 1). Among the lizards, there are some forms whose sinus venosus does not possess a well developed sinus septum. Such forms are *Hemidactylus flavivirdis* (Mahendra, 1942), *H. leschenaulti*, *Teratolepis fasciata*, *Riopa guentheri* (Kashyap, 1951), *Varanus monitor* (Mathur, 1944) and *Tiliqua scincoides* (Rau, 1924). Generally, however, the sinus septum is well developed in the lacertilian heart (Text-fig. 2). In those lizards in which it is absent, the junction between the left precaval vein and the sinus venosus does not show any constriction. In Ophidia, the structures inside the sinus venosus have undergone some reduction in conformity with the reduction in the size of the venous trunks and the elongation of the sinus venosus (Text-fig. 3). In the crocodiles, the sinus venosus is very much reduced, suggesting its ultimate disappearance in the hearts of birds and mammals.



TEXT-FIG. 2.

Dissection of the sinus venosus of *Calotes versicolor* showing a well developed cephalic rim at the junction of the sinus venosus with the dorsal wall of the right auricle. Note the large size of the venous trunks and the well developed sinus septum.

Auricles

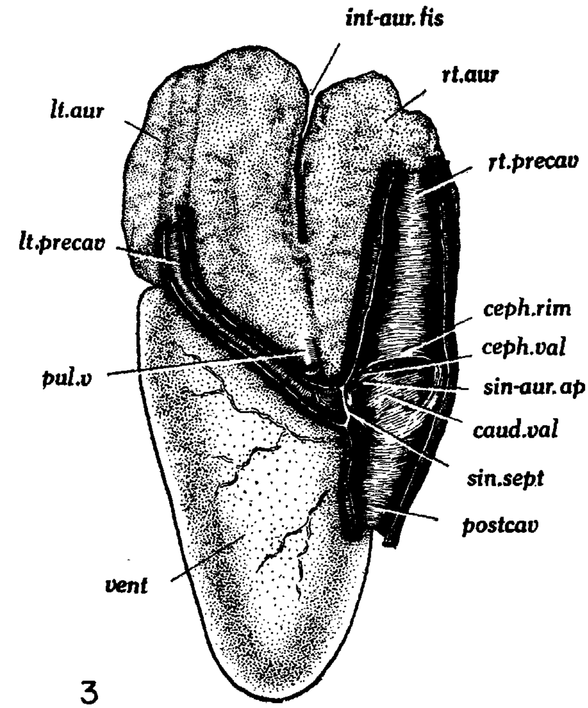
The auricles are thin walled and highly distensible. Hence when orgedwith blood they appear darker and larger than the ventricle. The difference in size between the two auricles is not so emphasised in the chelonian heart. The difference is moderate in lacertilian, rhynchocephalian and crocodilian hearts while it is extreme in the ophidian hearts. Along with the increase in disparity in the size of the auricles and lengthening of the heart as a whole, the interauricular fissure is also seen to become deep.

Diverticulum

The presence of a diverticulum on the auricle does not connote any special significance, as its formation is a specific peculiarity brought about by the disposition of the aortic trunks or their immediate branches and the presssure they exert on the auricles. Generally, it is the right auricle that bears the diverticulum and the right pulmonary artery is often responsible for its formation. An exception to this is the heart of *Ptyas mucosus* (Ray, 1934) in which the diverticulum is borne on the left auricle and is caused by the left systemic arch.

Valves

Regarding the disposition of the sinu-auricular valves, there is a remarkable uniformity in the hearts of all lower reptiles. The sinu-auricular aperture and the sinu-auricular valves that form its anterior and posterior margins are both obliquely transverse (Text-figs. 1–3). The ends of the valves towards the left side extend into the base of the left precaval vein and slightly overlap each other, the cephalic valve being ventral to the caudal. Towards the right side, the two valves run vertical and parallel to one another and gradually fuse to form a ridge called the suspensory ligament. The auriculo-ventricular aperatures are, each, guarded by a single large mesial valve and in some hearts by an additional small lateral valve (Text-figs. 4–6). The mesial valve is attached to the posterior end of the interauricular septum. Its dorsal and ventral margins are attached to the corresponding portions of the ventricular wall. The lateral margin alone is free, thin, notched and inflexed. It is this portion of the valve that plays an important part in preventing the regurgitation of blood during the ventricular systole. The mesial valve is bowl shaped, with the hump of the bowl towards the auriculo-ventricular opening and the cavity towards the ventricle. When the right valve is pushed towards the auriculo-ventricular aperature during the ventricular systole it is seen to fit snugly into a corresponding hollowness in the base of the ventricle, outside the rim of the auriculo ventricular aperture. In such a position, the inflexed lateral margin of the valve opens out and lies just against the opening of the right systemic trunk. This fact is of considerable significance in directing the two streams of blood into the systemic arches, the mixed blood finding its way into the left systemic arch whose opening lies just beyond the limits of the lateral margin of the valve when it has opened out and the arterial blood finding its way into the right systemic arch, which is the only channel left open for the blood during the last phase of the ventricular systole. The right mesial valve is usually larger and stronger than the left. The mesial-valves show a gradual increase in size and efficiency from Chelonia through Lacertilia, Ophidia and Crocodilia. In the last group, the openings of the aortic trunks are actually situated within the mesial valves, antero-mesially. Hence the valves act like funnels directing the blood into the aortic trunks, during the ventricular systole. The opening of the right systemic trunk is situated within the left mesial valve while those of the left systemic and pulmonary trunks are within the right mesial valve.



TEXT-FIG. 3.

Dissection of the sinus venosus of *Naja naja* showing the cephalic rim, sinu-auricular aperture with valves and the sinus septum. Note the oblique disposition of the left precaval and the elongation of the sinus venosus.

Cartilaginous support

A cartilaginous support is frequently present in the hearts of Chelonia, Lacertilia and Crocodilia. It is unifocal in the first two groups and multifocal in the last one. Ophidian hearts are usually devoid of a cartilaginous support. However, a small cartilaginous rod has been found in the heart of *Typhlops braminus* (Kashyap, 1950). The usual location of the cartilage is near the anterior end of the interventricular septum, in the vicinity of the pocket valves of the aortic trunks, sometimes extending slightly beyond the limits of the ventricle. The cartilage is generally of the hyaline type.

