

On the cardiac anatomy of the Sumatran rhinoceros

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(With 3 plates and 12 figures in the text)

A descriptive account is given of the cardiac anatomy of a Sumatran rhinoceros with special reference to the cardiac conducting system, hitherto undescribed for the Rhinocerotidae. In the specimen studied this system manifests a well-developed Tawara network of Purkinje tissue, marked by obtrusive taeniae vagae, and a comparable atrial network. The sinu-atrial and atrio-ventricular nodes are connected by a Wenckebach bundle. The primary dextral and sinistral branches of the Kent-His bundle arise directly from the atrio-ventricular node. In its general constitution the heart closely resembles its equid counterpart.

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Introduction

The splanchnology of the Indian, Javan and Sumatran rhinoceroses (*Rhinoceros unicornis*, *R. sondaicus*, *Didermoceros sumatrensis*) remains incompletely explored what time these forms move progressively towards extinction if only from increasing loss of habitat. Recorded splanchnological information derives from the anatomization of remarkably few specimens and thus stands in need of augmentation as opportunity may permit. The Sumatran rhinoceros has been more frequently dissected than any other rhinoceros form but information concerning its gross visceral anatomy remains confined to the memoirs of Garrod (1873, 1878), Forbes (1881) and Beddard & Treves (1889). These memoirs curiously devote scant attention to the cardiac anatomy of this rhinoceros form, the heart being summarily dismissed by Garrod (1873) and ignored altogether by Beddard & Treves (1889). It has therefore been considered desirable to examine the pathologized heart of an immature Sumatran rhinoceros from the Basel Zoo in order to enlarge understanding of the structure of this organ. The results of such examination are specified below.

Material and methods

The heart examined came from an immature female Sumatran rhinoceros ("Betina") captured (17 March 1959) near the Siak River in Central Sumatra and exhibited in the Basel Zoologischer Garten from July 1959 to September 1961. The animal was meticulously necropsied by Dr S. Lindt, of the University of Berne Institute of Veterinary Pathology, and its skeleton and viscera were duly preserved in the Zoological Department of the Basel Naturhistorisches Museum. By courtesy of Dr L. Forcart, Curator of that Department, the organs were subsequently made available for anatomical examination. These included the necessarily mutilated heart which was duly dissected, drawn and where necessary histologized. The endocardium proved readily reflectable thus facilitating study of the cardiac conducting system. The coronary blood vessels were too damaged to permit satisfactory injection. The organ manifested no pathological change.

Sumatran rhinoceros splanchnology

Available information concerning Sumatran rhinoceros "soft" anatomy remains based upon the examination of a few entire specimens and single organs. This particular rhinoceros form was originally distinguished from the other Asian rhinoceroses by Bell (1793) who gave a comprehensive account of the external characters of an immature male animal; in describing the external genitalia he made reference to the penile musculature but nowhere intimated that his specimen had undergone dissection either in whole or in part.

Thus Garrod (1873) provided the first and fullest account of the splanchnology of *Didermocerus* from his anatomization of an old female animal. He devoted most attention to the alimentary canal and the abdominal viscera, checking his findings against those of Owen (1862) in the Indian rhinoceros, Owen's paper being then the only published account of rhinoceros general anatomy. Concerning the heart Garrod merely commented that it presented "no unusual features" and dismissed its detailed structure with a reference to the prominence of the fossa ovalis and the thickness of the inter-ventricular septum. Later (Garrod, 1878) he described and figured the brain of a second female animal, the organ in question being subsequently preserved in the Royal College of Surgeons Museum as specimen D.400 of the Physiological Series.

Forbes (1881) detailed the penis configuration of yet another animal, emphasizing the distinctive nature of the glans processes. Beddard & Treves (1889) supplemented Garrod's earlier account of *Didermocerus* splanchnology from their anatomization of a male and a female animal and devoted particular attention to the myology of the head and forelimb. Concerning the viscera they had "not much to add to the description by Garrod" and concerning the heart said nothing.

Thus during the last century not more than five specimens of Sumatran rhinoceros (all from the menagerie of the Zoological Society of London) had undergone anatomical investigation of any kind and but three of these in systematic detail. More recently, however, a sixth animal, from the Basel Zoologischer Garten, has made possible some minor contributions to *Didermocerus* splanchnology in the shape of observations upon the histology of the lymph nodes, viscera and parathyroids (Cave & Aumonier, 1962, 1963, 1966) and upon the anatomy of the epipharyngeal bursa, thymus, thyroid and tonsil (Cave, 1964, 1973, 1976, 1979).

It is remarkable, in view of the detailed attention paid to other *Didermocerus* organs, that the heart should have been so summarily dismissed by Garrod (1873) and so ignored

by Beddard & Treves (1889) and that the Javan rhinoceros heart should have been equally neglected by these same observers (Garrod, 1878; Beddard & Treves, 1887). Such scant attention to cardiac anatomy may possibly reflect the example set by Owen (1862) in his nominative rather than descriptive account of the Indian rhinoceros heart, wherein reference is made to a single cardiac chamber only. For whatever reason, however, the rhinoceros heart has, to date, escaped that measure of anatomical attention commensurate with its physiological importance, so that even the limited information afforded by the present imperfect *Didermocerus* heart is not inopportune.

Observations

The heart in general

Though mutilated and impossible of vascular injection the heart provides certain information concerning its several chambers, the coronary vasculature and the cardiac conducting system. Its apex, non-bifid and formed by the left ventricle, is more obtuse than that of the equid heart. Owing to the obliquity of the diaphragm, the postcava has an intrathoracic course of 6.5 cm; its ostium in the dorso-caudal aspect of the right atrium lacks all trace of a Eustachian valve. The single, dextral precava enters this atrium ventro-cranially, the sinu-atrial node occupying the substance of the cavo-atrial junction.

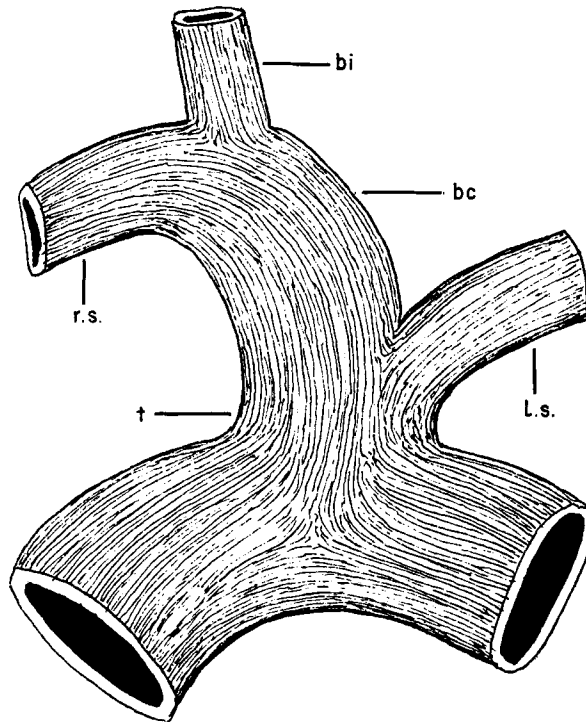


FIG. 1. Basal Sumatran rhinoceros. Aortic arch and branches. bc, truncus brachiocephalicus proprius; bi, arteria bicarotica; ls, left subclavian artery; rs, right subclavian artery; t, truncus brachiocephalicus communis.

