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JOURNAL OF ANATOMY

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(ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY)

CONDUCTED, ON BEHALF OF THE ANATOMICAL SOCIETY OF
GREAT BRITAIN AND IRELAND, BY

PROFESSOR THOMAS H. BRYCE, UNIVERSITY OF GLASGOW
PROFESSOR EDWARD FAWCETT, UNIVERSITY OF BRISTOL
PROFESSOR J. P. HILL, UNIVERSITY OF LONDON
PROFESSOR G. ELLIOT SMITH, UNIVERSITY OF MANCHESTER
PROFESSOR ARTHUR KEITH, ROYAL COLLEGE OF SURGEONS,
LINCOLN'S-INN-FIELDS, LONDON, W.C.

VOL. LI.

THIRD SERIES.—VOLUME XII.

WITH PLATES AND NUMEROUS ILLUSTRATIONS IN TEXT.

LONDON:
CHARLES GRIFFIN AND COMPANY, LTD.,
EXETER STREET, STRAND.
1917.

PRINTED IN GREAT BRITAIN BY
NEILL AND CO., LTD.,
EDINBURGH.

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PREFACE TO THE FIFTY-FIRST VOLUME

The issue of the first part of this volume of the Journal of Anatomy and Physiology coincides with a change in the management and control of the Journal. In future it will be named the Journal of Anatomy, and will be the official organ of the Anatomical Society of Great Britain and Ireland, whose property it now is.

It must, however, be clearly understood that the change of proprietorship does not involve any departure from the policy hitherto followed of accepting for publication in the pages of the Journal approved articles other than those read before the Anatomical Society.

The Journal was founded by the late Sir William Turner in 1866. In a preface which he contributed to the fortieth volume he gives his reasons for establishing the Journal, and mentions the changes which had occurred in its editorial staff up to that year. He also acknowledges the active part taken in the arrangements for the institution of the Journal by the late Sir George Murray Humphry, "who undertook for some years the duty of acting editor."

"On the completion of Volume XX. in 1887 a new series was commenced, with Professor Turner as acting editor." Although in later years others were responsible for the editorial work, "he retained to the end his interest in the Journal, and every sheet of each issue passed through his hands before going to the press." He died on the 15th of February of the present year: had he lived a few months longer he would have had the satisfaction of seeing the completion of the jubilee volume.

In 1906 Professors A. Macalister and D. J. Cunningham undertook the management of the Journal, and Macalister edited three volumes (XXXII. to XXXIV. inclusive). Cunningham followed with the next seven volumes (XXXV. to XLI. inclusive), and "under his auspices an important change in the size and appearance of the Journal was made in 1905 in the fortieth volume." Macalister resumed the duties of acting editor in 1908, and since that year has edited nine volumes (XLII. to L. inclusive). He has spared neither time nor trouble to improve the Journal and enhance its scientific value.

Professors A. Thomson and A. Keith joined the editorial staff in 1907, and Professor A. Robinson in 1909.

Until the year 1878 the Journal was the organ of the two sciences, Anatomy and Physiology. In that year the *Journal of Physiology* was established, and thereafter "physiological" papers became few and far between in this Journal, and finally ceased to appear. It has therefore been deemed advisable to drop the words "and Physiology" from its title.

ROBERT HOWDEN,
President of the Anatomical Society
of Great Britain and Ireland.

October 1916.

JOURNAL OF ANATOMY

THE SHAPE AND PERITONEAL RELATIONSHIPS OF THE SPLEEN IN MONOTREMES AND MARSUPIALS.

By W. Colin Mackenzie, M.D., F.R.C.S., F.R.S.E. *From the Laboratories of the Royal College of Surgeons of England.*

In the course of investigations on the comparative anatomy of Monotremes and Marsupials, which I have been conducting during the past six years, and which at first had special reference to the evolution of muscular action, my attention was arrested by certain peculiar features of the spleen, both as regards its shape and relationships, which throw light on the anatomy of the human spleen. A search through available literature relating to the two orders showed little reference to the subject, apart from the description originally given by Richard Owen. On account of the large amount of material I have had for dissection—the Monotremes alone numbering fifty specimens—individual variations have been excluded. In this monograph I propose to give first a general description of the spleen and its relations in the two orders, and, secondly, to offer an explanation of the apparent differences and their bearing on the shape and relationship of the human spleen.

The Spleen in Monotremes.

Platypus (Ornithorhynchus anatinus).

On opening the abdomen of the Platypus, concomitant with the presence of a diaphragm and great omentum one is struck by the large development of the spleen and pancreatic tissue, and the right stem of the former may extend from the left hypochondrium to the right iliac region.

The spleen (fig. 1) is somewhat V-shaped, and three portions are recognised, viz. a small body 2·5 to 3 cm. long directed towards the œsophagus and in the great omentum (lesser sac); a large right ventral (anterior) process lying freely in the abdominal cavity and suspended also in the great omentum, 12 to 15·5 cm. long, with the width varying from

2 to 2·5 cm. and thickness 1·5 cm.; and a shorter left dorsal (posterior) process 7 to 9 cm. long, with a width of 1·75 to 2 cm. and thickness of nearly 1 cm. This left process is outside the lesser sac in relation with a fold—the left lateral or lieno-mesocolic—connecting it to the mesocolon of the left or distal colon. The distal colon is never fixed dorsally, and the average maximum width of the mesocolon equals 5 cm. The pancreas is found diffusing itself on the left aspect of the mesocolon in relation with the left lateral fold. The fold with the left splenic process and pancreas can be lifted free from the ventrum of the left kidney and the dorsal wall.

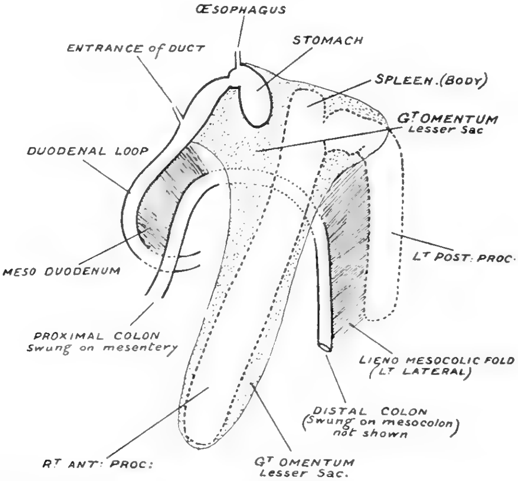

FIG. 1.—The peritoneal relations of the spleen in Platypus.

Whilst the right process and body of the spleen are continuous, the left process is arched and forms practically a right angle with the body. A deep notch is present at the cephalic margin between the two, and the actual width of attachment may be less than 2 cm. One or two small notches may be noted at the caudal border near the termination of the lesser process, and a notch directed towards the body between the right and left processes. It is interesting to note that in an Agama (Reptilia) measuring 30 cm. snout to vent and abdominal width of 7 cm. the spleen was 1·5 cm. long and ·4 cm. wide, while the snout to vent measurement of the Platypus is 37 cm. and width 13 cm.

Echidna (Echidna aculeata).

As in the Platypus, three main portions of the spleen may be recognised (fig. 2), viz. body and two processes; but while uniformity is characteristic of the spleen of the Platypus, although conforming to the general character it is rare in the Echidna to find two spleens alike.

(1) Body.—This is better defined than in Platypus and is in relation to the stomach fundus, being directed towards the œsophagus. It is suspended in the great omentum, the width of which, even in a male adult, only equals 1 cm.; and so at this early stage we obtain the definition of a gastro-splenic omentum. Its length varies from 3 to 5 cm. and the width ·5 to 1 cm.

(2) The right ventral process is the longer of the two and is also suspended in the great omentum (lesser sac), the width of which at its anterior extremity is 7 cm.; so that it is more mobile than the body. Its average length is 5 to 7 cm. and width ·5 to 1·5 cm.

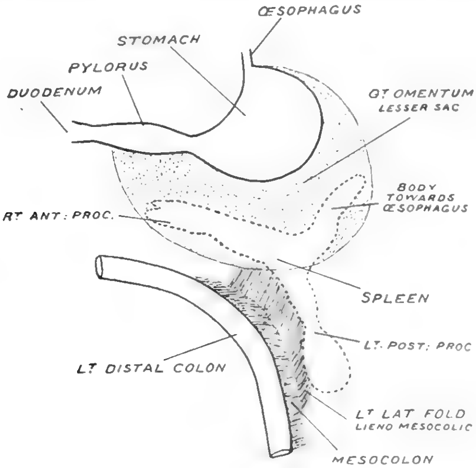

FIG. 2.—The peritoneal relations of the spleen in Echidna.

(3) Left dorsal process.—This is shorter than the anterior, and two portions may be recognised, viz. a stem terminating in a pear-shaped body, which may be smooth or (especially in smaller specimens) corrugated. The stem rarely runs directly into this portion. Usually there is narrowing at the point of attachment, and the connection between the two may be merely a slender fibrous thread. The stem varies from 1·5 to 3 cm. in length and average width ·5 cm., while the body varies from 2 to 3·5 cm. in length and circumference may reach 5 to 6 cm. This process, as in Platypus, lies outside the lesser sac in relation to the lieno-mesocolic fold, extending caudally towards the pelvis on the left of the distal colon. In one specimen out of a large number examined, I found the left stem included in the lesser sac. The distance between the pear-shaped body and colon may only equal

·75 cm. The pancreas is a less mobile organ than that of the Platypus, and in not one of the numerous specimens examined by me did it extend sinistral to the lesser sac, so as to come into relation with the lieno-mesocolic fold. The distal left colon is mobile, having a mesocolon. In one specimen this was greatly narrowed and the length of the distal colon in the abdomen only equalled 7 cm. In another—a male specimen—the pancreas was a "fixed" organ and on the right side was adherent to the lobus caudatus. The left or distal colon was fixed dorsally, describing an almost vertical course to the pelvis. In close relation in this specimen, and all fixed dorsally in the left lumbar region, were the left testis, kidney, pear-shaped process of spleen, and distal colon. The pancreas extended but a short distance on the left of the colon and apparently had little influence in the fixation of this structure, since it never extended to the left in relation with the lieno-mesocolic fold. Yet fixation has occurred. In this specimen, as well as the one with a shortened mesocolon, the distal left colon was relatively short; there was a failure to develop, with atrophy of the mesocolon. Instead of the distal colon from the duodeno-intestinal flexure to vestibule being 28 cm. long—the average adult male length—it only measured 13 cm.

THE SPLEEN IN MARSUPIALS.

In this order we meet not only with types of spleen presenting the early mammalian character seen in the Monotremes, but with types becoming dorsally fixed and resembling closely the human spleen.

Tasmanian Devil (*Dasyurus sarcophilus*).

In this Marsupial there is a well-defined great omentum extending from the pyloric region to the left along the great curve of the stomach. No duodenal loop is present, and no well-marked distinction between colon and small intestine as in other Marsupials. The intestinal tract is reptilian in character, consisting of a canal 157 cm. from pylorus to pelvis, swung apparently on a single mesentery 7 cm. long at its dorsal attachment. This latter consists of two portions—an upper 1·5 cm. long (superior mesenteric) and corresponding to the duodenum and small gut (135 cm.), and a lower (5 cm.) representing the original mesocolon and corresponding to the remaining 22 cm. of intestine, which is large gut.

As in Macropus, the spleen presents three distinct portions:—

(1) A large portion or body directed along the great curvature of the stomach towards the œsophagus. It is swung on the great omentum, which is 2 cm. wide at the left extremity and 10 cm. at the right. At the left extremity, in addition to the shortened omentum (gastro-splenic), a

peritoneal band stretches across the omentum between the stomach and spleen. The body varies from 7 to 8 cm. in length, and greatest width is 1·75 cm.

(2) The right ventral process is also in relation with the lesser sac, being swung freely on the great omentum. It varies from 4 to 5 cm. long and is about 1·75 cm. wide. This portion forms almost a right angle with the body.

(3) The left dorsal process, 2·5 cm. long and 2 cm. wide, is outside the lesser sac and gives attachment to the left lateral fold. This membrane is somewhat triangular in shape and measures 9 to 10 cm. long, and over it the main pancreatic tissue diffuses itself, but it never extends nearer than 2 cm. to the dorsal attachment. The basal portion of the membrane (5 to 6 cm. long) extends from the root of the mesentery out along the lower part of the lesser sac to the left dorsal process of the spleen. Its left margin is free. The right margin is not continuous dorsally with the mesocolon of the large intestine, but with the peritoneum slightly to its left. The left lateral fold, as in the Platypus and Kangaroo, is free from dorsal wall and ventrum of the left kidney.

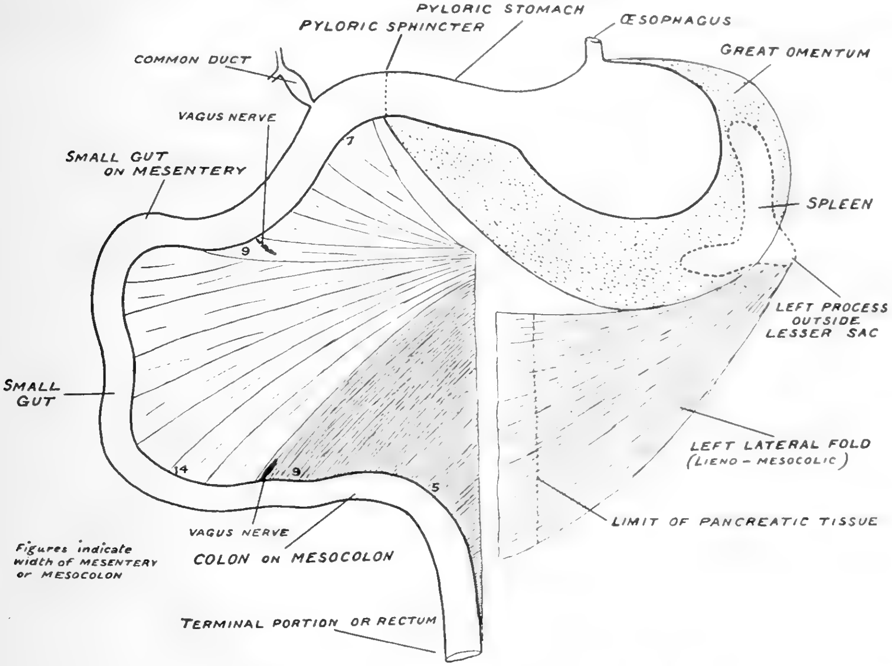

FIG. 3.—The gastro-intestine and spleen in Tasmanian Devil.

Koala (Phascolarctus cinereus).

