NOTE ON THE REPTILIAN HEART

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In a recent paper on the Classification of the Reptilia (1) I drew attention to the significance of the structure of the heart, and concluded that the Amniota diverged into two branches: the Sauropsidan branch culminating in the Aves, and the Theropsidan branch in the Mammalia. It was pointed out that although the highest forms in each of these branches are provided with a four-chambered heart, yet these hearts differ in fundamental structure, and must have been independently developed along diverging lines from a more primitive three-chambered heart with symmetrical aortic arches. The final conclusion was therefore reached that all living reptiles belong to the sauropsidan branch and must have been derived from a common sauropsidan ancestor in which the heart was already built on the sauropsidan plan, with the aortic trunk subdivided (the left aortic arch crossing the right), and most of the arterial blood passing through the right arch to reach the dorsal aorta. Thus, when an interventricular septum is completed, the arterial blood passes from the left ventricle into the undivided aortic trunk in the mammal, and into the right aorta in the bird. When, as in the crocodile, the left aortic arch persists it receives venous blood only from the right ventricle.

In the paper referred to above, the heart of the various orders of living reptiles was not described in detail; but diagrams were given, one of which purports to show the relation of the arches to the chambers in the Rhynchocephalia, Lacertilia, Ophidia, and Chelonia. O'Donoghue, in a contribution which appeared last year in this journal (5), while accepting my general conclusion that no modern reptilian heart can lead to the mammalian structure (5, p. 479), takes exception to my statement 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" (1, p. 271). He admits that this statement is correct with regard to the Crocodilia and Chelonia; but maintains that it is "incomplete and indeed somewhat misleading" as regards Lacertilia and Ophidia. But O'Donoghue's own statements, when discussing the heart of these two orders, are so extraordinary that they must be quoted in full. On p. 478 he writes:

"Thus the conditions in Ophidia and Lacertilia are quite different from what is implied by Goodrich both in the extract given above and in the dia-

gram. The ventricle in these two groups, containing by far the greater number of living species of reptiles, is indeed partially divided into a right and left chamber, but the two systemic arches came off from the right side and the pulmonary arch alone comes off from the left. There is thus a considerable difference in the relation of the septum to the arterial trunks between the Ophidia and Lacertilia on the one hand and the Crocodilia and Chelonia on

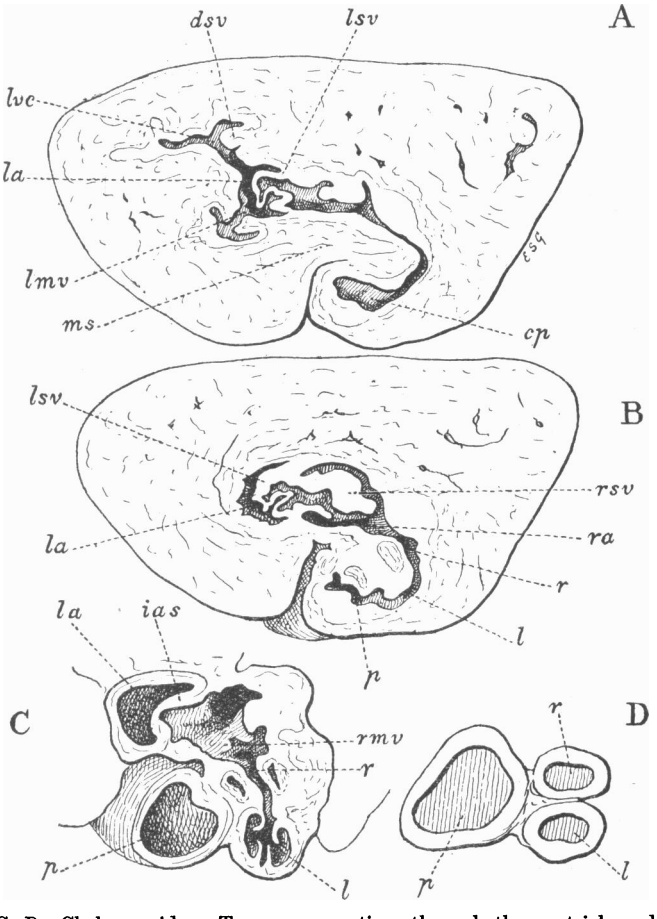

Fig. 1, *A*, *B*, *C*, *D*. Chelone midas. Transverse sections through the ventricle and base of the aortic arches seen from behind (posterior view) with dorsal edge above and ventral edge below. *A* is the most posterior, and *D* the most anterior section.