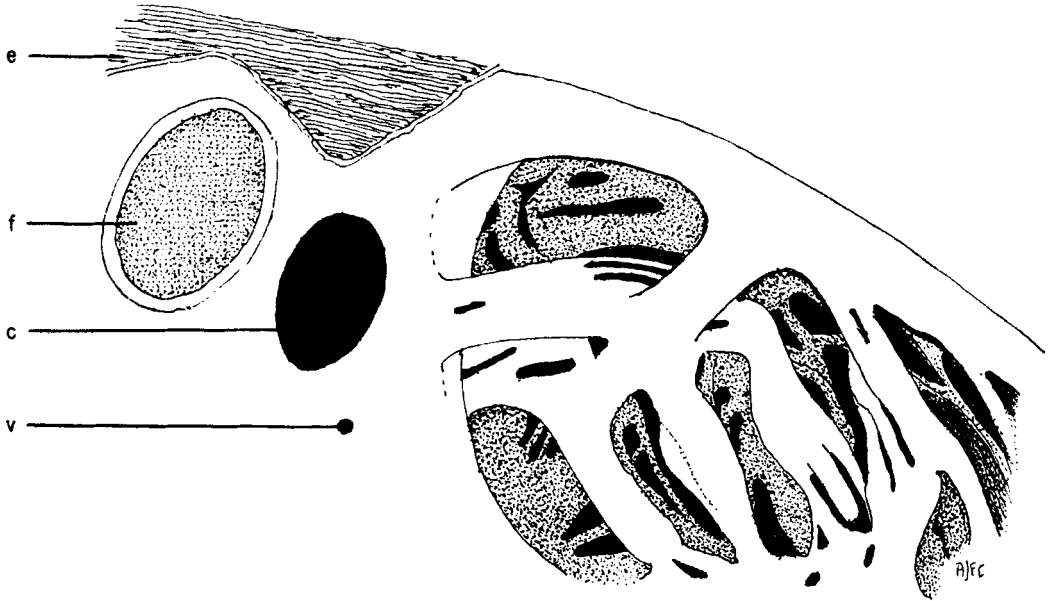


FIG. 2. Basel Sumatran rhinoceros. Dissection sketch showing coronary sinus ostium (c), endocardium *in situ* (e), fossa ovalis (f), vena minima (v) and pectenate musculature.

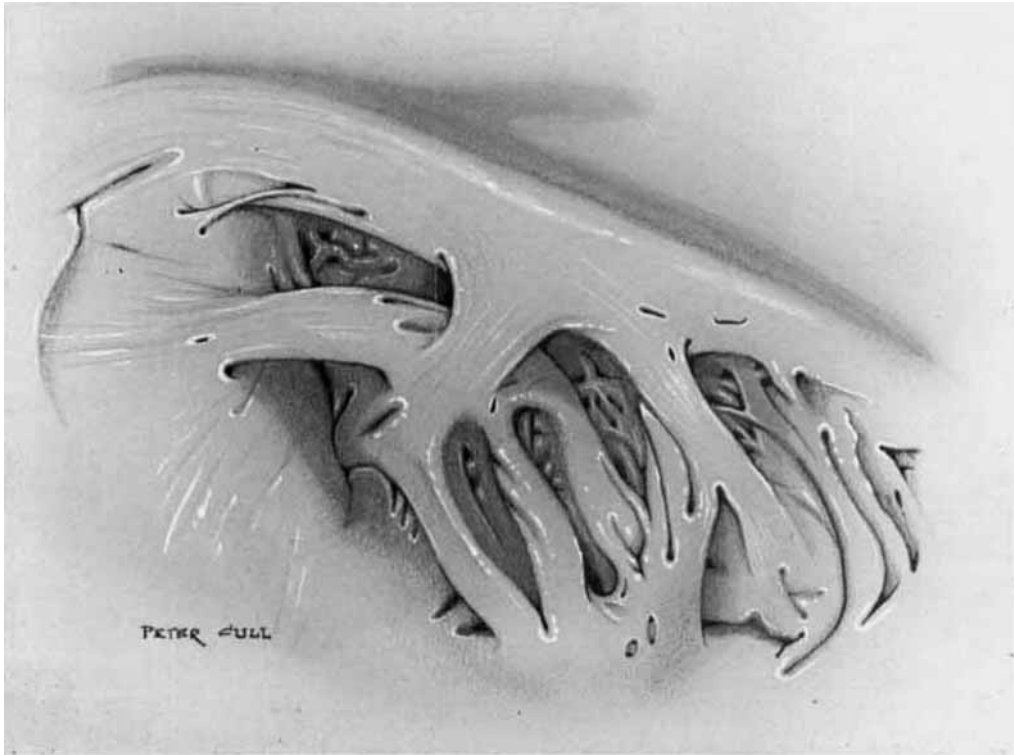


PLATE I. Basel Sumatran rhinoceros. Right atrium: interior showing crista terminalis and musculi pectinati.

The low-pitched aortic arch lacks definitive ascending and transverse portions but displays the canonical aortic (Valsalva) sinuses: its initial wall-thickness is 7 mm, its thickness in the region of the ligamentum arteriosum is 11 mm. Its summit gives off a single, large innominate artery (truncus brachiocephalicus communis) which divides almost immediately into left subclavian and truncus brachiocephalicus proprius: this last vessel courses cranialwards to divide into right subclavian and bicarotic arteris (Fig. 1). Those portions of the coronary arteries occupying the atrio-ventricular sulci are buried in an abundance of brownish epicardial fat. The atrial walls vary in local thickness from 4 to 7 mm; the interventricular septum is 25 mm thick cranially, 37 mm thick caudally. No os cordis is developed.

The cardiac chambers

The right atrium

This chamber has the sinu-atrial node embedded in its wall at the entrance of the precava. Exteriorly a broad, shallow sulcus terminalis runs from the nodal region to the postcava, demarcating atrium proper from auricle. Interiorly a topographically correspondent prominent crista terminalis gives rise to an elaborate complex of muscoli pectenati. An emphatic crista interveniens (tuberculum Loweri) separates precaval and postcaval ostia. On the interatrial septum a small but deep fossa ovalis is circumscribed by a raised annulus ovalis with a free sharp inner border overhanging the fossa. Medial thereto lies an oval (17×8 mm) coronary sinus ostium, devoid of Thebesian valve and sharp-rimmed from an embracing sphincteric arrangement of myocardial fibres. Ventrad of this ostium opens one of the venae minimae cordis and others open in the depressions of the pectenate musculature (Fig. 2). The muscoli pectenati, which radiate from the crista terminalis, are not comb-like in disposition, but form instead a complicated arborization of arciform fasciculi which subdivide and interlace over the auricle walls (Plate I).

Most, if not all, of these rounded, arched fasciculi contain a core of pale Purkinje tissue which divides *pari passu* with the subdivision of the containing fasciculus. Indeed the finest branches of the pectenate complex consist principally of such tissue, supported by some connective tissue, with or without a minimal admixture of ordinary myocardial fibres. From some of the larger fasciculi fine filaments of Purkinje tissue, recognizable macroscopically by their characteristic pale colour, emerge from the fascicular substance and thereon pursue a short subendocardial course before either re-entering that fasciculus or joining some other. Thus, as in the horse heart, there is some attempt at the formation of a subendocardial network of conducting tissue.

The entire pectenate muscle complex is permeated by an atrial Purkinje tissue network in direct association with the sinu-atrial node, one anatomically similar to the ventricular Tawara network associated with the atrio-ventricular node. The relationship of this atrial conducting tissue network to the atrial myocardium is so strikingly intimate as to suggest that the plexiform arrangement of the pectenate musculature is primarily determined by this network and is therefore more concerned with the propagation of the cardiac contractile impulse than with the dynamics of atrial systole.

The right ventricle

This somewhat bulbous chamber forms much of the dextral aspect of the heart, both ventrally and dorsally, save for the apical region. Its triangular outline has its base at the

atrio-ventricular sulci, its apex at a well-marked cornus arteriosus. Its septal wall is convex towards the ventricle cavity, its free wall is uniformly convex exteriorly. The main ventricular cavity is demarcated from the infundibular (conus) region by a prominent muscular ridge (crista supraventricularis) which sends a retiform series of columnae carnea into the free wall (Fig. 3). Save within the conus arteriosus columnae carnea are developed in great number and in all three varieties on the ventricular walls, especially towards the ventricle fundus. Columnae of the first order ("ridges") are mural elevations attached lengthwise to the ventricle wall; second-order columnae ("bridges") are mural elevations attached at their extremities only; third-order columnae ("papillary muscles") are conical elevations equipped apically with chordae tendineae. Their variety and multiplicity apart, the right ventricle columnae carnea are notable for the emergence from their substance in places of "false tendons", i.e. of pallid strands, some of which run a short subendocardial course prior to re-entering the ventricular parietes, while one such crosses the upper part of the ventricle as a "moderator band". These strands (taeniae vagae) are composed of Purkinje tissue supported by connective tissue which renders them obtrusively conspicuous against the darker-coloured myocardium; they are demonstrably the superficial component of an extensive Tawara network situated somewhat more deeply within the substance of the ventricle walls.