The spleen is suspended in the great omentum, being contained in the lesser sac, and is characterised by the relative shortness of the left dorsal process and the absence (this being the only instance among Marsupials and Monotremes) of the left lateral or lieno-mesocolic fold. The shape of the spleen varies slightly in different animals. In all there is an elongated right ventral process varying from 7 cm. to 12·5 cm. long. It is usually constricted and fissured where it joins the main splenic mass. The remainder of the spleen or body may approach somewhat in shape the human type, forming a triangular body 7 cm. long and 4 cm. across, with two small projections, one directed towards the œsophagus and the other representing the left dorsal process. The right process is much more mobile than the body, and while the width of great omentum between the left extremity and great curve of stomach equals 2·5 cm., at the right extremity this equals 9 to 10 cm. In some specimens the body is not relatively so large, and in place of the projections two processes are seen, separated by a well-defined interval or gap.

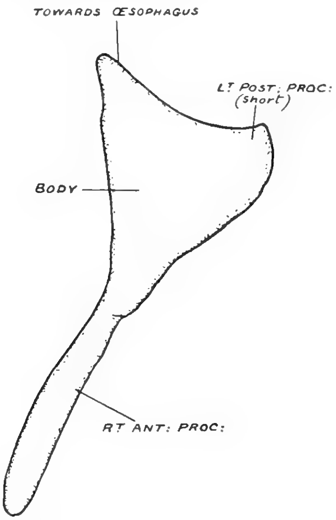

FIG. 4.—The spleen in Koala.

Macropodidæ (Kangaroos and Wallabies).

The spleen consists of three portions: (1) left, largest portion or body; (2) narrow elongate or right process; (3) wider, though shorter, dorsal left process.

The body varies from 11 to 15 cm. in length, with a maximum width of 4·5 cm. The short left process is 6 cm., with a maximum width of 3 cm.; and the right process 9·5 cm. long, and maximum width 1·75 cm.

Frequently the width of this process may only equal 1 cm., with a narrow attachment to the body—the connection being fibrous, with a sprinkling of splenic tissue. Such a process is one apparently undergoing a retrogressive evolution, and is found both in the Wallaby and Kangaroo. In the Tasmanian Wallaby I found the anterior process to be not only narrower but shorter than the left process. The great stomach in Macropus is a V-shaped organ with a large left and a smaller right limb, and the well-defined Spigelian lobe of the liver depending between the two. The body and elongated right process are suspended on the great omentum (lesser sac), being related to the greater curvature of the left limb as far to the right as the bend in the stomach. The process is less closely attached than the body. The short, wide left dorsal process is outside the lesser sac, being connected to the mesocolon of the distal colon by the triangular fold, the left lateral

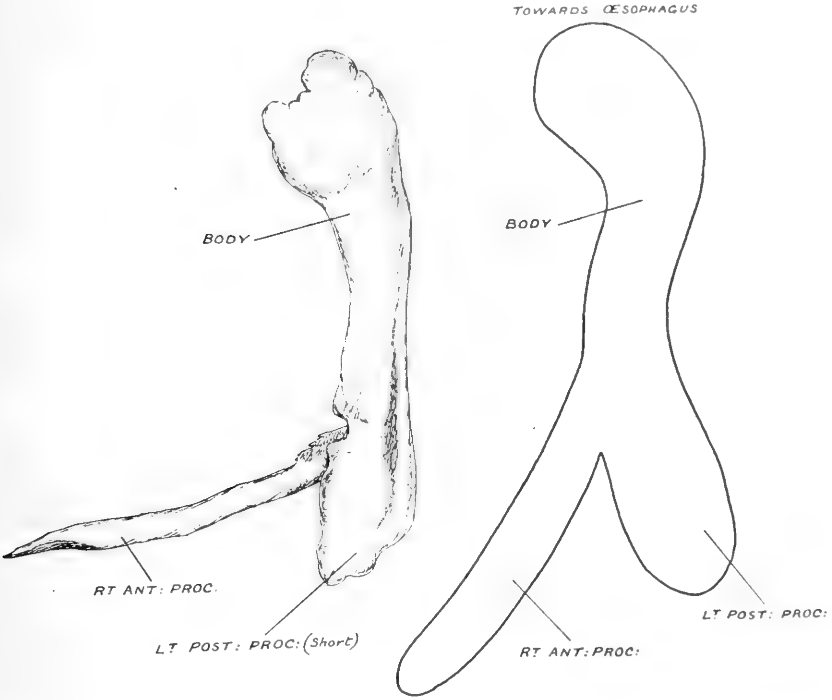

Fig. 5.—Spleens of Macropodidæ.

or lieno-mesocolic, which is more developed in some specimens than in others. It is free from the dorsal wall and ventrum of the left kidney. Both as regards its shape and the disposition of the left lateral fold, the spleen of the Macropod presents the primitive Mammalian type, and resembles closely that of the Monotreme.

Opossum (Trichosurus—Pseudochirus).

In Trichosurus a marked advance towards the human type of spleen is to be noted, and light is thrown on the formation of the lieno-renal ligament and the mode of fixation of the distal colon and spleen. Although three portions of the spleen are noted, viz. body, right and short left processes, the organ is more compact and the processes less defined than in the preceding mammals (fig. 9). The body is directed towards the œsophagus and is suspended—like the right ventral process, which is directed along the great curvature of the stomach—on the great omentum, *i.e.* lesser sac.

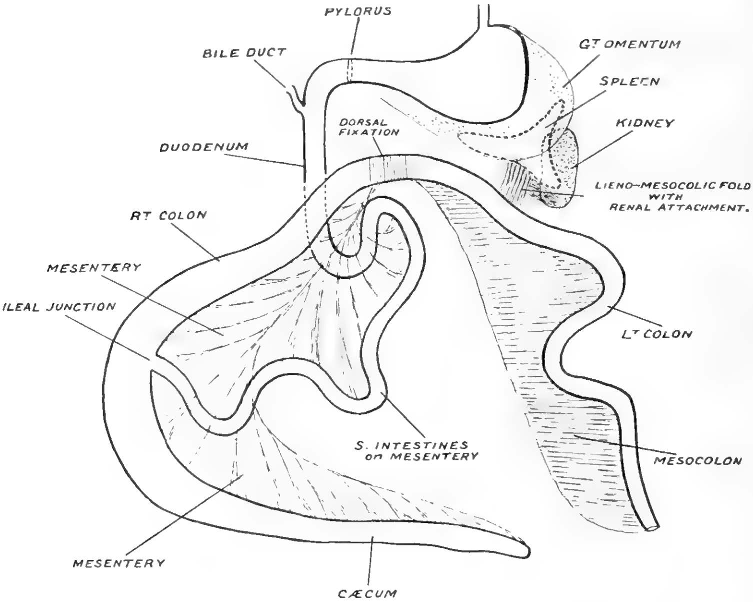

Fig. 6.—The gastro-intestine and spleen in Trichosurus.

The width of the great omentum (gastro-splenic) at the extremity of the body is 1·5 cm., and at the extremity of the right process the width is 5·5 cm., so that the narrowing gastro-splenic omentum is here well defined. The short left dorsal process is outside the lesser sac in relation with the left lateral fold. Its average length is only 1·5 to 2 cm The total average length of the spleen is 7 cm. and the width 1·5 to 2 cm. In addition to the outer or left and inner visceral or right surfaces, three margins can be defined, viz. renal or dorsal margin formed by the body and left process; right ventral margin formed by the body and right process; and left colic margin formed by the left dorsal and right anterior processes. On examining the inner or visceral surface (fig. 9) of the spleen we are struck with the resemblance borne to that of Man and the Wombat. We note a well-defined renal surface, concave, formed by the body and left process; a gastric surface formed by the body and right process, with the gastro-splenic omentum (great omentum) attached along a groove extending from the extremity of the body to the extremity of the anterior process. This surface is separated dorsally by a distinct raised edge from the renal surface, but unless there is a defined concavity this is not marked. From the gastro-splenic omentum, running down the left dorsal process, we see the attachment of the left lateral fold (lieno-mesocolic). This, with the anterior part of the gastro-splenic omentum, separates off the lower left or colic surface. Below the attachment of these two membranes we have a ridge simply the result of the impressions of the colon and stomach, just as the posterior ridge separating the renal from the gastric surface is the result of the renal impression. The lieno-mesocolic (left lateral fold), instead of being free as in the preceding specimens from the short left splenic process to the mesocolon of the distal colon, has, in addition, become attached to the ventrum and outer surface of the lower half of the left kidney. The result is that the spleen and left portion of the pancreas which is supported on the fold are brought into relation with the kidney, and so we have defined the concave renal surface of the spleen related to the upper and outer convex portion of the kidney—the pancreas lying ventral to that organ. Thus we see that we have a definitely formed lieno-renal fold which is really the upper part of the lieno-mesocolic fold, and the lower part of the fold is really now reno-mesocolic. A peritoneal band is noted in both Trichosurus and Pseudochirus from the middle of the convex border of the kidney to the lateral abdominal wall, and continuous over the kidney with the lieno-mesocolic fold. The attachment of the lieno-mesocolic fold to the left kidney (zygosis) is thus a factor in bringing the spleen into close relation with that organ, and this is more marked in some specimens than in others. In two specimens the pancreas lay ventral to the left kidney, and the renal surface of the spleen was related to the outer part; but all could be raised off the kidney, as they were suspended on the lieno-mesocolic fold, and this was not attached to the ventrum of the kidney as above described. The fold, however, was really lieno-renal, as its lower attachment was to the dorsal wall at the lower pole of the kidney, *i.e.* it did not extend to the mesocolon, the lower portion being atrophied. In a smaller variety of Australian Opossum (Pseudochirus), though the spleen is practically similar to that of Trichosurus, the fixation of structures in the left hypochondrium and lumbar regions is more pronounced. The renal surface of the spleen is in relation with the upper and outer convex surface of the kidney, and the left process of the spleen can be raised slightly off that organ. The pancreas, however, is seen to be in close relationship with the ventral and outer surface of the kidney. In Trichosurus the left distal colon and mesocolon are free of lesser sac, but in Pseudochirus they are included for about 8 cm. This inclusion must be an important factor in approximating colon to spleen, although in Pseudochirus it is associated with a large process of pancreatic tissue in the lesser sac and free from the dorsum. Whilst in Trichosurus the colon and mesocolon are not brought close to the kidney, in Pseudochirus the lieno-mesocolic fold is relatively shortened up and the mesocolon is brought in direct relation with the caudal pole of the kidney, so that we find in close connection pancreas, left process of spleen, kidney, and mesocolon, only the shortened remains of the lieno-mesocolic fold intervening. In these two varieties of Opossum important light is thrown on the combination of correlated factors necessary to produce the close relationship of spleen, pancreas, and colon in the left human hypochondrium.

Wombat (*Phascolomys*).

The spleen is placed in the left hypochondrium in relation with the left part of the stomach and upper portion of the left kidney. It may be described as triangular in shape, presenting three margins: (1) dorsal or renal; (2) right, gastric, or ventral; (3) left, lower, or colic.

We also note three extremities or angles, viz. œsophageal or upper, right ventral, and a left extremity. In addition, two main surfaces, viz. outer or left, and inner visceral or right. Its greatest length is 12 cm. and breadth 11 cm.

Extremities.—(*a*) The œsophageal or superior extremity is most dorsal and frequently the most pointed, and lies 3 to 4 cm. from the œsophagus. It is in relation with the great curvature of the stomach, to which it is connected by gastro-splenic omentum, *i.e.* upper part of the great omentum, and which is thickened in this region, with a width of only 1 cm. Frequently, as in the human, it bends towards the inner surface so as to give a rounded shape to the upper end of the spleen. This is probably an accommodation effect for a well-developed left hepatic lobe, with the lower and inner part of which it is related.

(*b*) The ventral or right extremity is usually rounded and corresponds to the right ventral process seen in the Monotremes and other Marsupials. It is connected to the great curve of the stomach by the gastro-splenic (great) omentum, the width of which is 4 cm., so that it is more mobile than the superior angle. It is to be noted that the gastro-splenic omentum does not extend to the tip of either extremity.

(*c*) The left extremity corresponds to the left process seen in other Marsupials and in the Monotremes, and is related to the outer margin of the left kidney about the middle.

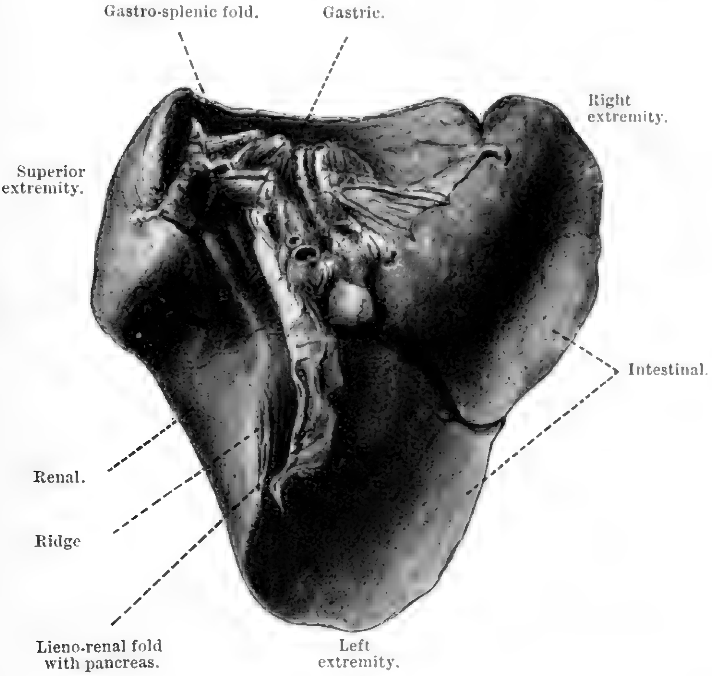

FIG. 7.—Inner or visceral surface of the spleen of Wombat (Phascolomys).

Margins.—(*a*) Right (anterior of human) lies between the superior and anterior extremities along the great curve of the stomach. It is thin, usually concave, frequently notched below, and formed by the body and right ventral process.

(*b*) The left margin extends between the right ventral and the left extremities. It is usually thin, is the longest of the three, and presents a well-defined notch about its middle or towards the left, so that the left process or extremity becomes differentiated off. It is free and comes into relation with the distal colon and the left portion of the stomach.

(*c*) The renal or dorsal margin extends between the superior and left extremities, being formed by the body and left posterior process. It is thicker and more dorsal than the others and is curved—being in relation with the outer convex margin of the left kidney.

Surfaces.—(*a*) The outer or left surface is usually smooth, slightly convex, corresponding to 8, 9, 10, 11, and 12 ribs. It is related to the diaphragm and the mesial or visceral surface of the left lobe of the liver.

