# THE CONDUCTING (CONNECTING) SYSTEM OF THE CROCODILIAN HEART

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## INTRODUCTION

Most of the observations by a large number of workers, reviewed by Davies & Francis (1946), are in favour of a myogenic rather than a neurogenic initiation and conduction of the impulse for contraction in the vertebrate heart, and the present histological study of the crocodilian heart is in consequence concerned with the investigation of the muscular connexions between its several chambers. In studying the problem of the phylogeny of the cardiac conducting system of mammals and birds the crocodilian heart assumes special importance since there occurs in it, for the first time in the vertebrate series, a complete ventricular septum. Thus such questions as the following arise. Does the presence of a complete ventricular septum modify the arrangement of the muscular atrioventricular connexions that exist in lower vertebrates so that the connexion is now situated solely or mainly in the ventricular septum, as in mammals and birds, or do the peripheral atrioventricular connexions, that precede any septal connexions in phylogeny, still form the main or only muscular connexion between atria and ventricles which could form a pathway for the passage of the impulse for cardiac contraction? Further, are the atrioventricular muscular connexions constituted by ordinary cardiac muscle or by specialized muscle fibres comparable in structure with those in mammals and birds?

In spite of the importance of these considerations, surprisingly few investigations have been made of the connexions between the sinus venosus and atria and between the atria and ventricles in the crocodilian heart. The older anatomical literature, now classic, was concerned purely with naked-eye morphology and not with matters that relate to the cardiac rhythm; it is well summarized by Röse (1890) and Hoffmann (1890). The most comprehensive anatomical description of the crocodilian heart (alligator and crocodile) is that of Greil (1903), who gave a detailed account of the morphology of the heart and its several chambers and of its valves and septa. Greil, however, did not clearly distinguish between striated cardiac muscle and smooth muscle or between structures derived from cardiac and from arterial sources. The work of Keith & Flack (1907), in which the sinu-atrial node of the mammalian heart was first described, following closely as it did on the observations on the atrioventricular node and bundle by Tawara (1906), was largely preoccupied with the phylogeny of these structures, and they claimed that they are remnants of more extensive tissues of similar nature that they stated were present at the junctions of the various cardiac chambers in lower vertebrates. Their colleague, Mackenzie (1913), studied the crocodilian heart (alligator and crocodile). He found that the sinus venosus established continuity with the right atrium by means of 'nodal tissue' situated on the left side of the sinu-atrial orifice. So far as the connexions of the atria with the ventricles are concerned, he maintained that continuity of the left atrium with the left ventricle is interrupted by fibrous tissue at the bases of the membranous atrioventricular valves, and that on the right side, in addition to occasional muscular continuity between the right atrium and right ventricle in the atrioventricular funnel, the right atrium is connected to the ventricular septum by means of 'nodal tissue'. Mackenzie believed that the connexions between the chambers of the crocodilian heart foreshadow the mammalian condition. Mangold (1914*a*, *b*) summarized the current views on the conducting system of the vertebrate heart but made only passing reference to the crocodilian heart, while Goodrich (1919), reviewing the morphological relations of the ventricular septum in the main reptilian orders (including Crocodilia), confined his attention to gross anatomy and made no reference to any connexions that might act as a conducting pathway or to any histological features. Swett (1923) described the muscular connexions between the several cardiac chambers of *Alligator mississippiensis* and was unable to confirm Mackenzie's description of 'nodal tissue' at the junctional sites. He found that the sinus muscle is continuous with the musculature of the right atrium all around the sinu-atrial orifice, that the musculatures of the atrial septum and of both atria are continuous with that of the dorsal part of the ventricular septum, and that peripheral connexions exist between the atrial and ventricular musculatures at the dorsal and right-dorsal quadrants of the right atrioventricular orifice and to a lesser extent at the dorsal and left-dorsal segments of the left atrioventricular orifice, these peripheral atrioventricular connexions involving the atrioventricular funnel. He also stated that 'experiments which have been carried out in Doctor Laurens's laboratory on the hearts of young alligators have substantiated the above anatomical description of the course of the auriculoventricular connection'. Lowman & Laurens (1924) took kymographic records from the right atrium and the apex of the ventricles before and after making scissors cuts in various segments of the atrioventricular junction and concluded that the most important single part of the atrioventricular connexion for coordinating atrioventricular rhythm is the right-lateral, other important parts being the left-lateral and left-ventrolateral, while the dorsal and right-dorsolateral parts are the least important. They also maintained that this differentiation agrees with the structure of the connexions as determined by Swett, but it appears to the present authors that these conclusions are at considerable variance with the anatomical muscular connexions determined by Swett and with those found in the present work.