the other. Not only is there a greater twist on the arterial trunks, which leave the top of the heart in relatively the same position, while the pulmonary leaves the ventricle more to the right in the latter, but the septum is actually situated on opposite sides of the pulmonary artery. In Ophidia and Lacertilia it lies between the pulmonary and left systemic, while in Crocodilia and Chelonia it lies between the pulmonary and right systemico-carotid."

"Another striking and important difference which has not been emphasised formerly is 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."

Now, I willingly admit that my description of the reptilian heart is very general, and in some respects incomplete, and that the diagram given may be somewhat misleading when applied to the Lacertilia and Ophidia (though correct for the Chelonia), for it is scarcely possible to represent the true state

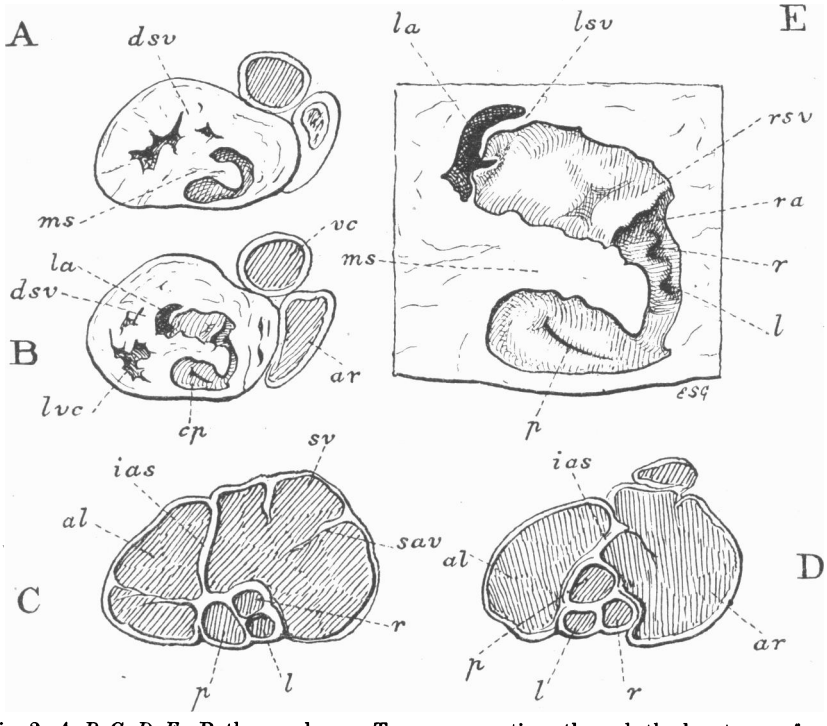

Fig. 2, *A, B, C, D, E.* Python molurus. Transverse sections through the heart, seen from behind, as in figure 1. *E*, portion of figure *B* on a larger scale.

of affairs in a single figure in one plane; but I am quite unable to accept O'Donoghue's interpretation, and am inclined to think that he has misunderstood some fundamental points in the structure of the heart of lizards and snakes.