(*b*) Inner right or visceral surface is more complex and presents, as in the human spleen, certain very definite areas, viz. right, gastric, or upper; left, lower, or colic; dorsal or renal. The attachment of the gastro-splenic omentum extends on the gastric surface close to the posterior boundary obliquely down and forward from within 1 cm. of the superior extremity to within 1 cm. of the tip of the right ventral extremity below. The lieno-mesocolic fold—which supports the left pancreas and the chief vessels—is attached on this aspect of the left process, and may or may not extend to the left angle or tip. Below it is attached to the ventrum of the caudal pole of the left kidney, so that it is lieno-renal. The left pancreas—unlike the human—can be raised from the front of the kidney. By means of this fold and the anterior part of the gastro-splenic omentum the lower or colic surface is defined. In addition, certain ridges are noticed on this aspect of the spleen. Along the attachments of the lieno-mesocolic and anterior parts of the gastro-splenic membranes is a blunt ridge, and following the curve of the upper part of the gastro-splenic membrane a slight ridge may be noticed. Dorsal to the upper part of the gastro-splenic membrane is a sharper ridge—renal ridge—the result of renal pressure, and separating off the renal and gastric surfaces. The renal ridge is traced along the left extremity, forming a prominence below.

(1) Gastric surface (right or upper) is somewhat triangular and concave for the fundus of the stomach. It corresponds to the body and right anterior process. Dorsally is the attachment of the gastro-splenic omentum with some small vessels, and below it is separated from the colic surface by the gastro-splenic membrane in front and the lieno-mesocolic behind. The pancreas, supported on the lieno-mesocolic fold, tends to encroach on the gastric surface between this fold, the renal ridge, and the gastro-splenic omentum. The dorsal limitation of this surface is the ridge behind the gastro-splenic omentum; or where the depression for the kidney is well marked a defined margin separates it from the renal surface.

(2) Left, lower, or colic surface.—This is separated from the gastric surface by the gastro-splenic omentum, and from the renal and gastric by

the lieno-mesocolic fold with pancreas, and more posteriorly the renal ridge, since the renal concavity extends to the left extremity. A well-defined fissure is seen a little below its middle, which, extending inwards, serves to define the left process. This surface corresponds to the right ventral and left dorsal processes of the Platypus, the notch on the edge leading to the fissure representing the original interval between the two. It is related to the distal colon, and when distended the stomach is seen to be related to the upper or ventral half (*i.e.* above the fissure), which portion is included in the gastric surface of the human.

(3) Dorsal or renal surface is the narrowest of all the surfaces and corresponds to the body and left posterior process. It is really a concavity for the upper part of the left kidney, and can be regarded as an accommodation effect. The concavity may extend almost along the whole length or be only limited to the lower four-fifths, since in cases with a well-developed left hepatic lobe the upper end of the spleen may be curved over towards the inner surface. The result of renal accommodation or pressure is to define on the inner and dorsal aspect of the spleen a ridge or margin—renal ridge—best defined below, where it forms a distinct projection or angle. This ridge separates the renal and gastric surfaces and, with the lieno-mesocolic fold, the renal from the colic below.

INTERPRETATION OF THE FOREGOING FACTS.

A study of the spleen in these two orders throws light on the significance of shape of the human spleen[1] and on the correlations associated with its fixation in the left hypochondrium The spleen of the Wombat (Phascolomys) (fig. 7), though conforming more to the primitive Mammalian type, yet resembles the human so closely as to be at times almost indistinguishable, and so the so-called anterior, posterior, and superior angles of the human spleen become significant. These all have their prototypes in the Platypus. Two spleens are illustrated, taken at random from full-time fœtuses (fig. 9). As one might expect, the anterior process (*i.e.* ventral, right process of the Platypus) is well defined, while the posterior (*i.e.* dorsal, left process of the Platypus) is poorly defined. In both, fissures are seen defining the body from the processes. From the point of view of biology, *i.e.* function, the human spleen of the text-books cannot be accused of affording much information. Post-mortem examinations made for a period of six years with Dr S. Strachan at a benevolent home for the aged showed

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[1] "The Notches and Fissures of the Spleen and their Meaning," F. G. Parsons, *Journ. of Anat. and Phys.*, vol. xxxv. pp. 416–427; "The Form of the Human Spleen," R. K. Shepherd, *Journ. of Anat. and Phys.*, vol. xxxvii. pp. 50–69.

me the great relative frequency of perigastric adhesions, perisplenitis, and old left pleuritis, all of which would profoundly modify shape. To throw light on the significance of shape it would be better if young subjects were chosen. One naturally wonders whether different portions of the Mammalian spleen have different functions. There is no biological evidence of this, nor can it be said to be borne out by histological examination, although important differences were noted in the spleen in the different members of the orders described. As regards the fixation of the human spleen, this, it must be borne in mind, is associated with fixation of the distal colon and left pancreas. The attempts made by nature can be studied in the Monotremes and Marsupials. In a study of the peritoneum of the members of these two orders, three primary folds are noted, which are traced in varying degree throughout the Mammalia, and play an important part in the fixation of the gut, which is coadjusted to the erect posture:—

(1) Mesial fold, approximating the colon to the pyloric region, and continuous in the Chameleon with the gastro-hepatic omentum or ventral mesogaster.

(2) Duodenal or right lateral, passing from the ascending duodenum to the right aspect of the mesocolon of the distal colon, which I regard as an acquired or physiological fold (zygosis).[1]

(3) Left lateral or lieno-mesocolic, from the left, dorsal, or posterior process of the spleen to the left aspect of the mesocolon of the distal colon. This, like the mesial, I regard as biological. The mesial fold is best defined in the Koala, the duodenal in Trichosurus, and the lieno-mesocolic fold in the Platypus. The origin of the left lateral or lieno-mesocolic fold was certainly very puzzling, and at first I was inclined to regard it as an acquired or physiological adhesion (zygosis) from a spleen which had wholly developed in relation to the lesser sac. A study of certain lizards supplied me, however, with a different explanation (fig. 8).

In Agama we notice the narrow splenic body in the mesogaster running parallel with the stomach. In Lygosoma (Scincidæ) the spleen was noticed passing almost vertically close to the dorsal wall and in relation not only with the mesogaster but with the mesentery and mesocolon as well. Correlated with the development of the Mammalian spleen we have the development of great omentum, and, in the case of the Agama, the enlargement would be wholly related to the lesser sac, as actually happens in Koala, in which the left process is insignificant; while in the case of Lygosoma an enlargement of the spleen would involve not only the mesogaster (great omentum, lesser sac) but the mesocolon as well. In Lygosoma the pancreas is noted as a single strand extending from the commencement of the

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[1] "The Nature of Peritoneal Adhesions," Arthur Keith, *Lancet*, 8th August 1914.

duodenum to the lower portion of the spleen. Diffusibility is characteristic of its early Mammalian development. In the Platypus it diffuses itself on the right in the meso-duodenum and on the left on the lieno-mesocolic fold. Mesially it is fixed, forming the lower dorsal boundary of the lesser sac.

With development of the spleen is a correlated great omentum, but no inclusion primarily by the great omentum (lesser sac) of distal colon or pancreas. The pancreas as we ascend in the Mammalian scale becomes more compact. From the point of view of selection it would not be advantageous for it to be included in the lesser sac. It could not then conform to the abdominal law of dorsal fixation of solid bodies by which torsion especially of ducts is prevented in the erect posture. In addition, the dorsal fixation of duodenum, spleen, and left distal colon, of which its own further dorsal fixation is an important factor, would be interfered with; and the significance of the relationship of the pancreas on the left to a fold (left lateral) connecting spleen and distal colon in the production of that arrangement becomes understood. This fold is completely absent in Koala, and in that Marsupial there is no fixation of distal colon, spleen, or left pancreas. Primary inclusion by the great omentum of the proximal 8 cm. of distal colon actually happens in Pseudochirus (Australian Opossum), and in this Marsupial, though distal colon, spleen, and kidney are proximal, there is a considerable amount of pancreatic tissue free in the lesser sac. Furthermore, a study of the Mammalia shows that for adaptability to a mixed diet selection requires not atrophy but development of the distal colon, which becomes ultimately fixed as in erect Man in the left hypochondrium. In the Echidna, whose diet is chiefly ants, a failure to develop or atrophy of the distal colon and mesocolon is correlated with the dorsal fixation of that gut and of the pancreas, but not of the spleen. I regard

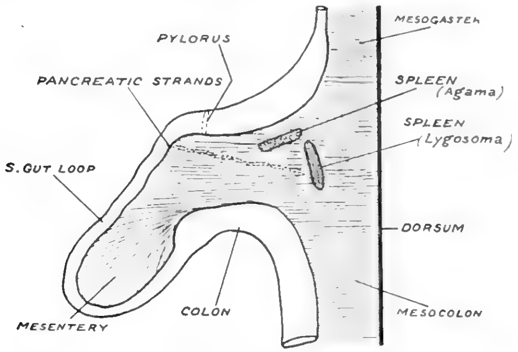

FIG. 8.—Diagram to show contrasted positions of spleen in Agama and Lygosoma.

that as the evolutionary tendency in the Echidna (since I have seen the various grades of shortening of the mesocolon), and nature does not retrace her steps. From the point of view of "selection" for the evolution of the human type, the arrangement in the Platypus is superior to that of the Echidna.

The "selection" factors would be:—

(*a*) Lieno-mesocolic fold lying ventral to left kidney, connecting spleen and mesocolon, and supporting pancreas.
(*b*) Pancreas outside the lesser sac.
(*c*) Shortening of the great omentum (gastro-splenic omentum) between the left extremity of the spleen and stomach fundus, with secondary peritoneal bands between the two.
(*d*) Development—not atrophy—of the distal colon.

As evolution proceeds, the pancreas, which even in the Platypus is fixed dorsally about the root of the mesentery, approaches the dorsum on the right and left sides (in the Echidna direct adhesions may be noted between pancreas and lobus caudatus), which means some approximation of spleen and mesocolon. Adhesions form between the lieno-mesocolic fold and ventrum of the left kidney as in Trichosurus—the fold ending in the Wombat at the lower pole of the kidney. Thus is developed the lieno-renal band. The development of the so-called human "intermediate" angle (which really represents the lower limitation of the renal ridge) is now easy to understand. Further evolution results in further atrophy or shortening of the lieno-renal (mesocolic) fold. The pancreas and colon become more closely related to the spleen, with an encroachment on the lower portion of the renal concavity and atrophy of the lower part of the renal ridge.

A new feature becomes added which can be effectively studied throughout the Primates, viz. the inclusion by great omentum first of the mesocolon and later of the distal colon—the pancreas now being a dorsal organ. This inclusion or fusion begins from right to left, and the importance of the mesial fold previously mentioned, between the colon and pyloric region, is seen. In a young Baboon (Catarrhina) (fig. 9), the "lieno-mesocolic" is simply a fold between the spleen and the upper part of the kidney, *i.e.* it is atrophying, and the ridge on the inner surface of the posterior angle or process has almost gone. The lower part of the renal and the colic surfaces are becoming continuous with the "intermediate" angle becoming evident. Here, however, the colon is not fixed, but the mesocolon at its commencement is partially applied to the great omentum. The colic surface is not, as in the human spleen, encroached on by the stomach, *i.e* the relationship of colon to spleen is not limited as in the human, and the gastro-splenic omentum goes almost to the tip of the anterior process. In a young Orang Utang, however (fig. 9), the colon is fixed dorsally. It is included (secondarily) in the lesser sac by the great omentum, and has only a limited relation to the spleen. The anterior portion of the colic surface is encroached on by the stomach as in the human spleen. Thus, with its fixation the colon comes into relation with a limited area of spleen only, though previously related to the whole colic surface. As to whether the stomach will encroach on the colic surface depends on the atrophy of the right or anterior part of the gastro-splenic omentum. With dorsal fixation of the spleen the membrane further atrophies and the stomach encroaches as in the human spleen. But where there is mobility, *i.e.* not good dorsal

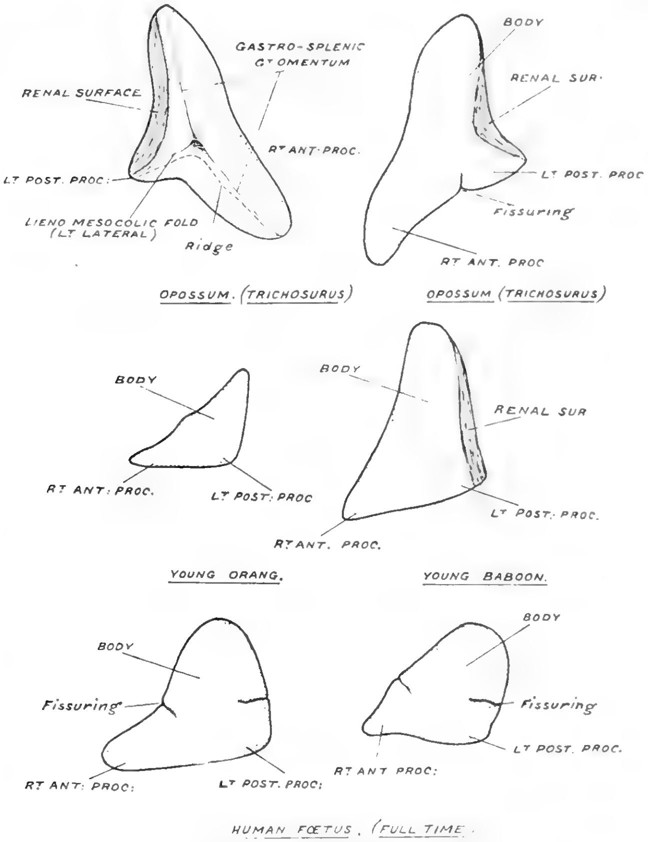

FIG. 9.—Spleens of Opossum, Orang, Baboon, and human fœtuses.

fixation, the anterior part of the lower surface is colic not gastric. Thus we may see the human foetal spleen with the remaining lieno-mesocolic (renal) fold and the anterior part of the gastro-splenic omentum extending to the extremities of the anterior and posterior processes, and practically shutting off the lower surface which is related to colon only. This is associated with a greater amount of mobility than is present in the human adult spleen.

It is worthy of note that broadening of the base of the mesentery, *i.e.* fixation of the proximal colon, begins from the mesial fold also, spreading from above downwards. Similarly, further fixation of the distal (descending) colon spreads downwards from the splenic fixation or flexure. The supporting phrenico-colic fold and the suspending lieno-phrenic, also lateral processes from the spleen to the abdominal wall, are not biological but physiological membranes freely modified to meet local conditions.

This article forms part of a monograph presented at the June meeting of the Anatomical Society on "The Digestive Glands and Spleens in Monotremes and Marsupials." As the research was carried out at the Royal College of Surgeons, it is scarcely necessary to add my indebtedness to Professor Keith, and especially to his Cavendish Lecture of last year, which gave us a new conception of the biology of the gastro-intestine. The drawings were made from my original dissections, now in the possession of the College, by Mr W. Finnerty.

