THE CONDUCTING SYSTEM OF THE MONOTREME HEART

By FRANCIS DAVIES, M.D. (Lond.)
Anatomy Department, King's College, London

INTRODUCTION

Keith, Mackenzie and Robertson (1, 2) after an extensive investigation of the hearts of vertebrates, decided that birds are unique amongst higher vertebrates in that the avian right auricle is connected to the right ventricle by multiple muscular strands not of a markedly specialised type, and these authors concluded that the auriculo-ventricular bundle, in the form of a specialised strand, is peculiar to mammals. Keith and Mackenzie admitted that the condition in the avian heart greatly puzzled them, and examined the heart of *Echidna* in the hope of obtaining a clue to their conception of the avian auriculo-ventricular connections. However, in the heart of *Echidna* they found (1, 3) a large and typical auriculo-ventricular bundle, like that in the hearts of ungulates. In addition they noted considerable remnants of the extensive auriculo-ventricular connection which prevails in lower vertebrate hearts, especially round the right auriculo-ventricular orifice, where they found a leash of fibres descending direct from the auriculo-ventricular node to the septal wall of the right ventricle. This leash they regarded as a remnant of the complete circle of inner ventricular fibres of the lower vertebrate heart. They also noted a connection, consisting of ordinary cardiac muscle, between the left auricle and left ventricle in the heart of *Echidna*. The present writer (4, 5) drew attention to the fact that in the avian heart the main auriculo-ventricular connection takes the form of a well-defined auriculo-ventricular bundle, consisting of specialised muscle, which descends from the auriculo-ventricular node into the depth of the ventricular septum and there divides into right and left limbs for distribution to the respective ventricles. Other auriculo-ventricular connections noted in the avian heart were those between the auricular and ventricular myocardial components of the muscular right auriculo-ventricular valve by means of the right auriculo-ventricular Purkinje ring. The present study (commenced at University College, London, and completed at King's College) consists of the histological examination of the hearts of *Platypus* (one) and *Echidna* (two), for which material I wish to express my gratitude to my former chief, Prof. J. P. Hill.

The specialised connections of the monotreme heart, as determined in the present work, are described below. The remarks apply equally to *Platypus* and *Echidna*, but any particular differences are mentioned. Further, the sinu-auricular and auriculo-ventricular connections thus determined are compared

with those in the placental mammalian, avian and lower vertebrate hearts, and the bearing is discussed which the condition in the monotreme heart has upon the significance of the arrangement of the specialised muscle in these other hearts.

PRESENT WORK

The sinu-auricular node

The three caval openings in the right auricle, right and left anterior, and posterior are surrounded by the right and left sinus valves. Between the left sinus valve and the inter-auricular septum is a well-defined region of the right auricle, *the intersepto-valvular space* (Plate I, fig. 1). Running upwards in the base of the right sinus valve and continued on to the roof of the right auricle is a muscular band, the crista terminalis. Beneath the epicardium, on the auricular side of the crista terminalis, is the sinu-auricular node (Plate I, fig. 2). It is ovoid in shape and tapers off above and below. It is situated mainly in relation to the crista on the roof of the right auricle, but also extends caudally in relation to about the upper half of the right sinus valve. In size it is relatively more massive than the sinu-auricular node of the hearts of placental mammals. Its specialised cells are arranged in interlacing strands with much connective tissue interspersed. The cells vary in size, some being almost as large as the ordinary auricular myocardial cells, though most are smaller (Plate I, fig. 3). Longitudinal myofibrillae are scarce and are limited to the extreme periphery of the cell, the wide perinuclear zone being clear and devoid of fibrillae. Transverse striation is not perceptible in the fibrillae. The nuclei are round or slightly oval and centrally situated; two nuclei can frequently be seen in the same cell in one section. These specialised cells of the sinu-auricular node pass into direct continuity with the neighbouring myocardial cells of the right auricle on the one hand, and on the other they merge with the myocardial cells of the cardiac end of the right anterior vena cava. The cephalic part of the sinu-auricular node is situated beneath the epicardium on the auricular (ventral) side of the crista terminalis. It is only the caudal, narrower part of the node which lies actually in the base of the right sinus valve and crista terminalis. There is no evidence of specialised nodal cells in relation to the left sinus valve in *Platypus* or *Echidna*. The arterial arrangement in relation to the monotreme sinu-auricular node differs in *Platypus* and *Echidna*. In *Platypus* (Plate I, fig. 3) the arrangement is similar to that in the sinu-auricular node of the bird and of the placental mammal in that two small arteries run longitudinally through the node and communicate by two or three branches in the node. In *Echidna* (Plate I, fig. 4) the outstanding feature is the extreme vascularity of the node, the nodal arteries being large and communicating very freely with each other. Many nerve fibres run into the sinu-auricular node from neighbouring nerve ganglia, and moreover a number of nerve cells lie actually in the node in both *Platypus* and *Echidna* (Plate II, fig. 5). Keith and Mackenzie (1) also noted

the presence of nerve cells in the sinu-auricular node in *Echidna*. In the hearts of placental mammals Meiklejohn (6) found nerve cells in the perinodal connective tissue only and not amongst the specialised nodal tissue. These details of the sinu-auricular node in the monotreme heart are of interest in considering the nature of the node in the heart of the higher mammal and bird and its relation to the sinu-auricular junctional tissues in piscine and lower reptilian hearts. It is commonly thought that the limitation of specialised nodal tissue in the higher mammalian heart to the base of the right sinus valve represents a reduction of the sinu-auricular ring of the lower reptile and the fish, and it is suggested by Mackenzie (7) and by Walmsley (8) that this reduction occurs *pari passu* with, and is caused by, the fusion of the left sinus valve with the inter-auricular septum, with consequent obliteration of the intersepto-valvular space and disappearance of the left part of the sinu-auricular ring. But, as described above, in the monotreme heart the sinu-auricular node is confined to the region of the right sinus valve (and crista terminalis) and the intersepto-valvular space is a well-defined region of the right auricle, between the left sinus valve and the inter-auricular septum. The obliteration of the intersepto-valvular space which occurs in the hearts of higher mammals cannot therefore be the prime factor in the reduction of the sinu-auricular ring of the lower vertebrate heart.

