

The anatomy of a twenty-two millimetre embryo of the African
Rhinceros (*Rhinceros bicornis*).

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(With Plates I–VI and 6 figures in the text.)

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The rhinoceroses of the Old World tropics are an exceptionally interesting group of odd-toed ungulates which were abundant in Eocene times but are now close to extinction. The embryo was made available to me through the kindness of Dr. W. L. H. Duckworth of the Anatomy School, Cambridge. He has supplied the following short history of it to show how it came into his possession.

HISTORY OF THE EMBRYO.

The embryo was collected in British East Africa by William Francis Cooper, Clare College, Cambridge, who was in residence 1898 to 1901 (B.A. 1901). Dr. Duckworth received the embryo from Mr. Cooper in a glass bottle bearing the label—"Embryo—from uterus of Rhinceros No. 1 shot at Punda Milia, British East Africa. 3.viii.1909. W. F. Cooper". About twelve years ago, after being photographed, it was transferred to paraffin wax for the purpose of obtaining serial sections. The embryo measured 19.3 mm. when first received, but was only 18.4 mm. after prolonged storage in 70 per cent alcohol. Before that time, an opportunity occurred of submitting it, as received, to Dr. Streeter, who was able to comment on the veins of the brain as seen through the delicate cuticle of the region. It was exhibited with the two photographs (Pl. I) at the Cambridge meeting of the Anatomical Society in July 1941. The preparation of serial sections (1,200 in number) was carried out by one of the laboratory technicians, Mr. J. W. Cash.

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The specimen is probably the embryo of the Black Rhinoceros and not of the White Rhinoceros which was threatened with extinction as long ago as 1898.

The study of the embryo reveals features resembling those of the horse and other perissodactyles. It is interesting to note that such distinctive features appear so early in foetal life.

The care bestowed by Mr. Cooper on collecting the specimen is confirmed by the preservation of a considerable part of the embryonic appendages, the microscopic characters of which associate the rhinoceros with the horse while they throw it into contrast with the sheep. W. L. H. D.

INTRODUCTION.

There are several accounts of the external appearance of the rhinoceros, notably those of Parsons (1743), Bell (1795) and Thomas (1801) whose description could not be bettered. Cuvier in his 'Animal Kingdom' (1827) discusses the disputed classification of the large family of rhinoceroses and gives a few details concerning them, especially about the teeth. Daubenton in Buffon's 'Histoire Naturelle' (1754) gives an excellent description of the habits of the animal in the wild state and in captivity. Of especial interest in his account is a brief description of a foetal rhinoceros from Java (p. 204). The foetus was near term and measured about three feet in length. The skin was soft, lacking the armoured plates of the adult animal. Like all early students of the rhinoceros, this author devotes much space to the enigmatical horn, which has been made famous by poets and depicted by artists from Roman times when the strange animal was an occasional spectacle in the amphitheatre. Concerning this horn, Bell writes: "there is nowhere a greater Instance of the Uncertainties that Mankind may be led into from Conjectural Reasoning than in this very Subject of the Rhinoceros's Horn". The horn, and the equally extraordinary penis of the animal, seem so to have occupied the minds of the early writers as to leave little space in their works for a systematic account of other and possibly more interesting details of its internal anatomy.

The only systematic accounts of the visceral anatomy of the rhinoceros are those of Owen (1850) and of Garrod (1873). The specimen of Owen was an Indian Rhinoceros and his masterly description of its anatomy remains the most complete in the literature. Garrod was chiefly concerned with the thoracic and abdominal viscera of the Sumatran Rhinoceros and his account accords well with that of Owen in the Indian form. The anatomy of the animal appears to be that of a typical perissodactyle and resembles that of the horse in many particulars.

There is little information available in the literature about the breeding habits of the rhinoceros and almost none about the character of the foetus and the details of its development. Daubenton, whose passing reference to a full term foetus of the Javanese Rhinoceros has been mentioned, stated that the animal bred at infrequent intervals and that the young were usually single. Bartlett (1873) gave an interesting account of the birth of a Sumatran Rhinoceros and also a tentative estimate of the gestation period. The mother was observed in the act of copulation just before falling into the pit in which she was captured. She gave birth to her calf on the ship seven months later. The little animal was three feet long and two feet high, weighed about fifty pounds and in its general appearance resembled a young ass. It was covered with short crisp black hairs. The hoofs were soft and inflected. Only the anterior of the two horns characteristic of the adult was visible as a small mound about three-quarters of an inch high. The little creature ran about freely within a short time of birth but died in a few days. No study of its anatomy seems to have been undertaken and the placental membranes were not preserved. No bleeding was observed at the time of birth. In his estimate

of the gestation period as seven months Bartlett was almost certainly in error. More recent and reliable statements of the gestation period are contained in Shortridge's book (1934) on the mammals of South West Africa. Quoting various authorities, he gives an average length of gestation of sixteen to eighteen months for both Black and the White Rhinoceroses. He comments on the infrequency of breeding, a second calf never being born until the first is about two-thirds full grown. The mating season in South Africa is apparently from November to December, the calves being born in February or later. It may be of interest to compare the rhinoceros with other ungulates of the same geographical distribution in respect to the gestation period. Thus that of the zebra is twelve months, of the hippopotamus nine to ten months, of the giraffe fourteen to fifteen months, of the wart-hog five months and of the elephant eighteen to twenty-two months. The gestation period of the horse, to which the rhinoceros is related, is about ten months. These figures are as given by Shortridge.

DESCRIPTION OF THE EMBRYO.

After clearing in oil of wintergreen, following many years immersion in alcohol, the embryo measured 18.4 mm. crown-rump length. Allowing for shrinkage, and after due consideration of the general degree of development of the embryo, its length in the fresh state was estimated as 22 to 23 mm. It corresponds fairly closely with a pig embryo of about 23 mm.

The embryo was serially sectioned at $10\ \mu$, a marker being incorporated in the wax block to facilitate reconstruction. The sections were stained with haematoxylin and eosin. The chorionic membrane and a portion of the yolk sac were also sectioned to determine the type of placenta.

External appearance.

The external appearance of the embryo as seen from the front and from the right side shows it to be clearly perissodactyle. The snout is rounded, the eyes are not yet overgrown by the lids. The general appearance corresponds fairly closely to Keibel's figure of a 23 mm. pig, artiodactyle though it be, in his *Normentafel* (1897; *Tafel 2*, no. 29). The most striking difference from the pig is the elongation of the trunk particularly in the thoracic and upper abdominal regions. The prominence of the hind-brain is well marked and this at first was thought to be due to an accidental extrusion of the brain substance. There was no histological evidence for this, however, as was shown by a study of the region after sectioning.

Internal anatomy.

An exhaustive account of every system in the body is clearly neither necessary nor useful and could only be tedious. Only those features are described in detail which seem to be of especial interest or which help to determine the affinities of the specimen.

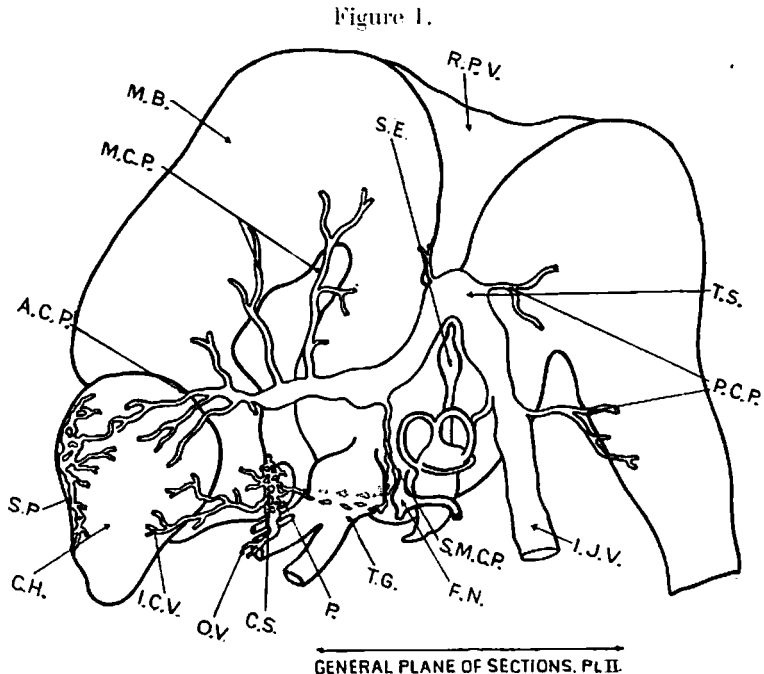
NERVOUS SYSTEM.

The brain and the arrangement of the cranial nerves are sufficiently like those of other mammalian embryos at this stage to merit only a brief description. They closely resemble the conditions in a pig embryo of about 23 mm. The general form of the brain is illustrated in fig. 1, which also shows the arrangement of the dural sinuses. The hemispheres are not remarkable: the cerebellum is represented by a cellular thickening of the rhombic lip of the hindbrain. The choroid plexuses are well differentiated (Pl. II, fig. 3).

The cranial nerves show no unusual features. The ganglion of the trigeminal nerve is large as in all ungulate embryos. The maxillary and the buccal branches of the trigeminal nerve in particular are very large as in the embryos of all forms which have a sensitive snout in the adult. The seventh

nerve and its geniculate ganglion are larger than in comparable human embryos, but not larger than in other ungulate embryos. Owen remarks on the size of the facial nerve, and on the great development of the facial musculature and the buccinator muscle in the Indian Rhinoceros.

