THE ANATOMY OF THE REPTILIAN HEART

Part II. Serpentes, Testudinata and Loricata

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1. INTRODUCTION

In the first part of the present series the heart of Varanus monitor (Linn.), an example of the Sauria, was described in detail in order to serve as a basis for the investigation of the hearts of other reptiles. In the present part, the hearts of the Serpentes, Testudinata and Loricata are dealt with. The following species were selected for intensive study, the method of investigation being the same as in the case of Varanus monitor.
Fig. 1. The heart of *Natrix piscator* (Dorsal View). c.c., the common carotid artery; l.a., the left auricle; l.p.c., the left precaval vein; l.s., the left systemic artery; p.a., the pulmonary trunk; p.c.v., the post-caval vein; p.v., the pulmonary vein; r.a., the right auricle; r.p.c., the right precaval vein; r.s., the right systemic artery; v., ventricle.

Fig. 2. The heart of *Natrix piscator* (ventral view) Abbreviations as in the previous figure.
1. Order **Squamata**: 
   Suborder **Serpentes**: *Natrix piscator* (Schn.): 12 specimens.
2. Order **Testudinata**:  
   *Lissemys punctata* (Bonnaterre): 12 specimens.
3. Order **Loricata**:  
   *Crocodilus palustris* Lesson: 3 specimens.

Specimens of *Natrix piscator* and *Lissemys punctata* were collected in the suburbs of Agra, while a number of hearts of *Crocodilus palustris* were presented to me by Prof. Beni Charan Mahendra from his personal collection. A number of snakes (e.g., *Python molurus*, *Eryx johni*, *E. conicus*, etc.) and some specimens of *Gavialis gangeticus* were used for confirmation and comparison.

As a comprehensive historical résumé and bibliography has already been given (Mathur, 1944), it is enough in the present part to refer to the relevant literature in the text and to give a list of the literature cited at the end.

II. **The Heart of the Serpentes**

(a) **General**

As the general structure of the ophidian heart has already been described by several workers, e.g., O'Donoghue (1912) in *Tropidonotus natrix*, Rau (1924) in *Eunectes murinus*, and Ray (1934) in *Ptyas mucosus*, it is scarcely necessary to give a detailed account of the heart of *Natrix piscator* (Schn.). I shall, therefore, confine myself only to those features which, although distinguishing the heart of this order from that of all other reptiles, have so far escaped the attention of anatomists.

In form the ophidian heart is considerably elongate, being generally about twice as long as broad. It lies generally in the anterior part of the *œmol*, between the body-wall on the one hand and the *œsophagus* on the other, although it differs in its relative position in various species within wide limits (Thomson, 1913).

Anatomically, perhaps, one of the most conspicuous features of the ophidian heart is its far-reaching asymmetry (Figs. 1 and 2). The right auricle in most snakes is twice or almost twice as large as the left\(^1\) and is nearly equal to the ventricle in its capacity. It extends farther back than in any other reptilian heart, covering a considerable part of the dorsal and ventral surfaces of the right side of the ventricle. The ventricle has its left

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\(^1\) Although such a disparity in the size of the auricles is the rule in *Colubridae*, the Broad Snakes *Eryx conicus* (Schn.) and *Eryx johni* (Russ.) show almost equal right and left auricles.
side nearly twice as long as the right, and the *coronary sulcus*, when seen in a ventral view, appears to be directed obliquely backwards from its left end to its right. The apex of the ventricle is displaced rather to the right side of the mid-longitudinal axis, and consequently the *posterior vena cava*, unlike that in other reptiles, occupies a sub-median position. The *sinus venosus* has its right half somewhat more developed than the left. The arterial trunks take their origin not exactly at the middle line of the heart but rather towards the left.

(b) *Minute Anatomy*

Although the general structure of the heart in snakes is well known, its minute anatomy has not been hitherto studied in serial sections. Goodrich's observations (1919) are apparently based on thick hand-cut sections and Rau (1924) had access to only a single heart of *Eunectes murinus* which he used for a study of "its gross structure in general and the relations of the interventricular septum to the opening of the arterial arches in particular." The following account which supplements the previous knowledge considerably, is almost entirely based on a scrutiny of successive transverse and longitudinal sections prepared by me and on dissections performed under the binocular microscope.