With regard to the position of the sinu-auricular node, A. Oppenheimer and B. S. Oppenheimer (9) described the node in the young human heart as lying on the venous side of the right sinus valve. Stiénon (10) from his study of foetal hearts of the rabbit, sheep and man, pushes the origin of the sinu-auricular node back to the cavo-sinus junction, while Shaner (11) finds that the sinu-auricular node in the foetal calf heart appears at the 100 mm. stage just above the cavo-atrial junction, and only just before birth sinks into the sulcus terminalis. In the adult monotreme heart, the cephalic part of the sinu-auricular node lies on the auricular side of the crista terminalis, only the caudal part lying actually in the base of the right sinus valve.

Purkinje fibres in the auricles

Much controversy has taken place concerning the presence of Purkinje fibres in the auricles in higher mammals. Keith, Flack and Mackenzie do not refer to them in their investigations. Koch (12) denies the presence of Purkinje fibres in the auricles of young human subjects and Monckeberg (13) considers that when present they are abnormal formations. Holmes (14) described Purkinje fibres in the right auricle of the calf heart, a small clump of Purkinje fibres lying near the superior vena cava and another in the musculi pectinati in the roof of the right auricle. Through the courtesy of Dr Holmes the present writer has seen his sections and has no hesitation in agreeing that the fibres he describes have all the characters of Purkinje fibres. Holmes was unable to find any Purkinje fibres in the auricles of any other mammalian heart he examined (sheep, ox, lamb, pig, camel, gazelle, human adult and child).

Tandler (15) noted the presence of Purkinje fibres in the human right auricle in the adult only. Walmsley (8) quotes Pace and Schwartz as finding Purkinje fibres in the auricles of many mammals, and Walmsley himself finds fibres agreeing in all respects with the ventricular Purkinje fibres in the following regions of the right auricle of the adult human heart: near the auriculo-ventricular node, though he is uncertain whether they are continuous with the node; at the lateral margin of the orifice of the inferior vena cava; round the orifice of the coronary sinus; and along the junction of the inter-auricular septum with the posterior wall of the right auricle.

It is noteworthy that the situations in which these Purkinje fibres have been described by the above workers are very variable, and moreover the fibres appear to form isolated strands, unconnected with the sinu-auricular or auriculo-ventricular node or with the ventricular Purkinje system. Thorel (16) described a connection between the sinu-auricular and auriculo-ventricular nodes consisting of specialised cardiac muscle, but this has not been confirmed by subsequent investigators. Todd and van der Stricht (17, 18) have gone to an extreme and state that in the adult human heart the Purkinje fibres form a network permeating the right (and probably the left) auricle just as fully as they do the ventricles. These authors concentrated their studies upon the right auricle and do not speak with the same certainty in the case of the left auricle. They also deny the right of the sinu-auricular and auriculo-ventricular nodes for special consideration, as they maintain that they are structurally identical with, and are non-specialised parts of, the general cardiac Purkinje system. The present writer (4) observed that in the bird's heart the Purkinje fibres in the right and left auricles formed a continuous system, both beneath the endocardium and around the coronary arteries in the myocardium. This avian auricular Purkinje system was found to be continuous on the one hand with the sinu-auricular node and on the other with the ordinary auricular myocardium; it was not directly continuous with the ventricular Purkinje system.

In view of the varying opinions concerning the presence and extent of distribution of Purkinje fibres in the auricles of placental mammals, the condition in the monotreme heart assumes special importance. In the present work no Purkinje fibres were found in either auricle of the Platypus heart, nor in those of one of the *Echidna* hearts examined. In the second *Echidna* heart studied, numerous cells were seen in the walls of both auricles having characters somewhat akin to those of Purkinje fibres (Plate II, figs. 6 and 7). These cells were most numerous in, and constituted the major thickness of the pectinate muscles of the left auricular appendix. They presented the following characters. Their transverse diameter averaged 12 μ, as compared with that of the auricular cells with more typical myocardial structure, which (in this particular heart of *Echidna*) had a diameter of about 10 μ. They contained two (occasionally three) nuclei, which were slightly oval in shape and central in position. The nuclei exhibited much basiphil chromatin material. About the nuclei there was a fairly wide zone devoid of longitudinal myo-

fibrillae, which were limited to the periphery of the cells. Transverse striation in these fibrillae was very distinct. The size of the cells, the very distinct transverse striation and the abundance of chromatin in the nuclei are evidence against considering these cells as Purkinje cells, although they are certainly different from the auricular muscle in the other *Echidna* heart and in the *Platypus* heart, and from the rest of the auricular musculature in this particular heart. They are of interest in relation to the description by Todd and van der Stricht (17, 18) of various types of Purkinje fibres in the heart of man. The present writer is not disposed to regard these fibres as Purkinje fibres. Their appearance does not suggest any pathological process known to the writer, nor does any improper fixation or peculiarity of staining appear to have had any action in the production of the microscopic appearance of these cells, which extend throughout the thickness of the auricular wall, and there is no suggestion of any sub-endocardial collection of definite Purkinje fibres in either auricle.

The specialised connection between auricles and ventricles

The only connection, of specialised structure, between the auricles and ventricles that could be made out in the present study was by means of the auriculo-ventricular node and its prolongations to the ventricles.

The auriculo-ventricular node
(Plate II, figs. 8 and 9)

In the heart of *Platypus* the auriculo-ventricular node lies mainly on the right side of the upper and posterior part of the cartilago cordis and partly in the lower border of the inter-auricular septum. In the two hearts of *Echidna* examined there was no cartilago cordis, but the auriculo-ventricular node occupied a corresponding site in relation to the trigonum fibrosum and to the inter-auricular septum. The auriculo-ventricular node in both *Platypus* and *Echidna* is a relatively massive structure. Its fibres resemble those of the sinu-auricular node in that they are smaller than the myocardial fibres and form a network by intercrossing in various directions, but there is not much connective tissue between the strands. Two rounded central nuclei are frequently seen in one cell, but the perinuclear clear zone is narrower and the peripheral zone exhibiting longitudinal myofibrillae is broader than the corresponding zones of the sinu-auricular nodal fibres. Transverse striation is not perceptible in the longitudinal myofibrillae. The dorsicephalic part of the auriculo-ventricular node in the *Platypus* heart is flattened transversely and its left surface is concave in adaptation to the convex right surface of the cartilago cordis, with which it lies in intimate contact. The fibres of this part of the node are continuous above and behind with the myocardial fibres of the inter-auricular septum. The ventrocaudal part of the node is ovoid in shape and is continued ventrally into the auriculo-ventricular bundle. The caudal part of the node is prolonged downwards for a short distance beneath the endocardium

on the right side of the ventricular septum at its posterior part. The fibres of this prolongation are similar in character to those of the main part of the node. They are smaller than the myocardial fibres of the ventricular septum and are quite unlike the very large Purkinje fibres of the auriculo-ventricular bundle. These nodal fibres become continuous with the superficial myocardial fibres of the ventricular septum. This prolongation of nodal fibres was noted by Keith and Mackenzie (1) in the heart of *Echidna*, and these authors also observed a similar prolongation of nodal fibres to the septal musculature in the heart of the rat. Wray Lloyd (19) describes a prolongation of specialised fibres in the rabbit heart which arises from the junction of the auriculo-ventricular node and auriculo-ventricular bundle and passes downwards beneath the attached border of the septal cusp of the tricuspid valve to become continuous with the myocardium of the ventricular septum. A similar nodal prolongation was observed (macroscopically) by Curran (20) in the heart of the calf (Plate II, fig. 10). It may be profitable here to repeat the warning, expressed by Wray Lloyd, that this septal prolongation of the auriculo-ventricular node must be borne in mind in experimental work on the conducting system of the higher mammalian heart.