## MATERIAL AND METHODS

Histological study was made of five hearts of *A. mississippiensis* (juvenile), which had been fixed in 10 % formalin and sectioned serially at $10\mu$ in each of the three conventional planes—transverse, frontal and sagittal, and of one heart of *Crocodilus niloticus* (juvenile), similarly fixed and sectioned serially at $10\mu$ in the transverse plane. The stains employed were iron haematoxylin and picrofuchsin, or haematoxylin and eosin, or Mallory's connective tissue stain, or Bodian's activated protargol. One alligator heart was impregnated in bulk by a silver pyridine method (Blair & Davies, 1935) and serially sectioned at $10\mu$ in the frontal plane. The grosser anatomical and topographical details, worked out from the sections, were supplemented by dissections of fresh hearts of *Alligator mississippiensis* and *Crocodilus niloticus*. Graphical reconstructions were made of the junctional regions to assist interpretation.

## OBSERVATIONS

The bulk of the histological observations were carried out on the alligator hearts, but no significant differences were observed in the single heart of the crocodile studied.

*The sinus venosus.* The sinus venosus, which forms a separate cardiac chamber, lies dorsal to the right atrium and has the form of an elongated pyramid, the short base of which lies cranially and the apex caudally (Pl. 1, fig. 2; Pl. 2, figs. 6, 7). The two precaval veins enter the lateral angles of its base, the postcaval and the two hepatic veins enter its apex, while the coronary vein enters its ventral surface near the apex. The muscle fibres constituting its dorsal wall run mainly transversely, though there is some criss-crossing of the fibres. Towards the ventral aspect, i.e. towards the junction of the sinus with the right atrium, the muscle fibres change their direction and become mainly longitudinal. At the actual site of junction of the sinus with the right atrium there is not a compact ring of muscle as in the Salamander (Davies & Francis, 1941); rather does the musculature of the sinus communicate with that of the right atrium through a broad meshwork of fibres, largely circular in direction (i.e. surrounding the orifice), but with a considerable admixture of connective tissue. A short distance proximal to the sinu-atrial junction, however, there is a thickened ring of circular muscle fibres in the sinus wall (Pl. 2, fig. 7). Two large muscular valves, right and left (Pl. 2, figs. 6, 7), guard the opening of the sinus into the right atrium. The muscular walls of both the sinus and the right atrium contribute to their formation, and there is quite free continuity between these two muscular components of the valves all around the sinu-atrial orifice. At the left margin of the sinu-atrial opening the wall of the right atrium is thickened (Pl. 2, fig. 7), the basket-work of atrial muscle fibres here being infiltrated with connective tissue. In the same area there are a few large nerve ganglia and many nerve fibres. It appears to the present writers that this arrangement of muscle, nerve cells and nerves is the structure described by Mackenzie (1913) in the crocodile as the sinu-atrial node, but it should be noted that the above arrangements involve the atrial and not the sinus muscle, and further that no histological differences could be made out between the muscle fibres here and those elsewhere in the atrial walls. The presence of nerve cells and the considerable admixture of connective tissue in this site do not warrant the identification of this site as 'nodal tissue'.

*The atria.* The right atrium lies rather to the ventral aspect, and the left atrium towards the dorsal aspect of the heart (Pl. 1, fig. 1). Each has an auricle (appendix) of considerable size. The atrial walls, as well as the atrial septum, consist of a basketwork of muscle fibres, with prominent muscular trabeculae which form a loose spongework projecting for a short distance into the atrial cavities.