1. **Sinus Venosus**.—In connection with the ophidian *sinus venosus* three facts, not hitherto pointed out, may be particularly mentioned.

First, the left precaval vein (Fig. 3) opens into the combined bases of the post-caval and the right precaval immediately posterior to, or almost at the level of, the hind end of the sinu-atrial aperture.

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![Fig. 3](image-url)

*Fig. 3* Transverse section through the heart of *Natrix piscator*, showing the posterior part of the *sinus venosus* (×10).

*a.v.*, the anterior extension of the ventricle; *r*, the ridge separating the bases of the post-caval and the right precaval vein from the base of the left precaval; *s.a.v.*, the sinu-atrial valve; *s.v.*, sinus venosus. (Other abbreviations as in previous figures.)
Secondly, the base of the left precaval vein (Fig. 3) is separated from the combined bases of the post-caval and right pre-caval by a prominent ridge hanging downwards from the dorsal wall and extending considerably cranially to the place where the left precaval opens into the sinus venosus. This structure corresponds in its position neither to a tuberculum intervenosum nor to a septum sinu-venosi.

Thirdly, the sinu-atrial aperture differs from that found in Varanus monitor in its form, position and direction. The suspending ligament and the sinu-atrial channel are absent and the sinus venosus, therefore, opens directly into the lumen of the right auricle. The sinu-atrial aperture (Fig. 3) is situated not on the dorso-lateral wall of the auricle as in Varanus monitor (Mathur, 1944), but almost in the middle of the dorsal surface. In all cases observed by me, the aperture is an elongated slit, not at right angles to the long axis of the heart, as reported for Eunectes murinus by Rau (1924), but disposed in a distinctly longitudinal direction. As a result of this, the sinu-atrial valves in snakes are situated not anterior and posterior to the aperture, but lateral to it.

2. Atrium Dextrum.—The right auricle, as already mentioned, is much larger than the left. It projects backwards behind the anterior border of the ventricle, and just anterior to the point of emergence of the arterial trunks from the ventricle, is divided by a neck-shaped constriction into a small left and a large right lobe (Fig. 3). The constriction broadens out anteriorly (Fig. 4) so that the two lobes pass on insensibly into each other. The left lobe opens posteriorly into the ventricle (Fig. 5) almost at the level of the coronary sulcus through the atrio-ventricular aperture. The right one forms the posterior extension of the auricle, already mentioned in the general account of the heart and has the sinu-atrial opening in its dorsal wall to the right side of the constriction. There is no atrium dextrum intraventriculare in snakes.

3. Atrium Sinistrum.—The left auricle is generally much smaller in size, and consequently in capacity, than the right. The quantity of aerated blood, therefore, entering the ventricle during the auricular systole is considerably less than that of the non-aerated.

Ray (1934) observed a prominent diverticulum at the inner antero-dorsal edge of the left auricle in Ptyas mucosus (Linn.) and compared it with a similar structure in the right auricle in Sphenodon punctatus (O'Donoghue, 1920), and Uromastix hardwicki (Bhatia, 1929). He thought that it might be due to "the constant pressure applied by the auricle on the underlined (sic.) left systemic arch." No such diverticulum was reported by O'Donoghue
FIG. 4. Transverse section through the auricular region of the heart of *Natrix piscator* × 10. (Abbreviations as in previous figures.)

FIG. 5 Horizontal longitudinal section through the heart of *Natrix piscator* (× 8)

l.a. and r.v., the left auriculo-ventricular valves, r.av.v. the right atrio-ventricular valves other abbreviations as in previous figures.

(1922) in *Tropidonotus natrix* and by Rau (1924) in *Eunectes murinus*. I have failed to find it also in *Python molurus* (Linn.), *Eryx conicus* (Schneid), *Eryx johni* (Russ.), *Lycodon aulicus* (Linn.), *Coluber diadema* Schleg, *Natrix piscator* (Schneid), and even specimens of *Ptyas mucosus* (Linn.) collected at Agra. The external configuration of such thin-walled chambers of the heart as the auricles and sinus venosus is considerably affected by the presence of coagulated blood, and it is as likely that the diverticulum described
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by Ray (1934) might be due to such a cause as that it characterises the specimens of this species found in Bengal.