Ventricle

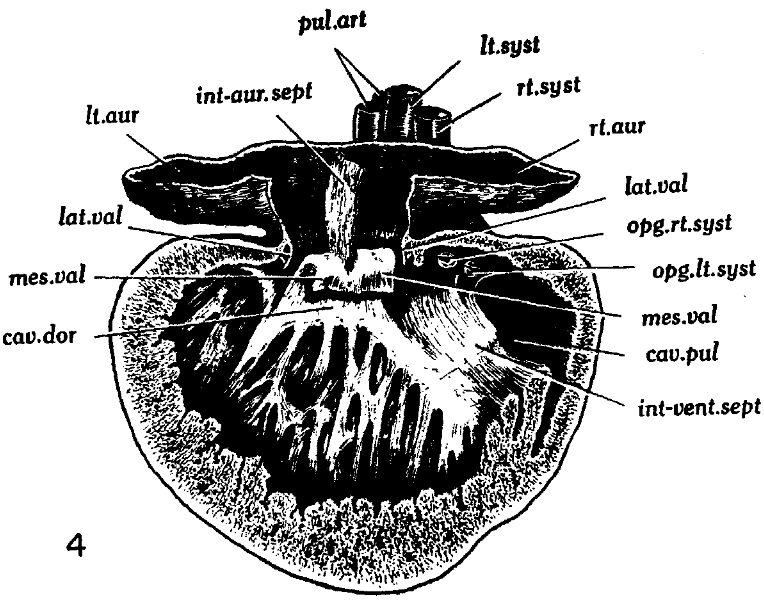
The ventricle is the most important part of the cardiac anatomy from the point of view of the shift from a three-chambered condition to a four-chambered one. In the ventricle of all lower reptiles there are two large cavities, a cavum dorsale situated antero-dorsally towards the left side and a cavum pulmonale situated ventrally towards the right. These two cavities are completely separated from one another in the caudal portion by the interventricular septum, while anteriorly, where the interventricular septum becomes incomplete, they communicate with each other freely. The present study has shown that the hearts of Chelonia, Lacertilia and Ophidia form a progressive series showing a gradual increase in the thickness of the wall of the ventricle, particularly towards the left side (Text-figs 4–6). This brings about a corresponding reduction in the extent of the cavum dorsale. The thickened ventricular wall, towards the left side, is broken up into numerous vertical ridges which lodge spacious crevices among them which will trap the arterial blood as it rushes into the ventricle and hold it till the venous and mixed blood reach the pulmonary and left systemic trunks.

It should be noted that the classical view regarding the selective distribution of blood to the three aortic trunks in Amphibia and Reptilia has been questioned by some authors recently. Thus Vandervael (1933) and Foxon (1947, 1951 and 1955) have brought out exprimental evidence to prove that mixing of blood takes within the amphibian ventricle. A similar view has been expressed by Prakash (1952) concerning the lizard, *Uromastix hardwickii*. However, Foxon and his associates (1956), using similar radiographical methods on another lizard, *Lacerta viridis*, have supported the selective distribution hypothesis. Simons and Michaelis (1953) using fluorescent dyes, have shown that in the heart of the frog, *Hyla caerulea* selective distribution of blood occurs under certain unknown circumstances while at others mixing of blood takes place. Thus experimental data are still inconclusive regarding the nature of the intracardiac circulation of blood in the amphibian and reptilian hearts. But looking at the problem from a purely anatomical point of view, one feels that several advanced features of the reptilian heart such as the absence of a truncus arteriosus; increased ridge formation towards the left side of the ventricle and relative lack of the same towards the right side; the presence of an incomplete interventricular septum whose incompleteness is such that the venous blood is obviously led on to the cavum pulmonale; all these and many more to be detailed presently, indicate an attempt at a selective distribution of blood within the reptilian ventricle. The degree of separation may, however, vary with different reptiles, depending upon the finer details of their cardiac anatomy.

The mesial auriculo-ventricular valves extend somewhat deeply into the cavum dorsale in the hearts of Lacertilia and Ophidia (Text-figs. 5–6). They are attached to the ventricular wall dorsally and ventrally and are free only laterally. Therefore, it could be expected that the arterial and venous streams of blood rushing into the ventricle push the lateral free margin of the valves, medially, as far as their fixed dorsal and ventral margins permit. By this the two mesial valves form a sort of a transient median vertical partition which is operative till the main volume of arterial and venous blood have found their respective places within the ventricle. Secondly, the incomplete interventricular septum is so situated that it permits the bulk of the venous blood to get into the cavum pulmonale from where it is carried forward by the pulmonary trunk. Towards the left side of the cavum dorsale, the absence of an exclusive arterial chamber is amply compensated by the numerous vertical crevices that cut deep into the wall of the ventricle. These locked-up spaces are decidedly more advantageous than open cavities as they do not permit a free movement of the blood lodged in them and hence prevent, to some extent, the mixing up of the two streams of blood.

The location of the openings of the three aortic trunks is also noteworthy. The opening of the pulmonary trunk is within the cavum pulmonale, ventral to the interventricular septum. The opening of the right systemic trunk is dorsal to the septum, very near the right auriculo-ventricular aperture in such a way that it is just coverd over by the lateral margin of the right auriculo-ventricular aperture during the ventricular systole. The opening of the left systemic trunk lies just beyond the lateral margin of the right auriculo ventricular valve when the latter is distended, opposite to the free margin of the inter ventricular septum. The disposition of these openings is very suggestive of a selective distribution of blood.

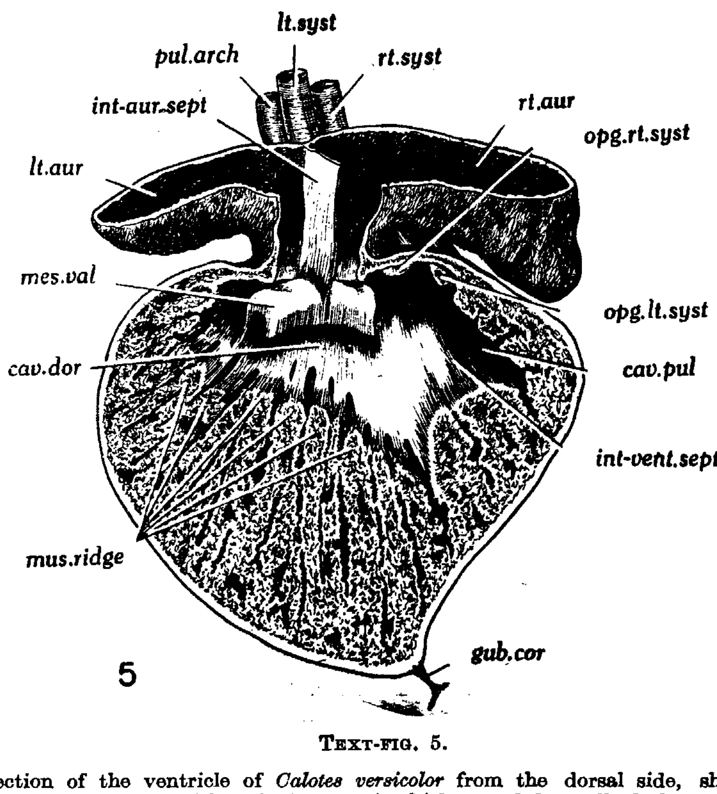
It has been suggested that the ventricle of the lower reptile has within it two incomplete septa disposed in different planes. One of these is the interventricular septum. The other one has been referred to as the "muscular ridge" by Rau (1924) and "vertical septum" by Leene and Vorstman (1930). The vertical septum is said to be situated about the middle of the cavum dorsale, in its caudal portion, disposed in a dorso-ventral plane. The vertical septum, by virtue of its location, appeared to them as significant and suggestive of the way in which the interventricular septum may have become complete. A similar opinion is implied when Foxon (1955) says that "it is this secondary septum which in crocodiles and birds become the definitive interventricular septum". The only thing that was required was to continue this incomplete, caudal and vertical septum, cranially, till it joins the region between the mesial valves of the auriculo-ventricular apertures. Before becoming complete, the vertical septum should, however, turn to the right so as to include the opening of the right systemic trunk. Leene and Vorstman (1930) summed up their hypothesis by saying that "in dividing the ventricle into two parts, two septa play a part, a vertical septum and a horizontal one". The horizontal septum referred to here is the interventricular septum. They also illustrated their hypothesis by means of two figures in which the vertical and the horizontal septa have been extended further, anteriorly, along the planes they occupy, till the ventricular cavity is completely divided into venous and arterial channels.