*The atrioventricular junctions.* The atria are slightly invaginated like a funnel into the base of the ventricles (Pl. 2, fig. 9), the connective tissue of the epicardium following this invagination and to a large extent effecting a separation of the musculatures of the atria and ventricles except towards the caudal extremities of the funnel, where in places the atrial muscular component of the funnel is continuous with the ventricular component (Pl. 2, fig. 10). The connective tissue invaginated into the funnel is more marked in the left chamber than in the right. On the right side some straggling muscle fibres penetrate the connective tissue at the base of the funnel to effect union between the atrial and ventricular muscle, but such muscular continuity is not present all round the atrioventricular orifice. On the ventral aspect of the atrioventricular orifice, where the bases of the large arteries are situated, there is no muscular continuity between the right atrium and right ventricle in the funnel, either at its base or in its caudal part. Thus atrioventricular continuity of the right side is limited to the dorsal, right-dorsal and right segments of the atrioventricular orifice. On the left side there is no penetration of muscle fibres through the connective tissue at the base of the funnel, and continuity of the left atrial and ventricular muscles at the caudal part of the funnel is limited to the dorsal and left-dorsal segments of the atrioventricular orifice, beneath the base of the marginal cusp of the atrioventricular valve. At the base of the funnel the muscle fibres of both atria take a circular direction and form an atrioventricular 'ring' (Pl. 2, figs. 9, 10), though the 'ring' is incomplete ventrally where the large arteries take their origin from the heart, and thus has a rather C-shaped form. It is, nevertheless, interposed between the general musculature of the atria and the atrioventricular funnel, and it is suggested that the time taken for the passage of the cardiac impulse through this 'ring' probably accounts for the interval between atrial and ventricular contraction, which was observed in the exposed heart of the living crocodile.

On the right side the atrioventricular funnel is much more extensive, and passes more deeply into the ventricle, than on the left side (Pl. 2, fig. 9). The caudal border of the right part of the funnel is to some extent free from attachment to the interior of the right ventricle, but it is doubtful whether it is free enough to allow the funnel to act as a valvular cusp (marginal cusp; Pl. 2, fig. 11) in the act of closure of the right atrioventricular orifice during ventricular systole in the manner suggested by Greil (1903). It would appear, judging solely from the morphological arrangements, that the only effective cusp at the right atrioventricular orifice is the septal cusp. It is fibrous in structure, and its basal attachment extends for about two-thirds of the circumference of the atrioventricular orifice. Its caudal border is free, except at its ventral part which is attached by a stout muscular band to the interior of the ventricular wall (Pl. 2, fig. 11). The contraction of this muscular band during ventricular systole would have the effect of shortening the free border of the cusp, thereby adjusting it to the contracting atrioventricular orifice and at the same time preventing evagination of the cusp into the right atrium. In the avian heart there is no septal cusp at the right atrioventricular orifice, and the closure of this opening during ventricular systole is effected solely by the muscular valve that lies in relation to the free wall of the ventricle. This avian valve is homologous with the right part of the atrioventricular funnel in the crocodilian heart described above, but the valvular function of the latter would appear to be incipient, rather than actually attained.

The left atrioventricular orifice is guarded by a pair of large membranous semilunar valves, one septal and one marginal (Pl. 1, fig. 5). The septal cusps of the right and left atrioventricular valves are attached to the corresponding surfaces of the pars membranacea septi, but the attachment of the septal cusp of the left valve is situated some distance cranial to that of the right valve, the part of the pars membranacea septi intervening between the two valves representing morphologically the proximal portion of the septal cusp of the right valve. No direct continuity of the musculatures of the atrial and ventricular septa was found, these being separated by the pars membranacea septi. The marginal cusp of the left atrioventricular valve is as well developed as the septal cusp and its base is attached to the caudal border of the atrioventricular funnel. The caudal margins of both cusps are free, there being no chordae tendineae.

So far as continuity of the musculature of the atria with that of the ventricular septum is concerned, the conditions differ in the case of the two atria. There is no continuity whatever between the left atrial musculature and the ventricular septum, a stout mass of connective tissue intervening between the dorsal wall of the left atrium and the dorsal part of the base of the ventricular septum (Pl. 1, figs. 4, 5). By contrast, the dorsal wall of the right atrium establishes an obvious muscular connexion with the base of the ventricular septum; indeed, the most substantial muscular connexion between the right atrium and the ventricles occurs at this site, the dorsal wall of the atrium being continuous with both the free wall of the right ventricle and the ventricular septum (Pl. 1, figs. 4, 5).

The above description of the peripheral muscular connexions between the atria and ventricles agrees with that of Swett so far as the actual limits of the connexions are concerned, but Swett claimed that the finer structure of the connecting musculature resembles that of the atrial muscle, and that its distribution to, and mingling with, the ventricular fibres are easily observed, inasmuch as the striations of the ventricular fibres are much wider and take the stain (iron haematoxylin) more deeply. With the staining techniques described above, or using phase-contrast microscopy of unstained sections, this has not been substantiated. No difference could be found in appearance or in size (breadth) between the junctional fibres and the ventricular or atrial muscle. In all parts of the heart there is some slight variation in the appearance of the striations in the fibres seen in any one histological section, and these differences are attributed to the actual state of the fibres at the time of fixation rather than to a constant histological difference.