There is a great deal of difference amongst previous authors about the opening of the pulmonary vein. Fritsch (1869) pointed out that it is not guarded by a valve. Sabatier (1874) suggested that a fold of the auricle in this region acts as a valve during systole and prevents regurgitation,—a view which O'Donoghue (1912) regarded as highly probable and Rau (1924) confirmed in Eunectes murinus. Ray (1934), however, did not observe any such structure in Ptyas mucosus, and suggested that the inter-atrial septum in this region, abutting against the pulmonary aperture, acts as a temporary valve.

I feel that Ray's view is correct as in Natrix piscator the dorsal part of the inner-atrial septum (Fig. 6) forms a prominent fold exactly at the place

Fig. 6. Transverse section through the heart of Natrix piscator, showing the opening of the pulmonary vein (×10). Abbreviations as in previous figures.

where the pulmonary vein opens. Moreover, the terminal part of the pulmonary vein in Natrix piscator is abruptly dilated to form a small chamber opening into the left auricle. This chamber might supplement the action of the temporary valve formed by the atrial septum during the auricular systole, since it would act as a sort of backwater to check the backward thrust of the blood and thereby minimise the risk of regurgitation.

4. Ventriculus and Arterial Trunks.—The Ophidian Ventricule differs both externally and internally from that of other reptiles. It is considerably elongated, lies asymmetrically rather towards the left of the mid-longitudinal axis, projects forwards in front of and lateral to the posterior end of the left auricle, and accommodates the posterior part of the auricles in its anteromesial border which extends from the anterior end obliquely backwards towards the right. It is mainly on account of such a form and
**Fig. 7**. Transverse sections through the ventricle of *Natrix piscator*—(A) through the apical region, (B) through the region of the muscular ridge, (C) just anterior to the free border of the muscular ridge, and (D) at the level where the auricles lead into the ventricle. (×10).

*b.m.r.*, the base of the muscular ridge; *c.d.*, cavum dorsale; *c.p.*, cavum pulmonale; *d.s.*, the dorsal septoid process; *l.c.d.*, the left part of the cavum dorsale; *p.r.a.*, the posterior part of the right auricle; *p.v.l.a.*, the part of the ventricle receiving blood from the left auricle; *r.c.d.*, the right part of the cavum dorsale; *v.l.s.*, valves of the left systemic trunk; *v.p.a.*, valves of the pulmonary trunk; *v.s.*, the ventral septoid process (other abbreviations as in previous figures).
disposition that it shows a remarkable difference from that of other reptiles in its internal anatomy. Its features, as a whole, however, indicate a simplification of the saurian type.

In the apical region the horizontal septum is absent and there is thus no distinction between the cavum apicis dorsale and the cavum apicis ventrale. Numerous well-developed trabeculae (Fig. 7A), however, are present, arranged more or less peripherally. These divide the internal space into a large number of lacunae, inter-communicating with each other and opening into a central space which is compressed dorso-ventrally. A little in front of the posterior end in this region, a minute space separate from others may be noticed, situated ventro-laterally on the right side and leading forwards into the cavum pulmonale. This is, sensu strictu, homologous to the cavum apicis ventrale of Varanus monitor.

With regard to the muscular ridge ("the interventricular septum") in the Ophidia, O'Donoghue (1918) observed that it "is very well developed and 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—in fact, nearly at right angles to it—and divides the ventricular cavity, at any rate in systole, into a right dorso-lateral and a left ventro-lateral chamber." Goodrich (1919), however, reported that the disposition of the ridge was essentially similar in the hearts of Chelone, Varanus and Python, and Rau (1924) found that in Eunectes murinus "there projects into the cavity from the posterior apex and running dorso-ventrally a muscular ridge which divides the ventricle into two main cavities, a small left and a large right."