Papillary muscles are developed upon both walls of the chamber—an anterior muscle

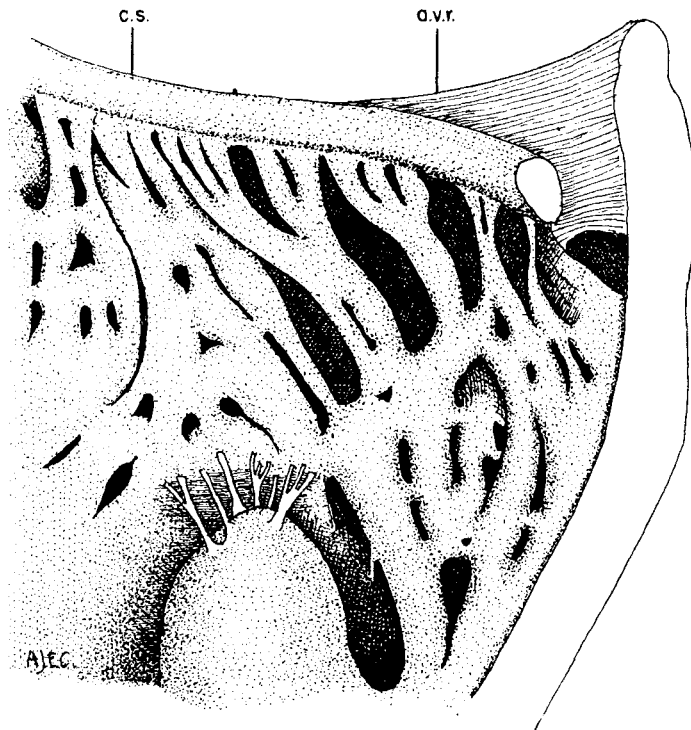


FIG. 3. Basel Sumatran rhinoceros. Right ventricle interior showing columnae carnea and anterior papillary muscle. avr, atrio-ventricular ring; cs, crista supraventricularis.

upon the free wall and two smaller muscles upon the septal wall. The former is a typically large, discrete, conical mass bearing six stout apical chordae tendineae which attach distally to the conus and marginal cusps of the tricuspid valve. The posterior papillary muscles are two smaller structures of unequal size. Of these the larger and more caudally situate springs from the septal wall near its junction with the free wall and its two stout apical chordae tendineae attach distally to the septal and marginal cusps of the tricuspid valve. The smaller papillary muscle arises from the septum nearer to the atrio-ventricular orifice and sends chordae tendineae to these same cusps.

Chordae tendineae of non-papillary origin also occur on the septal wall. An isolated flat chorda arises therefrom close to the attached margin of the tricuspid valve and is hidden in the open position of that valve; it divides and inserts into the septal cusp. An independent pair of chordae arises from the septum directly and likewise divides before inserting into the septal cusp. Craniad of this pair, another single chorda springs from the septum, showing a similar division and insertion. More craniad still a group of chordae arises from a faint, non-papillary septal elevation and gains insertion into the conus and septal cusps of the tricuspid valve (Fig. 4).

(The presence of two septal papillary muscles in the *Didermocerus* right ventricle is consonant with Owen's (1862) findings in *Rhinoceros unicornis* and the non-papillary origin of chordae tendineae with his observations (Owen, 1868) on the pig heart.)

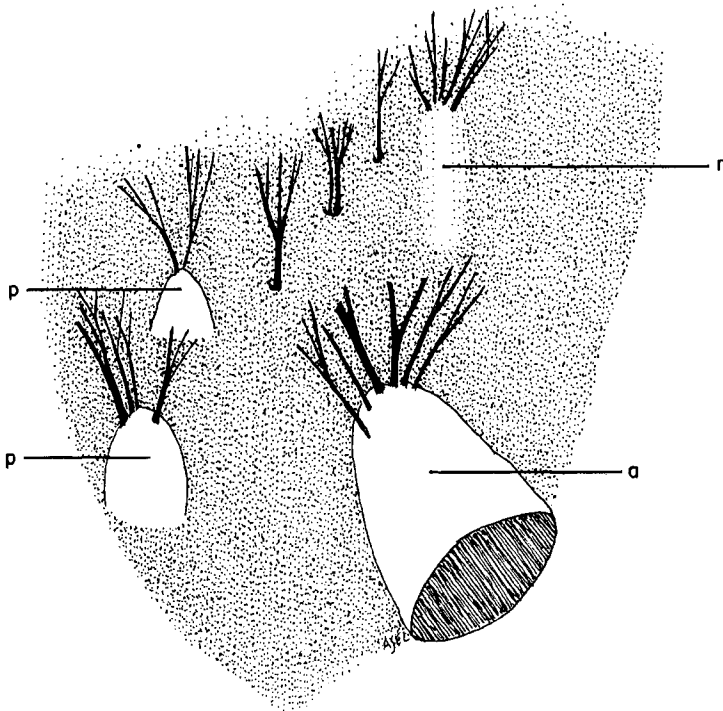


FIG. 4. Basel Sumatran rhinoceros. Right ventricle showing papillary muscles (white) and chordae tendineae (black) on septal wall. Semidiagrammatic. a, detached anterior papillary muscle; n, non-papillary elevation; p, p, posterior papillary muscles.

The infundibulum (conus arteriosus) of the ventricle is interiorly featureless: exteriorly it receives at least one branch of supply from the right coronary artery. As in *Equus* the pulmonary valve comprises a triad of equal-sized semilunar cusps, a caudal and a right and left cranial. The pulmonary trunk passes dorso-caudally between the atrial auricles; Valsalva sinuses are not detectable with certainty.