The relatively enormous autonomic ganglionic masses associated with the trigeminal nerve and its branches are typical of mammalian embryos at this stage of development. Of these the spheno-palatine mass is especially large and diffuse: into it may be traced the Vidian nerve carrying fibres of the facial nerve (greater superficial petrosal) and of the carotid sympathetic nerves (deep petrosal). The otic ganglionic mass is a large collection of small



Graphic reconstruction of the brain viewed from the left side and including the fifth and seventh cranial nerves, the inner ear and the venous sinuses. $\times 15$.

A.C.P., anterior cerebral plexus; C.H., cerebral hemisphere; C.S., cavernous sinus; F.N., facial nerve; I.C.V., inferior cerebral vein; I.J.V., internal jugular vein; M.B., mid-brain; M.C.P., middle cerebral plexus; O.V., ophthalmic vein; P., pituitary; P.C.P., posterior cerebral plexus; R.P.V., roof plate of fourth ventricle; S.E., saccus endolymphaticus; S.M.C.P., stem of middle cerebral plexus; S.P., sagittal plexus; T.G., trigeminal ganglion; T.S., transverse sinus.

cells between the mandibular nerve anteriorly and the middle ear cavity and Meckel's cartilage posteriorly (Pl. II, fig. 5). Into it may be traced the tympanic branch of the glossopharyngeal (Jacobson's nerve) which lies in its typical position relative to the middle ear cavity. The chorda tympani of the facial nerve may be traced into the mandibular nerve at a lower level and especially into its lingual branch: large submandibular and sublingual ganglionic masses are associated with it. Posterior to the middle ear the facial nerve is connected with the inferior ganglia of the ninth and tenth cranial nerves, both these connections containing conspicuous ganglionic cells of the autonomic type.

Superior and inferior ganglia of the glossopharyngeal and vagus nerves are present. No Frobiep's ganglion was found on the hypoglossal nerve, though it was sought carefully. The nodose ganglion of the vagus nerve and the superior cervical sympathetic ganglion are fused, the two being easily differentiated by the difference in size of the cells. There is thus a vago-sympathetic trunk in the neck region as in most ungulates. The vagus and sympathetic trunks separate at the root of the neck where there is a large inferior cervical ganglion on the neck of the first rib. (Pl. IV, figs. 11 & 12). The sympathetic chain is prolonged into the cranial cavity as a carotid nerve which is in the form of a large and discrete nerve cord unlike the plexiform arrangement found in the sheep and pig and most other mammalian embryos (Pl. II, fig. 4). In addition to its contribution to the Vidian nerve as the deep petrosal nerve, the carotid nerve terminates in relation to small ganglionic masses in the arterial rete mirabile at the base of the skull (Pl. II, fig. 5).

Owen on the Indian Rhinoceros, and Garrod on the Sumatran variety, agreed that the general anatomy and in particular the convolitional pattern of the brain closely resemble that of the horse.

DURAL VENOUS SINUSES.

The dural venous sinuses are described in detail at this point since they are most easily understood in relation to the brain with the development of which they are so closely bound up. They are illustrated in fig. 1 in which the Gasserian ganglion, the facial nerve and the auditory capsule are also indicated. The general terminology follows that of Streeter (1915) whose account of the development of the sinuses in the human embryo is the most complete.

The primary head vein of the mammalian embryo typically begins as the anterior cerebral plexus and passes backwards medial to the trigeminal ganglion. In the interval between the latter and the geniculate ganglion of the facial it receives the stem of the middle cerebral plexus and turns sharply laterally to pass outside the auditory capsule (*vena capitis lateralis*), receives the stem of the posterior cerebral plexus and finally drains into the anterior cardinal or primitive internal jugular vein. A transitory vein medial to the auditory capsule (*vena capitis medialis*) may link the primary head vein and the internal jugular vein. The basic pattern is modified in certain artiodactyles, especially the pig and sheep, by the presence of a large vein lateral to the trigeminal ganglion in addition to the main channel medial to it. The ganglion is thus virtually encircled by a collar of veins continuous caudally with the *vena capitis lateralis*. All these veins are present in sheep and pig embryos of size and general development comparable with the rhinoceros embryo and persist as permanent veins in the adult. The *vena capitis lateralis* is an important vein in the adult of these forms, being one of the main vessels draining the brain, and leaving the skull through a large postglenoid foramen to enter the external jugular vein. It is occasionally present in Man.

In the rhinoceros embryo the remnants of the venous collar around the trigeminal ganglion are readily identified (fig. 1). There is no *vena capitis lateralis* nor any vestige of a vein lateral or medial to the auditory capsule. A slender vein descending between the auditory capsule and the facial ganglion posteriorly and the trigeminal ganglion anteriorly may represent the old stem of the middle cerebral plexus. The three cerebral plexuses no longer drain into the primary head vein or its remnants but into a new and large vessel dorsal to the auditory capsule. This is the future transverse sinus and the stem of the middle cerebral plexus below it may persist as the superior petrosal sinus as in the human embryo (Streeter). The veins of the cerebral hemispheres drain in three directions: upwards into a sagittal plexus (primordium of the superior sagittal plexus), posteriorly into the transverse

sinus and below into a plexus associated with the arterial rete mirabile (cavernous sinus). The latter receives the ophthalmic veins in addition to the inferior cerebral veins and drains posteriorly into the remnant of the primary head vein.

The arrangement of the dural sinuses in the rhinoceros, with the exception of that part of it associated with the arterial rete mirabile, which is a special ungulate feature, strikingly resembles Streeter's Stage 4 in the human embryo of 21 mm. The forebrain plexuses are, of course, destined to undergo considerable change with progressive development of the brain as a whole, and especially of the rapidly expanding hemispheres. In the absence of the vena capitis lateralis at this early stage, and so presumably in the adult, the rhinoceros departs from the general pattern. This vein, which is large in the pig, sheep and cow, is small in the horse. In this respect the rhinoceros resembles more closely the horse, but detailed embryological observations on the latter form are entirely lacking. For this reason, whilst admitting the great differences between the perissodactyles and the artiodactyles, it is necessary to refer to the latter repeatedly, as so little is known of embryos of the former. A study of the skeleton of an African Rhinoceros in the Museum of the Zoology Department in Cambridge confirms the absence of a postglenoid foramen, which, where present, transmits this vein.

ARTERIES OF THE BRAIN.

A brief account of the arterial pattern of the brain in the embryo follows at this point, since it contains some features characteristic of the embryo and adult ungulates. The vessels are diagrammatically illustrated in fig. 2. The arterial pattern does not represent the adult arrangement except in the broadest particulars, since the brain is undergoing rapid expansion and change.

An extensive rete mirabile, supplied by a large internal carotid artery on each side (Pl. II, fig. 5) is present at the base of the brain surrounding the pituitary gland. This is a typical ungulate feature. In this respect, namely the importance of the internal carotid contribution to the rete mirabile, the rhinoceros resembles the pig and differs from the sheep in which the vessel is very small, the rete being supplied by numerous branches of the external carotid artery, chiefly from its maxillary branch. A large discrete carotico-sympathetic nerve accompanies the internal carotid artery and ends in relation to small aggregations of ganglion cells in the rete (Pl. II, fig. 4). Anterior cerebral and ophthalmic arteries are given off from the rete mirabile which supplies the brain as far caudally as the pontine flexure by recurrent branches. These recurrent branches consist of three "diencephalic" arteries; an unpaired median diencephalic and two lateral diencephalic arteries (fig. 2). They appear to supply the diencephalon and mid-brain and fuse posteriorly, forming a single vessel which immediately divides into a terminal vessel on either side. The two terminal vessels supply the developing cerebellum and adjacent parts of the hind-brain. No posterior cerebral nor definite middle cerebral artery can be identified at this stage, the hemispheres not having extended very far posteriorly.

The basilar artery is formed in the usual manner by the two vertebrals which are of moderate size. The branches of the basilar artery are illustrated and tentatively identified in fig. 2.

CARDIOVASCULAR SYSTEM.

Heart.

The heart shows no special features and corresponds in general development with that of a pig embryo of about 23 mm. Right and left venous valves are found guarding the sinu-atrial orifice. Of the inter-atrial septa only the septum primum is developed and there is no indication of the septum secundum in the

Figure 2.

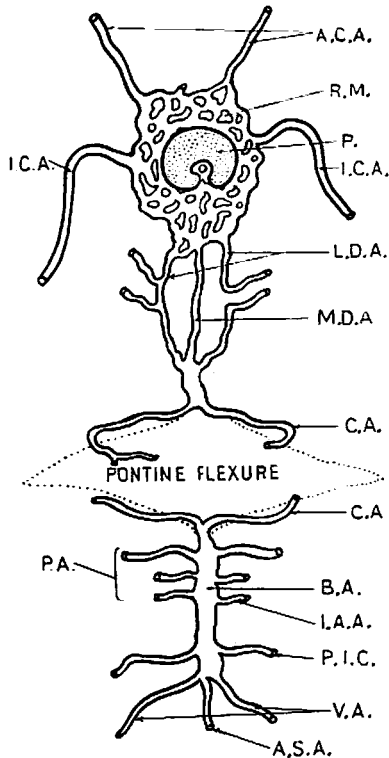


Diagram of the arteries of the brain viewed from the ventral surface. The dotted lines indicate the pontine flexure.