TEXT-FIG. 4.

Dissection of the ventricle of *Geomyda trijuga* from the dorsal side, showing the auricular ostia with valves, the cavum dorsale, the openings of the aortic trunks and the incomplete interventricular septum Note the spacious cavum dorsale and the moderately thick wall of the ventricle. The small ridge between the openings of the two systemic trunks indicates the position occupied by the pars endocardialis in the crocodilian ventricle.

The present study has afforded an opportunity to find out the validity of Leene and Vorstman's two-septa hypothesis. Transverse sections of the ventricle of many reptiles, particularly of Lacertilia and Ophidia show a medially situated and dorso-ventrally disposed muscular column which would answer to the descriptions of a vertical septum. It is situated in such a way as to divide the cavum dorsale into left and right halves, if extended anteriorly. Transverse sections, however, do not give the required topographical details which would indicate the real nature of this vertical septum. When the ventricle is dissected, it is often difficult to locate the vertical septum from among the numerous vertical ridges that project into the cavum dorsale from behind. In reality, the so-called vertical septum appears to be the most medial and prominent of these vertical ridges and nothing more. In Chelonia (Text-fig. 4), where the wall of the ventricle, which is responsible for these vertical ridges, is relatively thin these ridges do not extend far into the cavum dorsale and this is probably the reason why Leene and Vorstman (1930) were not able to find a well developed vertical septum in *Chelone*. In *Testudo* they reported that the vertical septum is much better developed and this may be due to a slight increase in the muscularity of the ventricular wall. Thus the vertical septum which is to be entrusted with so important a role as the completion of the interventricular septum is found to be very inconstant in its structure and position and is often poorly developed too.



TEXT-FIG. 5.

Dissection of the ventricle of *Calotes versicolor* from the dorsal side, showing the internal structure. Note the increase in thickness of the wall of the ventricle with a corresponding reduction in the extent of the cavum dorsale. The muscular ridges conceal deep crevices among them.

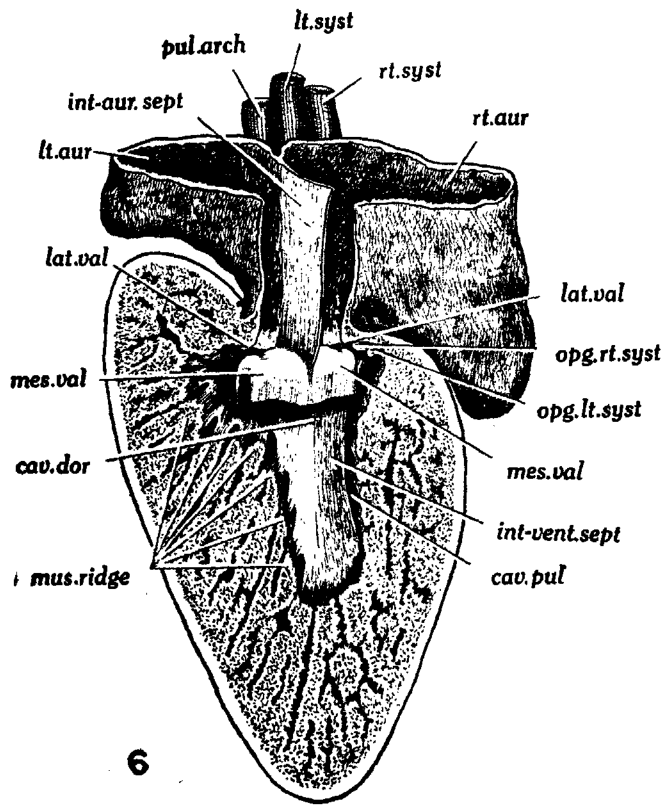
Besides, there is the problem of the opening of the right systemic trunk which has to be brought towards the left side of the ventricle before the vertical septum completes itself anteriorly. This problem is explained away by Leene and Vorstman

(1930) by assuming that "the vertical septum turns more or less to the right growing in a cranial direction". It is difficult to understand how the vertical septum, which is already within easy reach of the region between the two mesial valves, could turn to the right and include the opening of the right systemic trunk and at the same-time leave out the right auriculo-ventricular aperture.

It is also worth noting that most of the valves and septa are endocardial in origin and often remain in the same condition throughout, while the vertical septum is purely muscular except for an extremely thin covering of endocardial tissue in common with the lining of the cavum dorsale.

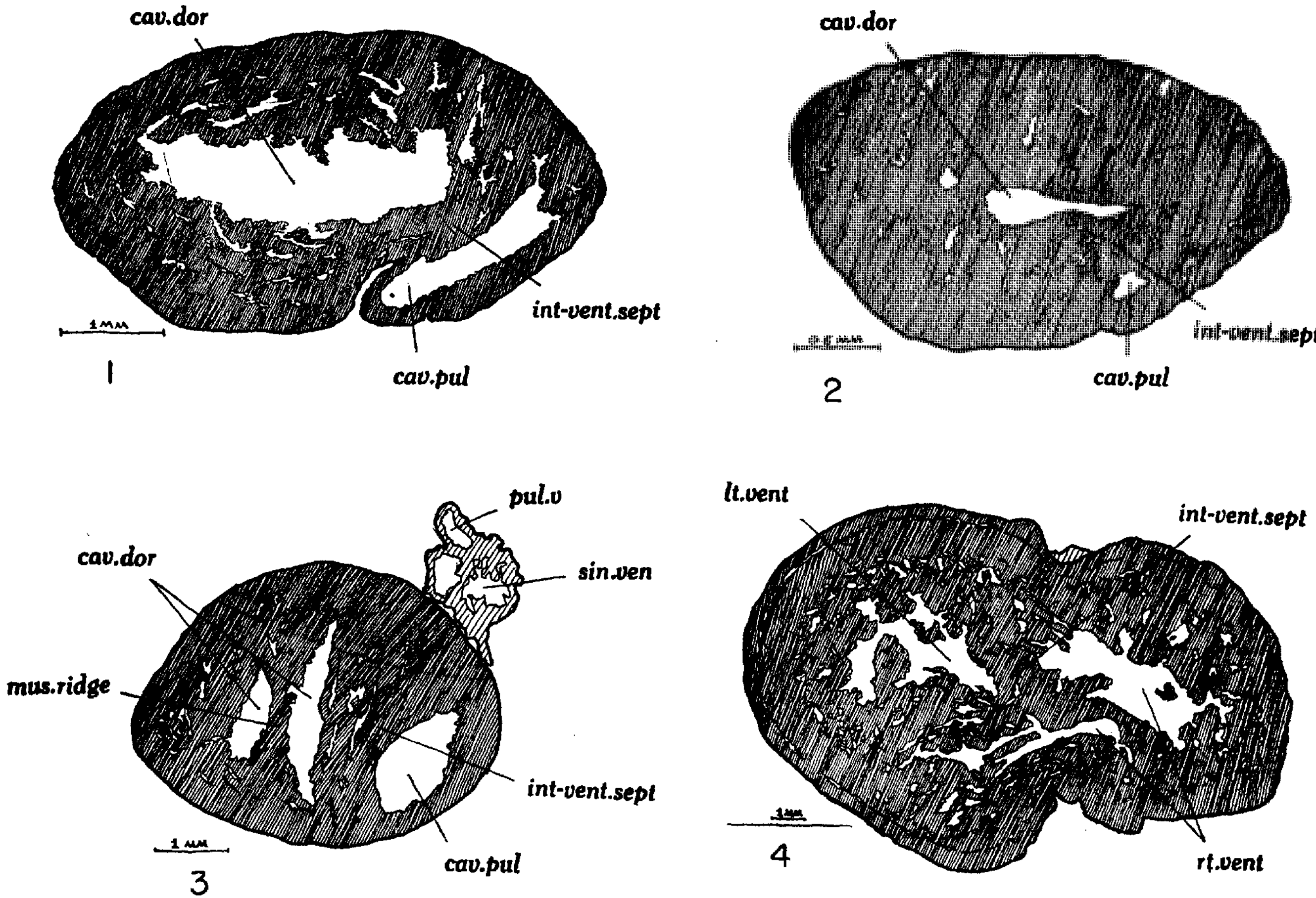
Further, it is difficult to believe that the completion of the interventricular septum is effected from the caudal end as Goodrich (1919) has opined, so far away from the region of the auricular ostia and the opening of the systemic trunks with which the finished septum is so intimately associated.