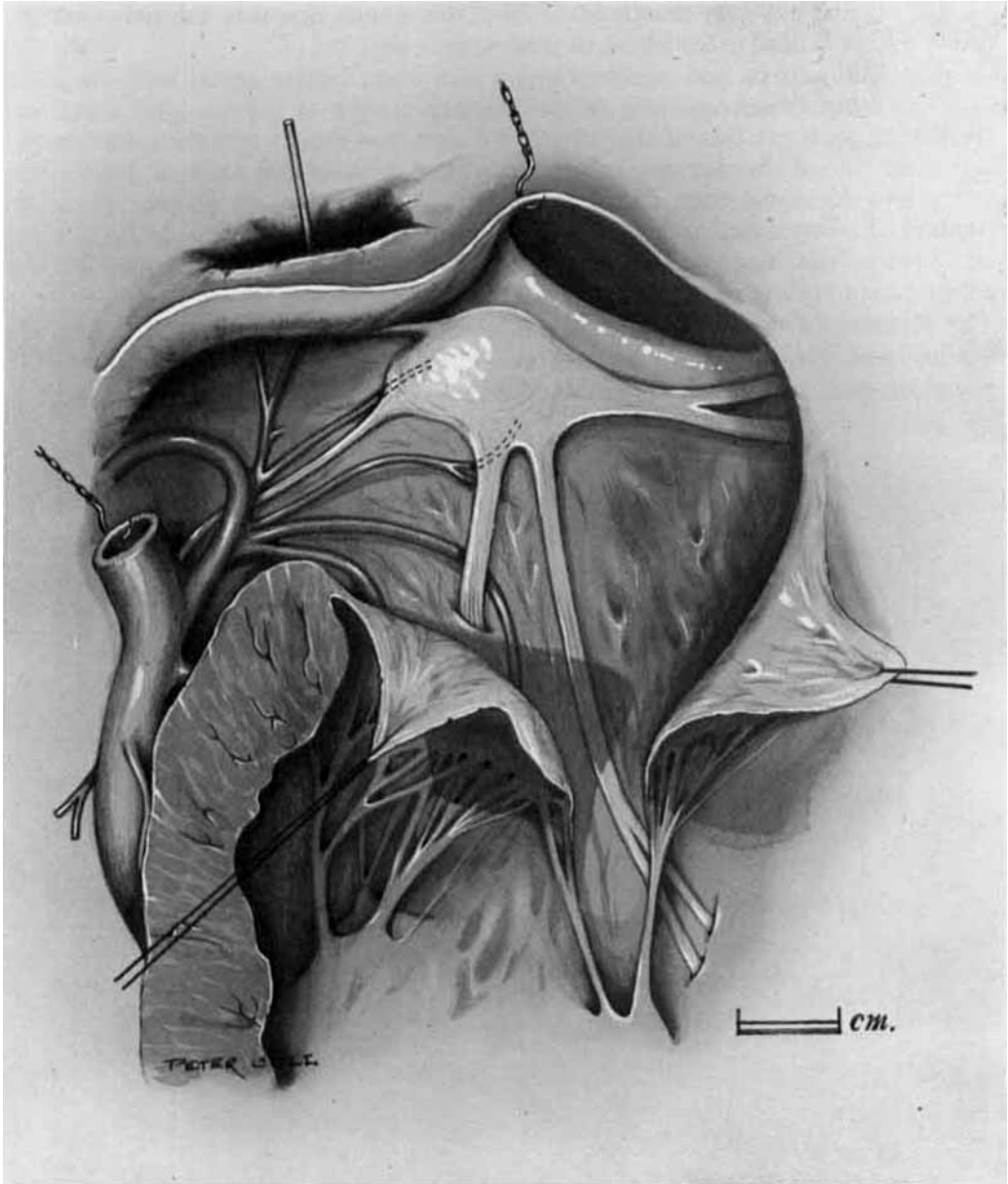


PLATE II. Basal Sumatran rhinoceros. Atrio-ventricular node dissected *in situ*, showing relations, vasculature, Wenckebach bundle and absence of a canonical Kent-His bundle.

The right atrio-ventricular (tricuspid) valve has a conus cusp, situate between the atrio-ventricular ring and the conus arteriosus, a septal cusp, attached above the interventricular septum and a marginal cusp attached to the atrio-ventricular ring opposite the septal cusp. Each cusp receives the insertion of chordae tendineae from more than one source. The site of such insertion includes the attached margins and the undersurfaces of the cusps as well as their free margins.

The atrio-ventricular node occupies the membranous portion of the interventricular septum; under cover of the attached margin of the septal cusp a double ribbon of conducting tissue from the node enters the right ventricle beneath the endocardium and represents the dextral branch of a canonical Kent-His bundle (Plate II).

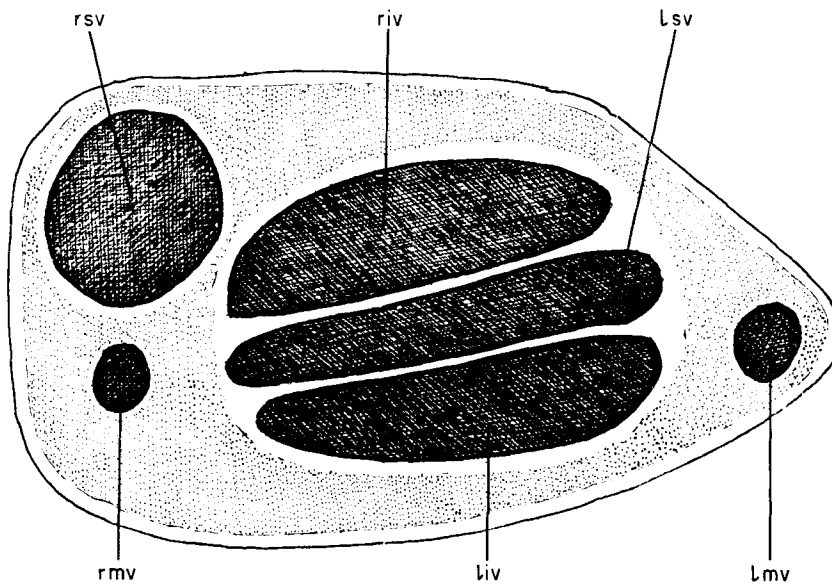


FIG. 5. Basal Sumatran rhinoceros. Left atrium interior showing pulmonary vein ostia. The right superior (rsv) and the right and left minor veins (rmv, lmv) have separate ostia: the right inferior vein (riv) shares a common ostium with the left superior and inferior veins (lsv, liv).

The left atrium

This chamber is somewhat transversely elongate and is formed by the confluence of the distal ends of the pulmonary veins. The cavity of the atrium proper is demarcated by a prominent myocardial ridge (*crista terminalis sinistra*) from the obtuse, ventrally-directed and marginally crenated auricle. The atrium wall is devoid of *musculi pectinati*, which are confined to the auricle wall upon which they radiate from the *crista*.

The pulmonary veins enter the dorsal aspect of the atrium in close mutual proximity, some indeed in a contiguity which compels their respective openings to share a virtually common, if partitioned, ostium (Fig. 5). Bilaterally three pulmonary veins are present—two subequal major vessels and a minor. The large veins are the superior (cranial) and inferior (caudal) pulmonary veins draining the greater part of the ipsilateral lung. The