In Natrix piscator, the muscular ridge (Fig. 7B) is a relatively small structure, arising from the ventral wall of the ventricle towards the right of the middle line and projecting obliquely upwards from its base. Its dorsal half, curving downwards towards the right, bounds an extremely small ventro-lateral space (cavum pulmonale) from a larger cavity on its dorsal side and its anterior portion is attached to form the dorsal and dorsolateral wall of the pulmonary trunk (Fig. 7C). The cavum dorsale is not divided into chambers but is continuous from its left end to its right. It has, however, two strong projections (Fig. 7B), one on its roof and the other on its floor. These may be called the septoid processes; they would press against each other during systole and thus prevent the blood on the left side from mixing with that on the right.

In this connection one might quote Rau (1924) who found that the "large right cavity" (cavum dorsale) in the ophidian ventricle is further
divided by a septum, the interventricular septum, into two cavities—the dorso-lateral right and the ventral one. The interventricular septum is particularly well developed. It is attached to the ventral wall of the ventricle and has a free dorsal border anteriorly which projects freely into the cavity of the ventricle. Posteriorly the septum is continued and separates the ventral cavity effectively from the others." As Rau gave a description of the muscular ridge in addition to this septum, it seems likely that the latter corresponds to the *ventral septoid process* described by me.

The auriculo-ventricular openings (Fig. 5) are situated more anteriorly than in *Varanus monitor* (cf. Mathur, 1944), and the auricles do not project into the lumen of the ventricle as *intraventricular atria*. As the ventricle projects forwards on the left side, the left auricle leads directly into the definitive lumen of the ventricle at its posterior end, but the right auricle...
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leads into a space, which has ventricular wall on its ventral and right sides and an atrial sort of covering on its dorsal aspect. It is only the left lobe of the right auricle which opens into the ventricle; the right lobe extends back behind this region as a structure quite separate from the ventricle.

Rau (1924) observed that in *Eunectes murinus* "the pulmonary artery arises ventrally from the cavum pulmonum (sic.); the left systemic artery springs as in *Tiliqua* at a short distance cranially from the origin of the pulmonary artery to the extreme right;" and "the right systemic arises even more cranially." I find a similar disposition in *Natrix piscator*. The openings of the pulmonary and left systemic arches appear to lie side by side almost at the same level in horizontal longitudinal sections (Fig. 8 A), but serial transverse sections leave no doubt that the latter (Fig. 7 C) is situated a little anteriorly to the former. The opening of the right systemic (Fig. 7 D and 8 B) as usual, lies immediately above that of the left systemic but is rather more anteriorly situated than the openings of the other two trunks. The pulmonary trunk takes its origin from the cavum pulmonale while the other two arise from the right part of the cavum dorsale. The origin of the systemic trunks almost from the same place where the right auricle leads into the lumen of the ventricle may be particularly noted.

III. The Heart of the Testudinata

The heart of testudinates, as first noted by Fritsch (1869) and later described by Hoffmann (1890) and Böninghoff (1932), corresponds in its external appearance to the general form of the body of these reptiles. It is broader than long (the ratio of width to length being 3:2 according to Fritsch), is dorso-ventrally flattened, and has the apex of the ventricle almost completely rounded. Its situation, considerably behind the anterior border of the corselet, is regarded as a concomitant of its higher grade of organization (Hoffmann, 1890).

The displacement of the testudinate heart from the mid-longitudinal axis of the body is worth noting. In *Lissemys punctata* (Fig. 9) not only does the heart lie to one (right) side of the axis, but it is also tilted in such a way that its mid-longitudinal axis lies not parallel but at an acute angle to that of the body. Such a displacement and tilting, which is probably due to the retractility of the neck into the antero-mesial part of the trunk, leads to

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*According to Rathke (1848), the heart in the embryos of *Chelone* is longer and narrower than in the adult, and according to Burne (1905) it was somewhat long and narrow in the specimen of *Dermochelys* (Sphargis) corticata, studied by him. O'Donoghue (1918) pointed out that Burne's specimen was probably a young one.*
considerable elongation of the left arteries and veins and a shortening of the right ones.