THE FORMATION OF THE PARS MEMBRANACEA SEPTI. By

J. ERNEST FRAZER, F.R.C.S., St Mary's Hospital, *Professor of Anatomy in the University of London.*

THE *pars membranacea* is not only the thinnest portion of the interventricular septum, but is also in part of its extent a structure separating the right auricle from the cavity of the aortic vestibule; it cannot therefore be considered as merely a part of a structural system, more or less simple, which divides the heart into right and left sides, for the aortic vestibule is formed to the right of the plane of the interventricular septum, and is associated with the region of the earlier bulb.

Some little time ago it was suggested to me by Sir John Broadbent that a series of models showing the main points in cardiac development would be of value in demonstrating to clinical students the bearing of these points on certain lesions of the organ. I undertook to make such a series, and used the sections of embryos of 5 mm. and upwards which I possess, in the work. Many of the models were so cut up in endeavouring to follow the development as exemplified in them that they were useless for subsequent demonstration: this, however, caused me little regret, for I had determined at an early stage that the purpose with which the work had been undertaken would be served best by constructing "schematic" models—made with a free hand, founded on the actual reconstructions, but only showing the general and main conditions, so that they would bear to the real models the same relation that a scheme or diagram on paper bears to the structure or conception of which it is used as an illustration of some particular aspect or condition. Anyone who has worked with reconstruction models of the heart will agree, I think, that they are very difficult to read, after the earlier stages, owing to the rapidly growing complexity of detail and inability to see more than a small part of each cavity at once, and such models would certainly be quite useless for the purpose of teaching students.

The subject of the present paper presented itself as an important one early in the work, because it seemed that clear-cut ideas on the formation of the region were necessary for a proper understanding of development in the immediate neighbourhood. Three of the schematic models illustrate this subject, and I propose to utilise the plan of their construction in the description; they represent the bulbar and ventricular parts as simple smooth-walled cavities, opened and exposed by the removal of the ventral wall, so that the continuous cavity, necessarily flatter than is actually the case, is seen from the atrial opening to the arterial extremity where the aortic stem begins.

A diagrammatic rendering of the state of things found at a relatively early stage is seen in fig. 1. The cavity of the bulb is still easily distinguished, being partly separated from that of the ventricle by the bulbo-ventricular ridge, elongated and spur-like on section; owing to the presence of this ridge, the cavities of bulb and ventricle become continuous to the right of the position occupied by the auriculo-ventricular opening. The interventricular septum is very low, leaving a wide passage between the two ventricles, and the lower end of the septum reaches the right tubercle of the lower a.-v. endocardial cushion, while its upper end runs into the bulbo-ventricular spur, near its base. The arterial endocardial cushions are shown at the upper end of the bulb; it must not be forgotten that these figures are only schemes, and that the cushions in an embryo whose ventricular development would be at about the stage seen in the

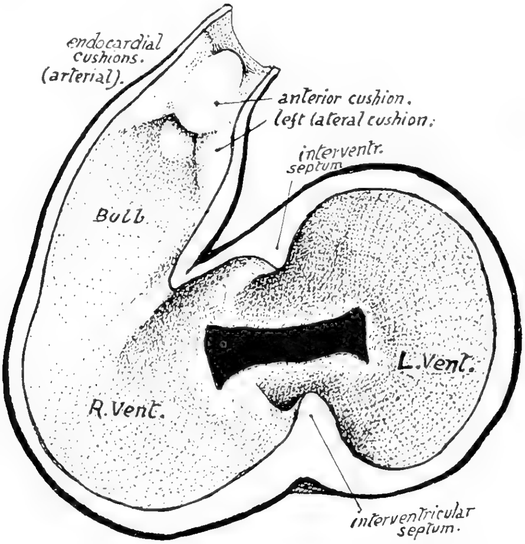

FIG. 1.—Diagram showing the relations at an early stage between the auriculo-ventricular opening and ventricles, the cavity of the bulb, and the bulbo-ventricular ridge. The distal cushions of the bulb are shown in a more differentiated state than they really exhibit at this stage.

drawing, would be merely indefinite thickenings. These cushions are four in number, and the two that are placed laterally are represented as not yet joined, so that a single opening exists between the anterior and posterior cushions leading from the undivided bulbar cavity to the single aortic stem.

It is plain that no direct passage can be made between the left ventricle and the aortic end of the bulb so long as the ridge exists between the bulbar and ventricular cavities, and this ridge now commences to atrophy, or at any rate to disappear, as is well known. I think that the process is more than a passive one, as is perhaps usually taught, and that, although there may be merely a failure in growth at first, there is an actual degeneration coming into play very soon: such, at least, is the opinion I have formed from the examination of sections, and the assumption appears to be necessary to account for the practically complete disappearance of the ridge and wall in its neighbourhood. But, whatever may be the nature of the agency bringing it about, there is no doubt of the fact of the disappearance of the ridge, and, with this, new possibilities open up for further development of the bulbo-ventricular complex.

The stage of its formation on which the heart enters now is illustrated in fig. 2; here the cavity of the "bulb" no longer opens downwards into the ventricle to the right of the a.-v. orifice, but directly over its right-hand portion. This new relationship is not attained by any special extension of the a.-v. opening towards the right: the opening has become wider with the increasing ventricular width, but that this growth is purely proportionate is evident when we look at the situation of the interventricular septum. It is, then, the disappearance of the intervening bulbo-ventricular ridge which allows the lower opening of the bulbar region of the cavity to present a wider lumen and to become continuous with the ventricle much more to the left than is possible in the earlier stages. The remains of the ridge are shown in the diagram as a low crest between the right end of the a.-v. opening and the posterior arterial cushion. The direction of the ridge, like the somewhat upturned extremity of the a.-v. opening, is perhaps to be referred to the combined effects of the growth of the right ventricle, and the disappearance of all but the basal portion of the ridge.

A change is seen in the arterial endocardial cushions, in that the two lateral cushions are now shown as fused across the centre of the lumen of this part of the bulb, thus dividing it into two openings, anterior and posterior, which are continuous in their turn with the two distinct arteries into which the arterial stem has been divided by the aortic septum. The aortic septum is not indicated in the figure: it would meet and become continuous with the upper aspect of the fused cushions if it were put in, so that the aorta would reach the posterior opening and the pulmonary artery the anterior one. The course which must be taken by the aortic blood from the left ventricle is indicated by the arrow: its channel must be still further hollowed by the complete disappearance of the bulbo-ventricular ridge, and the fusion of the a.-v. cushions will afford a continuous floor for it, separating it from the cavity of the right auricle and constituting therefore the upper part of the *pars membranacea septi*. In the meantime, other changes are taking place in this region, concerned with the closing in of the aortic channel and its separation from the corresponding aditus to the pulmonary artery. These are shown in the figure in the shape of two "bulbar" ridges: the left ridge is on the dorsal and left wall at its upper end and on the ventral and left wall below, while the right ridge is on the right wall, rather ventral in its upper part and decidedly more dorsal below, where it reaches the right side of the a.-v. opening. The ridges are continued above into the arterial cushions, which are fused, so that, when they meet, the ridges would form a roof to the aortic channel continuous with the spiral septum formed by the arterial cushions and the arterial septum above these.

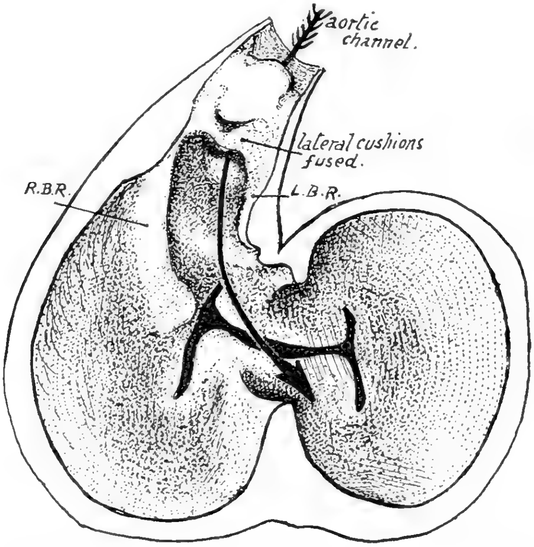

Fig. 2.—To illustrate the intermediate stages of the formation of the two channels and pars membranacea.

R.B.R., L.B.R., right and left bulbar ridges. The arrow marks the situation and direction of the aortic channel.

The lower end of the left ridge is at first separated from the upper part of the interventricular septum by the remains of the bulbo-ventricular ridge, but as this disappears the two structures become continuous, the left ridge, however, reaching the right side of the septum, as might naturally be expected, seeing that it is developed in the bulbar region.

These two ridges are, of course, the "proximal bulbar swellings" of Tandler's description. It is, perhaps, hardly necessary to point out that they and the whole bulbar region have been shown in the diagram as more elongated, for the sake of clearness, than they appear in the actual condition. Also, for similar reasons, the original direction of the arterial end of the heart has been preserved; actually, the ventral and dextral growth of the right ventricle leads, with the atrophy of the dorsal and left wall of the bulbar region, to an increasing obliquity, dorsally and to the left, of the arterial portion of the heart, but these are all non-essential points in the description of the mode of formation of the *pars membranacea septi*.

The essential matters are the apposition and junction of the upper and lower a.-v. cushions and the disappearance of the bulbo-ventricular ridge, so that the dorsal and left arterial cushions are brought very near to the right end of the a.-v. region. At the same time, or probably usually just before this, the aortic channel is separated from the pulmonary subdivision by the meeting of the bulbar ridges, the extension of the fused (lateral) arterial cushions, and the junction of this compound septum with that between the ventricles: it will perhaps be most convenient to deal shortly with this first—the septum between the right and left channels.

In fig. 3 the larger drawing represents the elements which enter into the composition of the septum between the two channels, in the way in which they are shown in the schematic model. The lower parts of the bulbar ridges meet, but they are separated above by the downgrowth of the fused lateral arterial cushions: the right ridge grows across the auriculo-ventricular opening[1] to join with the other ridge, and shortly after this the lower free edge of the septum formed in this way fuses with the free margin of the interventricular septum, with which the left ridge is, as has been seen, already continuous. The smaller drawing is from a model of a heart from an embryo of 16 mm. length, showing only this region, dissected to exhibit the composition of the dividing septum: in this the proper obliquity of the parts is, of course, a factor in the appearance, the pulmonary

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[1] This existence of a new transversely directed upper limit to the right a.-v. opening may afford an explanation of the presence of three cusps in the valve of this side, contrasting with the simpler original form of the left opening: this, however, is only a suggestion, in conformity with the disposition of the cusps on each side, for I have not investigated the matter further.

orifice looking almost directly toward the observer, and the aorta, where it is cut, being far above the level of the aortic valves. It is evident that, when the division between right and left sides is completed in this way, there is no closure of the true interventricular foramen, for the structures concerned in the separation between the two channels reach the margin of the foramen and leave its lumen patent, affording passage to the blood from the left ventricle to the aortic channel.

While this, then, is the way in which the aortic channel is being cut off from the rest of the region, the floor is formed in the manner indicated or foreshadowed in fig. 2. The fused a.-v. cushions make the main part of the bed of the channel, the bulbo-ventricular ridge has completely disappeared, and consequently the region of the arterial cushions lies just above the right end of the fused a.-v. cushions. Fig. 4 is from a reconstruction model (16 mm.), and shows the position of the cushions. A is the upper a.-v. cushion, and B the lower one, larger and better marked than the other in the model. The interventricular septum is partly cut away, but its area of contact with the lower cushion is indicated by interrupted lines: the same method is used to show the position of the right bulbar ridge, the base of which only is visible in the illustration. Evidently the right ridge, when

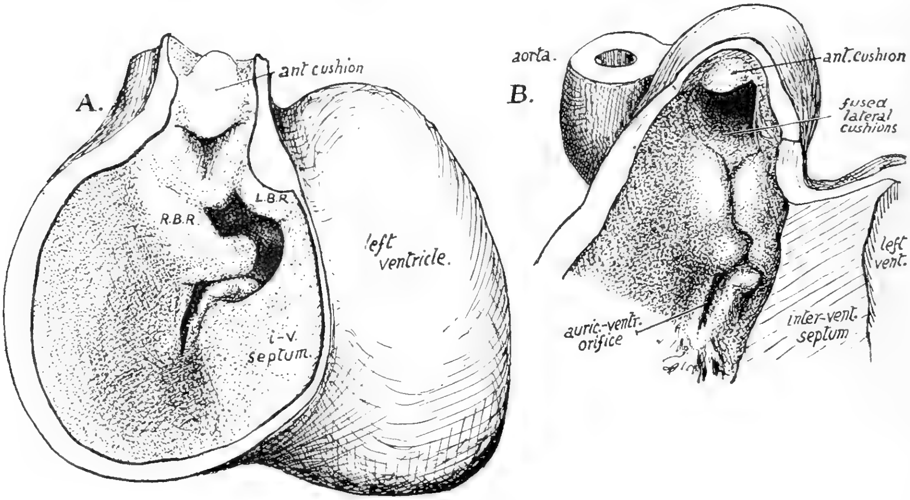

Fig. 3.

A. Diagram to illustrate the further growth of the bulbar ridges and arterial cushions to complete the division into two channels.

B. View of the infundibular aspect of the dividing septum, from the "dissected" reconstruction model, 16 mm.

it crosses the line of the right a.-v. opening, rests on the upper surface of the right tubercle of the lower cushion, the front part of which projects slightly below it (*cf.* fig. 2). Thus it is along this cushion that the right ridge comes into relation with the interventricular septum.

The bed of the aortic channel is seen to be made from a part of the lower cushion and the whole thickness of the right portion of the upper cushion. The right tubercle of the upper cushion is marked *x*, and just above this is seen the posterior arterial cushion. The proximity of the two structures is accounted for by the total disappearance of the bulbo-ventricular ridge, and probably of the left dorsal wall immediately adjacent to it. The right tubercle, *x*, is thus left with only a very narrow strip of tissue between it and the posterior arterial cushion.

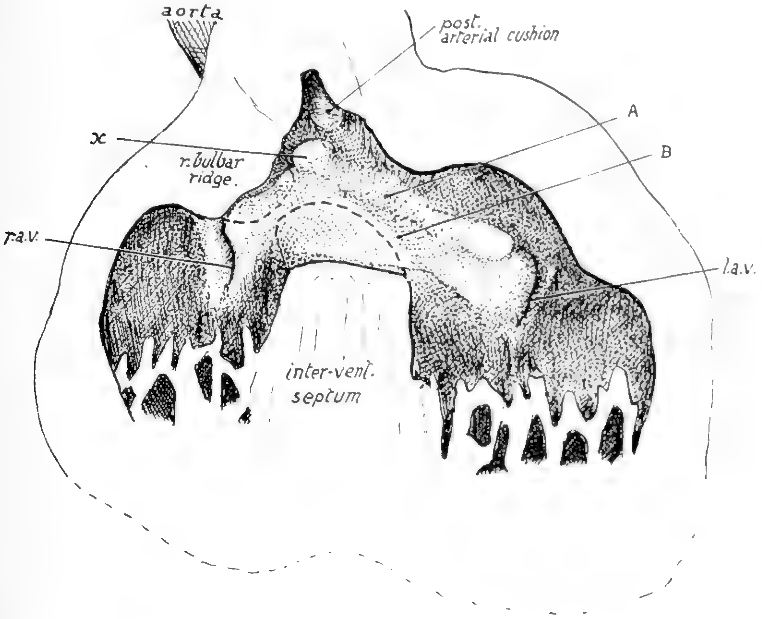

FIG. 4.—The floor or dorsal wall of the aortic vestibule, from the 16-mm. model, simplified.