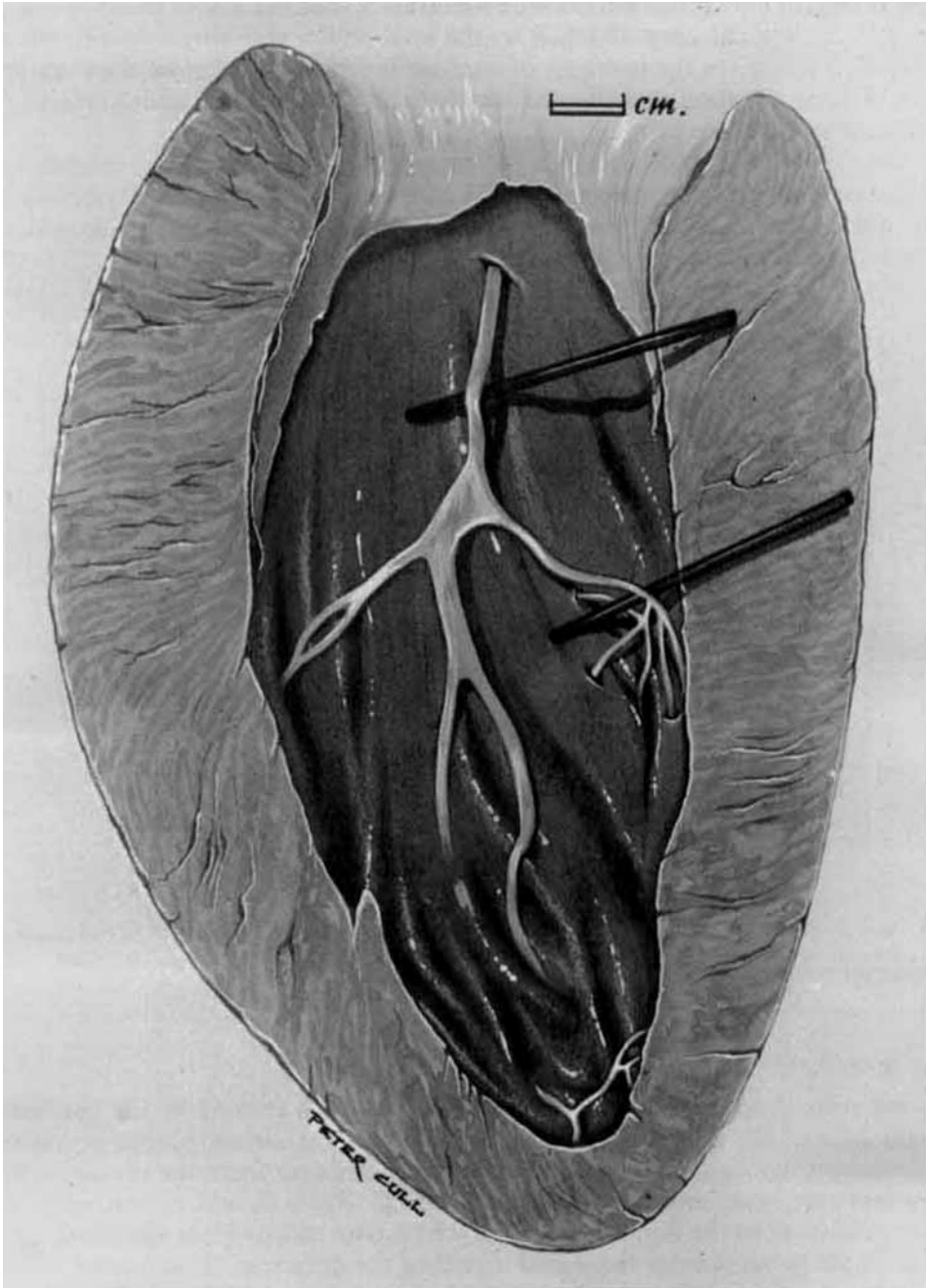


PLATE III. Basel Sumatran rhinoceros. Left ventricle: septal wall showing emergent branching taenia of Purkinje tissue.

dextral smaller vein drains the azgos "lobe" of the right lung; the provenance of the sinsitral smaller vein remains undetermined.

The right superior pulmonary vein and the right and left smaller veins enter the atrium by discrete ostia; the right inferior pulmonary vein shares a common ostium with the left superior and left inferior pulmonary veins.

The left ventricle

This chamber, more ovate than the right ventricle and thrice the wall-thickness thereof, forms the cardiac apex. It presents septal and free walls concave towards its interior. The oval left atrio-ventricular orifice has a mitral valve comprising anterior (ventral, cranial) and posterior (dorsal, caudal) cusps, which give attachment to chordae tendineae by their free margins and undersurfaces. On the chamber walls first- and second-order columnae carnae ("ridges" and "bridges") are minimally developed but third-order columnae ("papillary muscles") maximally so. The bases of many of these papillary muscles are compounded of individual columnae which coalesce to form the definitive conical muscle. From the papillary muscle apices arise independent groups of chordae tendineae, varying in thickness, which divide and insert into the mitral valve cusps. From some of the muscles pale ribbons or strands (taeniae vagae) of Purkinje tissue emerge and remain visible awhile through the endocardium before disappearing into the ventricle parietes. One particularly obtrusive ribbon emerges from the septal wall (Plate III), recalling arrangements frequently observable in the bovine heart.

A single papillary muscle is developed upon the anterior (free) ventricular wall, a multiplicity of muscles upon the posterior (septal) wall. The anterior papillary muscle is

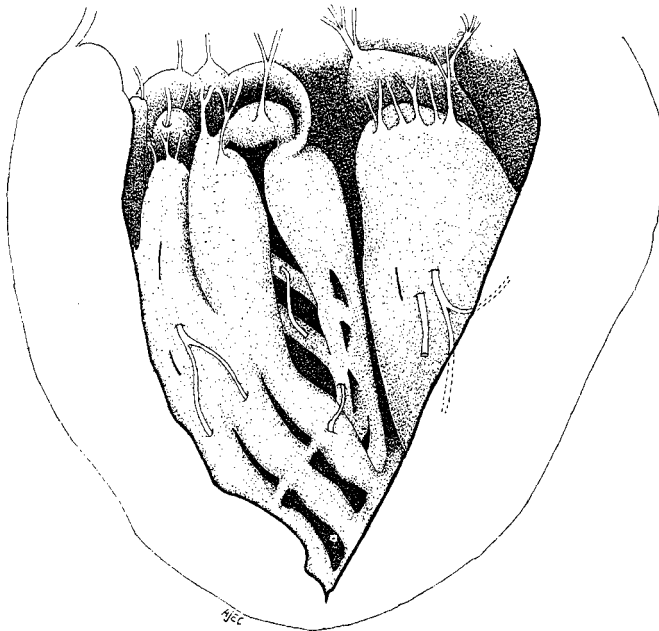


FIG. 6. Basel Sumatran rhinoceros. Left ventricle showing papillary muscles, chordae tendineae and five taeniae vagae of Purkinje tissue.

notably large and discrete, with a sulcated base and an apical set of seven chordae tendineae, two of which are particularly stout and some of which divide before inserting (apparently) into the mitral anterior cusp. From its substance emerge two strands of Purkinje tissue, the thicker of which divides before entering the ventricle wall (Fig. 6).

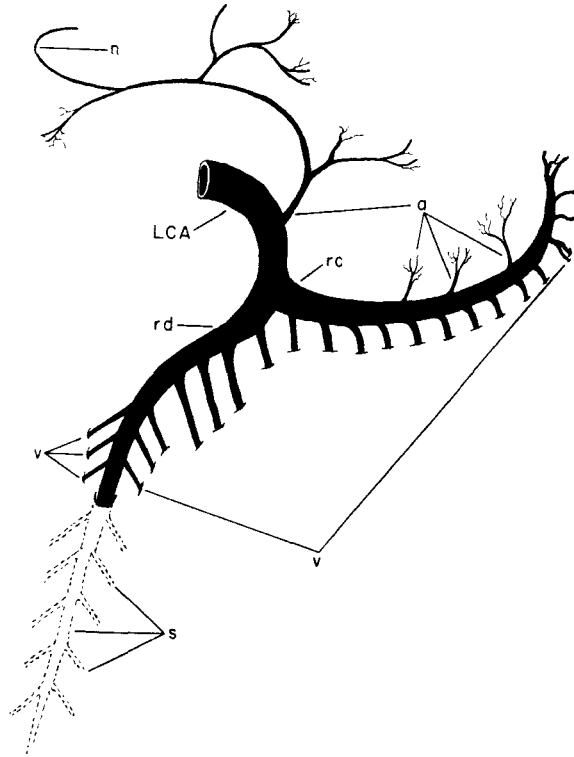


FIG. 7. Basal Sumatran rhinoceros. Distribution of left coronary artery (LCA). Semidiagrammatic: surface vessels black, intramuscular vessels in broken line. a, atrial branches; n, nodal branch; rc, ramus circumflexus; rd, ramus descendens; s, intraseptal branches; v, ventricular branches.

The posterior multiple papillary muscle-formation comprises major dextral and minor sinistral components. Of these the dextral is more readily delineated than described, being a conical mass of composite base subdivided into some seven papillary peaks, each beset with chordae tendineae inserting principally into the posterior mitral cusp (Fig. 6). The sinistral component is a minor, discrete muscle mass arising from the septal wall, bearing two groups of (now damaged) chordae tendineae. The entire posterior papillary formation may be interpreted as a much-divided single muscle of considerable size (the equivalent of the equid single muscle) or, alternatively, on the basis of topographically separate, chorda-bearing, conical masses, as a group of some eight papillary muscles.

The ventricular septal and free walls are connected by "moderator bands" of different thicknesses, composed principally of conducting tissue.

The three semi-lunar cusps of the aortic valve (a cranial and a right and left caudal)

are associated with corresponding aortic (Valsalva) sinuses: each manifests an apical corpus Arantii.