The heart of *Lissemys punctata* (ventral view), showing the mid-longitudinal axis (AB) of the body, the mid-longitudinal axis (ab) of the heart as established by comparison with other reptiles, and the plane (xy) parallel to which transverse sections were cut.

*Fig. 9.*

- g.c., gubernaculum cordis
- l.c.c., the left common carotid artery
- l.s.a., the left subclavian artery
- r.c.c., the right common carotid artery
- Other abbreviations as in previous figures.

As the general anatomy of the testudinate heart is well known (Rathke, 1848; Fritsch, 1869; Hoffmann, 1890; Burne, 1905; O'Donoghue, 1918; Hyman, 1922, etc.) we may deal here only with its minute anatomy. A careful study of the heart of *Lissemys punctata* (Bonnaterre) in serial sections (Fig. 10) shows that it resembles that of snakes to a great extent.

In the first place, the ventricle, like that of snakes, is seen in transverse sections to be produced forwards on the left side in front of the level of the auriculo-ventricular apertures. In superficial views, however, the extreme shortening of the heart in the antero-posterior direction almost completely conceals this left prolongation of the ventricle.

Secondly, the two auricles open almost at the same level close to the coronary sulcus. The left auricle opens into the left part of the *cavum dorsale* and the right auricle into the right.
Fig. 10. Transverse sections through the heart of Luscinus punctata, section A being the most anterior and section F the most posterior (×8).

$c.d^1$, the left portion, and $c.d^2$, the right portion of cavum dorsale, $m.r.$, the muscular ridge; $o.b.r.s.$, the open base of the right systemic trunk, $s.$, the septum formed by the union of the dorsal and ventral septoid processes; $v.s.$, the ventral septoid process. (Other abbreviations as in previous figures.)

Thirdly, the pulmonary trunk arises behind the point of origin of the systemic trunks. The left systemic lies at its origin just beneath the right; and the two systemics receive their blood from the right part of the cavum dorsale immediately behind the auriculo-ventricular apertures. Comparison of successive transverse sections also establishes the fact that the left
anterior prolongation of the ventricle receives, as in snakes, arterial blood from the left auricle, while the venous blood from the right auricle passes backwards on the right side of the heart to the dorsal aspect of the muscular ridge and then across its free border into the cavum pulmonale below.

Fourthly, the dorsal and ventral septoid processes are present in the cavum dorsale. They, however, differ from those of snakes in two important features: first (Fig. 10 D), in correlation with the dorso-ventrally compressed nature of the cavum dorsale, they are very broad and flattened. Secondly (Fig. 10 E), in the posterior part of the ventricle they unite with each other to form a complete partition separating the left part (cavum sinistrum) of the cavum dorsale entirely from its right part (cavum dextrum), the latter alone being in communication with the cavum pulmonale. Posteriorly, the muscular ridge, which is considerably broad in the region bearing the free septoid processes, diminishes gradually in width, until close to the apical end of the ventricle (Fig. 10 F) it is discernible only as a small blunt growth on the septum, formed by the union of the two septoid processes.

IV. The Heart of the Loricata

(a) General

The essential features of the crocodilian heart are very well known. As pointed out by previous authors (Parker and Wiedersheim, 1907; Kingsley, 1926; Goodrich, 1930, etc.) the sinus venosus is subdivided by a septum; the large atrio-ventricular aperture is guarded by a muscular flap on its right (outer) side; the ventricle is completely divided by a septum ventriculorum into right and left chambers, the former containing venous blood alone and the latter arterial; and a small aperture, the foramen Panizzae, puts the two systemic trunks into communication at their origin just distal to the valves.

(b) Minute Anatomy

The present account of the crocodilian heart, based on a thorough examination of successive transverse and horizontal sections of the heart of Crocodylus palustris Lesson, supplements our knowledge of this organ by a number of new important observations.