Thus from the above account it becomes clear that the vertical septum of the lower reptiles cannot possibly effect the completion of the interventricular septum. As shall be detailed later, the problem is intimately bound up with the incomplete interventricular septum of the lower reptiles.



TEXT-FIG. 6.

Dissection of the ventricle of *Naja naja* from the dorsal side, showing the internal structure. Note the thickness of the wall of the ventricle and the mesial shift of the interventricular septum.



TEXT-FIG. 7.

Transverse sections of the ventricle through the sub-apical region in the hearts of (1) *Geomyda trijuga*, (2) *Calotes versicolor*, (3) *Naja naja* and (4) *Crocodilus palustris*. The interventricular septum is complete and separates the large cavum dorsale from the small cavum pulmonale in 1, 2 and 3 and separates the right and left ventricles in 4.

The interventricular septum or the horizontal septum is the most important component of the ventricle and exhibits a remarkable constancy of structure, position and function in the heart of lower reptiles. It consits of two parts, a posterior complete (Text-fig. 7, figs. 1–3) and an anterior incomplete part (Text-fig. 7, figs. 5–7). The posterior portion is made up of a loose assemblage of muscle fibres and is recognised by its characteristic oblique position and the presence of the cavum pulmonale towards its right. The anterior portion is very clearly differentiated because of its smooth endocardial covering and its characteristic horizontal position. It forms the floor of the cavum dorsale towards the right side and its free margin overhangs the cavum pulmonale. In Chelonia, the horizontal septum is rather short and is situated diagonally towards the right anterior corner of the ventricle (Text-fig. 4). In Lacertilia, it is somewhat longer and more mesial than in Chelonia and therefore, the cavum pulmonale which lies towards its right appears to be more extensive (Text-fig. 5). The lengthening of the horizontal septum and its mesial shift is further emphasised in the Ophidian ventricle in which the free margin of the horizontal septum is brought almost in a line with the right auriculo-ventricular aperture (Text-fig. 6). This enables the cavum pulmonale to receive almost all of the venous blood as it rushes into the ventricle, thereby minimising the chances of its mixing with the arterial blood.

The free margin of the horizontal septum, particularly at its anterior end, has a thick covering of endocardial tissue which is continuous with that of the pocket valves of the aortic trunks.

Regarding the disposition of the openings of the aortic trunks Goodrich (1930) very aptly says that "the cavum arteriosum leads, antero-dorsally, to the septum towards the opening of the right carotico-systemic trunk, while the opening of the left systemic trunk is situated almost opposite the free edge of the septum. . . The position of the opening into the left systemic trunk varies a little in different forms, being nearer the opening of the right trunk in Ophidia, and of the pulmonary trunk in Chelonia; but the general disposition of the three openings is remarkably constant throughout Reptilia". The nearness of the opening of the left systemic trunk to the opening of one or the other of the remaining two aortic trunks has been the basis for attempts at dividing the lower reptiles into two groups, with some phylogenetic significance attached to such a division (O'Donoghue, 1918; von Hofsten, (1941). In reality, the nearness of the opening of the left systemic trunk to the opening of either the right systemic or the pulmonary trunk cannot form a clue to the actual position of the incomplete interventricular septum.

In the present study an attempt is made to mobilise all the indirect evidence which would establish the true position of the interventricular septum with reference to the opening of the aortic trunks. This shows that the interventricular septum of lower reptiles lies between the left systemic and pulmonary trunks, as figured for the Lepidosaurian type by von Hofsten (1941).

(1) In dissections of the ventricle in which the dorsal wall has been removed, the openings of both the systemic trunks are seen lying side by side, with a common wall between them, dorsal to the free margin of the interventricular septum. Only the ventrally situated opening of the pulmonary trunk is hidden from view.

(2) There is invariably a confluent space posterior to the openings of the two systemic trunks and their pocket valves are made up of the same continuous endocardial tissue. This fact is clearly seen in transverse sections of all the hearts studied (Text-fig. 9–11).

(3) On the other hand, transverse sections show clearly that the pulmonary trunk is completely separated from the two systemic trunks by a muscular wall. There is not a single instance of such an encroachment of muscular wall between the two sytemic trunks, within the limits of the ventricle. It should be noted that

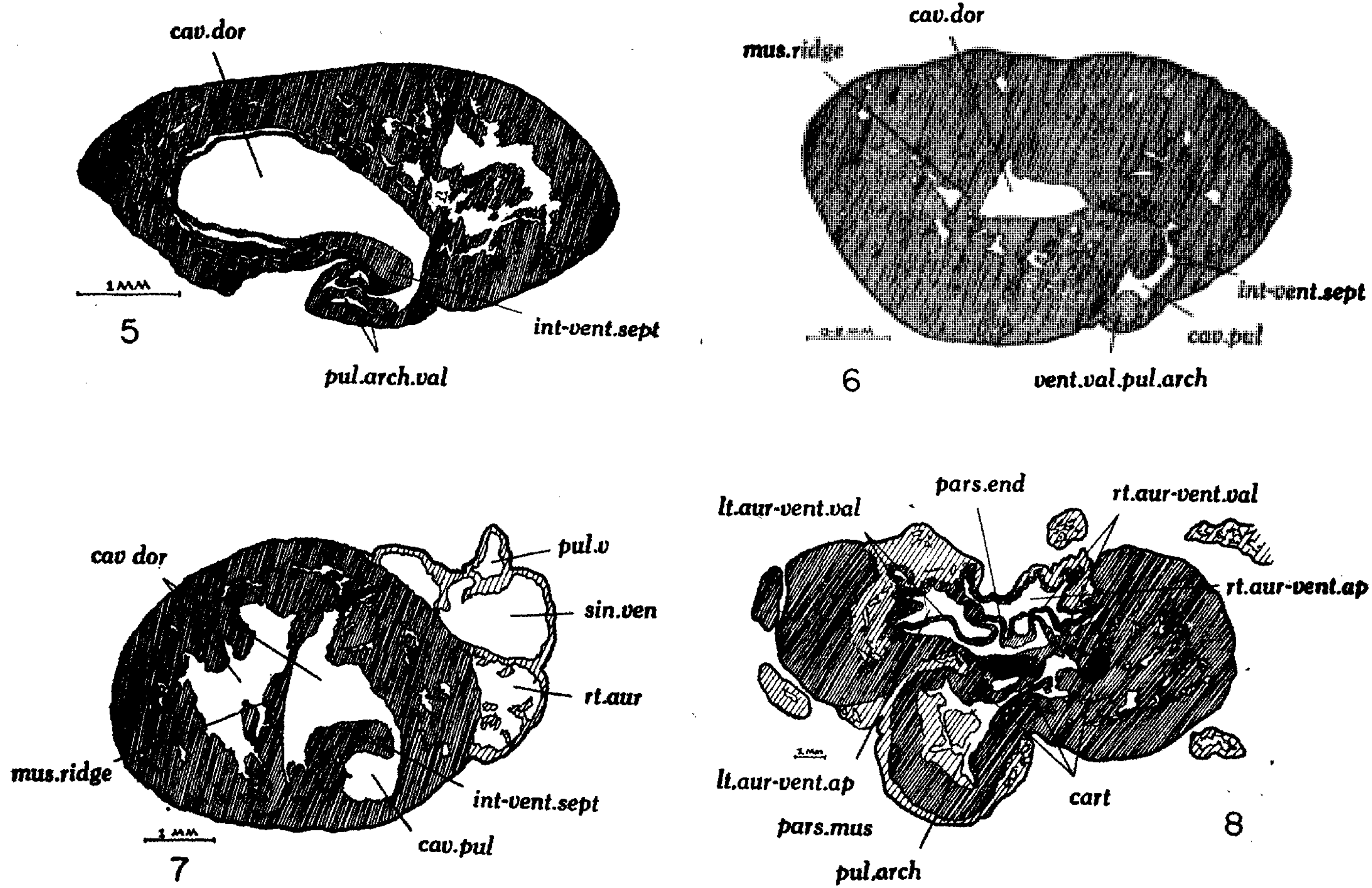
the muscular elements that are seen between the pulmonary and systemic trunks become continuous with the free margin of the interventricular septum, posteriorly.