A.C.A., anterior cerebral artery; A.S.A., anterior spinal artery; B.A., basilar artery; C.A., cerebellar arteries; I.A.A., internal auditory artery; I.C.A., internal carotid artery; L.D.A., lateral diencephalic artery; M.D.A., median diencephalic artery; P., pituitary; P.A., pontine arteries; R.M., rete mirabile; V.A., vertebral artery.

intersepto-valvular space dorsally. The coronary sinus and the arrangement of the great veins will be described later.

Pulmonary veins.

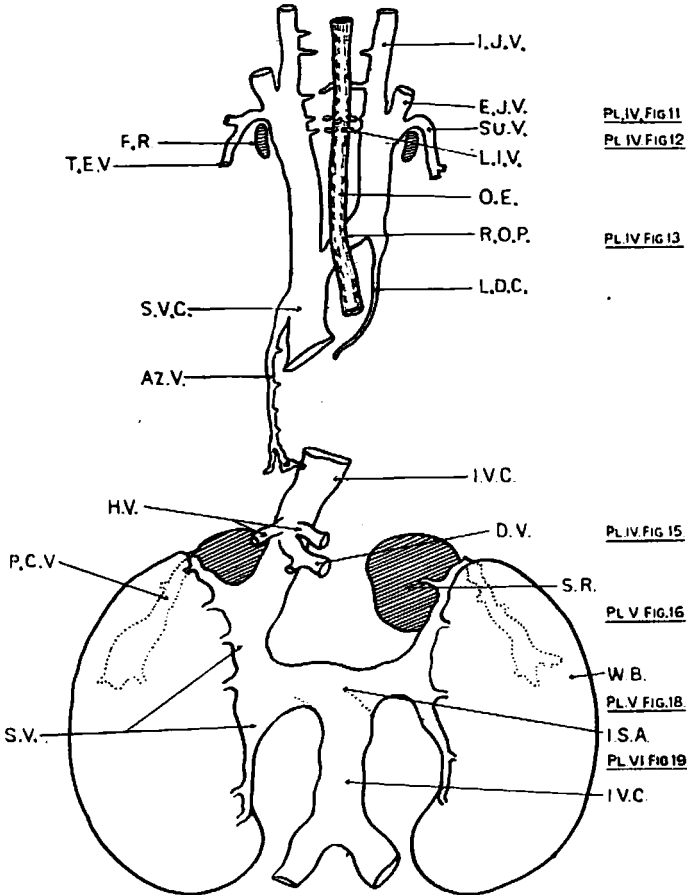
A single large pulmonary vein is present on each side and each opens low down into the left atrium. It leaves the substance of the developing lung where it receives a right and left tributary from each lobe (Pl. IV, fig. 14).

Superior (anterior) vena cava.

The venous system of the embryo is illustrated from a graphic reconstruction in fig. 3. The anterior cardinal or primitive internal jugular veins are prominent structures in the neck as in all mammalian embryos at this stage. Of especial interest are the unusually large jugular lymph sacs associated with them (Pl. III, fig. 8). The anterior cardinal veins are continuous above with the transverse sinuses of the cranial cavity and anastomose frequently in the neck by small veins passing dorsal to the oesophagus, ventral to it, and through the thymic plexuses ventral to the trachea. Several of the thymic veins are beginning to enlarge and foreshadow the left innominate vein (Pl. IV, fig. 11). At the root of the neck the anterior cardinal veins are joined by the external

jugular veins, the subclavian veins and the large thoraco-epigastric or milk-line veins. The lateral compression of the thoracic inlet is very marked as in all perissodactyles, especially the horse. This results in the close proximity of the two anterior cardinal veins at this point and favours the development of

Figure 3.



Graphic reconstruction of the superior and inferior vena caval systems of veins. The oesophagus, suprarenal gland and Wolffian body are also indicated. 125.

AZ.V., azygos vein; D.V., ductus venosus; E.J.V., external jugular vein; F.R., first rib; H.V., hepatic veins; I.J.V., internal jugular vein; I.S.A., inter-subcardinal anastomosis; I.V.C., inferior vena cava; L.D.C., left duct of Cuvier; L.I.V., left innominate vein; O.E., oesophagus; P.C.V., posterior cardinal vein; R.O.P., retro-oesophageal part of left anterior cardinal vein; S.U.V., subclavian vein; S.R., suprarenal; S.V., subcardinal vein; S.V.C., superior vena cava; T.E.V., thoraco-epigastric vein; W.B., Wolffian body.

Photographs at the levels indicated are to be found in the succeeding plates.

anastomoses between them (Pl. IV, figs. 11 & 12). These great veins are also more dorsally situated with respect to the oesophagus than in the pig embryo.

The arrangement of the anterior cardinal veins in the thorax is very unusual and deserves special note. At the level of the fourth thoracic vertebra,

the left anterior cardinal turns to the right and after passing *dorsal* to the oesophagus quickly fuses with the right anterior cardinal vein to form with it the superior vena cava (fig. 3 and Pl. IV, fig. 13). A small vein detaches itself from the parent vessel and continues the original course of the left anterior cardinal vein behind the pericardium to open low down into the right atrium close to the point of entry of the inferior vena cava. It is tentatively called the left duct of Cuvier in fig. 3 and Pl. IV, fig. 13, and probably becomes the oblique vein of Marshall and the coronary sinus of the adult. The portion of the left cardinal vein which passes behind the oesophagus is here termed the retro-oesophageal part of the left anterior cardinal vein since in the writer's experience it has no counterpart in any other mammalian embryo. It is not to be confused with the left innominate vein, which is in process of formation at a higher level and in the position typical of this vessel in all known mammalian embryos. It evidently represents an enlargement of a retro-oesophageal anastomosis between the two cardinal veins. The compression of the thoracic inlet and the resulting proximity of the veins has already been shown to favour this. It is impossible to say whether this unusual vein persists in the adult. Owen does not mention it in the Indian Rhinoceros though his account of the arrangement of the internal jugular veins is interesting. He writes (p. 46): "the upper part of the superior vena cava receives the two large jugular veins close together, so that a proper vena innominata can scarcely be said to exist". It is not easy to envisage the vessels described by Owen, whose account of the great veins is vague in other particulars. He states also that there was no distinct coronary sinus in the rhinoceros he studied.

The azygos vein is right-sided in the rhinoceros embryo as in the pig and the horse. It is left-sided in the sheep and the cow. Owen states that it is right-sided in the Indian Rhinoceros. The vein represents the posterior cardinal vein at least at its cranial end where it opens into the superior vena cava: it ceases to be a discrete vein opposite the tenth thoracic vertebra and here merges with an extensive prevertebral plexus lying between the two sympathetic chains. In this part it is confluent if not identical, with the prevertebral plexus described by Sabin (1915) in the pig and with the supracardinal or perisymphatic plexus described by Huntington & McClure (1920) in the cat.

In the rhinoceros the relationship of the posterior cardinal vein to the cranial tip of the Wolffian body is quite different from that in the pig. In the latter at this stage there are two veins on either side of the thorax, one medial to the sympathetic chain (supracardinal), the other ventral or ventromedial to the chain (posterior cardinal) and continuous with a large vein embedded in the dorsal part of the mesonephros. The continuity of the thoracic and Wolffian portions of the posterior cardinal veins is clearly demonstrated by Sabin (1915) in pig embryos as long as 28 mm. In the rhinoceros embryo there is no continuity between the venous system of the dorsal thoracic wall and that of the mesonephros, a caudal extension of the pleural cavities intervening (Pl. V, fig. 15). The reason for this difference seems to lie in the smaller size of the Wolffian body in the rhinoceros and in its lack of significant extension into the thorax as in the pig. In the latter the extension of the primitive pleural cavities takes place entirely ventral to the anterior end of the mesonephros, thus allowing continuity of the thoracic and mesonephric portions of the posterior cardinal vein. In the rhinoceros the extension of the pleural cavities passes dorsal to the anterior end of the mesonephros which is accordingly carried on to the pleuro-peritoneal membrane or primitive diaphragm. Continuity of the two segments of the posterior cardinal vein is thus impossible. This is probably the case for all mammalian embryos in which the mesonephros extends for only a moderate distance into the dorsal wall of the thorax and not for a considerable distance as in the pig.

Posterior (inferior) vena cava.

The inferior vena cava is illustrated in fig. 3 and sections across the embryo at the levels indicated in this figure are found in the Plates and will serve to indicate the relations of the great vessels at successive points in its course.

The thoracic part of the inferior vena cava is long as in many quadrupedal mammalia and possesses a pleural mesentery. It opens into the heart between the lower portions of the right and left venous valves. Owen states that there is no valve of the inferior vena cava in the adult Indian Rhinoceros. After piercing the diaphragm, the vein enters the liver and almost immediately receives a large hepatic vein on each side and the ductus venosus ventrally (Pl. V, fig. 15). The latter is more horizontally disposed than in the pig embryo in which it inclines upwards at an acute angle from the umbilicus to the liver. It receives at least one large hepatic vein within the liver. This fact, supported by the statements of Owen and of Garrod that there are three large hepatic veins in the rhinoceros, suggests that the ductus venosus may persist in its proximal part as a third hepatic vein instead of becoming wholly reduced to a fibrous vestige as in man.