1. Atrium Dextrum.—The sinus-atrial aperture (Fig. 11) leads rather laterally into the dorso-lateral outer wall of the right auricle some distance behind the latter's anterior border. It is guarded by a pair of cranial and caudal valves, hanging freely into the lumen of the auricle. The septum atriorum is complete and unperforated. The right auricle is definitely larger than the left and its posterior part covers more than half of the right side of the ventricle. It leads downwards into the right chamber of the ventricle by
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Fig. 11. Horizontal longitudinal section through the heart of Crocodilus palustris, showing the sinu-atrial aperture with its cranial and caudal valves. (×8).

d.s.v.m., the dorsal attachment of the septum ventriculorum; s.a., the septrum atrorumin; w.c.d., the wall of the cavum dextrum, w.c.s., the wall of the cavum sinistrum. Other abbreviations as in previous figures.

the right atrio-ventricular aperture, which is situated on the dorsal wall of the ventricle close to the dorsal edge of the septum ventriculorum. The aperture is guarded by a pair of right and left valves (Fig. 12 A), attached by their dorsal and anterior edges, but having their posterior and ventral borders hanging freely into the lumen of the ventricle.

2. Atrium Sinistrum.—The opening of the pulmonary vein lies almost midway between the anterior border of the left auricle and the coronary sulcus. It is not guarded by any valves. The left auricle leads into the left chamber of the ventricle by the left atrio-ventricular aperture (Fig. 12 B) which is similar in its disposition and valves to the right one, but lies a little dorsal to the plane of the latter. The inner valves of both the atrio-ventricular apertures are developed on the terminal part of the inter-auricular septum.

3. Ventriculus.—The ventricle is completely divided into right and left chambers by a vertical partition, the septum ventriculorum (Fig. 13 A). The left chamber which we may call cavum sinistrum is almost half the size of the right (cavum dextrum) and some distance in front of the apical region, it receives blood from the left auricle by the left atrio-ventricular aperture (Fig. 13 B), which is provided by a pair of outer and inner valves. At the
Fig. 12. Horizontal longitudinal sections through the heart of *Crocodilus palustris*, showing the right (A) and left (B) atrio-ventricular apertures with their valves. (× 10).

*c.d.m.*, cavum dextrum; *c.sm.*, cavum sinistrum; *s.vm.*, the septum ventriculorum. Other abbreviations as in previous figures.
Fig. 13. Transverse sections through the ventricle of *Crocodilus palustris*, showing (A) the disposition of the septum ventriculorum, (B) the atrio-ventricular apertures with their valves and (C) the formation of the arterial trunks. (×10).

c.n., the cartilaginous nodule. Other abbreviations as in previous figures.
same plane along the antero-posterior axis, the *cavum dextrum* is in communication with the right auricle by the right *atrio-ventricular aperture*, but the latter lies a little ventral to the level of the left *atrio-ventricular aperture* and is guarded only by an inner (mesial) valve. The inner valves of both apertures are developed on the ventral end of the *septum atriorum*, the latter being continuous with the ventricular septum. The position of the *atrio-ventricular* apertures definitely on the dorsal wall of the ventricle, although not noted by previous workers, is an important difference from other reptiles.

Anterior to the region of the *atrio-ventricular* apertures, the ventricle shows the formation of the arterial trunks. As we trace forwards the fate of the *atrio-ventricular valves* and the terminal part of the *septum atriorum*, we find (Fig. 13 C) that the free end of the left mesial valve gets attached to the outer valve of the left atrio-ventricular aperture and thus completes the dorsal wall of the *cavum sinistrum*. The latter chamber lies here dorso-laterally towards the left side in the lumen of the ventricle. A small nodule of cartilage is present at the place where the completed wall of the *cavum sinistrum* joins the wall of the ventricle.

In the same region (Fig. 13 C) the right mesial valve gets attached to the right dorso-lateral wall of the *cavum dextrum* and thus completes the dorsal wall of the latter. A nodule of cartilage similar to the left one is also present here, as well as at the ventral end of the extension of the *septum ventriculorum* found in this region.

Unlike the *cavum sinistrum*, the *cavum dextrum* is not restricted to the dorso-lateral part of the ventricular lumen, but extends downwards towards the left side beneath the *cavum sinistrum*. Thus it is almost four times as large as the *cavum sinistrum* and has a crescentic appearance in transverse sections.