First of all with regard to the incomplete interventricular septum; O'Donoghue states that in the Ophidia the septum is "attached to the left dorso-lateral side of the ventricle, running from base to apex, and directed towards the right ventro-lateral wall. Thus it runs in a direction entirely different from that of the septum in either Crocodilia or Chelonia," and further, that in the Lacertilia (*Varanus*) it "runs from the left latero-dorsal wall of the

ventricle across towards the right latero-ventral wall, but is decidedly more dorso-ventral in position," dividing the ventricle into "a right lateral, slightly dorsally situated chamber, and a smaller left lateral chamber lying slightly ventrally. The left chamber again gives off only the pulmonary artery, while the right systemo-carotid and left systemic arches both come off from the larger right chamber. Into this chamber also, as in Ophidia, both the auricles open." This description is entirely at variance with my own observations and the recent careful work of Greil on the heart of these reptiles (2), as well as that of older authors. The incomplete muscular septum, although it may shift somewhat laterally towards the posterior apex of the heart, is essentially always a ventral septum developed in relation to the sulcus interventricularis, which passes back from the bulbo-auricular infolding. The septum passes obliquely dorsalwards from the left ventral wall towards the right, and always tends to separate a left dorso-lateral chamber from a right ventro-lateral chamber (cavum pulmonale). This ventro-lateral chamber, leading to the pulmonary artery, is continued up on the right round the free edge of the septum into the more dorsal right region (cavum venosum) of the larger chamber. The true disposition of these structures is shown in the accompanying figures of transverse sections of the heart of Chelone, Varanus, and Python (figs. 1, 2, 3). In these three hearts the ostium of the pulmonary artery is always situated on the right of the base of the muscular septum, which passes between it and the more dorsally situated ostium of the right systemic arch (carotico-systemic). With the help of the medial septal auriculo-ventricular valves, the bulk of the venous blood passes ventrally at auricular systole round the free edge of the septum into the cavum pulmonale; while the bulk of the arterial blood passes across to the right systemic arch. The only important difference between the Chelonia on the one hand, and the Lacertilia and Ophidia on the other, is that, whereas in the former the left arch receives most of its blood from the cavum pulmonale, in the two latter groups by an extra twist upwards of the base of the left systemic arch its ostium comes to lie close to that of the right arch and dorsally to the free edge of the septum, thus receiving more of the arterial blood.

Although O'Donoghue states that in Sphenodon "there is no septum ventriculorum comparable with that of the other Reptilia," I find, like Greil (2), that it exists. The muscular incomplete septum of Sphenodon is small but distinct, and differs in no essential from that of the Lacertilia.

It will be gathered from the description given above that in the anterior region of the ventricle of these reptiles there are two streams of blood crossing each other almost at right angles. The more anterior arterial stream passes from the left region (cavum arteriosum) across to the right arch, and the more posterior stream passes downwards from the right region (cavum venosum) to the cavum pulmonale. Before reaching the base of the various arches the blood passes towards the apex of the heart; and if we follow backwards the three cavities mentioned above (cavum arteriosum, c. venosum, and c. pul-

monale) we find that the cavum arteriosum forms in all the three groups the incipient left ventricle (figs. 1–5), while the cavum venosum and c. pulmonale together belong to the incipient right ventricle. The next important step in the evolution of the sauropsidan heart leading to the four-chambered condition, is the separation of these left dorso-lateral and right ventro-lateral cavities. This appears to be brought about not by the 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