A, B, upper and lower auriculo-ventricular cushions; *x*, right tubercle of upper cushion; *r.a.v.*, right a.-v. opening; *l.a.v.*, left opening.

The model from which the last figure was drawn is one of two made from embryos of 13 and 16 mm. respectively, which were constructed with a view to showing the final position of the various parts described above. In these embryos junction of the several parts has occurred, but the lines of junction are still nearly altogether apparent. In the 16-mm. specimen the sections are particularly clear and good, and the model made from it gave the figures shown in figs. 4 and 3, B. The "suture lines" were drawn and cut with the rest of the sections in which they occurred, with the result that, when the models were made, the component parts were shown very clearly. The 13-mm. embryo was treated in the same way, and the model cut up afterwards: although the sections of this specimen are very good, yet an excessive amount of blood in the heart made it necessary to refer continuously to the higher powers of the microscope to decide doubtful points in the drawings, wherefore a larger model was not made from it; but the results obtained were practically the same as in the other case—in some ways even more definite. In an embryo of 18 mm. the sections did not exhibit the original divisions of the parts with enough clearness to lead one to make a similar kind of model.

By adopting these means, actual confirmation became possible of the impressions gained from the earlier stages as to the mode of formation of the membranous part of the septum. It was seen that the upper cushion—perhaps in association with the smaller growth of this part of the ventricle, and even, it may be, the atrophy towards the right—is much less extensive than the lower one, the size of which may possibly be connected with the greater growth of the lower parts of the ventricles. Moreover, it became evident that, to make a proper channel for the stream to the aorta, the ventricular surfaces of the cushions were rendered concave and hollowed in an oblique direction, the hollow (fig. 4) affecting the lower cushion more toward the left and the upper one more toward the right. This part of the channel wall is separated, therefore, on the left of the middle line from the left auricle, and further on from the right auricle, by the endocardial cushions. It is only that part which comes into relation with the right auricle, *i.e.* the part made by the right end of the upper cushion, which forms a portion of the described *pars membranacea*; but this limitation is in all likelihood due to the conception of the *pars membranacea* as a portion of the dividing septum between right and left sides, whereas it would perhaps be more reasonable to look on the separating wall between auricular and ventricular region as being of the same value on each side, made from the same structures, and to describe both these areas as continuous, *via* the lower cushion, with the proper interventricular septum.

When the a.-v. cushions fuse, the right and left openings remain as subvertical slits, bounded on their inner sides by the upper and lower tubercles of the corresponding cushions. When the right bulbar ridge grows across the right opening (fig. 4) it cuts off the upper part of this, and leaves the definite opening formed only from the lower portion of the vertical slit, that part which is bordered by the lower portion of the lower cushion. The upper part, beside the upper tubercle, closes and thus completes the bed of the channel, but the closure would appear to be subsequent to the formation of the roof of the channel: in the 13-mm. embryo a communication can still be followed between the channel and the auricle: in the 16-mm. specimen the track is closed at its aortic end for the thickness of some sections, while in the embryo of 18 mm. no indication of its former position could be recognised with any certainty. I could not be certain whether the upper part of the left opening persisted or not.

It is advisable, perhaps, to call attention again to the fact that not only are the figures illustrating the earlier modes of formation purely schematic but even the figures drawn from the actual model have had to be simplified to some extent to make them of use for the purposes of this paper—for the intricacies which make the models so hard to read when one can turn them about in the hand would render the drawings of their actual state quite unintelligible, in all probability, to the reader who has no opportunity of handling them. It might not be considered out of place, therefore, if a little consideration were given to some of the points which are not illustrated by the diagrams.

To take, for example, the two bulbar ridges. As has been already pointed out, these are not so long as they are represented in the diagrams, and they are, moreover, much thicker, so that their lower ends form, where they meet, a thick but low mass projecting somewhat into the cavity of the right ventricle (fig. 4). Thus a relatively thick septum exists between the two channels. The upper parts of the ridges are separated by the downgrowth of the fused (lateral) arterial cushions, which makes a mass of remarkable thickness: the prolongation downwards of the cushion-mass is in the form of a double tongue, each tongue fitting it between the pulmonary or aortic surface, as the case may be, of the ridges. Thus, in fig. 4, B, the tongue seen foreshortened between the upper parts of the ridges is only one of the downgrowths, for a corresponding formation lies between the ridges on their deep or aortic aspect, and the two tongues are separated for some distance by a cleft passing upwards between them, filled by the basal portions of the ridges. Moreover, the axis of each tongue passes in a different direction; that of the deep downgrowth, compared with that of the other, is directed markedly to the left. Thus the whole mass exhibits a twist in conformity with the general spiral seen in the structures which separate the aortic and pulmonary vessels and channels.

In the diagrams the interventricular septum is shown reaching the lower a.-v. cushion, close to the right tubercle, but I do not think it would be correct to look on the solid septum proper as actually reaching the cushion. It seems to reach its lower edge and, above this, only to be connected with it by loose trabecular structure, through which a partly interrupted passage can be traced between the ventricles. Even when the whole system is closing in, this arrangement seems to hold, and here, then, the septum is formed presumably by the aggregation of looser trabeculæ, and perhaps by part of the cushion above this. The addition of loose trabecular tissue to the septum would also appear to take place on its surface, particularly on the left side: the 13-mm. model shows such tissue, seemingly pushed against this surface of the septum by the pressure of the blood-stream passing to the aortic channel, and probably the thick septum seen in later stages owes some of its size to the addition of this trabecular structure to its surfaces as the ventricular cavities get more defined and the channels opened out.

It has also been pointed out that the arterial stem is really directed more obliquely than shown in the drawings. This is due to the degeneration and disappearance of the left and dorsal wall of the bulbar region. As a result this part of its wall necessarily shortens, and in fact its wall in this part practically disappears except in its distal portion, where the cushions lie which form the semilunar valves: in this way these (dorsal and left) valves come to lie just above the *pars membranacea*. But the atrophy does not affect the front and right walls of the bulb, so that in this part more of the original cavity of the bulb might be expected to persist; but whether the wall of this part is invaded by the ventricular musculature or is pushed up by it as it grows seems a difficult question to answer satisfactorily. It is sufficient for present purposes to recognise that the disappearance of the bulb-wall is most marked dorsally and on the left, in the region of the left channel, with resulting obliquity of the part: the floor of the aortic channel becomes very short, the septum between the two channels is longer, and the front wall of the infundibulum longer still.

Summing up shortly the results which I have endeavoured to set forth in the preceding pages, it may be said that the *pars membranacea* is made from the fused a.-v. cushions, the auriculo-vestibular part from the right end of the upper cushion, the interventricular part from the lower one with some trabecular structure joining this with the proper interventricular septum. The disappearance of the bulbo-ventricular ridge is a necessary preliminary to the formation of the aortic vestibule, and is also the cause of the shortness of the dorsal wall or floor of the vestibule, and the proximity of the *pars membranacea* and the dorsal and left aortic valves. The true interventricular foramen does not close, but remains patent as the opening into the aortic vestibule from the left ventricle. The septum separating the cavities of the aortic vestibule and the infundibulum is made by the junction of two bulbar ridges, which join the free edge of the interventricular foramen below, and are separated above by a marked downgrowth of the fused lateral endocardial cushions of the arterial end of the bulb. Only the lower portion of the right auriculo-ventricular opening remains as the permanent right opening, the upper part being closed and lying in the floor of the aortic vestibule: this upper moiety is cut off from the lower by the growth of the right bulbar ridge across the opening to meet the margin of the interventricular septum. It is doubtful whether the permanent left opening is the whole or only a part of the earlier one.

BILATERAL DUPLICATION OF THE URETER.

By Douglas G. Reid, M.B., Ch.B. Edin., M.A. Trin. Coll. Camb., *Anatomical Department, University of Cambridge.*

Cases of double ureter are so well known that little need be said regarding many of the features presented by the example (found in an old male) of bilateral double ureter to which I here refer, "distinctly rare" (especially when we exclude cases in which there are not four separate openings into the bladder) though it be.

There were no other outstanding variations in the urinogenital organs or in other parts.

There were no accessory renal arteries on the right side, although the right kidney lay somewhat lower than usual. On the left side a relatively small accessory renal artery (cut by the dissectors) entered the anterior, surface of the left kidney (normally placed) above the level of the hilum.

The kidneys were distinctly enlarged. Although this is doubtless usual, it was here, in part at least, due to pathological causes (amyloid degeneration apparently secondary to tuberculosis of the lungs); and the downward displacement of the right kidney was obviously secondary to enlargement of the liver. Anatomists are sometimes too prone to overlook associated pathological conditions. As they were present here, it is unnecessary to go into details regarding the size of the kidneys. Normal in general external form, there were no indications that the parts of either kidney corresponding to a ureter had ever been separate from one another.

The renal ducts passed from their upper ramifications (to which I shall again refer) downwards parallel to one another.

On each side they had the course and relations presented by the normal single ureter.

In the abdomen, and in the upper part of their intra-pelvic course, although lying close together, they could readily be separated from one another, and their coats were distinct. But in relation to the ductus deferens they became firmly welded together, so that even with the aid of a knife it was extremely difficult to indicate the line of separation between the two tubes. Indeed (see fig. 1), immediately before (on the right side) and after (on the left side) crossing the ductus deferens, the ducts were apparently "fused" into a single thick-walled tube, circular as seen in transverse

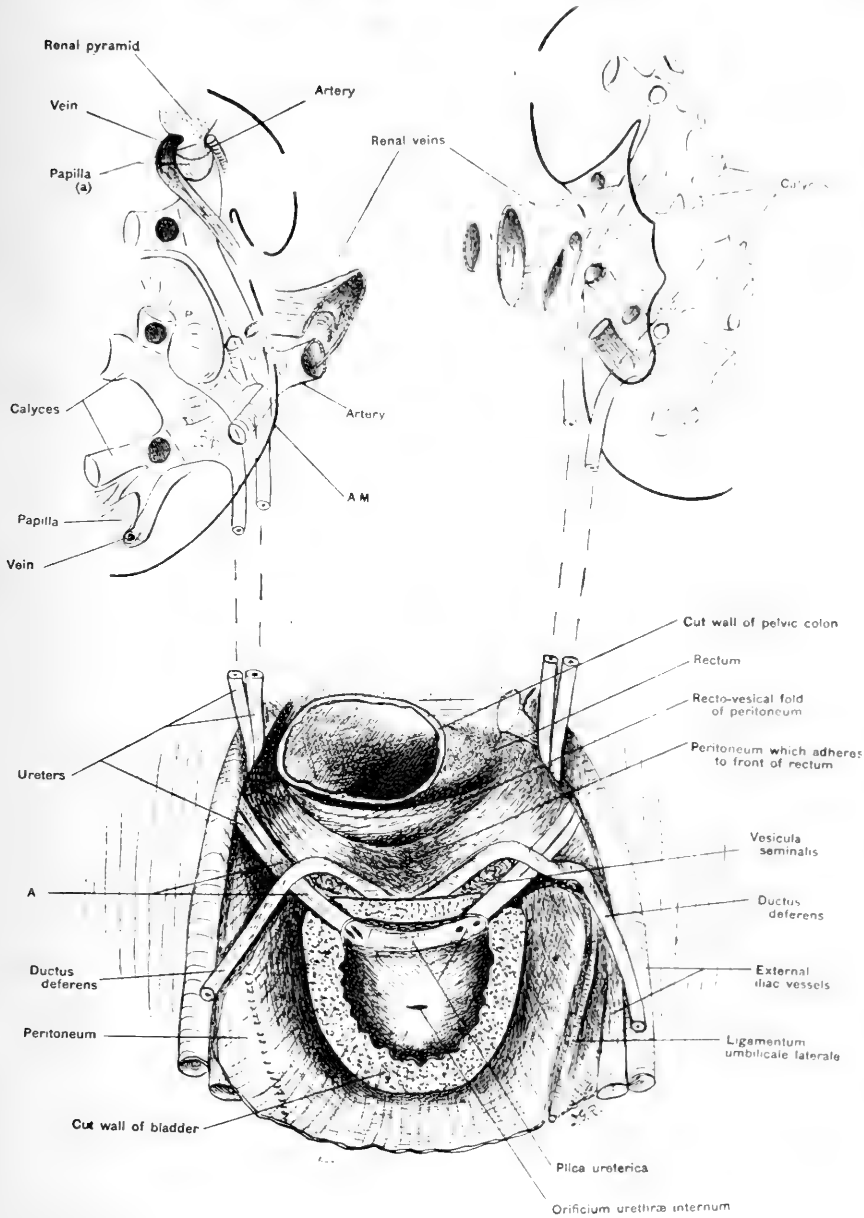

FIG. 1.—The kidneys are represented as lying lower than was the case. The bladder is viewed from above and slightly from in front. A indicates the apparently single portion of the right ducts. The whole of the convex border of the recto-vesical fold of peritoneum adheres to the rectum, so that the fold is purely rectal. One-half actual size.

section. Unless the interior of the bladder had been carefully examined, the fact that the lumen of each duct remained distinct might readily have been overlooked. As is usual, the ureter which drained the urine from the upper part of the kidney opened medial (more so on the left side, see fig. 1) to the opening of the ureter from the lower part. For this reason it "is more subject to compression" (Riesman, Hektoen-Riesman's *Pathology*, 1901).

The bladder was small and contracted. The medial openings of the ureters were one inch apart and nearly the same distance from the internal urethral orifice.

A transverse section (see fig. 2) for microscopic examination was made of the apparently single ureter (A, fig. 1).

The middle coats of the two tubes, in which the bundles of muscle-fibres were for the most part longitudinal, were completely blended over the line between them. Thus there was no indication of a connective-tissue partition between two sets of fibres; and the tunica adventitia formed a cylinder common to both tubes. Indeed, it was specially remarkable that some bundles of transverse muscle-fibres lay over the line between the tubes, so that these had undoubtedly been compressed, at the same time, by transverse fibres common to both.