(4) It is an accepted fact that a part of the bulbus arteriosus of the anamniote heart becomes incorporated into the reptilian ventricle during the latter's phylogeny and contributes to its definitive right wall (Greil, 1903; O'Donoghue, 1912; Robertson, 1914 ; Goodrich, 1930). For this reason, during the development of the reptiles, the posterior end of the spiral fold or its homologue and the anterior end of the interventricular septum meet at the ventral endocardial ridge of the auriculoventricular aperture and become continuous with each other. As the spiral fold is situated between the arterial and venous channels, it effects the complete separation of the pulmonary trunk fom the two systemic trunks during the development of the reptilian heart (Bremer, 1928; Goodrich, 1930). As the spiral fold is continuous with the anterior end of the interventricular septum it can be inferred that the real position of the latter is between the pulmonary and the systemic trunks.

(5) Another convincing proof that the opening of the left systemic trunk is definitely dorsal to the interventricular septum is the cartilaginous support. In those hearts in which there is a cartilaginous support, it is always situated at the free margin of the interventricular septum and extends, to a greater or lesser extent, between the pulmonary and the left systemic trunks.

Therefore, O'Donoghue's contention that the living reptiles can be divided into two groups regarding the position of the interventricular septum with reference to the opening of the aortic trunks is untenable. It should, however, be pointed out that the conclusion arrived at in this study refers to the condition seen in the living lower reptiles and not to the course phylogeny might have taken in the completion of the interventricular septum.

A careful comparison of the structure and position of the complete interventricular septum of the crocodile with the incomplete interventricular septum of lower reptiles, gives a clue to the manner in which it may have become complete. The crocodilian interventricular septum consists of two parts, an antero-dorsal and a postero-ventral (Text-fig. 7, fig. 4; Text-fig. 8, fig. 8; Text-fig. 9, fig. 12). The two parts are sharply marked off from one another in their structure and position although, they form a single continuous septum. The postero-ventral portion is very thick and muscular and is called pars muscularis. It bears a striking resemblance to the incomplete interventricular septum of lower reptiles. In transverse sections of the ventricle the appearance of the two is exactly the same, both regarding the bend towards the right side and the position of the openings of the aortic trunks. Instead of having a free marign, as in lower reptiles, the pars muscularis is continued dorsally by the antero-dorsal portion of the interventricular septum, pars endocardialis. If the pars endocardialis is removed from the crocodilian ventricle its internal structure would be very similar to that of the ventricle of a lizard or snake. In accordance with this interpretation, the pars endocardialis and the pars muscularis should meet at an angle along a line which corresponds to the free margin of the interventricular septum of lower reptiles. Dissections as well as transverse sections of the corcodilian ventricle show that this is precisely the case and the fold formed at the junction of the dorsal and ventral portions of the interventricular septum is clearly seen in them. From the above account it becomes evident that the right ventricle of the crocodilian heart is merely the cavum pulmonale of the lower reptile with parts of the cavum dorsale about the free margin of the interventricular spetum added to it. The pars endocardialis of the crocodilian ventricle has no counter-part within the ventricle of lower reptiles It is not homologous to the so-called vertical septum because the latter is merely one of the numerous ridges present towards the left side of the ventricle and is very inconstant in structure and position. Further, the vertical septum joins the interventricular septum, ventrally, at the



TEXT-FIG. 8.

Transverse sections of the ventricle through the middle region in the hearts of (5) *Geomyda trijuga*, (6) *Calotes versicolor*, (7) *Naja naja* and (8) *Crocodilus palustris*. The interventricular septum is incomplete and horizontal in 5, 6 and 7, and is complete in 8. Note that in 8, the interventricular septum consists of two parts, a dorsal thin pars endocardialis and a ventral thick pars muscularis. The latter bears cartilaginous nodules.