4. The Arterial Trunks.—The exact mode of origin of the arterial trunks is especially interesting as it shows several features not observed so far. The *cavum sinistrum* is subdivided anteriorly (Fig. 14 A) by an oblique septum into a large dorsal space (*a*), and a small ventral one (*b*), the two spaces being continuous behind as the septum has its posterior border free. The ventral space, a little anteriorly (Fig. 14 B), has a horizontal projecting process (*p*), developed from its left wall and incompletely dividing its lumen into dorsal and ventral sub-spaces (*b*1 and *b*2). It is clear that all these spaces (*a*, *b*1 and *b*2) can receive only aerated blood from the *cavum sinistrum*. The anterior extension (*c + d*) of the *cavum dextrum*, is seen to be a single undivided space in this region, has no point of communication with the spaces (*a*, *b*1 and *b*2) which really pertain to the *cavum sinistrum*. Further anteriorly (Fig. 14 C) the extension of the *cavum dextrum* is divided into a
Fig. 14. Transverse sections through the heart of *Crocodilus palustris* showing the mode of origin of the three arterial trunks. The section figured in A is the most posterior, that in F the most anterior. (×10).

r.c.dm., the right wall of the cavum dextrum; v.c.dm., the ventral wall of the cavum dextrum. Other abbreviations as in previous figures.

dorso-lateral (c) and a ventro-lateral space (d), both spaces receiving non-aerated blood from the *cavum dextrum*. The ventro-lateral space (d) extends forwards as the *pulmonary trunk* and is distinctly cut off from the others in its forward course (Fig. 4, D, E and F). The spaces of the *cavum sinistrum* (a, b₁ and b₂), as well as the dorso-lateral space (c) of the *cavum dextrum*, however, show certain points of communication with each other before they form the systemic arches. The right systemic is formed by the spaces
(a and b1) of the cavum sinistrum, but the ventral part (b2) of its ventral space is excluded from this trunk. It, therefore, contains almost unmixed aerated blood. The left systemic comprises the ventral part (b2) of the ventral space of the cavum sinistrum and the dorso-lateral space (c) of the cavum dextrum and, therefore, contains a mixture of aerated and non-aerated blood. According to previous authors, "a small aperture of communication (the foramen of Panizza) exists between the two aortic roots at their origin, just distal to the valves". I have very carefully scrutinised successive transverse and horizontal sections of the heart of Crocodilus palustris, but have not found any communication between the arches distal to their valve-containing bases. The pulmonary trunk (Fig. 15 A) arises ventrally to the points of origin of the systemic trunks, and at the horizontal plane at which it takes its origin from the cavum dextrum, it completely separates the right systemic from the left, so that there is no communication of these arches at this level.

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**FIG. 15 A**

**FIG. 15 B**

**FIG. 15.** Horizontal longitudinal sections through the heart of Crocodilus palustris, showing the pulmonary trunk with its valves, and the absence of communication between the two systemic trunks. (×8).

b.p.a., the base of the pulmonary trunk; v.r.s., valves of the right systemic trunk; v.c.v.m., the base of the septum ventriculorum; other abbreviations as in previous figures.

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* Quoted from Parker and Wiedersheim. 1907, p 410.
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A little dorsal to this plane the two systemics no doubt come to lie adjacent to each other, but the separating wall between them is devoid of any perforation (Fig. 15 B).

Although there is no communication in *Crocodilus palustris* between the systemic arches distal to their valves, as reported by Panizza and believed generally by comparative anatomists, there is, as shown by me in the account of the origin of the two trunks (Fig. 14) a small space (b*), which, arising from the lumen of the cavum sinistrum becomes confluent with an extension of the cavum dextrum to form the left systemic. This space corresponds in my opinion to the communication between the bases of the right and the left systemic arches in *Varanus monitor* (cf. Mathur, 1944).

V. SUMMARY

In the present paper, the author has studied the hearts of *Natrix piscator*, *Lissemys punctata* and *Crocodilus palustris* in the same way as he previously studied the heart of *Varanus monitor*. The more important features discovered by him are as follows:

(a) **Serpentes**

(1) The *sinu-atrial* aperture in snakes is not a transverse opening at right angles to the long axis of the heart, as generally believed, but is an elongated slit parallel to it. There is neither a *suspending ligament* nor a *sinu-atrial channel* as in *Varanus monitor*.