The coronary vasculature

The right coronary artery

The right coronary artery (Fig. 8) arises from the dorsal (cranial) aortic sinus and passes at first dorsally between the pulmonary trunk and right atrium and then dextrally and caudally into the right portion of the coronary sulcus, wherein, overhung by the right auricle, it continues to the cranial end of the right interventricular sulcus. Here it divides into two terminal branches, viz. a larger ramus descendens and a smaller ramus circumflexus. The ramus descendens, the main continuation of the parent vessel, runs caudalwards within the right interventricular sulcus for a short distance, then disappears from the heart surface by sinking into the interventricular septum and continuing therein to its caudal end. The ramus circumflexus, a somewhat sinuous vessel, first loops cranialwards and gives fine branches to the left atrium before entering the left portion of the coronary sulcus, wherein it terminates without anastomozing with the circumflex branch of the left coronary artery.

Recognizable branches of this vessel are:

(a) from the parent artery in the coronary sulcus—(i) a right marginal artery which proceeds caudalwards upon the surface of the right ventricle almost to the cardiac

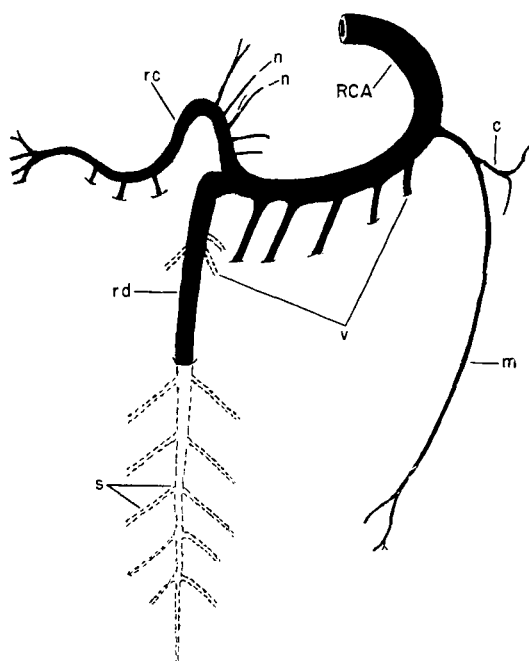


FIG. 8. Basal Sumatran rhinoceros. Distribution of right coronary artery (RCA). Semidiagrammatic: surface vessels black, intramuscular vessels in broken line. c, conus artery; m, marginal artery; n, nodal branches; rc, ramus circumflexus; rd, ramus descendens; s, intraseptal branches; v, ventricular branches.

apex, giving off close to its origin a branch to the wall of the conus arteriosus, (ii) a series of eight or nine ventricular branches which run caudally for some 25 mm on the right ventricle wall and then enter the wall substance;

(b) from the ramus descendens—a cranio-caudal succession of septal branches from its intraseptal portion;

(c) from the ramus circumflexus—(i) a number of small ventricular branches which disappear rapidly into the cranial portion of the right ventricle free wall, (ii) two fine nodal branches to the atrio-ventricular node, (iii) fine branches to the interatrial septum. The vessel appears not to supply the right atrium.

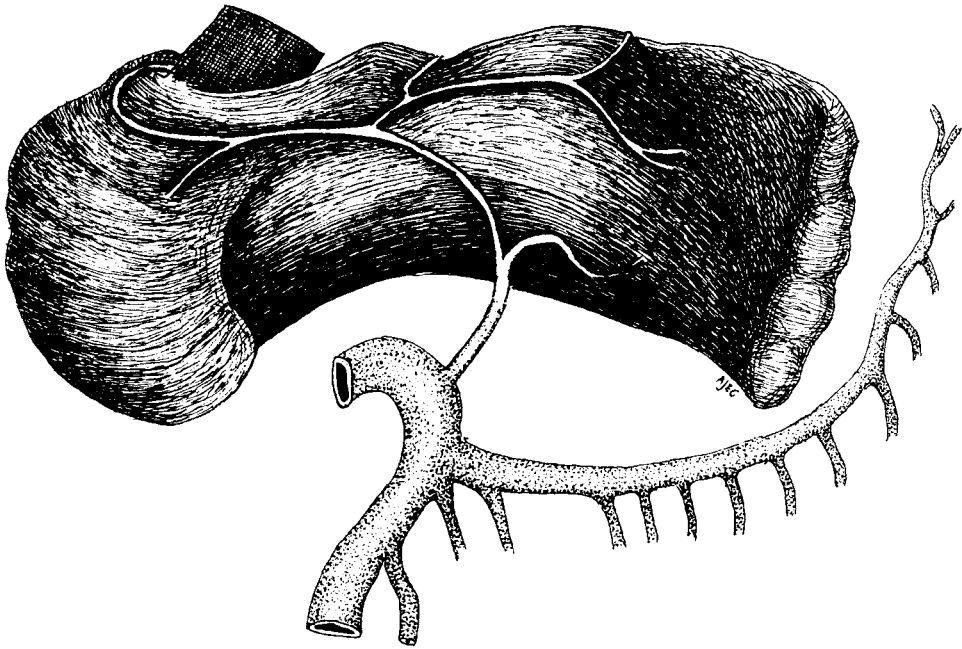


FIG. 9. Basel Sumatran rhinoceros. Oblique ventral view of atria, showing their vascularization from the left coronary artery.

The left coronary artery (Figs 7, 9)

This arises from the left ventral (caudal) aortic sinus and passes between the pulmonary trunk and left atrium to gain the junction of the coronary and left interventricular sulci. Here it divides into a smaller ramus circumflexus and a larger ramus descendens. The ramus circumflexus occupies the left portion of the coronary sulcus and terminates therein by dividing into a number of non-anastomosing twigs near the cranial end of the right interventricular sulcus. The ramus descendens enters the ventral interventricular sulcus and runs therein towards the cardiac apex; short of the apex, however, it leaves the heart surface and enters the caudal portion of the interventricular septum wherein it terminates.

Recognizable branches of this vessel are:

(a) from the parent artery—(i) a long, slender atrial branch which passes dorsal to the

aorta to supply the walls of the right and left atria and which gives (ii) a special nodal branch to the sinu-atrial node;

(b) from the ramus circumflexus—(i) a series of small atrial branches to the left atrium, (ii) a series of some dozen and larger ventricular branches to the right ventricle which runs a short course upon the ventricle free wall before disappearing into its substance;

(c) from the ramus descendens—(i) from its exposed portion, a series of ventricular branches to the contiguous free walls of the two ventricles, (ii) from its intraseptal portion numerous branches to the interventricular septum and the columnae carnae of the two ventricles.

Additional branches of the coronary arteries may well have escaped notice owing to the impracticability of any vascular injection of the specimen.

The coronary veins

These resemble in disposition those of the horse. The capacious coronary sinus is devoid of a Thebesian valve but provided with an ostial sphincter. Sinistrally it receives an oblique vein of Marshall; its other tributaries include a vena magna cordis, ascending to the sinus in the right interventricular and coronary sulci and a vena media cordis accompanying the ramus descendens of the right coronary artery.

The cardiac conducting system

This system, peculiar to the heart of the warm-blooded vertebrate, is responsible for the initiation and propagation of the cardiac contractile impulse and thus controls the rhythmicity of cardiac contraction. In the mammal heart its apparatus comprises (1) a sinu-atrial (Keith-Flack) node, (2) an atrio-ventricular (Tawara) node, (3) an atrio-ventricular (Kent-His) bundle having two primary branches and (4) a ventricular (Tawara) network formed by the repeated subdivision of those branches. The component tissue of the system (Purkinje tissue, conducting tissue) differs histologically and developmentally from the ordinary myocardium in which it is embedded.

Conventional physiological doctrine envisages no atrial counterpart of the Tawara ventricular network nor any direct connexion of the two cardiac nodes by means of Purkinje tissue. After generation at the sinu-atrial node the cardiac contractile impulse is held to reach the atrio-ventricular node through the unspecialized atrial myocardium alone (Davies, 1942; Davies & Francis, 1946). But as indicated below, this conventional view of the internodal transmission of the contractile impulse is challenged by anatomical evidence from a variety of sources, including arrangements found to be present in the present *Didermocerus* heart. For therein the conducting system manifests both an atrial Purkinje tissue network (comparable to the accepted ventricular Tawara network) and a direct internodal connexion by a Wenckebach bundle of Purkinje tissue.