No nerve cells are seen in the auriculo-ventricular node itself, but a number of nerve fibres pass into the node from nerve cells which are situated in the lower part of the inter-auricular septum. With regard to the position of the auriculo-ventricular node in relation to the sinus valves, in both *Platypus* and *Echidna* the node lies outside the region of the sinus valves. Walmsley (8) is of the opinion that in the human heart the auriculo-ventricular node lies in the proper atrial region, that is, outside the area enclosed by the sinus valves, and that therefore the auriculo-ventricular node is a derivative of the auriculo-ventricular ring of lower reptilian and piscine hearts. Mackenzie (7), on the other hand, believes that the auriculo-ventricular node is a derivative of the sinu-auricular ring of the lower vertebrate heart, and states that in the kangaroo heart the auriculo-ventricular node lies within the limits of the sinus valves. The view favoured by Mackenzie therefore is that the sinu-auricular and auriculo-ventricular nodes are right and left derivatives of the primitive sinu-auricular ring. Experimental evidence that is considered to support this view is that the right vagus and right sympathetic nerves are associated with the sinu-auricular node, while the left vagus and left sympathetic influence the auriculo-ventricular node. The present work on the monotreme heart supports Walmsley's opinion that the auriculo-ventricular node lies outside the sinus region of the right auricle. Moreover, Shaner (11) finds that the auriculo-ventricular node first appears in the 9 mm. calf embryo behind the posterior endocardial cushion, at which time the auriculo-ventricular ring is a complete and unbroken muscular ring around the auriculo-ventricular canal, continuous above with the auricular muscle and below with the ventricular muscle.

The auriculo-ventricular bundle and its divisions
(Plate II, fig. 8; Plate III, figs. 12 and 13)

From the ventrocaudal part of the auriculo-ventricular node the auriculo-ventricular bundle passes forwards, at first through the connective tissue on the right side of the cartilago cordis in *Platypus*, or through the trigonum fibrosum in *Echidna*, thence continuing embedded in connective tissue on the upper border of the muscular ventricular septum. Here it lies nearer the right than the left side of the septum, being close to the endocardium on the right side, but separated from the endocardium on the left side of the septum by a thick layer of connective tissue. At the anterior part of the upper border of the muscular septum the bundle divides into right and left limbs, the bifurcation of the bundle sitting saddle-wise on the upper border of the muscular part of the ventricular septum (Plate III, fig. 13). The auriculo-ventricular bundle is a relatively massive structure in both *Platypus* and *Echidna*, and consists of a compact rounded bundle of parallel Purkinje fibres (Plate III, fig. 11). These fibres are large, having an average diameter of about 20 μ, and contain two, or occasionally three, round, central nuclei. Around the nuclei there is a clear cytoplasmic zone, longitudinal myofibrillae being limited to the periphery of the cell. Transverse striation is easily recognisable in these fibrillae, but is not so marked as in the myocardial fibres proper. Although the auriculo-ventricular bundle is surrounded by connective tissue, some of the specialised fibres appear to establish continuity with the myocardial fibres of the upper part of the ventricular septum, and the lower part of the bundle presents a streaky appearance (in the stained sections, Plate III, fig. 12) owing to the fact that some of the more deeply staining septal myocardial fibres are interspersed among the specialised fibres of the bundle. A few nerve fibres can be identified among the special bundle fibres and can be traced into continuity with those in the auriculo-ventricular node.

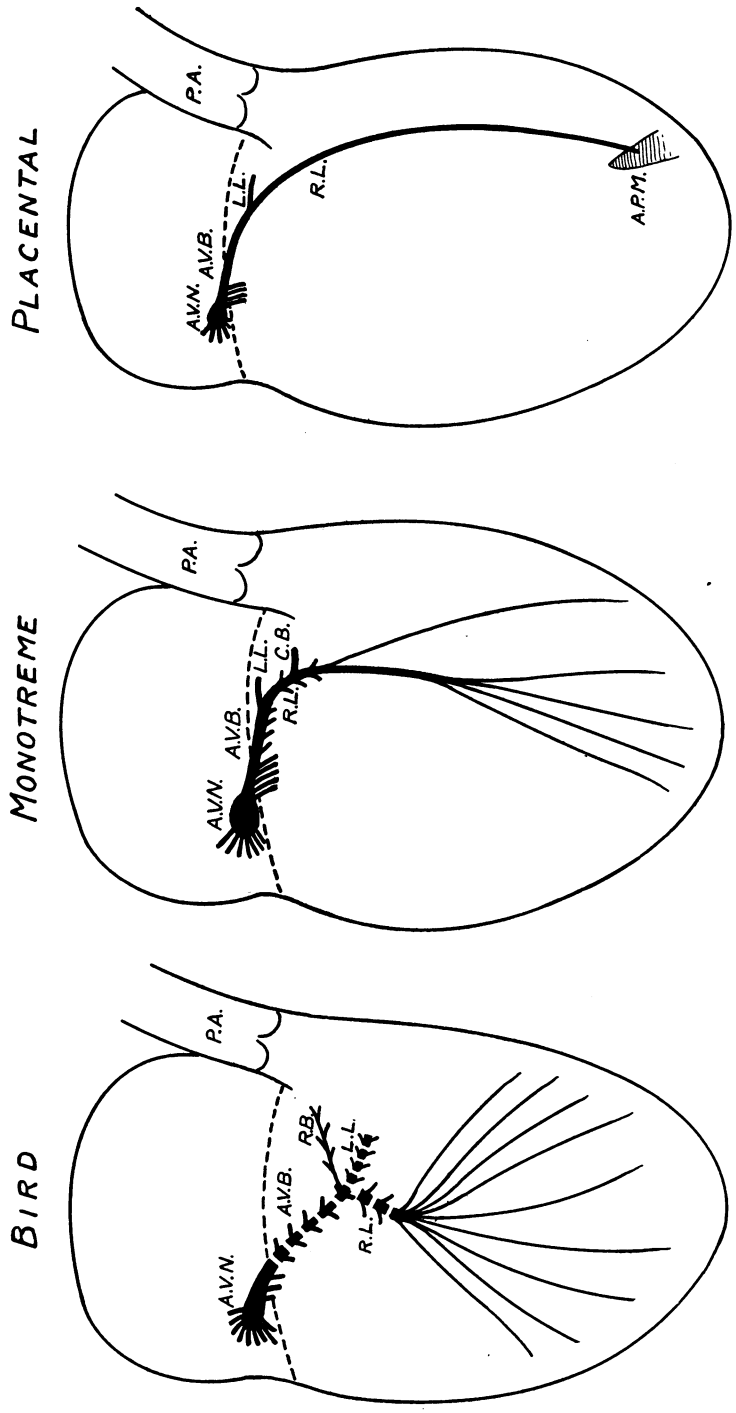
The right limb of the auriculo-ventricular bundle