Below the liver the inferior vena cava ("subhepatic segment") inclines dorsally and to the right to become continuous with the great intersubcardinal anastomosis. Here the aorta is virtually surrounded by veins forming the familiar renal collar (Huntington & McClure, 1920) (Pl. V, fig. 18). Into this renal collar drain the two subcardinal veins, the dorsal veins of the Wolffian bodies, the suprarenal, the renal and testicular veins. From this point, which represents the subcardinal segment of the inferior vena cava, the great vessel is continued dorsally and takes up its position in front of the vertebral column and between the two sympathetic chains. In this part of its course to the point where it is joined by the common iliac veins, the inferior vena cava forms a large median vessel still showing, however, evidence of a bilateral origin (Pl. VI, fig. 19). This is the postrenal or supracardinal segment of the inferior vena cava which is bilateral in the pig embryo, at least as late as the 28 mm. stage (Sabin, 1915).

Thus in the rhinoceros embryo the development of the inferior vena cava seems to conform to a generalized mammalian pattern.

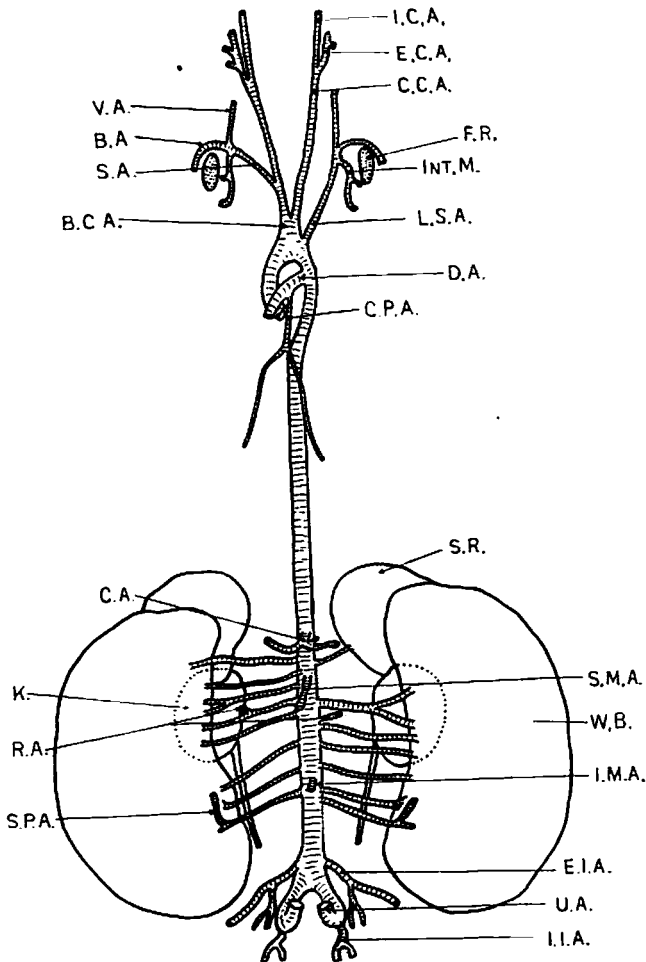
Portal vein.

This is formed by the union of the splenic and superior mesenteric (vitelline) veins below the pancreas. The latter vein in turn receives the inferior mesenteric vein at a lower level. The relations of the portal vein to the dorsal and ventral components of the pancreas and to the lesser omentum are typically mammalian (Pl. V, fig. 16).

Arterial system.

The main details of this system, which is characteristically ungulate, are illustrated in fig. 4. The high aortic arch and the arrangement of the great vessels are typical of perissodaactyles and reflect the marked lateral compression of the thoracic inlet. Thus two vessels arise from the aortic arch, a large brachiocephalic and a small left subclavian artery. The brachiocephalic artery then divides into an innominate and a left common carotid artery (fig. 4). This differs slightly from the arrangement described by Garrod and Owen in the adult rhinoceros. In both the Sumatran and the Indian forms a single vessel arises from the aortic arch, namely the brachiocephalic trunk which in turn divides into the right and left subclavian arteries and a bicarotid trunk. The latter divides into the two common carotid arteries. The arrangement is typical of most quadrupeds and is readily derived from the condition present in this embryo by a migration of the left subclavian artery on to the brachiocephalic artery and by a minor rearrangement of the other vessels.

Figure 4.



Graphic reconstruction of the arterial system. The first rib, suprarenal gland, Wolffian body and kidney are also indicated. $\times 12.5$.

B.A., brachial artery; B.C.A., brachio-cephalic artery; C.A., coeliac artery; C.C.A., common carotid artery; C.P.A., common pulmonary artery; D.A., ductus arteriosus; E.C.A., external carotid artery; E.I.A., external iliac artery; F.R., first rib; I.C.A., internal carotid artery; I.I.A., internal iliac artery; I.M.A., inferior mesenteric artery; INT.M., internal mammary artery; K., kidney; L.S.A., left subclavian artery; R.A., renal artery; S.A., subclavian artery; S.M.A., superior mesenteric artery; SP.A., spermatic artery; S.R., suprarenal gland; U.A., umbilical artery; V.A., vertebral artery; W.B., Wolffian body.

Such a process is common in embryonic development as may be seen in sheep and pig embryos.

The internal carotid artery is large and supplies the rete mirabile; the external carotid artery is small and makes no contribution to the rete. A single small pulmonary trunk arises from the under side of the ductus arteriosus and after a short course divides into the right and left pulmonary arteries. This differs from the arrangement in man and is typical of ungulate embryos. The

abdominal branches of the aorta are the typical coeliac, superior and inferior mesenteric arteries which have the distribution common to other mammalian forms. The lumbar arteries arise on each side as separate branches from the aorta and not as Y-shaped vessels as in the pig, where the abdominal aorta is more ventrally situated relative to the vertebral column. The arteries to the Wolffian body number about eight on each side and resemble those of a pig embryo of 20 to 28 mm. (Hill, 1907). The more cranial ones pass dorsal to or through the developing suprarenal body and doubtless supply it. A small renal artery is present on each side, as a branch of the fourth mesonephric artery on the right side and as an independent branch of the aorta on the left side. The stroma of the metanephros is accordingly vascularized early, though there are no functional glomeruli at this stage. A spermatic artery is present on each side and is a recurrent branch of the last mesonephric artery. It approaches the gonad (testis) from below and ramifies on the anterior surface of the tunica albuginea, an arrangement typical of mammalian embryos of the male sex. The remaining branches of the abdominal aorta are not remarkable. They include the external and internal iliac arteries and the large umbilical arteries. The umbilical cord contains two arteries and one umbilical vein (left) as in man.

Respiratory system.

A detailed account of the system will not be given since it contains no features of unusual interest. A general impression of the stage of development reached by the nasal and laryngeal regions and also of the trachea and lungs may be obtained from the illustrations.

ALIMENTARY SYSTEM.

No information could be obtained about the teeth and dental formula at this stage since only the primary dental lamina was differentiated. This information would have been welcome since the teeth of the rhinoceros show considerable variations. Thus the incisors may be absent, or number four in each jaw, or four including two degenerate teeth laterally. The canines are invariably absent and the cheek teeth vary from six to seven (Cuvier, 1827).

Of the salivary glands the submandibular gland alone is differentiated and consists of a short tube opening into the floor on the mouth lateral to the tongue and dividing posteriorly into a few solid acini.

The oesophagus shows a well-developed musculature and a well-marked lumen except at the lower end where there is a tendency to occlusion and epithelial vacuolization (Pl. III, fig. 9; Pl. V, fig. 15). The stomach is simple and lined throughout by an even glandular epithelium. Garrod (1898) states that the cardiac portion of the stomach is lined by squamous epithelium in all perissodactyles. Owen states that the stomach in the Indian Rhinoceros is simple and resembles that of a horse. Garrod, however, describes a curious cardiac diverticulum in the Sumatran form, the stomach being simple in other respects. The rest of the intestinal tract presents nothing of note. The umbilical hernia is not entirely reduced, a few coils still remaining outside the umbilical opening.

The liver and the manner of its lobulation are illustrated in Pl. V, figs. 15 & 16. It appears to conform in general with Garrod's account of the liver in the Sumatran Rhinoceros in which the following lobes were recognized: right lateral lobe, right central lobe, left central lobe, left lateral lobe and a definite caudate or Spigelian lobe. The gall-bladder is absent, as in the rhinoceroses described by Owen and Garrod.

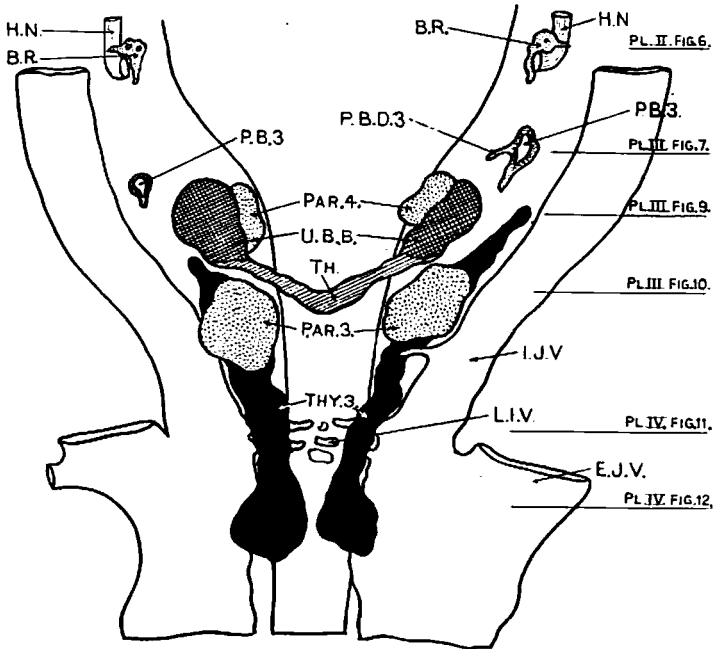
Nothing noteworthy is seen in the spleen, the dorsal and ventral pancreas or in the bursa omentalis (Pl. V, fig. 16).