The structure labelled 'bulbus' by Swett is really the bases of the aortic arches bound together in a common sheath, and consists solely of fibrous tissue and smooth muscle, with some cartilage, at the bases of the vessels where they join the ventricles. Greil (1903) also regarded these structures as bulbus tissue. There is, however, a remnant of the bulbus in the form of a muscular band, composed of cardiac muscle, which spirals around the base of the pulmonary arch, and the pulmonary arch alone (Pl. 2, fig. 8). Naturally it is continuous with the musculature of the right ventricle. It was recognized by Mackenzie but Swett appears to have overlooked it.

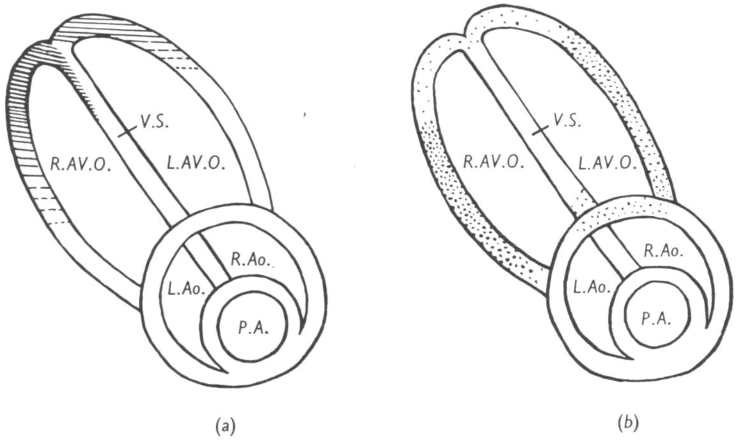
From the ventral surface of the sinus venosus the epicardium is reflected to the dorsal surface of the base of the right ventricle, near the dorsal interventricular sulcus, in the form of the dorsal ligament or sinuventricular fold (Pl. 1, figs. 2, 3). As Swett observed, it consists of fibrous tissue and contains the coronary vein, a small artery, and some nerve fibres and nerve cells. It does not contain any muscle and, therefore, does not constitute a muscular connexion between the cardiac chambers. It is comparable in structure and position with the dorsal ligament described by Laurens (1913*a*, *b*) in the lizard and tortoise and shown experimentally by this author, contrary to the findings of Dogiel (1907) and Imchanitzky (1909), to have no significance for the co-ordination of the heart's action.

*Microscopic structure of the cardiac musculature.* So far as the finer structure of the muscle in the crocodilian heart is concerned, no differences were found between the characters of the fibres of the several chambers. Measurements of numerous fibres taken at random from each chamber in the heart of the alligator show that the breadth of the fibres ranges from 7·5 to 10 $\mu$, the great majority being 8·3 $\mu$ broad. These figures hold uniformly for each of the chambers and for the connecting muscle fibres at the sinu-atrial and atrioventricular junctions. The coarseness of the striations also varies somewhat, but the differences between the fibres of any one chamber are quite as great as can be found between those of different parts of the heart. The whole myocardium of the heart, therefore, presents a very uniform histological picture, and no histological specialization has been found in any part of the heart of the alligator or crocodile comparable with nodal tissue or Purkinje fibres in the hearts of mammals and birds.

## DISCUSSION

The results of the present study of the crocodilian heart indicate that the muscular connexions between the sinus venosus and the right atrium, and between the atria and ventricles consist of ordinary heart muscle, and that the cardiac muscle of the several chambers and at the junctional sites presents a uniform histology throughout. It is suggested that the pauses between the contractions of the sinus and atrium on the one hand, and between the systole of the atria and that of the ventricles on the other, such as were observed in the heart of the living crocodile, are due to the ring-like arrangement of the muscle fibres situated proximal to each junctional site, operating on a similar principle to that described in the heart of the salamander (Davies & Francis, 1941). At the sinu-atrial junction the ring is complete, but at the atrioventricular junction the ring is interrupted ventrally by the fibrous tissue at the bases of the large arteries so that the delaying musculature here forms a 'C' rather than a complete ring.