From the bifurcation of the auriculo-ventricular bundle the right limb runs caudally beneath the endocardium on the right side of the ventricular septum, immediately behind the conus arteriosus. At first it has the form of a round bundle (Plate III, fig. 14), but about one-quarter of the way down the right side of the ventricular septum it broadens out and divides into an anterior and a posterior branch (Plate IV, fig. 15). The specialised fibres of the right limb of the auriculo-ventricular bundle have the same characters as those of the main bundle. The right limb has a delicate connective tissue investment, but some of the deeper specialised fibres come into apposition with the neighbouring septal myocardial fibres, and indeed appear to establish continuity with them. Also, just beyond the commencement of the right limb, many of its specialised fibres become continuous with the myocardial fibres of the conus arteriosus. The anterior, smaller, branch of the right limb of the auriculo-

ventricular bundle (Plate IV, fig. 16) runs caudally and ventrally, as a single rounded bundle, beneath the endocardium on the right side of the ventricular septum. About two-thirds of the distance down the septum it passes beneath the endocardium of a large muscle bundle (the septo-marginal bundle) which conveys it from the septum to the free wall of the right ventricle, which it reaches a short distance above the apex (Plate IV, fig. 17). Here it passes into continuity with the sub-endocardial Purkinje network of the free wall of the right ventricle. The posterior, larger, branch of the right limb of the auriculo-ventricular bundle (Plate IV, fig. 18) runs downwards beneath the endocardium on the right side of the ventricular septum, becoming markedly flattened out, and, more than halfway down the septum, divides into four subsidiary branches (Plate IV, fig. 19). These branches, after a short course downwards beneath the septal endocardium, are conveyed from the septum to the free wall of the right ventricle in "false tendons" to become continuous with the sub-endocardial Purkinje network of the free wall of the right ventricle (Plate IV, fig. 20). On their way down beneath the endocardium on the right side of the ventricular septum, all the branches of the right limb of the auriculo-ventricular bundle are embedded in connective tissue, but in many places the deeper specialised fibres appear to establish continuity with the immediately subjacent septal myocardial fibres.

It is interesting to compare the septal disposition of the right limb of the auriculo-ventricular bundle in the monotreme heart with that in the avian heart on the one hand and with that in the heart of the placental mammal on the other (text-figure 1).

The present writer drew attention in previous communications (4, 5) to the fact that the right limb of the auriculo-ventricular bundle in the bird's heart passes from the bifurcation of the bundle (which is situated in the *depth* of the ventricular septum, about one-quarter of the distance down) to the endocardium on the right side of the ventricular septum, and there divides into several strands of Purkinje fibres which pass to the free wall of the right ventricle. The right limb of the auriculo-ventricular bundle in the heart of the placental mammal is generally described as a single, *unbranched* bundle, enveloped in a well-defined connective tissue sheath, passing down on the right side of the ventricular septum (immediately behind the conus arteriosus) and thence to the base of the anterior papillary muscle by means of the "moderator band" (septo-marginal bundle). The right limb of the bundle in the placental mammal is thus considered not to give off any branches until it reaches the base of the papillary muscle, where it passes into continuity with the sub-endocardial Purkinje network of the right ventricle. The present study shows that the right limb of the auriculo-ventricular bundle in the monotreme heart, which reaches the free wall of the right ventricle in the form of five branches, is intermediate in its arrangement on the right side of the ventricular septum between that of the much-branched right limb of the avian bundle and that of the (as usually described) single unbranched right limb of the bundle in



Text-fig. 1. Diagram to illustrate comparison of auriculo-ventricular node and bundle and right limb of bundle in avian, monotreme and placental heart. (For explanation see text.)

the heart of the placental mammal. It may be observed that the anterior branch of the right limb of the auriculo-ventricular bundle in the monotreme heart pursues a course on the right side of the ventricular septum similar to that of the entire right limb of the bundle in the heart of the placental mammal, namely, immediately behind the conus arteriosus and thence to the free wall of the right ventricle by means of the septo-marginal bundle.

The description of the unbranched course of the right limb of the auriculo-ventricular bundle in the heart of the placental mammal, from its point of commencement to its arrival at the base of the papillary muscle, is supported by Indian ink injections of the sheath of the auriculo-ventricular bundle and its divisions in the ox heart (King (21), Aagaard and Hall (22)), and by the detailed reconstructions of the system in the heart of the calf and of man (de Witt (23)).

Lewis (24), however, noted that an experimental lesion of the right limb of the auriculo-ventricular bundle in the dog's heart produced a more pronounced effect upon the subsequent electrocardiographic tracing the higher up the limb the lesion was situated. He therefore concluded that there must be early outgoing branches from the right limb of the bundle, though such have not been demonstrated anatomically.

Curran (20) in one of his figures (Plate II, fig. 10), though no special importance is attributed to it in the general text, shows a dissection of a branch given off from the right limb of the auriculo-ventricular bundle in the calf heart. This branch is given off just before the right limb enters the "moderator band," and it passes upwards and to the left into the musculature of the conus arteriosus. Ungar (25) has noted that when a well-developed septal papillary muscle is present in the right ventricle of the human heart, the right limb of the auriculo-ventricular bundle occasionally gives a branch to it. The branch of the right limb of the bundle to the conus musculature in the calf heart figured by Curran recalls the continuity of some of the specialised fibres of the right limb of the monotreme bundle with the adjacent myocardium of the conus. It also has its parallel in the recurrent branch of the auriculo-ventricular bundle in the heart of the bird, which passes upwards and to the left from the bifurcation of the bundle into the depth of the conus musculature (Davies (4, 5)). The results of Lewis's experiments and the present observations of the branching of the right limb of the monotreme bundle and the continuity of the specialised fibres of the right limb with the septal myocardium certainly warrant a careful histological re-investigation of the right limb in the heart of the placental mammal.