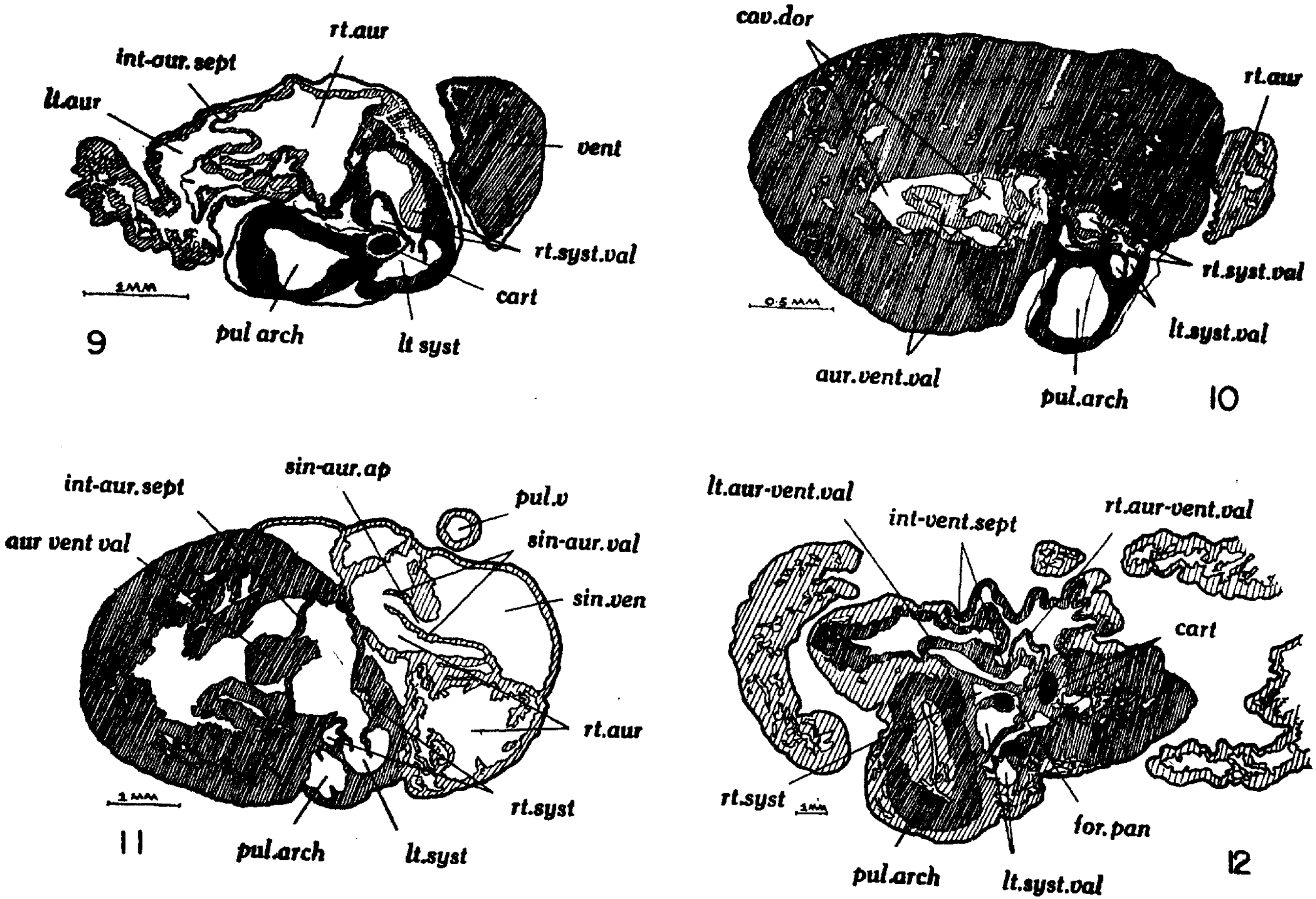
base of the latter, while the pars endocardialis joins the pars muscularis along a line which corresponds to the free margin of the incomplete interventricular septum. The pars endocardialis is, therefore, a new formation.

It is known that there are four endocardial ridges in the embryonic bulbus of reptiles (Text-fig. 10 fig. 16). These are termed the ventral, dorsal, left and right ridges (Bremer, 1928; Goodrich, 1930). Of these, the ventral one is the largest and corresponds to the amphibian spiral fold. The fusion across of the ventral and dorsal ridges results in the formation of the septum pulmo-aorticum which separates the pulmonary arch from the two systemic trunks. The fusion across of the right and left ridges results in the formation of the septum aorticum which separates the right and left systemic trunks. The right endocardial ridge is, however, rudimentary and hence the pulmonary channel remains a single undivided arch in the region of the bulbus. As already mentioned, the interventricular septum is in continuity with the ventral endocardial ridge. On analogy, it could be suggested that the pars endocardialis is in a line with the left ridge that separates the two systemic trunks and thus forms its ventricular extension. If such a condition is drawn, the diagram bears a striking resemblance to the cross section of a crocodilian ventricle in all details (Text-fig. 10, fig. 16). The dorsal ridge is not represented in this hypothetical cross section because it restricts itself to the region of the bulbus and does not extend into the ventricle in any reptile. The right ridge is also not to be represented because, as already pointed out, it is rudimentary even in the region of the bulbus.

In the formation of the complete interventricular septum, therefore, the endocardial elements play an important part as is normally the case (Robertson, 1913; Davis, 1927). The thick covering of endocardial tissue at the anterior end of the incomplete interventricular septum makes this hypothesis probable. Further, in *Geomyda trijuga* the anterior end of the interventricular septum gives off a small endocardial ridge which passes between the openings of the two systemic trunks (Text-fig. 4). This is exactly the position of the pars endocardialis in the crocodilian ventricle.

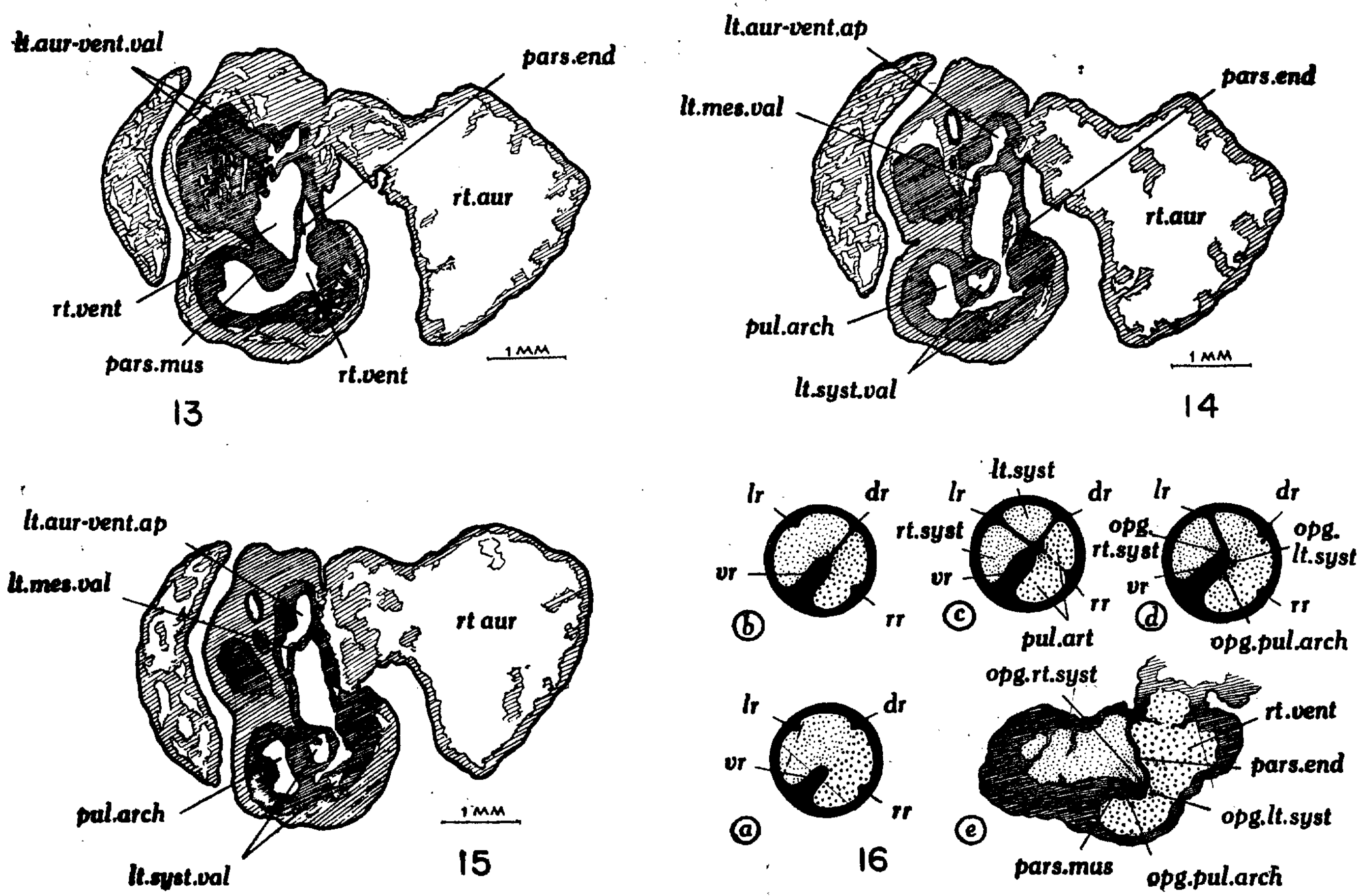
It will also be seen that by such a hypothesis the openings of the three aortic trunks are automatically set in the position they occupy in the crocodilian ventricle, without involving the turning and twisting of any structure that is already present in the ventricle of living reptiles. In order to bring the region of the auricular ostia in a line with the two systemic trunks, as seen in the crocodilian heart, one other change is necessary in the ventricle of a lower reptile. The interventricular septum with the openings of the aortic trunks at its anterior end should move towards the middle of the ventricle at a plane ventral to that of the auriculo-ventricular apertures. It has already been pointed out that such a shift is seen, to a slight degree, in the lacertilian and, to a marked degree, in the ophidian ventricles. This suggests the way by which a mesial shift of the interventricular septum may have taken place in the evolution of the crocodilian condition and to that extent the mesial shift recorded in the lacertilian and ophidian hearts is a proof to the hypothesis that has been put forth.