Many muscle-bundles, for the most part longitudinal but some transverse, were also present between the tubes, without there being any line of demarcation between longitudinal bundles special to either, although at places the transverse fibres appeared to belong more to one than to the other tube (fig. 2). Thus transverse fibres were present capable of acting on either duct, and also of compressing both together.

Thus, in double ureter, although the middle and outer coats of the tubes may fuse together below and the duct appear single, one should always be careful to determine if there is not really a double tube.

The manner in which the ducts terminated in relation to the sinus of each kidney is accurately shown in fig. 1. A greater number of calyces (6 as compared with 3, and 8 as compared with 7 minor calyces) are in connection with the two shorter ducts than with those which extend more cranially. This is especially the case on the right side; and a similar condition, present in cases of double ureter recorded by A. T. Kerr (*The Anatomical Record*, Feb. 1911, p. 55), is regarded as a reason why the view expressed by Huntington should not apply to such cases. But doubtless it might to Huntington's case. In this connection, see also Keibel and Mall's *Embryology*, vol. ii. pp. 867–8.

On each side (see fig. 1) the arteries (and veins) which passed through the hilum and came into relation with the shorter duct crossed first in front of the longer duct, and then passed one in front and the other behind the shorter duct. The arteries (and veins), in relation to the longer ducts alone, lay in front of the duct on the right side, where there was only a relatively small twig representing a retro-pelvic artery, and on the left side passed one in front and another, equally large, behind the duct (fig. 1).

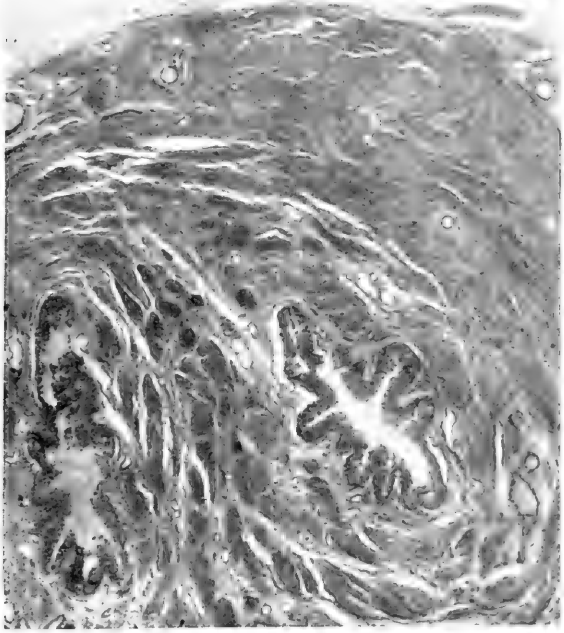

FIG. 2.—Microphotograph. The two lumina are seen. The dark areas are muscle-bundles. Only a relatively small part of the tunica adventitia is shown at the top of the photograph.

The left kidney was distinctly larger than the right; and it will be seen that there was a considerable difference on the two sides, both in the number of calyces and in the size of the ducts. Lateral to the anterior margin of the hilum the ducts of the right kidney were distinctly expanded (fig. 1). This obvious expansion was not present on the left side. These points are most noteworthy. Ralph Thompson (*Journ. Anat. and Phys.*, vol. xlviii., April 1914) states his belief that in certain conditions, owing to differences in anatomical relations, "blood, at any rate, escapes with greater difficulty from the right kidney than from the left, and that therefore the flow of urine along the right ureter may be retarded also."

The expansion of the upper parts of the right ducts was in part due to a pathological cause which I shall indicate. But it might be worth while looking for indications of the features which I describe in other specimens in which the conditions tend to be similar, and especially in thin subjects, where there is a relatively small amount of protective adipose capsule. It is noteworthy that this is prolonged into the slit-like renal sinus.

In the adult the hilum of the kidney usually looks inwards and forwards, although its anterior border is normally convex, and its posterior border straight or somewhat notched. But in this connection one must, of course, remember the orientation of the kidney. "La face antérieure regardant fortement en dehors il en résulte que la partie postérieure du bord interne est plus rapprochée du plan médian."

The direction is due, of course, to the forward projection of the bodies of the lumbar vertebræ coated by psoas major, against which the anterior margin of the hilum is not normally pressed.[1]

But on the right side, doubtless in association with the disposition of the main arteries,[2] the anterior margin of the hilum was convex and extended unusually far medially, so that the hilum looked directly inwards, and its anterior margin lay in close relation to the psoas major. At its lower part it was separated from this muscle only by the ducts and a small

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[1] As in the case of the head and neck (the visceral septum), I have found in the abdomen what may be termed a foundation stone (the posterior abdominal wall) of great value to the student in building up his anatomy of the part to the best advantage. Others must, I feel sure, follow this plan. Before touching on the intra-abdominal viscera in detail, the bones, muscles, and all the parts which enter into the formation of the posterior abdominal wall are described, and the form of this wall in relation to the form and direction of the viscera, diaphragm, etc., is dealt with. Special attention is thus early directed to the forward projection of the lumbar vertebræ because it helps the student to understand, and keep in mind, what are often mere statements made in the books regarding the direction of the viscera and their ducts and the blood-vessels. In addition to explaining why the kidneys and suprarenal glands face in a certain direction, it explains, *e.g.*, why the body and head of the pancreas of the adult face in different directions, why the pancreatic duct in the head of the pancreas inclines backwards, the backward course taken by the renal and splenic vessels, etc. It helps to explain, in association with the presence of the inferior vena cava and aorta, and, as Jonnesco points out, with the relatively smaller size of the adult kidney as compared with that of the child at birth, why the second part of the duodenum lies in a plane posterior to the more median parts. The parts are built up very largely upon the posterior abdominal wall as a "foundation stone." Thus, before dealing in detail with the stomach and intestines, the kidneys and their ducts are described, and then the suprarenal glands, liver, spleen, pancreas.

[2] See A. H. Young and Peter Thompson, *Journ. Anat. and Phys.*, vol. xxxviii. p. 1.

In connection with this, it was noteworthy that the calyces represented by the dark circles in fig. 1 were directed forwards to be attached around their associated papillæ, whilst, on the left side, the calyces represented by the light circles passed backwards. On this side the anterior "labium" of the hilum was poorly developed.

amount of adipose capsule. The liver was enlarged, and the ducts, where they crossed the anterior margin of the hilum, had undoubtedly been unduly compressed between this and psoas major coating the unyielding vertebræ. Indeed, a distinct groove was present on the kidney, indicating where the shorter duct had been compressed. In this way, on the right side, a slight hydronephrosis had been produced.

In the normal kidney, vessels may be found moulded over any convexity of the sinus wall. This moulding of the renal vessels was very obvious in the specimen, especially on the right side, where the formation of a cortex-coated convexity (P, surrounding the highest of the lower set of calyces in fig. 1), between the upper and lower parts of the sinus, had caused three large arteries and veins to be moulded around it in the form of a circle, incomplete only in one-fourth of its circumference.

In the normal kidney a vessel may sometimes be found grooving the sinus wall; and sometimes a papilla may be grooved by a vessel which is wedged in between it and the adjacent cortex. The grooving of the projection P and of the renal papilla (*a*) (see fig. 1) was especially well marked, and was due especially to the veins. The grooving of the papillæ was not so obvious on the left side, where also the veins in relation to the papillæ—which, however, were more numerous—were decidedly smaller than on the right side.

There seemed little doubt that the blood had escaped "with greater difficulty from the right kidney than from the left."

From the close anatomical relationship that the vessels may bear to a papilla, one can imagine that if pathologically enlarged they might, in some cases, interfere with the outflow of urine from the collecting tubes.

In diseases of the kidney "one astonishing feature stands out quite clearly. The right kidney is affected much more frequently than the left" (Ralph Thompson).

This is a consequent of special normal relations, in some cases associated it may be, with the anatomical conditions I have indicated.

THE GENITALIA OF THE CHEIROPTERA. By Frederic Wood Jones, *Professor of Anatomy in the University of London, The London School of Medicine for Women.*

Part I.: THE MEGACHEIROPTERA.

Material.

Of the fruit-eating bats I have examined examples of *Pteropus medius* (Dobson Cat., p. 51), of which species I have had spirit specimens of both sexes, which I owe to the kindness of Professor G. Elliot Smith, and fresh material from the Zoological Society of London.

For many specimens of *Cynonycteris ægyptiaca* (Dobson Cat., p. 74) I am indebted to Lord Rothschild. This series includes adult males and females, and one female which is apparently newly born. Other examples of the same species I have collected for myself.

Reproduction.

The presence of a more or less extensive uropatagium in many species would seem to offer an effectual impediment to copulation in the normal quadrupedal manner. I have been told by several non-scientific observers that this interfemoral membrane is circumvented in the act of copulation by the approximation of the ventral surfaces of the two individuals. Dr C. W. Andrews, who during his residence on Christmas Island had exceptional opportunities for observing the life-history of *Pteropus natalis*, confirms this account, and has been good enough to furnish me with some details. "The female," he tells me, "hung head down from a branch in the usual position, and the male hung facing her from the same branch, or from her legs, I am not sure which. Then there was a great flapping of wings and most horrid screeching which lasted for a considerable time."

On the other hand, Knud Andersen, writing of *Cynonycteris collaris* = *Rousettus leachi* and quoting (Wunderlich, *Zool. Garten*, xxxii. pp. 78–81, 1891), says that "during the act of copulation the male is suspended (as usual by the hind feet) behind the female, its underparts being in contact with the lower back of the female; an embracing with the anterior extremities does not take place."

Although some fruit bats, especially the members of the genus *Pteropus*, are easily kept and observed in confinement, it is, for some reason, difficult to obtain females. The living Pteropines imported into the London markets are usually males.

This state of affairs may result from a real numerical disproportion of the sexes, or to some sexual difference of life habit which renders the males more easily obtained. In collecting a series of embryos of *Pteropus natalis* Dr C. W. Andrews reckoned on obtaining only one female among every nine individuals shot. This rather striking feature of the economy of bats will be referred to again in dealing with the Microcheiroptera. Pteropine bats have been known to produce young in captivity, and both in London and Cologne these young have been reared at the Zoological Gardens.

Apparently all the Megacheiroptera produce but one offspring at a birth, and the reproductive life of the individual is probably late in its onset.

Sclater records the birth of a young *Cynonycteris collaris* in the gardens of the Zoological Society of London in 1870. The female was purchased on 1st November 1869, and was placed in a cage with a male of the same species: copulation was never witnessed. The young one was born on 27th February 1870, and, as Sclater says, "it is therefore possible, though not probable, that the female might have been pregnant when received." According to Andersen (*op. et loc. cit.*) the period of gestation of this species (which he indicates by the name *Rousettus leachi*) has been determined at the Zoological Gardens at Cologne to be fifteen weeks.

The young are born covered with short smooth hair (Sclater), and they cling tight to the mother's nipples, under cover of her folded wing membrane, until they are four months old (Andersen); at eight months they are not yet fully grown.

REPRODUCTIVE SYSTEM.

Robin has described the anatomy of the internal genitalia of nine species. The examples which he examined embraced the following species: *Epomophorus monstrosus* (Dobson Cat., p. 6), *E. comptus* (Dobson Cat., p. 13), *Pteropus medius* (Dobson Cat., p. 51), *P. rubricollis* (Dobson Cat., p. 24), *Cynonycteris amplexicaudata* (Dobson Cat., p. 72), *Cynopterus scherzeri* (Dobson Cat., p. 84), *C. jagorii* (Dobson Cat., p. 87), *Harpyia cephalotes* (Dobson Cat., p. 88), male only, and *Eonycteris spelæa* (Dobson Cat., p. 94).

The description and illustration of the internal genitalia, as given in this monograph, leave but little room for additional observations: but the external genitalia are not treated in an exhaustive manner.

Dobson, in his Catalogue of the Cheiroptera, has given some account of a few general features of the reproductive system, but, again, the external genitalia receive but little attention. In the second edition of this Catalogue, by Knud Andersen, even these meagre details of anatomy are omitted. There are a few papers, scattered in the literature, which deal with special points in the anatomy of the reproductive organs; but the accounts given in most works upon the Mammals may be traced to the researches of Robin. In the following descriptions I shall therefore make only brief reference to the anatomy of the internal genitalia, most attention being paid to those details of the external genitalia which seem not to have been fully described.

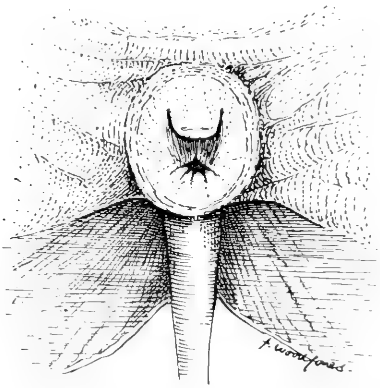

Fig. 1.—*Cynonycteris ægyptiaca.* External genitalia of a young female.

Female.—The internal genitalia of the female exhibit the curiously primitive condition of completely separated uteri. In some forms (as *Epomophorus* and *Cynonycteris*) each uterus possesses its own separate os uteri which opens into the common vagina; whilst in others (as *Pteropus*) two elongated uterine cornua are united outwardly in their lower portions into a corpus uteri, but this uterine body is completely septate within. In both cases the vagina terminates at the vulva in common with the urethra, there being no urogenital sinus. A hymen has not been described, and I am unable to detect it in any of my specimens.

There is a very complete ovarian capsule in all species. The Fallopian tubes are narrow, short, and not very tortuous.

The external genitalia of the female exhibit several points of interest. In the young female of *Cynonycteris ægyptiaca* (see fig. 1) the lips of the extroverted cloaca surround, as a prominent raised margin, the genital tubercle, the urogenital orifice, and the anus. The genital tubercle is bent caudad, and covers the urogenital orifice completely, while the clitoris, with its inconspicuous ridges, has already taken on that flattened form which is so characteristic of the adult.

In the adult female (see fig. 2) the prominence of the cloacal margins has practically disappeared; so that defined labia majora do not exist. There is, however, a depressed area which immediately surrounds the urogenital area as a sulcus. This sulcus represents the cloacal recess, and corresponds to a sulcus nympho-labialis in such animals as have well-developed labia majora. The region of the cloacal margins is defined by well-differentiated pubic hair, which differs from the general body hair in texture and in colour. The clitoris has become remarkably flattened, so that it, and its labia minora, form a leaf-like flap which covers the urogenital orifice and causes the vulva to appear as a slit-like orifice disposed transversely to the body axis. This transverse disposition of the vulva is very characteristic of the Megacheiroptera, and its similarity to the condition present in *Galeopithecus* is very striking.