The left limb of the auriculo-ventricular bundle

From the bifurcation of the main bundle the left limb passes downwards immediately beneath the endocardium on the left side of the ventricular septum. It first reaches the left side of the septum immediately below the right cusp of the aortic valve, and takes the form of a broad flattened band

of specialised fibres which have the same histological characters as those of the main auriculo-ventricular bundle. It is larger than the right limb and its fibres are more loosely arranged with much connective tissue lying between groups of the specialised fibres. Some of the deeper fibres of the left limb come into apposition with the subjacent septal myocardial fibres and appear to establish continuity with them. About one-quarter of the distance down the left side of the ventricular septum the left limb divides into four branches (two main central and two small marginal) which radiate from each other as they pass downwards beneath the endocardium on the left side of the septum. These branches subdivide and eventually reach the free wall of the left ventricle to become continuous with the sub-endocardial Purkinje network on the free wall of the left ventricle either by means of "false tendons" or at the junction of the septum and free wall. The disposition of the left limb of the monotreme bundle is very similar to that of the left limb of the bundle in the heart of the placental mammal.

A marked feature of the Purkinje system in the heart of the bird is the penetration of the sub-endocardial Purkinje fibres of the auricles and ventricles into the myocardium, especially in relation to the branches of the coronary arteries (4). No myocardial penetration of the sub-endocardial Purkinje fibres of the right or left ventricle in the monotreme heart was observed in the present study; the sub-endocardial Purkinje fibres of both ventricles become continuous immediately with the adjacent myocardial fibres.

SUMMARY

1. The conducting system, of specialised structure, of the monotreme heart (*Platypus* and *Echidna*) is described.

2. The limitation of sinu-auricular nodal tissue to the region of the right sinus valve in the presence of the intersepto-valvular space of the right auricle is evidence that the disappearance of the intersepto-valvular space in the higher mammalian heart is not the prime factor in the "condensation" of the sinu-auricular ring of the lower vertebrate (piscine and reptilian) heart.

3. The position of the sinu-auricular and auriculo-ventricular nodes in relation to the sinus valves is discussed.

4. The branched arrangement of the right limb of the auriculo-ventricular bundle in the monotreme heart is described and compared with that of the right limb of the bundle in the bird's heart previously described by the present writer, and with the present conception of the right limb of the bundle in the heart of the placental mammal.

I wish to express my gratitude to my former chiefs, Prof. G. Elliot Smith and Prof. J. P. Hill, and to my present chief, Prof. D. M. Blair, for their interest and advice, also to Mr F. Pittock and Mr E. O. Lloyd, technical assistants at University College, for the preparation of the material to illustrate the present work.

DESCRIPTION OF PLATES I–IV

Plate I

Fig. 1. Transverse section through lower part of right auricle of *Platypus* heart. Low power.
Fig. 2. Transverse section of upper part of free wall of right auricle. *Platypus*. Low power.
Fig. 3. High power view of part of fig. 2.
Fig. 4. Transverse section of upper part of free wall of right auricle. *Echidna*. Low power.

Plate II

Fig. 5. Transverse section of upper part of free wall of right auricle. *Platypus*. Low power.
Fig. 6. Transverse section through appendix of left auricle. *Echidna*. High power.
Fig. 7. Transverse section of left auricular appendix. *Echidna*. High power.
Fig. 8. Transverse section through upper border of ventricular septum. *Platypus*. Low power.
Fig. 9. Transverse section through lower border of auricular septum. *Platypus*. High power.
Fig. 10. Figure of Curran's dissection of auriculo-ventricular node and bundle in heart of calf.

Plate III

Fig. 11. High power view of transverse section through auriculo-ventricular bundle. *Platypus*.
Fig. 12. Transverse section through upper border of ventricular septum. *Platypus*. Low power.
Fig. 13. Transverse section through upper border of ventricular septum a little below fig. 12. *Platypus*. Low power.
Fig. 14. Transverse section through upper part of ventricular septum. *Platypus*. Low power.

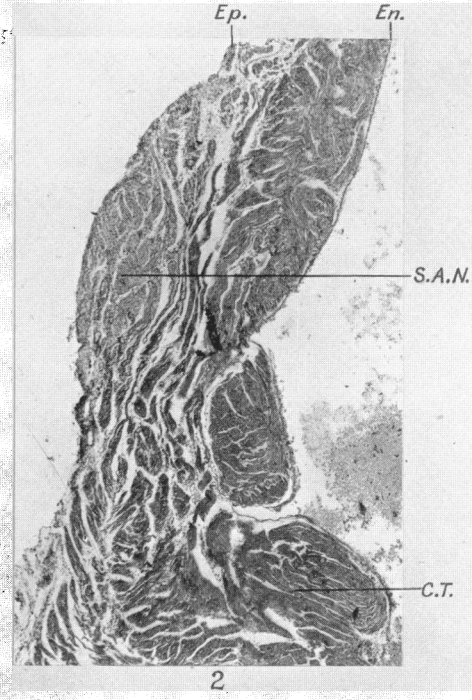
Plate IV

Fig. 15. Transverse section of ventricular septum about one-quarter of the distance down the septum. *Platypus*. Low power.
Fig. 16. Transverse section through ventricular septum below fig. 15. *Platypus*. Low power.
Fig. 17. Transverse section through ventricular septum about two-thirds of the distance down the septum. *Platypus*. Low power.
Fig. 18. Transverse section through ventricular septum about halfway down the septum. *Platypus*. Low power.
Fig. 19. Transverse section through ventricular septum below fig. 18. *Platypus*. Low power.
Fig. 20. Transverse section through ventricular septum a short distance above the apex. *Platypus*. Low power.