The *Didermocerus* sinu-atrial node (Fig. 10) occupies the canonical mammalian position within the medial aspect of the terminal precava. It is composed of relatively broad, striated Purkinje fibrils disposed in an interlacing network of bundles, accompanied by connective tissue cells, ganglion cells and numerous fine blood vessels. Macroscopically, it is a crescentic mass of irregular outline and somewhat reticular constitution, 23 mm long, distinguishable by its consistency and greyish colour from the cavo-atrial musculature but anchored thereto by peripheral strands. It is continuous with the Purkinje tissue within the crista terminalis and the pectenate muscle fasciculi radiating therefrom.

From its immediate neighbourhood a discrete band (Wenckebach bundle) of conducting tissue crosses the inter-atrial septum to the atrio-ventricular node, recalling the presence of such a bundle in the *Equus* heart (Tagand & Barone, 1956).

The *Didermocerus* atrial walls manifest an intrinsic Purkinje tissue network which permeates the plexiform pectenate musculature exactly as the Tawara network permeates the ventricular columnae carnea. Individual pectenate fasciculi display upon cross section a pale core of what proves histologically to be Purkinje tissue, the core dividing *pari passu* with the containing fasciculus. Such a core is not necessarily central to the fasciculus and is more commonly closer to its endocardial surface; in places it is directly subendocardial in position and is thus visible as a pallid filament for a greater or shorter distance. Filaments of this nature are observable also passing from one fasciculus to another. The slender Wenckebach bundle is an integral part of this atrial Purkinje tissue network.

The *Didermocerus* atrio-ventricular node (Plate II) is canonical in position on the pars membranacea of the interventricular septum. It is a compact greyish mass, of somewhat triangular outline, with an 18 mm long base and a vertical height therefrom of 16 mm. It receives at least two fine nodal branches from the ramus circumflexus of the right coronary artery. Dextro-cranially it receives the Wenckebach bundle which passes to it caudad of the coronary sinus ostium. From its caudal aspect three ribbons of conducting tissue arise, two of which are double strands, representing respectively the primary

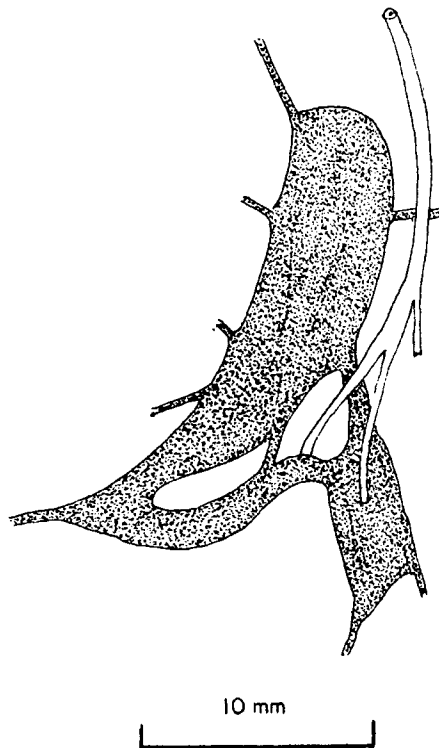


FIG. 10. Basel Sumatran rhinoceros. Sinu-atrial node and (displaced) nodal artery.

dextral and sinistral branches of a Kent–His bundle not developed as an anatomical entity. The first and most dextral ribbon is a narrow flat band passing deep to the nodal arteries on to the right ventricle wall; the second and most caudal is a flat double ribbon (the effective dextral branch of a His bundle) running from the node deep to the septal cusp of the tricuspid valve on to the interventricular septum; the third and most sinistral ribbon is likewise a flat double band (the effective sinistral branch of a His bundle) which runs deep to the tricuspid attachment and through the left atrio-ventricular ring on to the sinistral aspect of the interventricular septum (Plate II). Upon and within the superficial stratum of the septum the double ribbons divide repeatedly to form a typical Tawara network which extends thence into the columnae carnae of the two ventricles. The ventricular distribution of the conducting tissue is enhanced by numerous “moderator bands” uniting the septal and free walls and consisting of Purkinje fibres supported by connective tissue and sometimes also by a minimum of ordinary myocardium.

Since the Tawara network is situated within the juxta-endocardial layer of the ventricular walls, it makes its presence manifest in places in the shape of macroscopically recognizable subendocardial threads and ribbons (*taeniae vagae*) of paler colour (the traditional “false tendons” of the heart) which emerge temporarily from the darker ventricular parietes and remain observable awhile before disappearing into the ventricular musculature. The largest of these subendocardial *taeniae* emerge from the interventricular septum (Plate III).

The absence in the present *Didermocerus* heart of a definitive atrio-ventricular (Kent–His) bundle may be a mere individual anatomical variation rather than a canonical disposition of parts: opinion must remain suspended until arrangements in the Rhinocerotidae in general shall have been determined. In other particulars, however, the conducting system of the Sumatran rhinoceros heart would appear to resemble closely that of the horse, both of these perissodactyl forms manifesting an atrial Purkinje tissue network and an internodal Wenckebach bundle.

Discussion

The present examination of a *Didermocerus* heart amplifies knowledge of rhinoceros cardiac anatomy and provides a first-time description of the rhinoceros cardiac conducting system. Understandably, earlier accounts of the rhinoceros heart (Owen, 1862; Garrod, 1873) made no reference to this system, for although its constituent tissue had already been described by Purkinje (1843) its several morphological features were not identified until much later—the atrio-ventricular bundle by His (1893) and Kent (1893) independently, the atrio-ventricular node and ventricular network by Tawara (1906) and the sinu-atrial node by Keith & Flack (1907).

The present specimen shows the rhinoceros conducting system to be elaborately developed and to conform to the known perissodactyl pattern. The *Didermocerus* sinu-atrial node is structurally similar to that of *Equus*, *Asinus* and *Tapirus* and its emission of Purkinje tissue is closely matched by the equid node which likewise sends strands of such tissue into the precaval and atrial walls (Zimmerman, 1923; Meyling & Borgh, 1957), a Wenckebach bundle to the atrio-ventricular node (Tagone & Barone, 1956) and filaments into a potential subendocardial atrial network. The node’s relationship to the intrinsic atrial Purkinje tissue network is exactly similar to that obtaining between the atrio-ventricular node and the ventricular Tawara network.

The *Didermocerus* atrio-ventricular node is compact like the *Equus* node and thus differs from the *Tapirus* node described by Chiodi & Bortolami (1967) as mesh-like in structure. The absence from the node, in the present specimen, of a definitive Kent-His bundle may well be a mere anatomical variation, since the primary branches of a canonical bundle are duly represented. The *Didermocerus* Tawara network resembles that of *Equus* and *Asinus* in its topographical complexity, and in places becomes macroscopically evident in the form of subendocardial ribbons and filaments (taeniae vagae) of Purkinje tissue. The intimate topographical relationship which exists between the atrial Purkinje tissue network and the musculi pectenati on the one hand, and between the Tawara network and the columnae carnae on the other, suggests that (excluding the valve-controlling papillary muscles) the trabeculation of the myocardium of atria and ventricles alike is primarily designed to ensure a rapid and equable distribution of conducting tissue throughout the heart walls.

Purkinje tissue is more easily identifiable in the ungulate than in the rodent, carnivore or primate heart. Its disposition in the present *Didermocerus* organ is supportive of evidence from other sources challenging the validity of the conventional concept of the mode of internodal transmission of the cardiac contractile impulse, a concept open to criticism on several grounds. Firstly, the conventional view is inconsistent with the admittedly more rapid passage of the contractile impulse through Purkinje tissue than through ordinary myocardium. Secondly, it leaves unexplained the anomalous co-existence of two contrasted modes of impulse conduction in the adjacent and equally contractile atrial and ventricular heart segments, wherein, *a priori*, a uniform mode of conduction is expectable. Thirdly, it fails to explain why internodal impulse-transmission should take place in the mammalian heart through the unspecialized atrial myocardium but in the equally homoiothermal avian heart "through an extensive network of Purkinje tissue" (Davies & Francis, 1946). Fourthly, it attempts no explanation of the functional significance of such Purkinje tissue formations as have been periodically reported in the atrial walls of the mammalian heart.