THYROID, PARATHYROID AND THYMUS.

These derivatives of the embryonic pharynx, which show marked variation from one species to another, are of especial interest in the rhinoceros embryo. They are illustrated from a graphic reconstruction in fig. 5 and are compared in fig. 6 with the conditions found in a pig embryo of 21.5 mm. reconstructed to the same scale.

The researches, notably of Katschenko (1887) and more recently of Badertscher (1914-15, 1918), have revealed a characteristic relationship between the developing thymus and the hypoglossal nerve in certain ungulates.

Figure 5.



Graphic reconstruction of the pharynx and related structures showing especially the thyroid, parathyroids, thymus, ultimo-branchial body and certain vestiges of doubtful significance. 38.

B.R., remnant of a branchial pouch (3rd ?) or of a cervical sinus; E.J.V., external jugular vein; H.N., hypoglossal nerve; I.J.V., internal jugular vein; L.I.V., left innominate vein; P.B.3, remnant of third branchial pouch (?); PAR.3, parathyroid 3; PAR.4, parathyroid 4; P.B.D.3, remnant of ductus pharyngo-branchialis 3; TH., thyroid; THY.3, thymus 3; U.B.B., ultimo-branchial body.

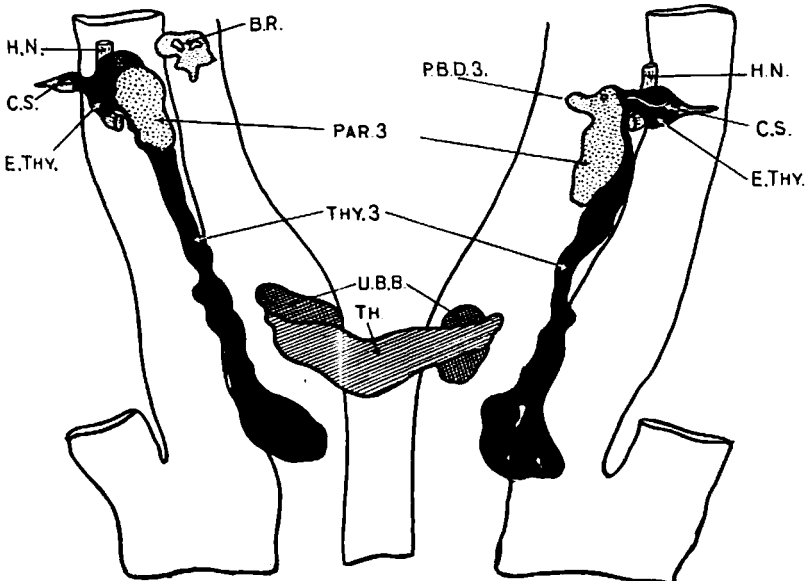
Photographs at the levels indicated are to be found in the succeeding plates.

in particular the pig. In this form, a portion of the thymus appears to be developed from the cervical sinus (or vesicle) of His and is therefore of ectodermal origin, the so-called "thymus superficialis of Katschenko" or ecto-thymus. It is fused with the endodermal thymus, derived from the third pharyngeal pouch by a connecting strand of thymic tissue which forms a loop across the hypoglossal nerve (fig. 6). This characteristic relationship is readily explained by the forward migration of the hypoglossal nerve and its associated somatic musculature and their subsequent arrest at the point of fusion between the ecto-thymus and the endodermal thymus of the third pouch. This connecting strand may persist in the pig until birth or later and accounts for the relatively high position of the thymus in the neck of this animal at birth

(Badertscher). Careful study of the region of the hypoglossal nerve was made in the rhinoceros, since in this area remnants of the cervical sinus and ecto-thymus may reasonably be expected to persist.

No part of the thymus is found in the rhinoceros in relation to the hypoglossal nerve (fig. 5). A small whorl of cells containing a suggestion of a lumen is, however, present on each side and may represent a remnant of the cervical sinus or vesicle (Pl. II, fig. 6). Some distance caudal to this is a well-defined vesicle related to the thyroid cartilage and to the loop of the superior laryngeal nerve (fig. 5; Pl. III, fig. 7). A slender cellular cord connects the vesicle to the perichondrium of the thyroid cartilage and may represent the remains of a pharyngo-branchial duct, suggesting that the vesicle may be a remnant of the third pharyngeal pouch. Such vestiges are commonly found in the neighbourhood of the larynx in a large variety of mammalian embryos.

Figure 6.



Graphic reconstruction of the pharyngeal derivatives in a pig of 21.5 mm. at the same magnification as fig. 5 and for comparison with this figure. Note the absence of parathyroid 4.

B.R., remnant of branchial pouch, probably 3rd; C.S., remains of cervical sinus and of cervical duct; E.THY., ectodermal thymus; H.N., hypoglossal nerve; PAR.3, parathyroid 3; P.B.D.3., remnant of ductus pharyngo-branchialis 3 (?); TH., thyroid; THY.3, thymus; U.B.B., ultimo-branchial body.

Thymus.

A thymus superficialis, as found in the pig embryo, is not present in the rhinoceros embryo. The thymus begins as an insignificant cord ventrolateral to the common carotid artery and at the level of the large ultimo-branchial body (Pl. III, fig. 9). It extends from this point throughout the neck as an irregular swollen cord, showing occasional vacuoles suggestive of a lumen, to end at the thoracic inlet and dorsal to the upper extremity of the pericardial cavity (Pl. IV, figs. 11 & 12).

Parathyroids.

The parathyroids are two in number, an upper parathyroid (parathyroid 4) fused with the ultimo-branchial body (Pl. III, fig. 9) and an inferior parathyroid

(parathyroid 3) fused with the thymic cord some distance below its upper end (Pl. III, fig. 10). Histologically they are easily distinguished from the thymus by their system of anastomosing epithelial cords enclosing islands of vascular mesoderm.

Only one parathyroid (parathyroid 3) is generally found in the pig embryo (fig. 6).

Professor F. Wood Jones, of the Hunterian Museum of the Royal College of Surgeons has supplied the following historical note :

" In February, 1850, Richard Owen gave his paper ' On the Anatomy of the Indian Rhinoceros '. The animal had died in the London Zoological Gardens and some of Owen's dissections were incorporated in the Hunterian Museum.

The specimen shown is a dissection of the larynx, on the left side of which the thyroid gland is exposed. Of the thyroid gland Owen observed (Trans. Zool. Soc. Lond. vol. iv, p. 48) : ' The structure of this body is more distinctly lobular than is usually seen : *a small compact yellow glandular body was attached to the thyroid at the place where the veins emerge* '.

This is the earliest reference to the existence of the parathyroid glands, which remained otherwise unrecognized and unnamed until Sandström's work was published in 1880. Owen apparently made no further investigations into the nature of these bodies, but his recognition of their existence antedates the usually accepted time of their discovery by 30 years."

Ultimo-branchial body.

The ultimo-branchial body is a conspicuous structure in the rhinoceros as in all ungulate embryos (Pl. III, fig. 9). Its densely staining cells and irregular lumen are very characteristic. It is fused with the superior parathyroid (parathyroid 4) and is continuous below with the thyroid gland (fig. 5).

Thyroid.

The thyroid is small in the rhinoceros embryo (fig. 5 and Pl. III, fig. 10). Owen comments on the small size of the thyroid isthmus in the adult rhinoceros. In this respect the rhinoceros resembles the horse, in which the isthmus is often little more than a fibrous cord across the trachea.

The rhinoceros embryo thus resembles other ungulate embryos in the large size of the ultimo-branchial body. It differs markedly from the pig in the absence of thymic tissue derived from the cervical sinus and in the absence of a connecting loop over the hypoglossal nerve. It differs from the pig in having two parathyroids on either side, derived in all probability from the third and fourth endodermal pharyngeal pouches, in which respect it more closely resembles the sheep. According to Verdun (1898, quoted by Maurer, 1906) parathyroids are developed from the third and fourth pouches in the rabbit, bat, cat, horse, deer, camel and man ; from the third pouches alone in the pig, guinea pig, rat, mouse, mole, goat, seal and hedgehog. Verdun's illustrations of the pharyngeal derivatives in the embryos of rabbit and man show an arrangement almost identical with that in the rhinoceros embryo. Sisson's account of the parathyroids in the horse is too vague to permit a proper comparison with the rhinoceros, to which it is perhaps most nearly related.

UROGENITAL SYSTEM.