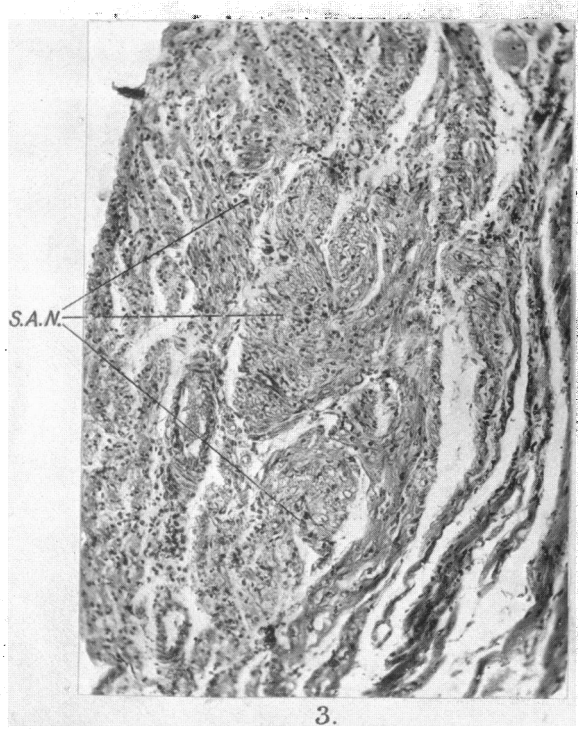
ABBREVIATIONS USED IN PLATES AND TEXT-FIGURE

A.S.	Auricular septum.
A.V.B.	Auriculo-ventricular bundle.
A.V.N.	Auriculo-ventricular node.
B.	Bifurcation of A.-V. bundle.
C.B.	Branch of right limb of A.-V. bundle to conus arteriosus.
C.C.	Cartilago cordis.
En.	Endocardium.
Ep.	Epicardium.
F.T.	False tendons.
I.S.	Intersepto-valvular space.
L.A.C.	Left auricle cavity.
L.L.	Left limb of A.-V. bundle.
L.S.V.	Left sinus valve.
L.V.C.	Left ventricle cavity.
N.C.	Nerve cells.
N.P.	Nodal prolongation.

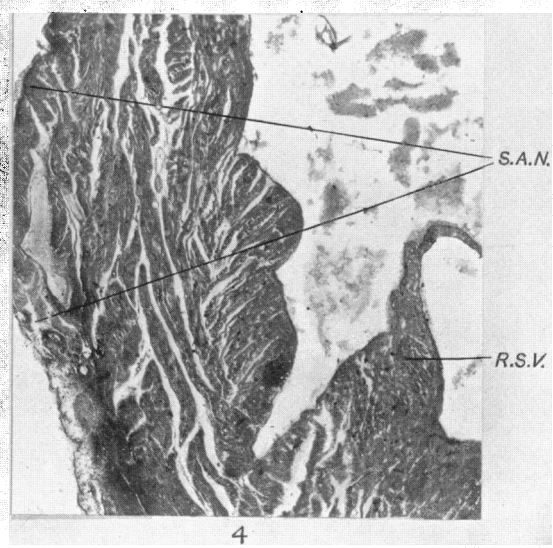
1.



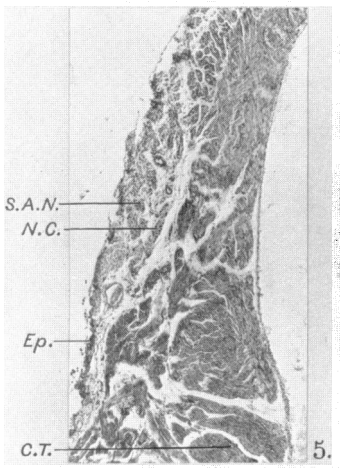
2



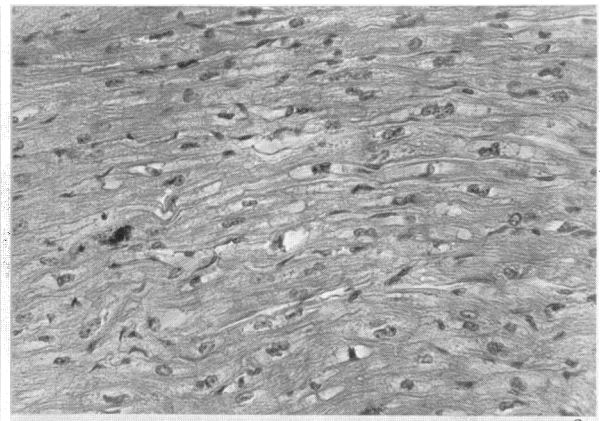
3.



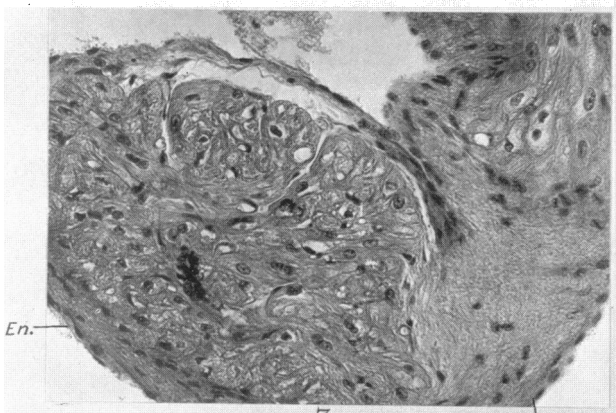
4



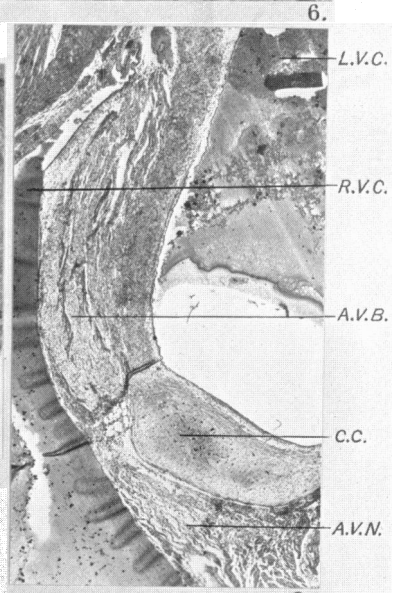
5.



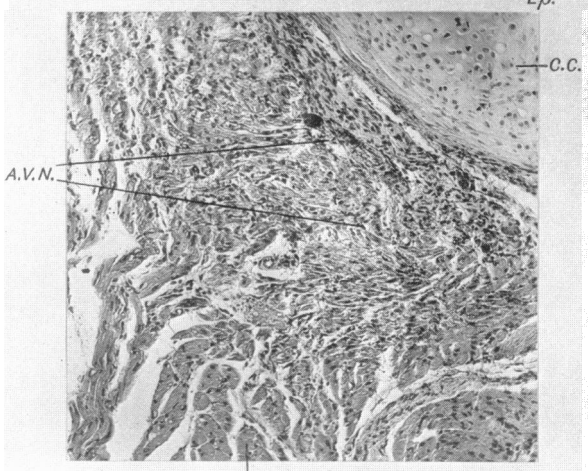
6.