The advent of the ventricular septum has resulted in the establishment of a substantial connexion between its musculature and that of the right atrial wall. This muscular connexion occupies a different morphological site from that of the atrioventricular node and bundle of the mammal and bird, and it is believed that it is not the true homologue of these latter structures. Davies & Francis (1941) have suggested that the sinu-atrial node, the atrioventricular node and the atrioventricular bundle and its branches are neomorphic developments in mammals and birds and it is now maintained that they are not foreshadowed in the crocodilian heart. It may be affirmed with certainty that in the crocodilian heart the sinu-atrial and atrioventricular muscular connexions show no histological specialization comparable with those in mammals and birds. Further, the peripheral atrioventricular connexions, which involve the atrioventricular funnel and which precede phylogenetically the septal connexions, persist to some extent in the crocodilian heart, though unlike those in lower vertebrates they are interrupted ventrally by fibrous tissue. In mammals and birds these peripheral connexions are normally entirely interrupted by fibrous tissue, the sole atrioventricular muscular connexions in these animals being by means of the specialized atrioventricular bundle and its branches. It has already been reported (Davies, Francis & King, 1951) that there are a number of differences between the electrocardiographic tracings obtained from *C. niloticus* and those from man, which may be accounted for by the absence of specialized conducting muscle in the crocodilian heart.




**Text-fig. 1. Diagrams of the atrioventricular junctional region of the heart of the alligator. (*a*) The muscular connexions between the atria and ventricles described in the present paper are indicated by cross-hatching. They are most marked, as shown by denser cross-hatching, in relation to the dorsal segment of the right atrioventricular orifice, but are also present in relation to the right-dorsal and right segments of the right atrioventricular orifice and the dorsal and left-dorsal segments of the left atrioventricular orifice. (*b*) The parts of the atrioventricular junctional region found by Lowman & Laurens (1924) to be important for co-ordinating atrioventricular rhythm are indicated by stippling. The most important, indicated by denser stippling, were the right-lateral segment of the right atrioventricular junction and the left-lateral and left ventro-lateral segments of the left atrioventricular junction. It will be seen that they do not correspond with the disposition of the muscular connexions shown in (*a*).**

The most important differences between the findings of Swett and those here described are that: first, while Swett described muscular continuity of both atria with the dorsal part of the ventricular septum, the present work indicates that the dorsal wall of the left atrium is separated from the ventricular septum by dense fibrous tissue and that only the right atrium establishes direct muscular continuity with the ventricular septum; and secondly, that the direct muscular continuity between the atrial and ventricular septa described by Swett could not be substantiated.

Finally, there is the question whether the morphological features described above support the conclusions drawn by Lowman & Laurens (1924) from their experiments. Text-fig. 1 indicates the arrangement of the muscular connexions between the atria and ventricles in the heart of *Alligator mississippiensis* here described (*a*), compared with the results obtained by Lowman & Laurens (*b*) after cutting various segments of the atrioventricular junctional regions and noting their effect on atrioventricular co-ordination. The segments which, on cutting, they found to produce the most marked atrioventricular dissociation do not correspond with those in which muscular atrioventricular continuity was noted both by Swett and ourselves to be best developed. Indeed, they claimed that one of the least important segments for atrioventricular conduction was situated dorsally, where we found the muscular continuity to be most marked. It is concluded that the results of these experiments fail to substantiate the arrangements of the muscular connexions, and it is suggested that the severe injuries inflicted on the heart in these experiments may cause upset of the function of the heart that may not be a reliable guide to the normal paths of conduction of the impulse for cardiac contraction from atria to ventricles.

## SUMMARY

1. In the hearts of *Alligator mississippiensis* and *Crocodilus niloticus* the musculature of the several chambers and that connecting one chamber to the next have a uniform histological structure, and no specialized nodal tissue or Purkinje fibres were found in any part of the hearts.

2. The sinus venosus is continuous with the right atrium all around the sinu-atrial orifice, the continuity involving the musculature of the sinu-atrial valves.

3. The right atrium is continuous with the right ventricle in the dorsal (principally), right-dorsal and right segments of the atrioventricular funnel, while continuity of the left atrium and left ventricle is limited to the dorsal and left-dorsal segments of the funnel.

4. The advent of a ventricular septum in the crocodilian heart has resulted in the establishment of a substantial muscular connexion between the right atrium and the dorsal part of the ventricular septum, but there is no direct muscular continuity between the left atrium and ventricular septum or between the atrial and ventricular septa.

5. It is believed that the muscular connexion between the right atrium and ventricular septum is not the homologue of the atrioventricular node and bundle of the mammalian or avian heart.