Another proof for the hypothesis comes from a developmental anomaly found in the heart of a crocodile embryo. Transverse sections of the heart of this embryo crocodile, which was fully developed and measured 10 cms., showed that the interventricular septum is incomplete anteriorly (Text-fig. 10, figs. 13–15). About the level of the mesial valve of the left systemic trunk, the pars endocardialis is found to be dissociated from the pars muscularis, just where they meet at an angle. Anterior to this point, the pars endocardialis is seen to gradually dwindle away from the pars muscularis and finally disappear altogether. That this is not an artefact is evident by the fact that after its dissociation from pars muscularis, the pars endocardialis could be followed up serially in a number of sections, each section showing



TEXT-FIG. 9.

Transverse sections of the ventricle through the aortic trunks in the hearts of (9) *Geomyda trijuga*, (10) *Calotes versicolor*, (11) *Naja naja* and (12) *Crocodilus palustris*. Note that in 9, 10 and 11 the right and left systemics are confluent with one another, and cut off from the pulmonary trunk by a muscular wall. A similar situation is seen in *Corcodilus palustris* in the region of the foramen of Panizzae.



Text-fig. 10.

Figures 13, 14 and 15.—Transverse sections of the ventricle of *Crocodilus palustr* showing an anomalous incompleteness in the interventricular septum. Figure 16 is a comparison between the embryonic bulbus of reptiles with the crocodilian ventricle. Explanation in the text.

it slightly shorter than it is in the previous one, till it completely disappears in the anterior sections. This anomaly points out to the fundamental duality of the crocodilian interventricular septum, a new endocardial septum becoming associated, in the course of phylongey, with a pars muscularis already existing in the ventricle of lower reptiles in the form of an incomplete interventricular septum.

Summary

The present study, based on the hearts of 29 species of reptiles, has brought to light the following facts concerning the structure of the reptilian heart.

1. The shape of the heart bears a direct relation to the external form of the body. In forms in which the shape of the body is in any way modified, the shape of the heart is also seen to be altered.

2. An auricular diverticulum is commonly seen in the hearts of lizards. It is usually borne on the antero-mesial aspect of the right auricle.

3. The junction of the left precaval vein with the sinus venosus is constricted in some lizards and most snakes. The presence of such a constriction is associated with a well developed sinus septum within the sinus venosus.

4. The sinu-auricular aperture is elliptical and placed obliquely transverse. It is bound by well developed cephalic and caudal valves.

5. The ventricular wall is particularly thick towards the left side and is beset with numerous vertical ridges and spacious crevices. These crevices trap the arterial blood as it enters the ventricle and hold it till the main current of venous blood reaches the cavum pulmonale.

6. The vertical septum which is supposed to divide the cavum dorsale into right and left halves is found to be inconstant in structure and position. It is merely one of the many vertical ridges found in the wall of the ventricle towards the left side. It is unlikely that it plays any significant role in the completion of the interventricular septum.

7. The incomplete interventricular septum of lower reptiles shows a remarkable uniformity of structure. It is complete and vertical posteriorly and incomplete and horizontal anteriorly.

8. It has been found that, in all the lower reptiles, the anterior end of the incomplete interventricular septum lies between the pulmonary and systemic trunks and the division of the lower reptiles into two groups on the basis of the position of the interventricular septum is, therefore, untenable.

9. Hearts of Chelonia, Lacertilia and Ophidia form a progressive series showing a gradual increase in the thickness of the ventricular wall towards the left side and a shifting of the interventricular septum towards the middle of the ventricle, indicating the line of evolution the ancestors of the crocodiles may have adopted to effect the complete division of their ventricle.

10. Pars muscularis of the crocodilian interventricular septum is homologous with the incomplete interventricular septum of lower reptiles. Pars endocardialis is a new formation without any corresponding structure within the ventricle of living lower reptiles. It is, presumably, an elaboration of the endocardial covering of the free marign of the incomplete interventricular septum, in a line with the left endocardial ridge of the embryonic bulbus.

ACKNOWLEDGEMENTS

The author wishes to record his gratitude to Prof. P. W. Gideon, Head of the Department of Zoology, Karnatak College, Dharwar, at the time when this study was undertaken, for his kindly encouragement and helpful suggestions. The author also considers himself fortunate in having the unstinted co-operation and expert guidance from Dr. K. R. Karandikar who succeeded Prof. P. W. Gideon as the Head of the Zoology Department, Karnatak College, Dharwar.

List of Abbreviations

aur. vent. val : aurieulo-ventricular valve.
cart : castilage.
caud. val : caudal valve of the sinu-auricular aperture.
cav. dor : cavum dorsale.
cav. pul : cavum pulmonale.
ceph. rim : cephalic of the sinu-auricular aperture.
ceph. val : cephalic valve of the sinu-auricular aperture.
com. car : common carotid trunk.
divert : diverticulum.
dr : dorsal endocardial ridge.
for. pan : foramen of Panizza.
gub. cord : gubernaculum cordis.
int. aur. fis : interauricular fissure.
int. aur. sept : interauricular septum.
int. vent. sept : interventricular septum.
lr : left endocardial ridge
lat. val : lateral valve of the auriculo-ventricular aperture.
lt. aur : left auricle
lt. aur. vent. apert : left auriculo-ventricular aperture
lt. car : left carotid artery.
lt. mes. val. : left mesial valve of the auriculo-ventricular aperture.
lt. precav : left precavel vein.
lt. pul. v : left pulmonary vein.
lt. syst : left systemic trunk.
lt. syst. val : valve of the left systemic trunk.
lt. vent : left ventricle.
mes. val : mesial valve of the auriculo-ventricular aperture.
mus. ridge : muscular ridge.
opg. lt. syst : opening of the left systemic trunk.
opg. pul. arch : opening of the pulmonary arch.
opg. rt. syst : opening of the right systemic trunk.
pars. end : pars endocardialis.
pars. mus : pars muscularis.
postcav : postcaval vein.
pul. arch : pulmonary arch.
pul. arch. val : valve of the pulmonary arch.
pul. art : pulmonary artery.
pul. v : pulmonary vein.
rt. aur : right auricle.
rt. aur. vent. apert : right auriculo-ventricular aperture.
rt. aur. vent. val : righr auriculo-ventricular valve.
rt. car : right carotid artery.
rt. precav. : right precaval vein.
rt. pul. v : right pulmonary vein.
rr. : right endocardial ridge.
rt. syst : right systemic trunk.
rt. syst. val : valve of the right systemic trunk.
rt. vent : right ventricle.
sin. aur. apert : sinu-auricular aperture.
sin. aur. val : sinu-auricular valve.
sin. sept : sinus septum.
sin. ven : sinus venosus.
vent : ventricle.
vr : ventral endocardial ridge.
vent. val. pul. arch : ventral valve of the pulmonar arch.