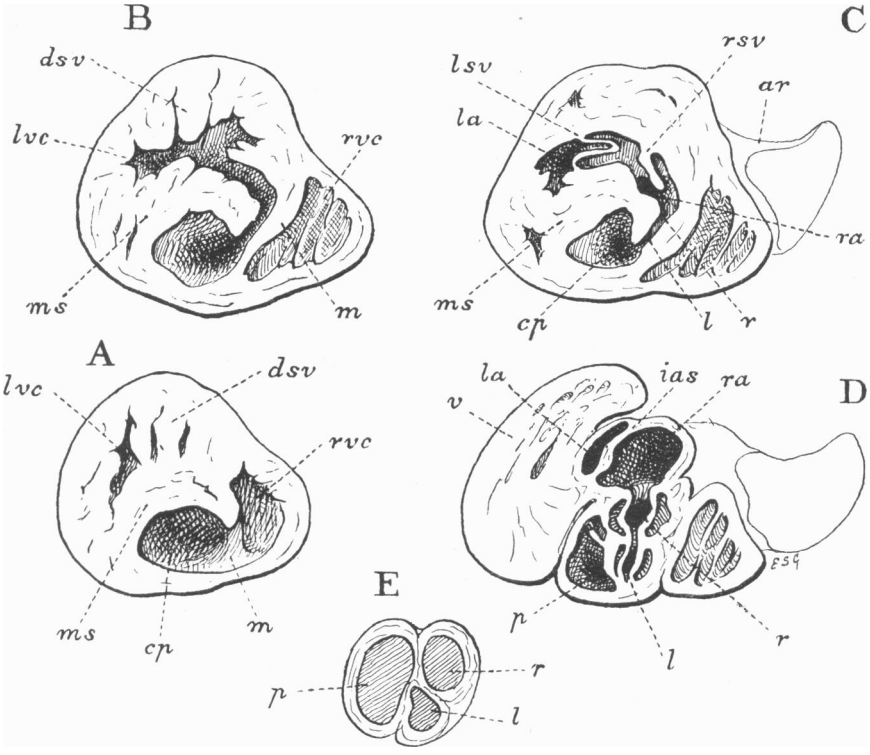

Fig. 3, *A*, *B*, *C*, *D*, *E*. Varanus sp. Transverse sections through the heart, seen from behind, as in fig. 1.

(figs. 2, 3, 5, Greil(2)). Eventually the completed interventricular septum meets the endothelial cushion thickening the posterior free edge of the interauricular septum, and so a right ventricle corresponding to the cavum arteriosum becomes cut off, from a left ventricle corresponding to the combined c. venosum and c. pulmonale. But before this interventricular septum can be completed it is obviously necessary to ensure that the arterial blood from the left side may reach the ostium of the right carotico-systemic arch. We find, therefore, that in the Crocodilia, where the interventricular septum has joined the interauricular endocardial cushion, the dorso-ventral venous

stream becomes quite cut off from the left to right arterial stream, and for this purpose the base of the right aorta passes over to the left to open more directly into the left ventricle. The formation of the necessary partition has been described in the chick by Greil and Hochstetter (3), and a good account

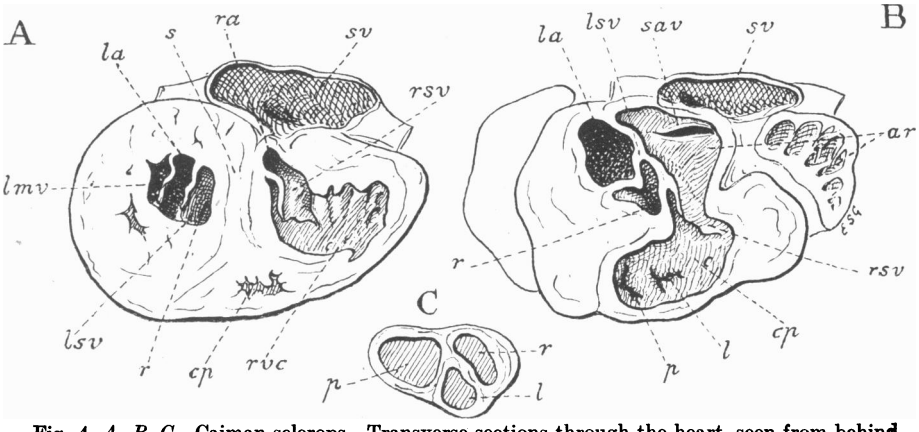

Fig. 4, *A*, *B*, *C*. Caiman sclerops. Transverse sections through the heart, seen from behind, as in fig. 1.