6. It is suggested that the observed pause between the contraction of the sinus and atrium and that between the systole of atria and ventricles are due to the circular arrangements of the muscle fibres proximal to each junctional site (sinu-atrial and atrioventricular 'rings').

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## EXPLANATION OF PLATES

(All the illustrations are of the heart of *Alligator mississippiensis.*)

### PLATE 1

Fig. 1. Photograph of ventral aspect of heart. ×3.

Fig. 2. Photograph of dorsal aspect of heart. ×3.

Fig. 3. Photograph of right side of heart. ×3.

Fig. 4. Transverse section of heart to show continuity between the right atrium and the ventricular septum, and the fibrous tissue separating the left atrial muscle from that of the ventricular septum. Mallory. ×6·2.

Fig. 5. Part of fig. 4 to show the same features more clearly. Mallory. ×14·5.

### PLATE 2

Fig. 6. Transverse section through the sinu-atrial orifice and the bases of the aortae and pulmonary arch. Mallory. ×6·2.

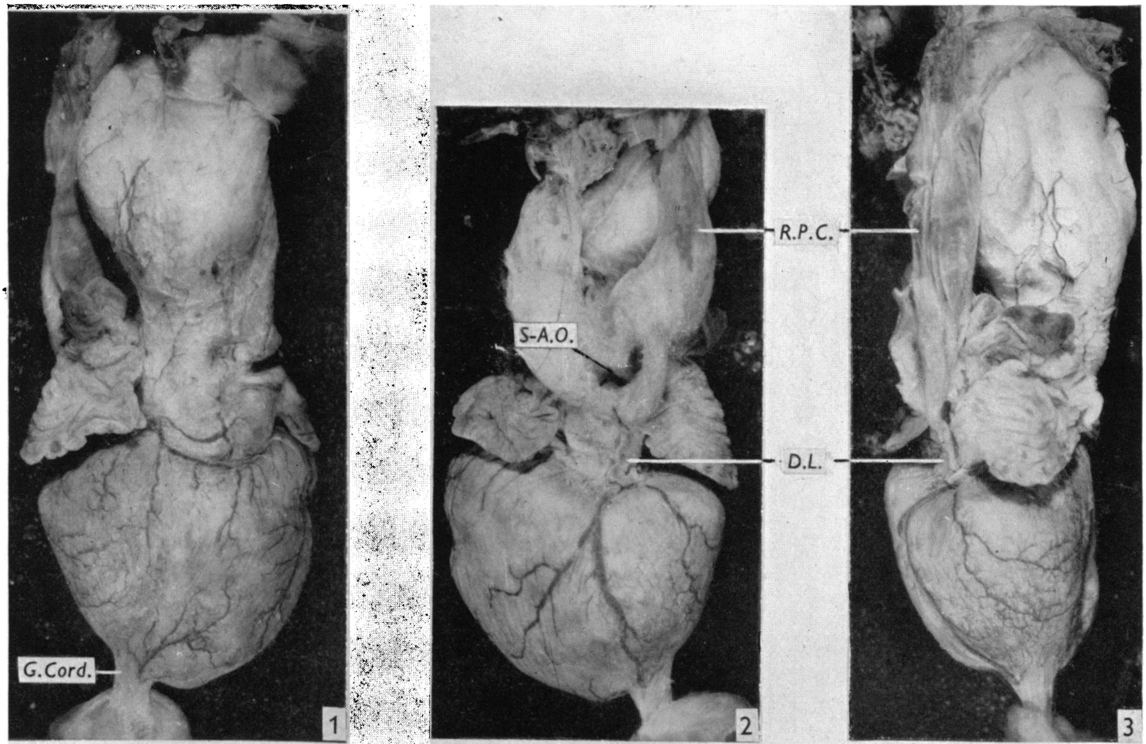
Fig. 7. Part of fig. 6 to show details of the sinu-atrial ring and sinu-atrial valves. Mallory. ×14.