It is relevant to recall that opinion is by no means unanimous touching the direct continuity of sinu-atrial node tissue and the atrial myocardium, opinions differing among authorities and histological findings varying according to the particular mammalian species investigated. Thus for man such continuity was denied by Wakefield & Chandler (1924) and Walmsley (1929) but vigorously maintained by Blair & Davies (1935). In the non-human heart it was found by Shaner (1929) to obtain in the foetal calf but not in the pig, sheep or camel.

Purkinje tissue has been reported in the atrial walls of man by Todd & Stricht (1919), of man, dog and various ungulates by Glomset & Glomset (1940) and of the horse by Zimmerman (1923), Borgh (1937) and Meyling & Borgh (1957). An internodal pathway of Purkinje tissue has been described for the adult human heart by Thorel (1910), for the 24 mm human embryo by Jones (1932) and for the 22 mm embryo by Gardner & O'Rahilly (1973) and three such pathways of mixed myocardial and Purkinje tissue have been described for the human heart by James (1963). Reviewing the relevant literature Le Gros Clark (1945) commented that, in the large ungulate heart, Purkinje fibres "may be found in the atrial musculature linking-up the sino-atrial and the atrio-ventricular nodes".

Thus evidence is not wanting to suggest, at least, that the anatomical apparatus sub-

serving the propagation of the cardiac contractile impulse may be less standardized in pattern than conventional physiological doctrine might imply. And the evidence provided by the present *Didermocerus* heart indicates that such apparatus might well include both a canonical atrial Purkinje tissue network and a direct internodal pathway of Purkinje tissue. Further it would seem unlikely that such an arrangement of the cardiac conducting system should be confined to the perissodactyls alone among mammals—indeed an internodal Purkinje connexion is observable in the giraffe (Fig. 12).

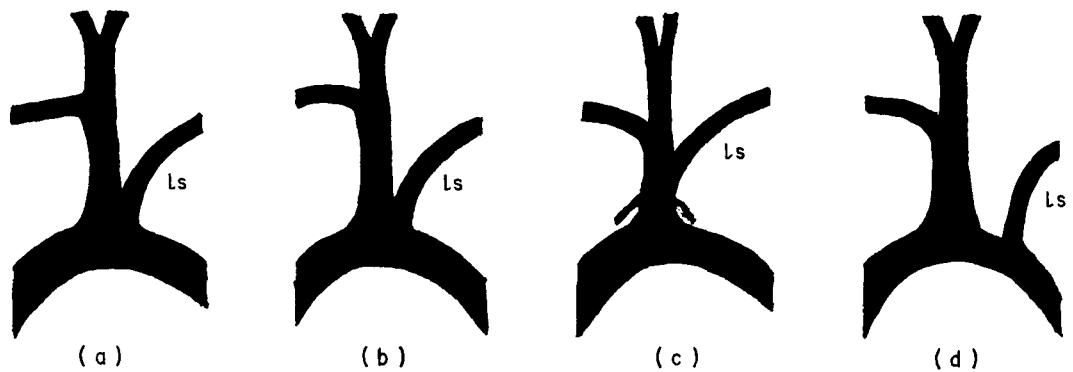


FIG. 11. Pattern of aortic arch vessels in Rhinocerotidae, illustrating variable origin of left subclavian artery (ls). Specimens represented are (a) the Basel Sumatran rhinoceros, (b) Garrod's (1873) Sumatran rhinoceros, (c) Owen's (1862) Indian rhinoceros and (d) Beddard & Treves' (1887) Javan rhinoceros.

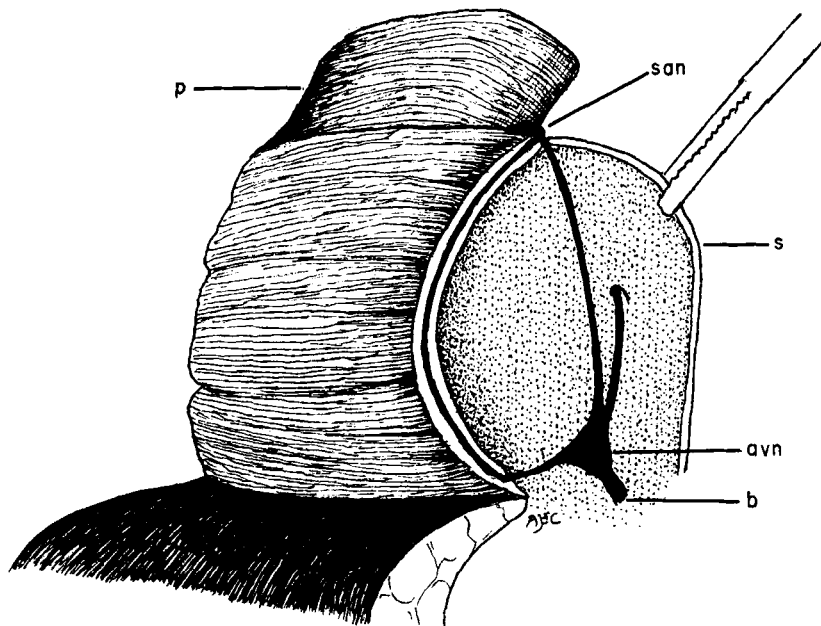


FIG. 12. Giraffe. Dissection sketch showing Purkinje internodal strands. avn, atrio-ventricular node; b, Kent-His bundle; p, precava; s, interatrial septum; san, sinu-atrial node.

The scant available information on rhinoceros cardiac anatomy precludes any detailed comparison of the present *Didermocerus* heart with that of other rhinoceros forms. It is, however, observable that in the Rhinocerotidae the left subclavian artery manifests a not unexpected variability of origin. In the present Sumatran rhinoceros heart it arose almost immediately from the truncus brachiocephalicus communis of the aortic arch, as in Garrod's (1873) specimen: in Owen's (1862) Indian rhinoceros specimen it arose more distally therefrom whilst in Beddard & Treves' (1887) Javan rhinoceros it arose, not from the arch, but from the trunk of the aorta (Fig. 11).

The *Didermocerus* coronary vasculature resembles that of *Equus*. The coronary sinus (as in *Rhinoceros unicornis*, *Ceratotherium simum* and *Diceros bicornis*) receives an oblique vein of Marshall. The left coronary artery supplies the sinu-atrial node, the right coronary artery the atrio-ventricular node. The arrangement of the *Didermocerus* pectenate musculature in the form of a tangle of subdividing and interlacing fascicular arcades is paralleled in the *Ceratotherium* and the *Diceros* heart and in all these three forms the presence of an atrial Purkinje tissue network is indicated macroscopically by observable subendocardial filaments of such tissue.

Summary

Some account is given of the cardiac morphology of a Sumatran rhinoceros including a first-time description of the rhinoceros cardiac conducting system. The atria manifest a Purkinje tissue network related to the sinu-atrial node and the ventricles an obtrusive Tawara network related to the atrio-ventricular node and notable for the presence of taeniae vagae. A Wenckebach bundle connects the two nodes. The primary dextral and sinistral branches of the Kent-His bundle arise directly from the atrio-ventricular node. Such anatomical arrangements suggest that the internodal mode of transmission of the cardiac contractile impulse may be other than that maintained in conventional physiological doctrine. In its general constitution the *Didermocerus* heart resembles that of *Equus* save for a greater complexity of its papillary musculature.

Gratitude is hereby tendered to Dr L. Forcart of the Basel Natural History Museum for the opportunity of studying the organs of a Sumatran rhinoceros and to Dr F. J. Aumonier of St Bartholomew's Hospital Medical College, London, for authoritative opinion on histological preparations made of the heart. The Plates are the work of Mr Peter Cull.

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