The mesonephros is very large and in the mid-abdominal region its general appearance strongly resembles that of the pig (Pl. VI, fig. 19). It is degenerating cranially and is in relation at this point with the pleuro-peritoneal membrane or primitive diaphragm (Pl. V, fig. 16) and separated from the dorsal body

wall by a caudal extension of the pleural cavity. The size and extent of the Wolffian body in the rhinoceros embryo seems to be about midway between that of the pig and that of the sheep. A pig embryo of 23 mm. showed no significant degeneration cranially, whereas in a sheep of this size degeneration is at least as extensive as in the rhinoceros embryo. In all other respects the mesonephros of this embryo is similar to that of the pig but differs fundamentally from that of the sheep and other ruminants in lacking a glomerular complex in its cranial third which is wholly characteristic of these forms (Davies & Davies, 1950). A count of the degenerating glomeruli and of the number of tubules leaving the capsules of the highly complicated and irregular Malpighian bodies caudal to the degenerating area, gives an approximate number of fifty nephrons, of which the cranial eight to ten are degenerate. This number of nephrons is typical of the ungulate mesonephros and is slightly less than the total number (seventy) found in the embryos of the pig and the sheep when the organ is at the height of its development. In the arrangement of the glomeruli, their large size and degree of fusion and in the complexity of the tubules, the mesonephros of the rhinoceros closely resembles that of the pig. The tubules show the usual secreting and collecting segments, the former lined with a columnar epithelium which is deeply eosinophilic and presents a swollen surface towards the lumen, and the latter lined with a cuboidal epithelium which stains more darkly with haematoxylin and is more regular. The lumen, especially in its secretory portion, and the capsular cavities of the Malpighian bodies also are filled with eosinophilic, protein-like debris. One of the tubules on the left side (Pl. V, figs. 16 & 17) shows an unusual metaplasia which is unique in the writer's experience. The lining epithelium is altered to a stratified (transitional?) epithelium accompanied by extensive desquamation of cells into the lumen. The metaplasia involves only the collecting segment of the tubule and ceases abruptly at its opening into the Wolffian duct. It does not seem to represent a degenerative change, since the affected tubule is situated in the middle of the mesonephros a considerable distance caudal to the area of degeneration which is proceeding in a strictly cranio-caudal sequence.

The Wolffian duct shows no unusual features and opens in the usual manner into the dorsal wall of the urogenital sinus where the lining epithelium changes abruptly (Pl. VI, fig. 20). The Müllerian duct stretches almost horizontally across the degenerating cranial end of the Wolffian body and opens by a single small ostium close to the pleuro-peritoneal membrane. There are no accessory ostia. The duct passes caudally and ventral to the Wolffian duct to about the middle of the mesonephros where it loses its lumen and quickly ends as a solid cord having no connection with the urogenital sinus.

The general appearance of the metanephros is illustrated in Pl. V, fig. 18 and resembles that of other ungulate embryos at this stage. The ureter opens caudally into the urogenital sinus (Pl. VI, fig. 20), independently of the Wolffian duct. At its cranial end it enters the renal hilum, which is medially placed, and divides there into an ascending and a descending tubule. The descending tubule on the left side may be seen in Pl. V, fig. 18. These tubules may be considered the primary divisions of the ureter and each in turn divides into secondary and tertiary tubules or collecting ducts. Developing glomeruli and nephrons are found only in relation to the tertiary collecting tubules and form a single row peripherally in the metanephros. The glomeruli are rudimentary, though the renal artery and vein are present and the stroma of the kidney is very vascular. It is difficult to determine how far this arrangement of the metanephros in the rhinoceros embryo foreshadows the rather unusual arrangement of the calyx system in the adult. It does not appear to differ markedly from that to be found in any ungulate embryo at this stage, but in the latter considerable modification of the embryonic pattern, involving

absorption of the early generations of collecting ducts, occurs during later development. Owen remarks on the peculiar arrangement of the calyces in the adult Indian rhinoceros. The ureter divides within the kidney into an ascending and a descending duct which together form a narrow duct-like pelvis running the full length of the kidney. The collecting tubules open in clusters into this channel along its length and without the formation of papillae. This arrangement, which differs fundamentally from that found in the pig, sheep, cow and other mammals, is not, however, a unique feature of the rhinoceros but is found also in the horse (Sisson, 1935). The kidney is lobulated in the adult rhinoceros (Owen, Garrod).

The suprarenal gland shows no distinctive features at this stage.

The gonad is sufficiently differentiated to allow its identification as a testis (Pl. V, figs. 16 & 18). Thus there is a well-developed tunica albuginea and a system of primordial seminiferous tubules embedded in a richly cellular stroma. The seminiferous tubules consist of deeply eosinophilic syncytial cords converging on a dark cellular mass which is the so-called rete blastema. The latter shows no formation of rete tubules and extends deeply into the upper end of the mesonephros as a series of cellular strands. They are here intimately related to the capsules of the degenerating Malpighian bodies of the mesonephros through which they are destined at a later stage to establish the continuity of the rete with the remnants of the mesonephric tubules. In all these features the rhinoceros embryo is typical of all mammalian embryos. The degenerative changes in the mesonephric units preparatory to the urogenital union are characteristic and consist of fibrosis of the Malpighian bodies, metaplasia of their capsules to a cuboidal epithelium, and shrinkage and fragmentation of the associated tubules (Pl. V, fig. 15).

The appearance of the phallic tubercle and related parts is illustrated in Pl. VI, figs. 21 & 22. A cellular outgrowth from the urethral plate (Pl. VI, fig. 22) probably represents the primordium of Cowper's gland.

SKELETAL SYSTEM.

Little will be said about the skeletal system since it shows no unusual features. The skeleton, except for the usual areas of membrane bone, is cartilaginous throughout. The first (Meckel's) and second (Reichert's) visceral cartilages are as in other mammalian embryos. The mandible is represented by a lamina of membrane bone lateral to Meckel's cartilage which is upturned at its anterior end as in the pig. A general conception of the skeleton may be obtained from a study of the photographic plates, and of the limb girdles in particular from Pl. IV, figs. 11 & 12, and Pl. VI, fig. 21. The short massive bones of the fore and hind limb characteristic of the rhinoceros are already foreshadowed. Some details of the skull may be found in Pl. II, figs. 4 & 5, also Pl. III, fig. 8.

The spinal column consists of seven cervical vertebrae, eighteen thoracic or rib-bearing vertebrae, four lumbar and about twenty-five sacral and caudal vertebrae. A study of the skeleton of a two-horned rhinoceros in the Museum of the Zoological Department in Cambridge shows that this number of vertebrae is typical of that form. According to Flower & Lydeker (1871) the perissodactyles possess never fewer than twenty-two, usually twenty-three thoraco-lumbar vertebrae in the existing species.

FOETAL MEMBRANES AND PLACENTA.

It is fortunate that a sufficient portion of the foetal membranes was preserved to indicate the type of placentation, about which no information has been available hitherto (Mossman, 1937). The placenta is diffuse and epithelio-chorial (Pl. VI, fig. 23) as in the pig and other non-ruminant ungulates such as the elephant, tapir and hippopotamus. The yolk sac is a small

crumpled vesicle free in the chorionic sac and consisting of a vascular splanchnopleure and an atrophic endoderm (Pl. VI, fig. 24). It is not in contact at any point with the chorion which is therefore entirely allantoic.

SUMMARY.

The rhinoceros embryo resembles other perissodactyle embryos in the following particulars:

(1) The general external appearance, especially the snout region, the relatively elongated trunk, the small head, the appearance of the limbs and digits. The embryo is three-toed and perissodactyle.

(2) The large size of the trigeminal ganglia and nerves, especially the buccal and maxillary branches.

(3) The arterial rete mirabile at the base of the brain.

(4) The lateral compression of the thoracic inlet and the arrangement of the great vessels.

(5) The common pulmonary trunk arising from the ductus arteriosus.

(6) The arrangement of the inferior vena cava, particularly in its subcardinal segment associated with the large mesonephros.

(7) The large size of the mesonephros, the number and size of its tubules and glomeruli.

(8) The arrangement of the glandular derivatives of the embryonic pharynx, namely the thyroid, parathyroids, thymus and especially the large ultimobranchial body.

(9) The diffuse epithelio-chorial placenta.

In the following features the embryo is distinctive though this does not imply that these are not ungulate features:

(1) The arrangement of the dural venous sinuses and especially the small size or absence of the vena capitis lateralis. This vein is conspicuously large in most ungulates but is subject to considerable variation.

(2) The absence of a gall-bladder; this character occurs however, in the horse and some other mammals.

(3) The large size of the carotico-sympathetic nerve which is a discrete cord and not plexiform as is usually the case in mammals.

(4) The anastomosis of the left and right anterior cardinal veins *dorsal* to the oesophagus in the thoracic region. The occurrence of such anastomoses is favoured by the position of the anterior cardinal veins immediately lateral to the oesophagus instead of ventro-lateral to it as in the pig.

The adult anatomy of the rhinoceros strikingly resembles that of the horse as is amply attested by Owen and Garrod. It is impossible to say, except in a very general way, whether these resemblances are reflected also in the embryo, owing to the regrettable lack of detailed information on the embryology of both forms.

ACKNOWLEDGMENTS.

It is a pleasure to acknowledge my indebtedness to Dr. W. L. H. Duckworth for placing this rare specimen at my disposal and for his stimulating advice and encouragement during the progress of the work. I also wish to thank Prof. F. Wood Jones, Prof. H. A. Harris and Dr. N. Balankura for their help on many points of comparative anatomy. I am indebted to Mr. J. A. F. Fozzard for the photographs and to Mr. J. W. Cash for the sections.