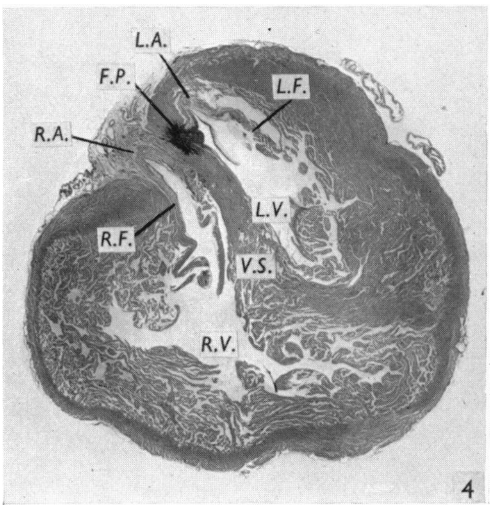
Fig. 8. Transverse section through heart, just caudal to the sinu-atrial orifice, to show the foramen of Panizza between the left and right aortae and the bulbar muscle encircling the base of the pulmonary arch. Mallory. ×6·2.

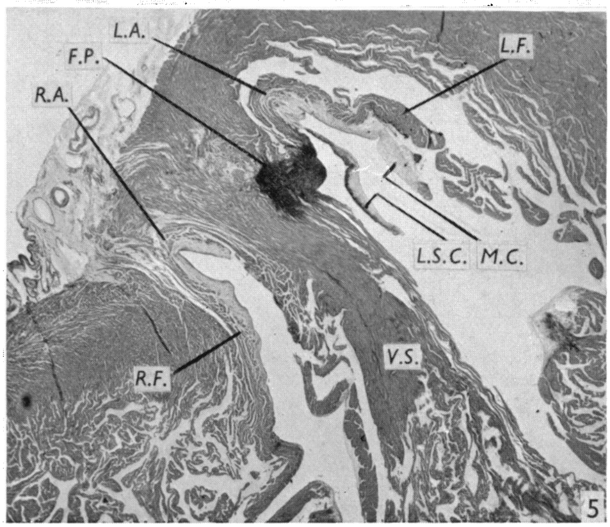
Fig. 9. Frontal section through the atrioventricular junction to show the atrioventricular funnel and atrioventricular 'ring'. Silver-pyridine. ×22.

Fig. 10. Frontal section through the atrioventricular junction to show details of the left part of the atrioventricular funnel and of the atrioventricular 'ring'. Silver-pyridine. ×35.

Fig. 11. Frontal section through the atrioventricular junction to show the right septal cusp with its attached muscle, and the 'incipient' muscular cusp on the marginal aspect of the right atrioventricular orifice. Haematoxylin and eosin. ×16.

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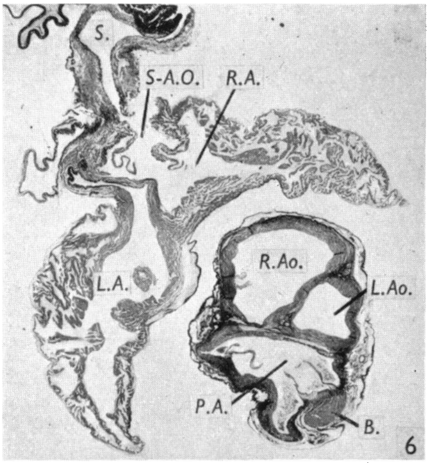