(2) The absence of valves at the opening of the pulmonary vein has been confirmed. Ray's suggestion about the rôle of the inter-atrial septum in prevention of regurgitation has been substantiated, and a subsidiary device for this purpose (dilatation of the terminal part of the pulmonary vein) is described for the first time.

(3) The auricles in snakes are not incorporated into the lumen of the ventricle and thus there are no *atria intraventriculare*.

(4) The ventricle is elongated and asymmetric, and its left side extends anterior to the level of the atrio-ventricular apertures as the *anterior extension of the ventricle*. The coronary sulcus is oblique.

(5) In the *apical region* there is no *horizontal septum* and consequently no *cavum apicis dorsale* and *cavum apicis ventrale*, as in *Varanus monitor*.

(6) The muscular ridge, though very similar in its general disposition to that of *Varanus monitor*, is smaller.

(7) The cavum pulmonale is an extremely small ventro-lateral space while the cavum dorsale is a single undivided cavity; the latter has two
strong projections, the *septoid processes*, developed one on its roof and the other on its floor. These processes, apparently, press against each other during systole and thereby prevent the blood on the left side from mixing with that on the right side.

(8) The *auriculo-ventricular apertures* and their valves in snakes are accurately described and their differences from those in the Sauria noted.

(9) The *pulmonary trunk* arises from the *cavum pulmonale*, and the left and right systemics from the right part of the *cavum dorsale*.

(b) *Testudinata*

(10) The asymmetrical disposition of the testudinate heart, due to the retractility of the neck, has been described and discussed.

(11) The sinu-atrial aperture is an oval and oblique slit, inclined towards the right side and opening into the terminal part of the right pre-caval vein.

(12) The two auricles open into the ventricle at almost the same level. The left auricle leads into the left part of the *cavum dorsale* and the right into its right part.

(13) There are no *atria intra-ventriculare* in turtles.

(14) An anterior extension of the ventricle is present on the left side as in snakes.

(15) In the *apical region* of the ventricle the *horizontal septum, cavum apicis dorsale* and *cavum apicis ventrale* are absent.

(16) As in snakes, *septoid processes* are developed in the *cavum dorsale* dividing the cavity into a left (*cavum sinistrum*) and a right one (*cavum dextrum*). It is noteworthy, however, that these processes in the Testudinata are fused together posteriorly to form a complete septum.

(c) *Loricata*

(17) The *sinu-atrial aperture* is situated on the outer dorso-lateral wall of the right auricle and has a pair of cranial and caudal valves.

(18) The *right atrio-ventricular aperture* is situated on the dorsal wall of the ventricle close to the dorsal edge of the septum ventricularum and is guarded by a pair of right and left valves.

(19) The left *atrio-ventricular aperture* and its valves are similar to those of the right. This aperture, however, lies dorsal to the plane of the right.
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(20) The opening of the pulmonary vein into the left auricle lies almost midway between the anterior border of the left auricle and the coronary sulcus.

(21) The ventricle is divided by a vertical partition (the septum ventriculorum) into right and left chambers. These have been designated, in view of their homologues in other reptiles, as the cavum sinistrum and the cavum dextrum.

(22) Anterior to the region of the atrio-ventricular apertures, the ventricle shows the formation of the arterial trunks. The free end of the left mesial valve gets attached to the outer valve of the left atrio-ventricular aperture and thus completes the dorsal wall of the cavum sinistrum. Similarly the right mesial valve in the same region fuses with the dorso-lateral wall of the cavum dextrum and thus completes its dorsal wall. The two cavities, when traced forwards, give rise to the three arterial trunks.

(23) The exact origin of the pulmonary trunk has been established. It is found that the pulmonary trunk receives blood entirely from the cavum dextrum. The left systemic receives it partially from the cavum sinistrum, and the right systemic exclusive from the cavum sinistrum.

(24) The Foramen Panizza, generally believed to be of universal occurrence in the Crocodilia, is found to be absent in Crocodylus palustris.

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