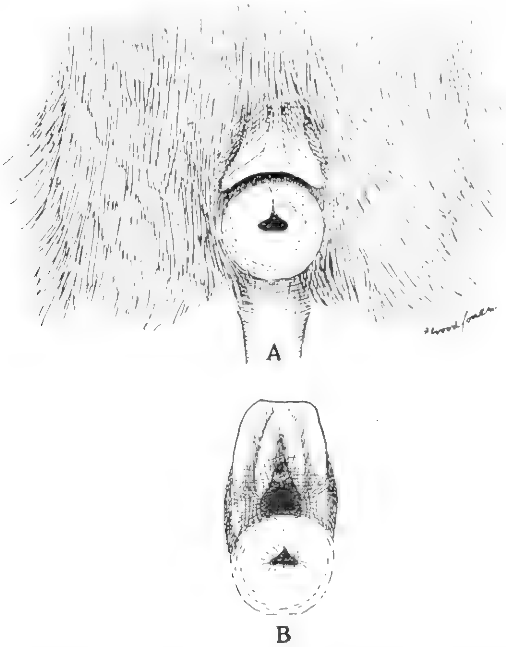

Fig. 2.—*Cynonycteris ægyptiaca.* A. External genitalia of adult female. B. External genitalia of another example with the clitoris raised.

The vulva itself is large, and the urethra opens just within its anterior margin.

In *Pteropus medius* the condition differs from the above in minor details only, the underlying plan being evidently the same.

The labia majora are rather more developed, and, over the separated pubic bones, make considerable eminences which correspond to a partially subdivided Mons Veneris: the sulcus nympho-labialis is rather better marked: but the flattening of the clitoris and its folds has not proceeded so far. The urethral orifice opens at the base of the clitoris, the vagina is large, but the vulva is not so markedly elongated from side to side. The differentiation of pubic hair is better marked than in *Cynonycteris*.

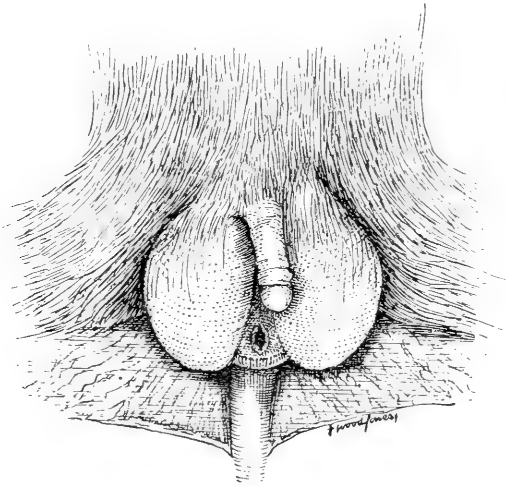

Fig. 3.—*Cynonycteris ægyptiaca.* External genitalia of an adult male, which, judging from the state of development of the testes, etc., is probably at the breeding period.

Male.—There is nothing of particular note concerning the internal genitalia of the male, and all the details have been described by Robin. The testes in all the examples that I have examined have been in the scrotal pouches. This finding is apparently merely the result of too limited a survey of material, for it is generally stated that the descensus is periodic in all bats, Megacheiroptera and Microcheiroptera alike. The testes are rounded rather than oval, and the epididymis is large. The surface of both testis and epididymis is covered with a fine meshwork of pigmented lines in *Pteropus*, but this pigment is not present in *Cynonycteris*, nor, according to Robin, in the members of any other genera dissected by him. The tunica vaginalis communicates freely with the peritoneal cavity. The vesiculæ seminales are large; the prostate does not entirely surround the urethra in all species, and when this is the case the deficiency is posterior, the anterior portion being developed. Glands of Cowper are present, and are generally very well developed.

The male external genitalia are principally noteworthy for that striking resemblance to the primate and human organs which attracted the attention of Linnæus. The penis in all is free and pendulous. It is covered by a fine skin, which is usually pigmented, and is devoid of hair except at its extreme base. A slight frænulum is present, and the well-marked median raphé runs along the lower surface of the penis and extends across the perineum to the verge of the anus. A small broad ossicle is present in the glans. In *Harpyia* the ossicle is said by Dobson to be elongated, as it is in most of the Microcheiroptera.

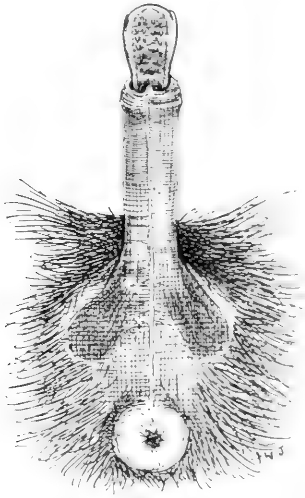

FIG. 4.—*Pteropus medius.* External genitalia of an adult male.

In *Cynonycteris ægyptiaca* (see fig. 3) the glans is simple, and the urethral orifice is terminal. The testes in all the specimens that I have examined are very large, and the scrotum, which is pre-anal in position, is pigmented in most specimens. There is a small broad ossicle in the glans.

In *Pteropus medius* (see fig. 4) the penis is deeply pigmented, the glans being black. The urethral orifice is situated upon the upper surface of the glans, which has a slightly lobulated extremity. Upon the under surface of the glans are a number of backwardly-directed corneous elevations which give a distinctly barbed character to this structure. These copulatory spurs are of interest not only as being reminiscent of the much larger structures present in some lower Mammals, but also because they have their representatives in human anatomy.

The scrotal area of *Pteropus* is deeply pigmented, but the pigment is confined to two definite patches which do not extend over the whole of the fully distended scrotal area. Distinct pubic hair is well marked. There is a small broad ossicle in the glans.

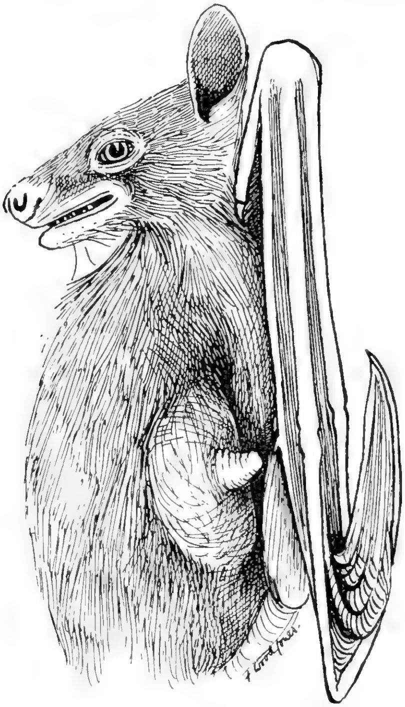

Fig. 5.—*Cynonycteris ægyptiaca*. Mammary gland of an adult female.

Mammary Glands.

The mammary glands are two in number and pectoral in position (see fig. 5). The nipples are large, and in old specimens the breast tends to become pendulous. The gland tissue, as in all bats, extends for a remarkable distance backwards upon the surface of the M. serratus magnus; much of it being actually situated upon the dorsal surface of the animal. This is evidently an adaptation to aerial life, and presumably is to permit of freedom of movement on the part of the great M. pectoralis major.

PELVIC SYMPHYSIS

In none of the Megacheiroptera is there a ventral meeting of the pubic bones. In the females the gap between the two sides of the bony pelvis is considerable, and the divided pubis form well-marked elevations beneath the skin. In the males the approximation of the two sides is closer, but an osseous union seems never to occur.

PLACENTATION.

The placenta is uniformly discoidal in the Megacheiroptera. Robin has given an admirable figure of the fœtus and placenta of *Pteropus Edwardsi* (*op. cit.*, plate viii., fig. 57), and Gervais has figured and described the fœtus and placenta of *Gnopterus marginatus*.

SUMMARY.

The Megacheiroptera, judging by their genitalia, form a fairly well-defined group, characterised by a rather extraordinary blend of characters which are stigmatised as low with characters which are ranked as high. In many of these characters they overlap with the Microcheiroptera. The entirely double uterus is matched in but few Eutherian Mammals; it cannot fail to be regarded as primitive, and its presence in an animal producing a single offspring at a birth is noteworthy. The absence of a urogenital sinus might be regarded as remarkable were it not considered in conjunction with the condition of the pelvic symphysis. The whole form of the external genitalia shows obvious cloacal outfolding, and although I have not had the opportunity of studying the actual embryonic stages, I conceive it to be certain, from the examination of the young specimen of *Cynonycteris*, that this is the process followed in development. The Megacheiroptera, therefore, fall into the ranks of the Cloacaexplicata. The apparently transverse opening of the vulva, and the marked flattening of the clitoris and its associated structures, are features which, well developed in *Galeopithecus*, are seen again in certain Microcheiroptera.

I regret that so far I have had no opportunity of dissecting *Harpyia*, since in so many points of its visceral anatomy it appears to diverge from the rest of the Megacheiroptera.

PART II.: THE MICROCHEIROPTERA.

MATERIAL.

Of the Microcheiroptera I have had material comprising numerous examples of a fair number of species. M. Robin has recorded the conditions present in many species that I have been unable to obtain, and, as a result, some knowledge is to be had of a considerable array of members of most genera. But though the combined lists of species might at first sight seem fairly comprehensive, they represent but a very small contribution towards the work to be done in investigating the anatomy of the insectivorous bats, since, in so many cases, the systematic arrangement of genera and species seems to have but little natural basis when reference is made to the anatomy of the reproductive system.

Within the limits of a genus the genitalia may display very profound modifications in apparently closely allied species. Nothing short of a thorough examination, not of skins and teeth alone, but of the detailed anatomy of a thoroughly representative collection, could clear up some of the many uncertainties still existing as to the interrelationships of the extremely large number of species.

I append a list of the species that I have dissected, and in nearly every case the species has been represented by a large number of examples. I have added in brackets the name of the donor to whose kindness I am indebted for the material, and where no such name is inserted I have collected the specimens myself.

Rhinolophidæ.

(1) *Phyllorhina tridens*, Dobs., p. 127.

Vespertilionidæ.

(2) *Synotus barbastellus*, Dobs., p. 176.
(3) *Plecotus auritus*, Dobs., 178.
(4) *Vesperugo serotinus*, Dobs., p. 191.
(5) *V. noctula*, Dobs., p. 212.
(6) *V. pipistrellus*, Dobs., p. 223.
(7) *V. temminckii*, Dobs., p. 233, ♂ only.
(8) *Vespertilio nattereri*, Dobs., p. 307.
(9) *V. murinus*, Dobs., p. 309 (Lord Rothschild).
(10) *V. nigricans*, Dobs., p. 319 (Lord Rothschild).
(11) *Natulus stramineus*, Dobs., p. 342 (Lord Rothschild).

Emballonurinæ.

(12) *Taphozus perforatus*, Dobs., p. 383 (Lord Rothschild).
(13) *Cheiromeles torquatus*, Dobs., p. 405 (C. Hose, per Prof. Elliot Smith).
(14) *Molossus abrasus*, Dobs., p. 415, embryos only (purchased).
(15) *Nyctinomus gracilis*, Dobs., p. 436 (Lord Rothschild).

Phyllostomidæ.

(16) *Chilonycteris davyi*, Dobs., p. 453 (Lord Rothschild).
(17) *Brachyphylla cavernarum*, Dobs., p. 541 (Lord Rothschild); and female embryo (purchased).

M. Robin's list includes 37 species, which overlap with the types that I have examined in five instances only.

REPRODUCTION.

It would seem obvious that, whatever obstacle the uropatagium may offer to normal quadrupedal copulation in the case of the Megacheiroptera, the impediment will be much increased in the Microcheiroptera, since, in the majority of them, this membrane is far more extensive. Further observation seems to be needed to settle the whole question. I have kept the two sexes of *V. noctula*, and some of the other common English bats, in captivity during their normal pairing season, but their unnatural surroundings appeared to preclude all manifestations of the sexual instinct. Duval, however, claims to have witnessed the act, and his account is best quoted in full. His observations were made in the spring, upon some Rhinolophids which had recently been captured. "La première fois je crus que le deux animaux se battaient, l'un d'eux reposant sur le plancher par sa région dorsal, et l'autre étant placé dessus, thorax contre thorax; je separai les deux individus, et, ayant saisi celui qui était dessus, j'interprétai facilement la véritable signification de l'acte en constatant l'état d'érection de son penis." If this be the normal method, it is certainly very strange, for it is remarkable that, whatever the actual details, the position of suspension should be departed from. It must not be overlooked that in accepting this description as a record of normal habits, one must take into account that the bats were unnaturally confined in a box, that the actual act cannot be said to have been witnessed, and that Duval was naturally predisposed to attach the most importance to what he saw, since he was endeavouring to prove that bats copulate in the spring, contrary to the opinions of most observers.

Concerning the reproductive history of the tropical and non-hybernating

Microcheiroptera there appears to be but little recorded: the observations of Gosse upon the habits of some West Indian bats seem to be unique.

Of the insectivorous bats inhabiting temperate regions, the details have been very thoroughly gathered together and woven into a complete history, thanks mostly to the outstanding work of MM. Rollinat and Trouessart. Concerning the Rhinolophid bats of France, and some of the members of the *Vespertilionidæ*, these observers have made a most interesting record of the breeding habits. Their observations were carried out upon some cave colonies of bats in various districts of central France (department of Indre) in 1896, and their conclusions may be given in the form of a brief summary, supplemented in places by additional observations culled from other sources.

Individuals apparently arrive at sexual maturity somewhat late in life, for breeding does not take place (with *Rhinolophus ferrum-equinum*, *R. hippsideros*, and *R. euryale*) until the second year at the earliest. Pairing takes place at the end of the summer season of activity. It is not till the first week of October that any spermatozoa are found in the genital tracts of the impregnated females; and only the mature second-year females taken at this time show signs of recent copulation.

During September a great change has been going on in the reproductive system of the males, and a marked enlargement of all parts of the system proceeds with great rapidity. The descended testes increase remarkably in size, and spermatozoa are liberated in enormous numbers. So great is the outpouring of spermatozoa at this time that the enlarged epididymis and vesiculæ seminales become filled, and a very remarkable overflow takes place into the bladder, causing a considerable deposit which separates from the urine. At copulation the spermatozoa are passed into the uterine cavity, and immediately there commences that activity of the glandular cervix which appears to be a universal concomitant of impregnation. In this case, however, the cervical secretion, possibly under the influence of the prostatic secretion in the seminal fluid, entirely plugs the female genital passages with a mucous "bouchon." The spermatozoa are sealed off inside the uterine cavity, and large numbers of them pass into the cornua; but their exit from the os uteri is effectively barred by the mucous plug which, becoming inspissated, forms a very intimate connection with the lining mucous membrane of the female genital tract. According to Rollinat and Trouessart, a somewhat similar plug forms about the orifice of the male genital ducts; but this male bouchon does not become so developed as does the vaginal bouchon of the female. When the formation of the bouchon is completed the animals suspend themselves in their winter retreats, and hybernate. Hybernation lasts throughout the winter months, and during the whole of this time all metabolic processes are at their lowest ebb, and the spermatozoa within the uterine cavity appear to share in this lethargy, and the whole process of reproduction remains at a standstill.