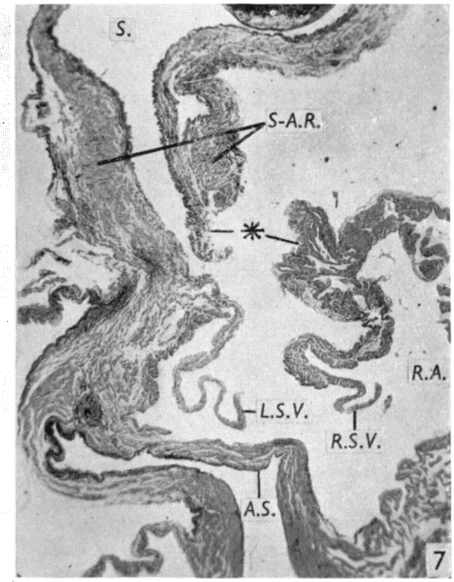


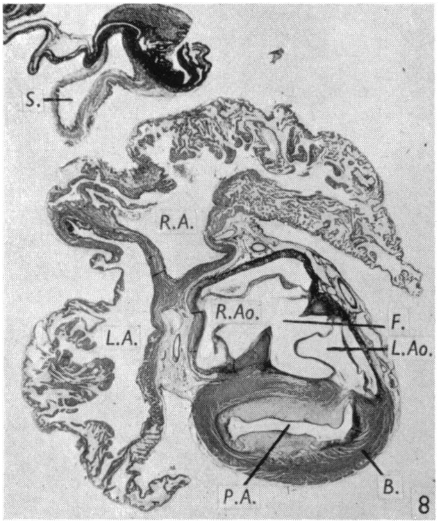


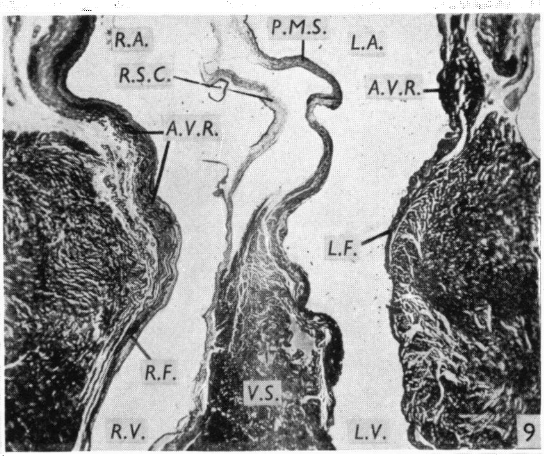


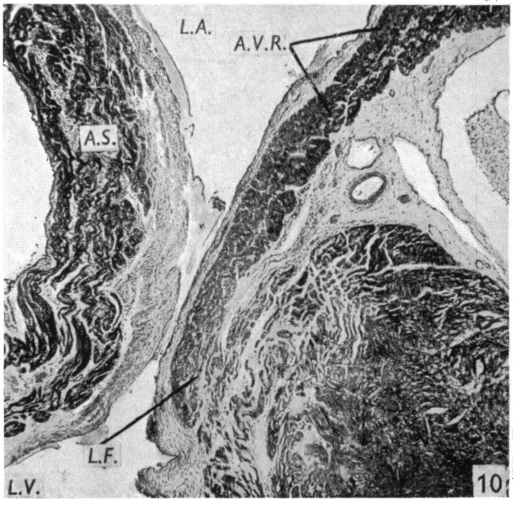


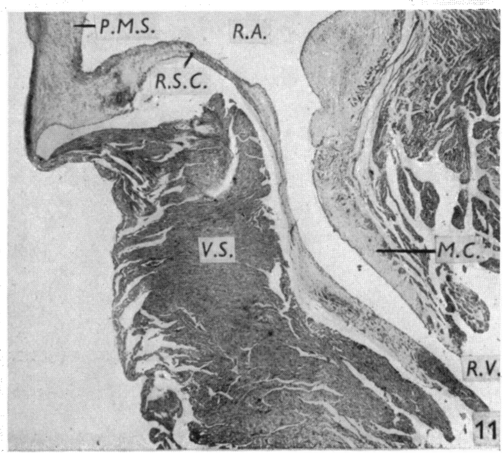


DAVIES, FRANCIS AND KING—The conducting (connecting) system of the crocodilian heart

## LIST OF ABBREVIATIONS IN TEXT-FIGURE AND PLATES

| | |
|---|---|
| *A.S.* | Atrial septum |
| *A.V.R.* | Atrioventricular ring |
| *B.* | Bulbar muscle |
| *D.L.* | Dorsal ligament |
| *F.* | Foramen of Panizza |
| *F.P.* | Fibrous tissue separating muscle of the left atrium from that of the ventricular septum. |
| *G.Cord.* | Gubernaculum cordis |
| *L.A.* | Left atrium |
| *L.Ao.* | Left aorta |
| *L.AV.O.* | Left atrioventricular orifice |
| *L.F.* | Left atrioventricular funnel |
| *L.S.C.* | Septal cusp of left atrioventricular valve |
| *L.S.V.* | Left sinus valve |
| *L.V.* | Left ventricle |
| *M.C.* | Marginal cusp of right atrioventricular orifice |
| *P.A.* | Pulmonary arch |
| *P.M.S.* | Pars membranacea septi |
| *R.A.* | Right atrium |
| *R.Ao.* | Right aorta |
| *R.AV.O.* | Right atrioventricular orifice |
| *R.F.* | Right atrioventricular funnel |
| *R.P.C.* | Right precaval vein |
| *R.S.C.* | Septal cusp of right atrioventricular valve |
| *R.S.V.* | Right sinus valve |
| *R.V.* | Right ventricle |
| *S.* | Sinus venosus |
| *S-A.O.* | Sinu-atrial orifice |
| *S-A.R.* | Sinu-atrial ring |
| *V.S.* | Ventricular septum |
| * | Artificial break at the base of the right sinus valve. |