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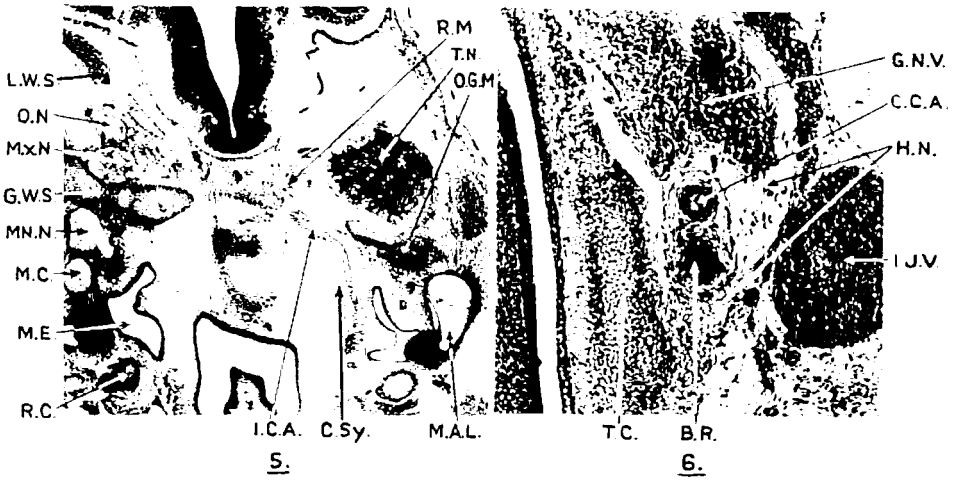
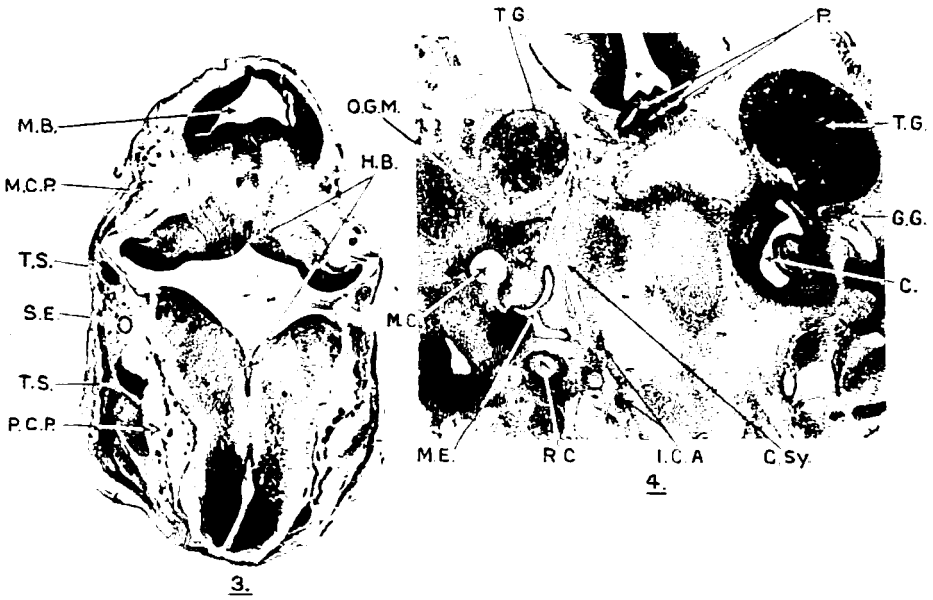
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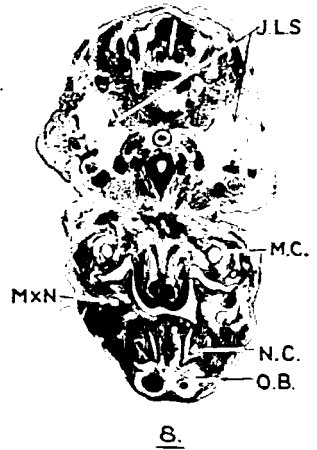
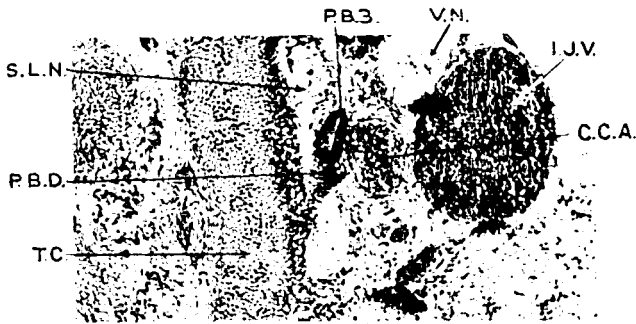
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Lateral view

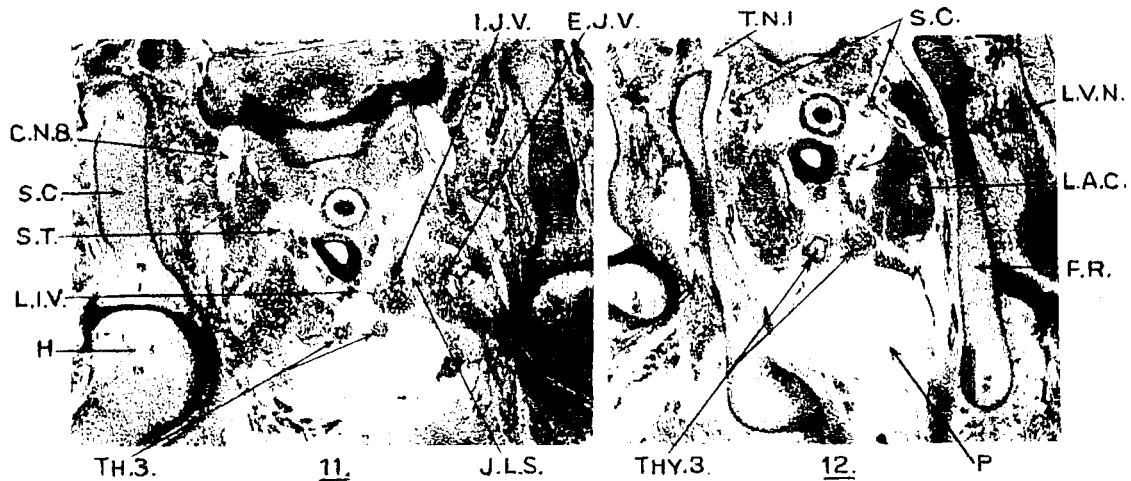
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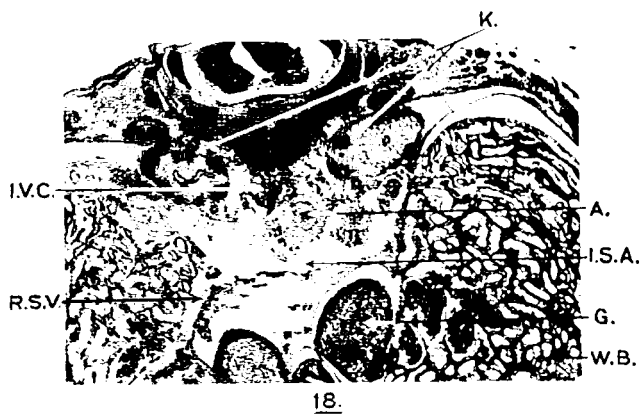
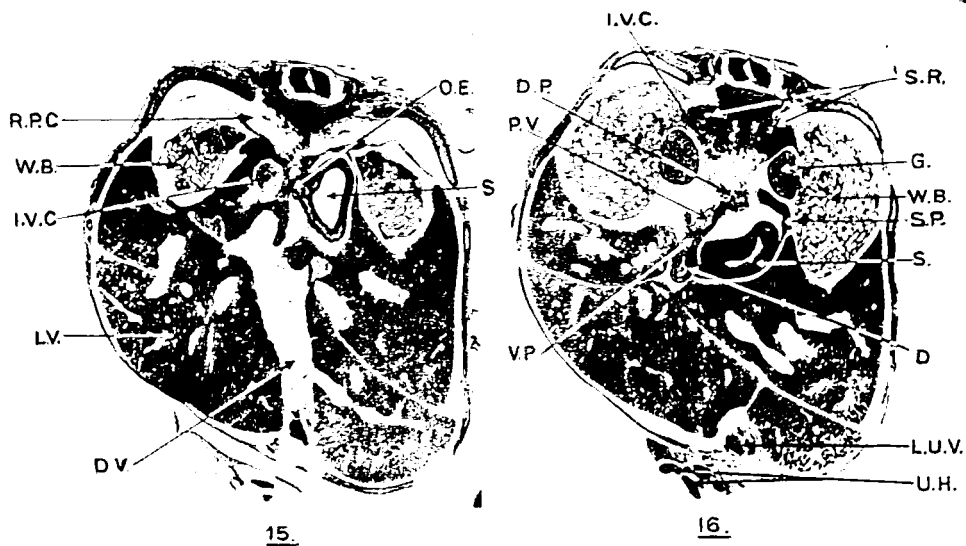
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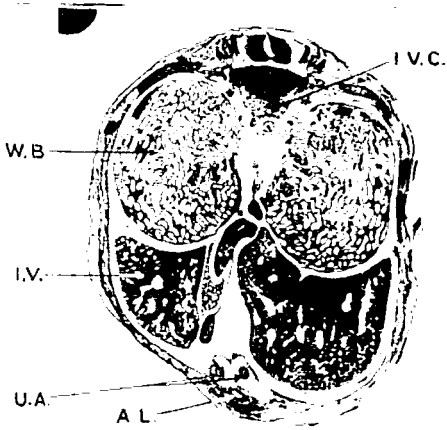
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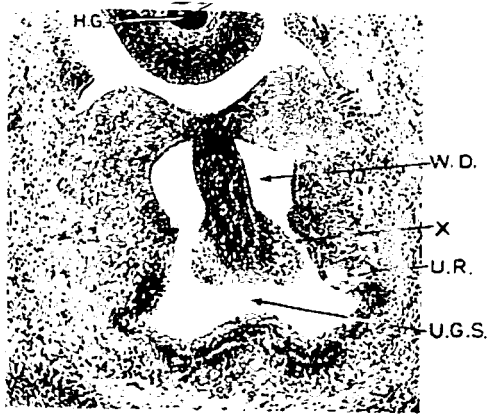
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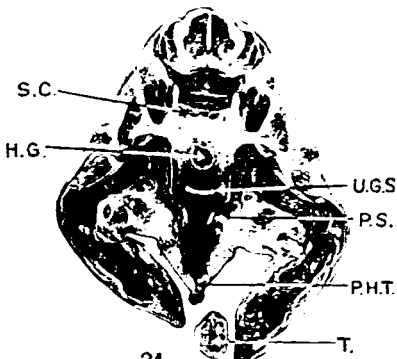
Embryo of African Rhinoceros.