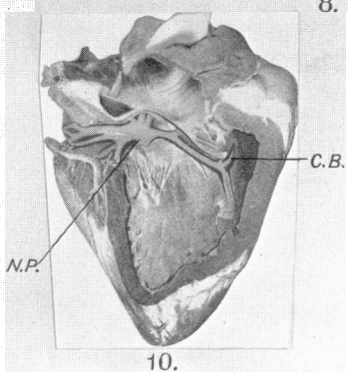
7.



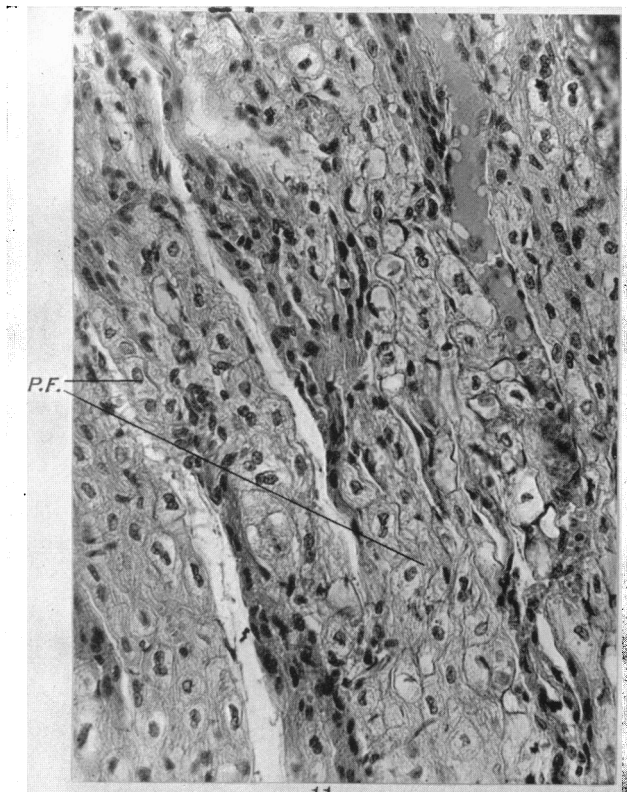
8.



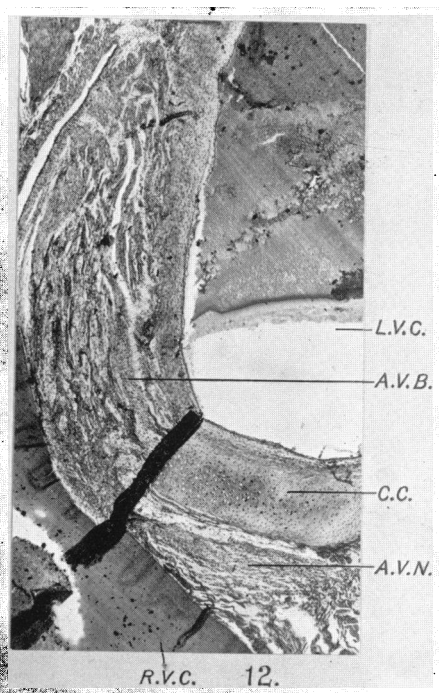
9.



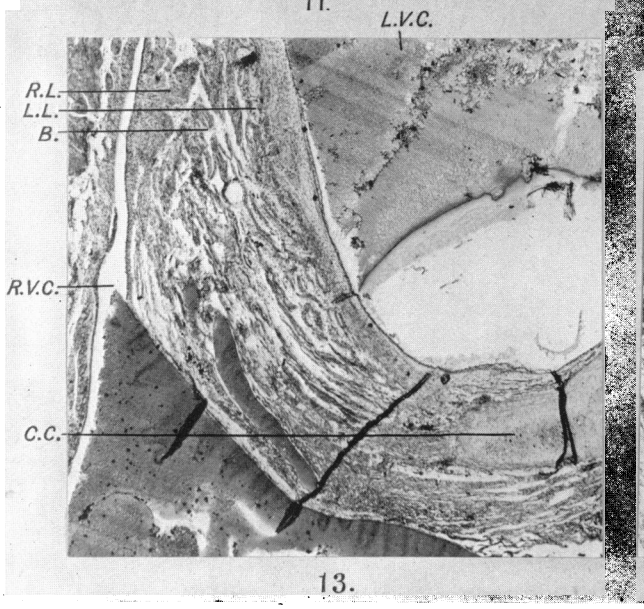
10.



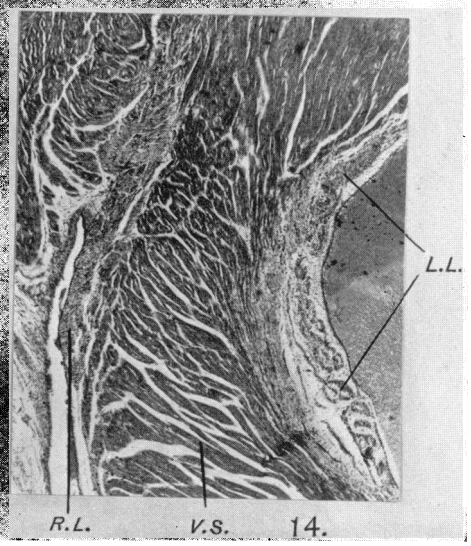
11.