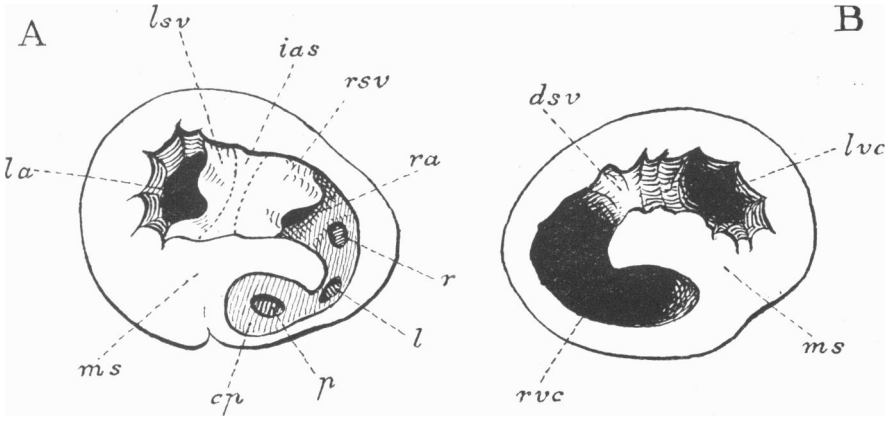

Fig. 5, *A*, *B*. Diagrams of the ventricle of a Reptilian heart (not Crocodilian). *A*, cut transversely and seen from behind; the position of the interauricular septum is indicated by dotted lines. *B*, cut transversely and seen from in front.

of it will be found in Lillie's book (4). It is clear that the essential relations of the right venous and left arterial streams in the single or divided ventricle remain unchanged throughout the Sauropsida, and that there is no foundation for O'Donoghue's statement that they are reversed in the Lacertilia and Ophidia. Indeed these fundamental relations, already foreshadowed in the Pisces and Amphibia, were doubtless definitely established in the common ancestor of all the Amniota, and were determined by the early differentiation of a right venous and a left arterial auricle.

SUMMARY

There is in the ventricle of all living Reptilia a muscular septum attached to the ventral wall, and passing forwards between the left auriculo-ventricular opening and the ostium of the pulmonary artery. Dorsally and to the left of this septum is the cavum arteriosum, while on the right the dorsal cavum venosum passes ventrally round the free edge of the septum to the cavum pulmonale. Muscular strands from the base of the septum to the dorsal wall of the ventricle separate incipient left from incipient right chambers. In the Crocodilia these strands form a wall which together with the septum unite with the endocardial cushion of the interauricular septum, and complete the division of the cavity into a left ventricle corresponding to the cavum arteriosum, and a right ventricle corresponding to the cavum venosum and the c. pulmonale. The left ventricle leads to the right aortic arch, and the right ventricle to the pulmonary artery and the left aortic arch. Whereas in the Chelonia, as in the Crocodilia, the left arch receives most of its blood from the cavum pulmonale, in the Lacertilia and Ophidia it opens more dorsally so as to receive arterial blood as well.

LIST OF REFERENCE LETTERS FOR FIGURES 1, 2, 3, 4, 5

a.l. left auricle; *a.r.* right auricle; *c.p.* cavum pulmonale; *d.s.v.* muscles representing dorsal region of septum ventriculorum; *i.a.s.* interauricular septum; *l.* left aortic arch; *l.a.* left auriculo-ventricular opening; *l.m.v.* left auriculo-ventricular marginal valve; *l.s.v.* left septal (medial) auriculo-ventricular valve; *l.v.c.* left ventricular chamber; *m.* muscle ridge; *m.s.* muscular inter-ventricular incomplete septum; *p.* pulmonary arch; *r.* right aortic arch; *r.a.* right auriculo-ventricular opening; *r.m.v.* right auriculo-ventricular marginal valve; *r.s.v.* right septal (medial) auriculo-ventricular valve; *r.v.c.* right ventricular chamber; *s.* interventricular septum; *s.a.v.* sinu-auricular valve; *s.v.* sinus venosus; *v.* ventricle; *v.c.* vena cava inferior.

LIST OF REFERENCES

(1) Goodrich, E. S. "On the Classification of the Reptilia." *Proc. Royal Soc.* B., vol. lxxxix. 1916.

(2) Greil, A. "Beitr. z. vergl. Anat. u. Entw. des Herzens." *Morph. Jahrb.* vol. xxxi. 1903.

(3) Hochstetter. "Die Entw. des Blutgefässsystems." Hertwig's *Handbuch d. Entw. der Wirbeltiere*, vol. iii. 1906.

(4) Lillie. *The Development of the Chick.*

(5) O'Donoghue, C. H. "The heart of the Leathery Turtle." *Journ. of Anat.* vol. lii. 1918.