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Embryo of African Rhinoceros.

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EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Ventral view of rhinoceros embryo. × 6·2. (Photograph retouched by A. K. Maxwell.)
2. Lateral view of rhinoceros embryo. × 6·2. (Photograph retouched by A. K. Maxwell.)

PLATE II.

- Fig. 3. Section through the mid-brain and hind-brain to show the cerebral plexuses and transverse sinus. The latter is cut twice as it arches over the saccus endolymphaticus (see text-fig. 1). *× c.* 11·3.
- H.B., hind-brain; M.B., mid-brain; M.C.P., middle cerebral plexus; P.C.P., posterior cerebral plexus; S.E., saccus endolymphaticus; T.S., transverse sinus.
4. Section through the head at the level of the trigeminal ganglia showing the general relations of the middle ear and particularly the large sympathetic branch accompanying the internal carotid artery. *× c.* 17·5.
- C., cochlea; C.Sy., sympathetic branch accompanying internal carotid artery and helping to form nerve of pterygoid canal; G.G., geniculate ganglion of facial nerve; I.C.A., internal carotid artery; M.C., Meckel's cartilage; M.E., middle ear; O.G.M., "otic" ganglionic mass; P., pituitary; R.C., Reichert's cartilage.

Fig. 5. Section through the head to show the internal carotid artery and the rete mirabile. The three main branches of the trigeminal nerve are also shown on the right. $\times c. 17.5$.

C.S.Y., carotid sympathetic nerve; G.W.S., greater wing of sphenoid; I.C.A., internal carotid artery; L.W.S., lesser wing of sphenoid; MAL., malleus; M.C., Meckel's cartilage; M.E., middle ear; MN.N., mandibular nerve; MX.N., maxillary nerve; O.G.M., "otic" ganglion mass; O.N., ophthalmic nerve; R.C., Reichert's cartilage; R.M., rete mirabile; T.N., trigeminal nerve and ganglion.

6. Section at the level of the thyroid cartilage and hypoglossal nerve showing a doubtful branchial remnant, possibly of the cervical sinus or third branchial pouch (see text-fig. 5). $\times c. 64.5$.

B.R., branchial remnant; C.C.A., common carotid artery; G.N.V., ganglion nodosum of vagus plus superior cervical sympathetic ganglion; H.N., hypoglossal nerve; I.J.V., internal jugular vein; T.C., thyroid cartilage.

PLATE III.

Fig. 7. Section at the level of the larynx and passing through the superior laryngeal nerve to show the vesicular remnants of a branchial pouch, probably the third (see text-fig. 5). $\times 74$.

C.C.A., common carotid artery; I.J.V., internal jugular vein; P.B.3, remnant of third (?) branchial pouch; P.B.D., cellular cord, possibly remnant of third pharyngo-branchial duct; S.L.N., superior laryngeal nerve; T.C., thyroid cartilage.

8. Low power view of section showing the general features of the neck and snout regions. Note the large jugular lymph sacs. $\times 7.5$.

J.L.S., jugular lymph sac; M.C., Meckel's cartilage; MX.N., maxillary nerve; N.C., nasal cavity; O.B., olfactory bulb.

9. Section at the level of the ultimobranchial body, the cranial tip of the thymus and parathyroid 3 (see text-fig. 5). This is the area outlined by a rectangle in fig. 8. $\times 64$.

OE., oesophagus; PAR. 4, parathyroid 4; R.L.N., recurrent laryngeal nerve; T., trachea; THY. 3, thymus 3; U.B.B., ultimobranchial body.

10. Section through the isthmus of the thyroid gland and also showing the thymic cord and parathyroid 3 (see text-fig. 5). $\times 64$.

C.C.A., common carotid artery; PAR. 3, parathyroid 3; TH., thyroid; THY.3, thymus 3; V.N., vago-sympathetic nerve.

PLATE IV.

Fig. 11. Section through the seventh cervical vertebra showing the components of the shoulder girdle, the developing left innominate vein and the lower end of the thymic cord. The right and left common carotid arteries and the left subclavian artery may be seen grouped around the trachea (see text-fig. 3). $\times c. 19.3$.

C.N.8, eighth cervical nerve; E.J.V., external jugular vein; H., humerus; I.J.V., internal jugular vein; L.I.V., left innominate vein; S.C., scapula; THY.3, thymus 3; S.T., sympathetic trunk.

12. Section at the level of the first rib to show the compression of the thoracic inlet. Note the vertical position of the first ribs which is typical of the unguleds (see text-fig. 3). $\times c. 19.3$.

F.R., first rib; L.A.C., left anterior cardinal vein; L.V.N., left vagus nerve; P., pericardium; S.C., inferior cervical sympathetic ganglion; THY.3, thymus 3; T.N.1, first thoracic nerve.

13. Section at the level of the disc between the fourth and fifth thoracic vertebrae showing the left anterior cardinal vein passing behind the oesophagus to join the right vein (see text-fig. 3). $\times c. 19.3$.

A.A., ascending aorta; L.D.C., left duct of Cuvier (oblique vein of the left atrium); P.A., pulmonary arch; R.O.P., retro-oesophageal part of the left anterior cardinal vein.

14. Section at the level of the eighth thoracic vertebra and at the point of entry of the inferior vena cava into the right atrium. Note the T-shaped pulmonary vein. $\times c. 19.3$.

I.V.C., inferior vena cava; L.A., left atrium; L., lung; P.V., pulmonary vein; R.A., right atrium.

PLATE V.

Fig. 15. Section at the level of the twelfth thoracic vertebra showing the lobulation of the liver, the cardio-oesophageal junction, the ductus venosus and the degenerating cranial extremities of the Wolffian bodies (see text-fig. 3). $\times 7.5$. D.V., ductus venosus; I.V.C., inferior vena cava; LV., liver; OE., oesophagus; R.P.C., right pleural cavity; S., stomach; W.B., Wolffian body.

- Fig. 16. Section at the level of the fourteenth thoracic vertebra showing the bursa omentalis, pancreas, spleen, stomach and duodenum. The suprarenal glands and Wolffian bodies are also seen. Note the absence of the gall-bladder (see text-fig. 3). $\times 7.5$.
 D., duodenum; D.P., dorsal pancreas; G., gonad (testis); I.V.C., inferior vena cava (sub-hepatic segment); P.V., portal vein; S.R., suprarenal glands; S., stomach; SP., spleen; U.H., umbilical hernia; W.B., Wolffian body; L.U.V., left umbilical vein; V.P., ventral pancreas.
17. High power view of the unusual mesonephric tubule seen in the left Wolffian body in fig. 16 and showing the metaplasia of the lining epithelium. $\times 70$.
18. Section at the level of the sixteenth thoracic vertebra; epithelium showing the "renal collar" of veins around the aorta (see text-fig. 3). $\times 16.5$.
 A., aorta; G., gonad; I.S.A., intersubcardinal anastomosis; I.V.C., inferior vena cava (beginning of post-renal or supracardinal segment); K., kidneys; R.S.V., right subcardinal vein; W.B., Wolffian body.

PLATE VI.

- Fig. 19. Section at the level of the seventeenth thoracic vertebra showing the large pig-like mesonephros. Note the inferior vena cava lying between the sympathetic chains and still showing indications of a bilateral origin (see text-fig. 3). $\times c. 7.8$.
 AL., allantoic duct (urachus); I.V.C., inferior vena cava; LV., liver; U.A., umbilical arteries; W.B., Wolffian bodies.
20. Section at the level of the fourth lumbar vertebra showing the opening of the Wolffian ducts into the urogenital sinus. Note the sudden change on the epithelium at X. $\times 64$.
 UR., ureter; U.G.S., urogenital sinus; W.D., Wolffian duct.
21. Section showing the hip joint and the phallic tubercle. $\times c. 7.7$.
 H.G., hind-gut; P.S., pelvic splanchnic nerves; PH.T., phallic tubercle; S.C., sympathetic chain; T., tail; U.G.S., urogenital sinus.
22. Section through the urethral plate showing the glandular outgrowth, probably Cowper's gland. $\times 17$.
 C.G., Cowper's gland; H.G., hind-gut; H.L., hind-limb; P.S., pelvic splanchnic nerves; T., tail; URE., urethral plate.
23. Section of part of the chorionic sac of rhinoceros embryo. The placenta is diffuse and epithelio-chorial. $\times c. 202$.
24. Section of the yolk sac which is a free collapsed vesicle within the chorionic sac. It consists of a vascular splanchnopleure and a lining of atrophic endoderm. $\times 245$.