LIST OF REPTILES STUDIED

Chelonia	1.	*Geomyda trijuga*, Schweigger (Emydidae).
	2.	*Testudo elegans*, Schoepff (Testudinidae).
	3.	*Lissemys punctata*, Bonaterre (Trionychidae).
Lacertilia	4.	*Hemidactylus leschenaulti*, Dum and Bibr (Gekkonidae).
	5.	*Teratolepis fasciata*, Blyth (Gekkonidae).
	6.	*Calotes versicolor*, Daudin (Agamidae).
	7.	*Chamaeleon zeylanicus*, Laurenti (Chamaeleonidae).
	8.	*Mabuya carinata*, Schneider (Scincidae).
	9.	*Riopa guentheri*, *Peters* (Scincidae).
	10.	*Barkudia insularis*, Annandale (Scincidae).
	11.	*Ophisops beddomei*, Jerdon (Lacertidae).
	12.	*Varanus monitor*, Linn (Varanidae).
Ophidia	13.	*Typhlops acutus*, Dum and Bibr (Typhlopidae).
	14.	*Typhlops braminus*, Daudin (Typhlopidae).
	15.	*Uropeltis phipsoni*, Mason (Uropeltidae).
	16.	*Python molurus*, Linn. (Boidae).
	17.	*Eryx johni*, Russel (Boidae).
	18.	*Acrochordus granulatus*, Schneider (Colubridae).
	19.	*Oligodon taeniolatus*, Jerdon (Colubridae).
	20.	*Lycodon striatus*, Shaw (Colubridae).
	21.	*Dryocalamus nympha*, Daudin (Colubridae).
	22.	*Balanophis ceylonensis*, Gunther (Colubridae).
	23.	*Macropisthodon plumbicolor*, Cantor (Colubridae).
	24.	*Boiga trigonata*, Schneider (Colubridae).
	25.	*Dryophis pulverulentus*, Dum and Bibr (Colubridae).
	26.	*Naja naja*, Linn. (Elapidae).
	27.	*Vipera russelli*, Shaw (Viperidae).
	28.	*Trimeresurus gramineus*, Shaw (Viperidae).
Crocodilia	29.	*Crocodilus palustris*, Lesson (Crocodilidae).

References

Bremer, J. L. (1928). Part I. An interpretation of the development of the heart. Part II. The left aorta of reptiles. *Amer. J. Anat.*, **42**, 307–350.

Davis, C. L. (1927). Development of the human heart from the first appearance to the stage found in embryos of twenty paired somites. Contr. Embryol. Carneg. Instn., **107**, 19, 245–284.

Foxon, G. E. H. (1947). The mode of action of the heart of frog. *Proc. zool. Soc. London.*, **116**, 565–574.

——— (1951). A radiographic study of the passage of blood through the heart in the frog and toad. *Ibid.*, **121**, 529–538.

——— (1955). Problems of the double circulation in vertebrates. *Biol. Rev.*, **30**, 196–228.

Foxon, G. E. H., Griffith, J. and Price, M. (1956). The mode of action of the heart of the green lizard, *Lacerta viridis*. *Proc. zool. Soc. London.*, **126**, (1) 145–157.

Goodrich, E. S. (1916). On the classification of the Reptilia. *Proc. roy. Soc.* B. **89**, 261–276.

——— (1919). Note on the reptilian heart. *J. Anat., Lond.*, **53**, 298–304.

——— (1930). Studies on the structure and development of Vertebrates. Macmillan, London.

Greil, A. (1903). Beitrage zur vergleichenden Anatomie und Entwicklungs-geschichte des Herzens und des Truncus Arteriosus der Wirbelthiere. *Morph. Jb.*, **31**, 123–310.

Hofsten N. von, (1941). On the phylogeny of the Reptilia. *Zool. Bidr. Upsala.*, **20**, 501–521,

Kashyap, H. V. (1950). The structure of the heart of *Typhlops*. *J. zool. Soc. India.*, **2** (1), 42–48.

——— (1951). Structure of the heart of *Riopa guentheri*. *Ibid.*, 3(1) 31–10.

Leene, J. E. and Vorstman, A. G. (1930). Note on the structure of the heart of *Varanus* as compared with other reptilian hearts. *Tijdschr. ned. dierk. yer.* 3de serie, Deel II, Aflevering 2, 62–66.

Mahendra, B. C. (1942). Contribution to the bionomics anatomy, reproduction and development of the Indian house-Gecko, *Hemidactylus flaviviridis* (Ruppel). Part III. The Heart and the venous system. *Proc. Indian Acad. Sci., B*, **15**, 5.

Mathur, P. N. (1944). The Anatomy of the Reptilian Heart. Part I, *Varanus monitor*. *Ibid.*, B, **20**, (1), 1–29.

——— (1946). The Anatomy of the Reptilian Heart. Part II. Serpentes, Testudinata and Loricata. *Ibid.*, B**23**, 129–152.

O'Donoghue, C. H. (1918). The Heart of the leathery turtle, *Demochelys (Sphargis) coriacea*, with a note on the septum ventriculorum in the Reptilia. *J. Anat., London.*, **52**, 467–480.

——— (1921). The blood vascular system of Tuatara, *Sphenodon punctatus*. *Phil. Trans.*, B, **210**, 175–252.

Prakash, R. (1952). Radiographic demonstration of the mode of action of the heart of a lizard, *Uromastix hardwickii* Gray. *Indian J. Radiol.*. **6**, 126–128.

Rau, A. S. (1924). Observations on the anatomy of the heart of *Tiliqua scincoides* and *Eunectes murinus*. *J. Anat., Lond.*, **59**, 60–71.

Ray, H. C. (1934). On the arterial system of the common Indian Rat-snake, *Ptyas mucosus*. *J. Morph.*, **56**, 3.

Robertson, J. I. (1913). The development of the heart and vascular system of *Lepidosiren paradoxa*. *Quart. J. micr. Sci.*, **59**, 53–132.

——— (1914). The comparative anatomy of the bulbus cordis, with special reference to abnormal positions of the great vessels in the human heart. *J. Path. Bact.*, **18**, 191–210.

Simons, J. R. and Michaelis, A. R. (1953). A cinematographic technique, using ultra-violet illumination, for amphibian blood circulation. *Nature, Lond.*, **171**, 801.

Vandervael, F. (1933). Recherches sur le mechanisme de la circulation du sang dans le coer des Amphibiens anoures. *Arch. Biol., Paris.*, **44**, 571–605.