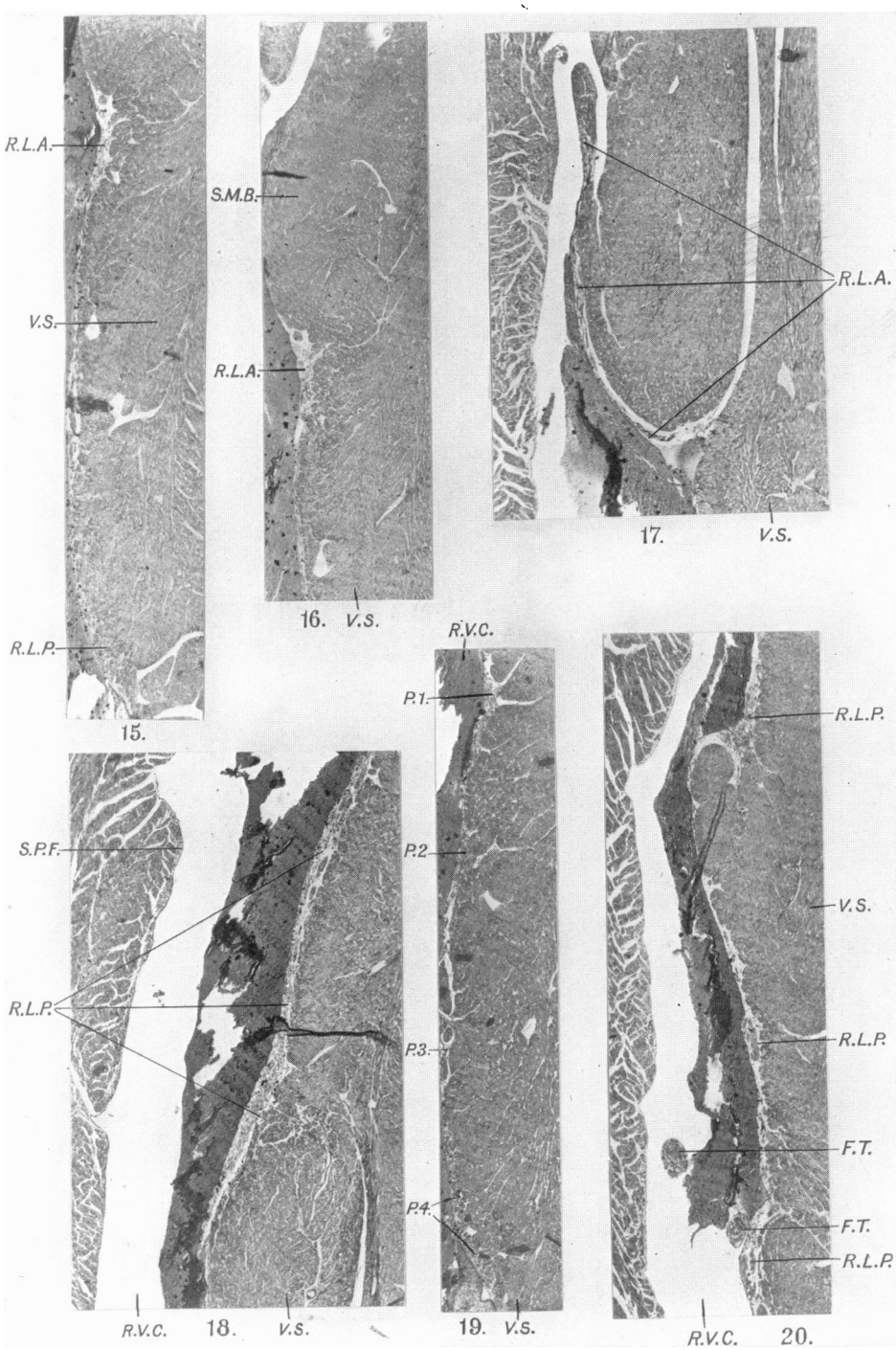
12.



13.



14.


R.L.A.
V.S.
R.L.P.
15.
S.M.B.
R.L.A.
16. V.S.
R.L.A.
17. V.S.
R.V.C.
P.1.
P.2
P.3.
P.4.
19. V.S.
R.L.P.
V.S.
R.L.P.
F.T.
F.T.
R.L.P.
R.V.C. 20.
S.P.F.
R.L.P.
R.V.C. 18. V.S.

P.F. Purkinje fibres.
R.A.C. Right auricle cavity.
R.L. Right limb of A.-V. bundle.
R.L.A. Anterior branch of right limb of A.-V. bundle.
R.L.P. Posterior branch of right limb of A.-V. bundle.
(P 1, P 2, P 3, P 4. Subdivisions of *R.L.P.*)
R.S.V. Right sinus valve.
R.V.C. Right ventricle cavity.
S.A.N. Sinu-auricular node.
S.M.B. Septomarginal bundle.
S.P.F. Sub-endocardial Purkinje fibres.
V.S. Ventricular septum.

REFERENCES

(1) KEITH, A. and MACKENZIE, I. (1910). *Lancet*, Jan. 8.
(2) MACKENZIE, I. and ROBERTSON, J. (1910). *Brit. Med. J.* pt 2.
(3) MACKENZIE, I. (1910). *Verhand. d. Deutsch. Path. Gesellsch.*
(4) DAVIES, F. (1930). *J. Anat.* vol. LXIV, pp. 129–46.
(5) —— (1930). *J. Anat.* vol. LXIV, pp. 319–23.
(6) MEIKLEJOHN, J. (1913). *J. Anat.* vol. XLVIII.
(7) MACKENZIE, I. (1913). *17th Internat. Congr. of Medicine, Anat. Sect.* pt 1.
(8) WALMSLEY, T. (1929). Quain's *Anatomy*, vol. IV, pt 3.
(9) OPPENHEIMER, A. and OPPENHEIMER, B. S. (1912). *Anat. Rec.* vol. VI.
(10) STIÉNON, L. (1927). *Archiv. de Biol.* T. XXXVI.
(11) SHANER, F. (1929–30). *Anat. Rec.* vol. XLIV.
(12) KOCH, W. (1909). *Münch. med. Wochenschr.*
(13) MONCKEBERG, J. G. (1924). *Handb. d. spez. path. Anat. u. Histol.* Henke u. Lubarsch.
(14) HOLMES, A. H. (1921). *J. Anat.* vol. LV.
(15) TANDLER, J. (1913). *Anat. des Herzens.*
(16) THOREL, C. (1906). *Münch. med. Wochenschr.* Jahr. LVI, No. 42.
(17) TODD, T. W. and VAN DER STRICHT, O. (1919). *Johns Hopkins Hosp. Rep.* vol. XIX.
(18) —— (1928). Cowdry's *Special Histology*, vol. II.
(19) LLOYD, W. (1930). *Amer. J. Anat.* May.
(20) CURRAN, E. J. (1903). *Anat. Rec.* vol. III.
(21) KING, M. R. (1916). *Amer. J. Anat.* vol. XIX.
(22) AAGAARD, O. C. and HALL, H. C. (1914). *Anat. Hefte*, Bd. LI.
(23) DE WITT, L. (1909). *Anat. Rec.* vol. III.
(24) LEWIS, T. (1911). *Mechanism and Graphic Registration of the Heart Beat.* London.
(25) UNGAR, M. (1924). "Das specifischen System der menschlichen Herzen." *Lotos.* Prague.