In the early months of spring (in March in Indre) the bats again become active, and ovarian activity is manifested by enlargement and vascularisation of the female organs. Ovulation takes place towards the end of the month, and early in April the right uterine horn is obviously enlarged by a pregnancy.

As soon as fertilisation is effected by the waiting spermatozoa the bouchon liquefies, and shortly disappears. When pregnancy has started there is displayed a tendency for the females to segregate themselves. Among Rhinolophids the pregnant females associate in colonies, which also contain males and females in their first year, and even some males in their breeding year. In some other cases the only males found in such colonies are first-year males, and in the case of *Vespertilio murinus* not even these males are tolerated in the female camps. In some cave colonies studied by Duval the pregnant females remained isolated from the unimpregnated first-year females. There is apparently some sexual difference in habits brought about at this time, and there are several problems awaiting solution by the field naturalist. It would appear that the pregnant females not only isolate themselves in their retreats, but that they do not even fly in company with the males in the early part of the summer. It is not impossible that they choose some different period of the night for their activities. At this time of the year I have shot a series of over twenty *Vesperugo noctula* and larger numbers of *V. pipistrellus* in the early hours of the evening without ever obtaining a female. I have never succeeded in shooting a pregnant female of any species, although at the end of the summer young females, and females in which parturition has occurred during the year, are not so difficult to obtain in this way. The pregnancy, which commenced in the Rhinolophids during the first few days of April, is completed about the 20th of June or a few days later. The period of actual gestation is therefore about (*R. ferrum-equinum*) 80 days, which is a remarkably long one; while the interval between copulation and the termination of pregnancy is little short of nine months. A most interesting account of the parturition of a bat has been given by Mr H. A. Blake, the then Governor of the Bahamas. The species on which the observations were made was said to be new to science, and I do not know if a determination of it was ever published. The female was one of a cave colony into which shots were fired to obtain specimens. She was picked up among those that fell, and was found to be alive and uninjured. She was confined in a cage, and during next morning parturition commenced. The mother suspended herself by one foot only, and used the other to assist the process of birth.

The membranes presented, and the left hind limb of the fœtus was the first part to be free of the maternal passages. The mother then used her free foot to rupture the membranes, and the liberated foot of the fœtus at once grasped the leg of the mother. Ten minues afterwards the other foot of the fœtus was extruded, and this also grasped the mother's free leg. In another five minutes the whole fœtus was entirely free of the maternal passages; it being born with its dorsal surface anterior. Directly it was born the mother lowered the young one with her leg, licked it all over, and placed it at the breast, while it was still tethered by its umbilical cord.

She bit through the cord, but carried out the process very slowly, not completing the severance till an hour after the young one was born. About ten hours after the birth of the young the placenta was extruded; the extrusion was assisted by the mother, and all the constituents of the afterbirth were eaten. It may be, considering the circumstances which led to the capture of this female, that the presentation was not a normal one; but I know of no other observations by which this may be checked. It would seem, however, that the ordered behaviour of the mother was natural enough.

The young bats are born with their eyes closed, and they remain blind for some considerable time. In the Rhinolophids the new-born young are clothed with fine hair, and the nose leaf already has its adult form; but the young of some species, such as *Vesperugo noctula*, are born quite naked, and hair is developed only at a later period. The milk dentition is present at birth. The nipple is seized at once in all species that have been observed; but in the Rhinolophids it is seized only for the purpose of actual suckling, for the inguinal anchoring nipples serve for mere fixation. The growth of the young is apparently fairly rapid, for *R. ferrum-equinum* is said to be nearly of adult size at the end of three months. In all the species that have been observed the young remain in the same colonies with their mothers, and hybernate in their company. There is evidence of a display of a rather noteworthy degree of maternal care in many species of which details have been recorded.

REPRODUCTIVE SYSTEM.

It has appeared to me to be useless to attempt a description of the reproductive system in those types that I have examined, basing the order of description upon the systematic position of the species. If this plan had been adopted it would have been possible, by combining my results with those of M. Robin, to give detailed descriptions of the internal genitalia of some fifty species, but chaos would have been the keynote of such a series of descriptions. Within the limits of a family, and even within the limits of a genus, such very wide differences are found to exist in certain details of the anatomy of the reproductive system that all sense of order becomes lost in the endless contrasting and comparison of different forms. I have therefore attempted another plan, and if there is any reliance to be placed upon the features of the external genitalia as taxonomic criteria, the findings obtained by this method might suggest a starting-point for further work upon the order. The basis of the present description depends upon the fact that there are two very distinct types of female external genitalia present in the Microcheiroptera. Type I. is in most essential respects similar to the condition seen in the Megacheiroptera. Type II. is absolutely distinct from that prevalent in that group.

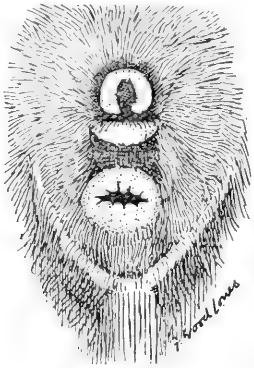

Fig. 1.—*Taphozus perforatus.* External genitalia of adult female. (An example of genitalia of Type I.)

These two types will therefore be treated separately, and the modifications seen within the limits of each type will be discussed so far as my own dissections and the published accounts will permit.

Type I.—The external genitalia of the female present as their most outstanding feature a transverse opening of the vulva such as is seen in the Megacheiroptera (and also in *Galeopithecus*). Combined with this feature, and obviously an essential part of the picture, is the abbreviation and flattening of the clitoris and its associated structures (see fig. 1). There is no well-marked Mons Veneris, and no apparent labia area. There is but poor differentiation of pubic hair, and usually there is some development of a post-anal or circum-anal fold. The external genitalia of the female of this type may be described as inconspicuous or little prominent. Combined with this type of external genitalia very varying conditions of the internal genitalia are met with.

(*a*) The uteri may be as completely separated as in the Megacheiroptera: the whole tract consisting of long separate tubes and a short and septate uterine body, each uterus having its own separated os uteri. This condition is seen in *Taphozus melanopogon* (Robin).

(*b*) The very small corpus uteri may be septate, but the septum does not continue to the os uteri, which is single. An example of this arrangement is *Taphozus perforatus.*

(*c*) The uterine cornua are very long and lead into a very short median uterine body which is not septate. *Molossus abrasus*, and, according to Robin, *Rhynconycteris naso*, *Saccopterix plicata*, and *Emballonura nigrescens* are examples of this development. The genus *Nyctinomys* presents some variability in the extent of formation of the corpus uteri. In *N. gracilis* a short uterine body is present.

(*d*) The uterine horns may be about equal to the length of the corpus uteri, as in *Phylorrhina tridens*, *Rhinolophus* (Robin), and *Nycteris* with some specific differences (Robin).

(*e*) The corpus uteri may be longer and larger than the cornua in varying degree. This development of the corpus at the expense of the cornua reaches its maximum in some such stages as *Plecotus*, *Synotus*, *Vesperugo*, and certain *Vespertilionidæ.*

(*f*) Finally, in certain *Vespertilionidæ*, the cornua have practically disappeared and the uterus becomes a simple corpus uteri, merely showing traces of the presence of cornua at its angles.

Within the limits of the forms displaying this Type I. of the external genitalia there is therefore displayed the whole evolution of the uterus from the condition of two separated uteri to a perfectly simple uterus consisting solely of a median corpus and bilateral Fallopian tubes.

Type II.—The other type of external genitalia differs utterly from that just described (see fig. 2). The outstanding feature of this type is the antero-posterior elongation of the vulva, such as is seen (amongst other Mammals) in the Primates. Combined with this feature, and as a definite component element of it, is the elongation of the clitoris and its associated embryological structures. There is usually a well-marked Mons Veneris, and some indications of a labia area. As a rule there is a pronounced development of pubic hair. A post-anal or circum-anal fold is not conspicuously developed, and the external genitalia of the female of this type can only be described as prominent. So far as the material at my command goes, I have met with this type only among the *Phyllostomidæ*, and Robin, whose material embraced more forms, records the same finding. Combined with this type of external genitalia there is but little variation displayed by the internal genitalia, the form of the uterus being practically constant. In *Chilonycteris davyi* the uterine body is produced into short cornua which are less than the uterine body in length, and, as is the rule with all bats, the right cornu exceeds the left in size. In *Desmodus* the uterus is cordiform (Robin), the cornua having been still further reduced; in *Artibeus* it is pyriform (Robin), and in *Brachyphylla cavernarum* it is in all respects like a human uterus in miniature.

The ovary in all is approximated to the sides of the uterus, and the Fallopian tubes make a rather tortuous course from the uterus to the spacious bursa ovarica.

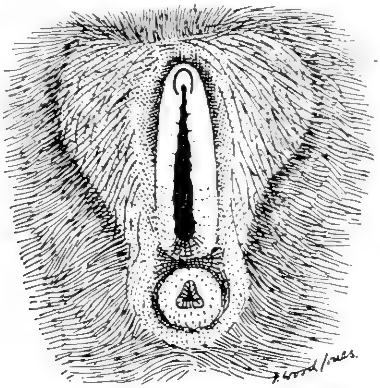

FIG. 2.—*Brachyphylla cavernarum.* External genitalia of adult female. (An example of genitalia of Type II.)

According to Dobson, *Noctilio* and its immediate allies show characters of this Type II. in so far as the vulval orifice is elongated in the anteroposterior direction. Certainly the genitalia of *Noctilio leporinus* as described by Robin differ somewhat widely from the condition seen in other *Emballonuridæ*, but according to this author the vulval orifice is in reality transverse and the unusual appearance is due to the elongation (instead of the usual flattening) of the clitoris. The *Noctilio* group is an extremely interesting one, and there are evidently a great many structural details in which it allies itself with the *Phyllostomidæ*, and especially with *Chilonycteris.* So far the opportunity of making a detailed study of the genitalia has not occurred. I am therefore uncertain which interpretation, that of Dobson or that of Robin, is the correct one.

Another candidate for Phyllostomid rank is the genus *Natulus*, and the claim is made on the strength of embryological evidence put forward by

Harrison Allen. There are apparently some characters of the embryo of *Natulus stramineus* which appear to point in the direction of such an alliance. In the adult female the clitoris is certainly elongated, but the other characters of the genitalia seem to be in harmony with the conditions seen in Type I. The vaginal orifice is rounded, but inclines more to the transverse type; the uterus is bicornuate. In the male the most remarkable feature is the elongation and tapering form of the penis. These characters possibly have some relation to the enormously enlarged uropatagium, and on the whole *Natulus* seems to range itself most naturally with the forms which fall under the first type of genitalia.

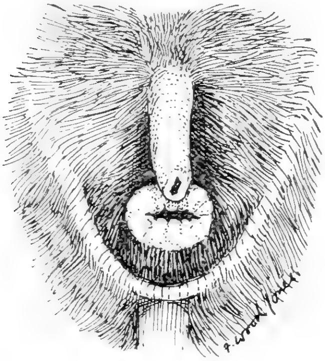

FIG. 3.—*Taphozus perforatus.* External genitalia of adult male.

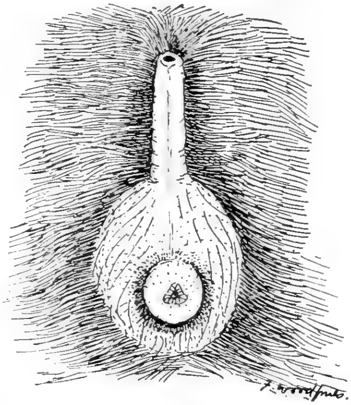

FIG. 4.—*Brachyphylia cavernarum.* External genitalia of adult male.

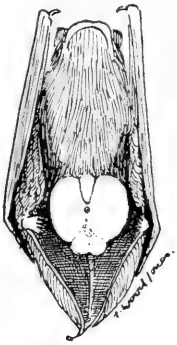

FIG. 5.—Male of *Vesperugo temminckii* during the breeding season, showing the enormous proportions of the descended genital glands at this time.

Male.—In the male the form of the external genitalia is almost identical in the two types. Illustration is made of *Taphozus perforatus* (fig. 3) and of *Brachyphylla cavernarum* (fig. 4), and further description is not needed in detail. In *Taphozus* (as an example of Type I.) the post-anal pouch seen in *Galeopithecus* and in the Megacheiroptera is well marked, and traces of it are present in the males of most Microcheiroptera of this type. In *Brachyphylla* (Type II.) and other Phyllostomids it is not nearly so well developed. The glans penis in all contains an elongated ossicle, and therein the Microcheiroptera differ from all the Megacheiroptera with the exception of *Harpyia* (Dobson). The internal genitalia of the males, however, show well-marked distinctions which separate them sharply into the same two types as are indicated by the external genitalia of the female. In Type I. the vesiculæ seminales are large and complex, while in Type II. they are reduced and simple. In Type I. the prostate has, as a rule, an anterior portion, and it usually surrounds the urethra with a ring of glandular tissue; in Type II. the prostate, though well developed, is confined to the back of the urethra. The descensus of the testes is periodic in all forms, and during the breeding season the descended organs reach to remarkable dimensions when compared to the body size of some of the very diminutive species. The condition in *Vesperugo temminckii* is illustrated from specimens shot on the wing during the breeding season in Nubia (see fig. 5). The site of the scrotal area varies. In many species of Type I. the scrotum is

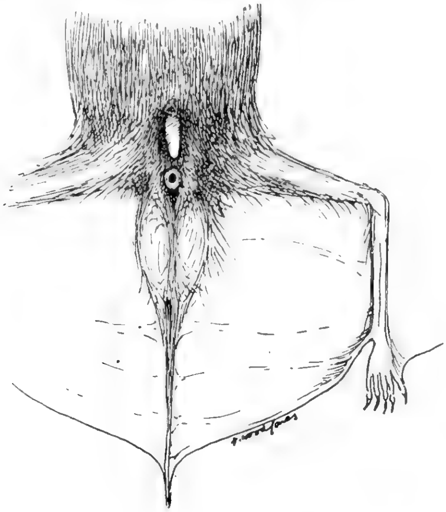

Fig. 6.—*Vesperugo serotinus.* External genitalia of an adult male.

post-anal, and this condition is figured as it occurs in *Vesperugo serotinus* (see fig. 6). A post-anal scrotum does not occur in any members of the Phyllostomids of which I have accounts or specimens.

EMBRYONIC STAGES.

The developmental stages, in such embryos as I have been able to obtain, leave no doubt that the evolution of the genitalia follows the lines of the cloaca explicata, and is effected by outfolding of the cloaca upon the surface of the body, the circum-anal or retro-anal pouch being a remnant of the cloacal margin. The phase seen in a 9-mm. male embryo of *Plecotus auritus* may serve to illustrate this point (see fig. 7). In the male

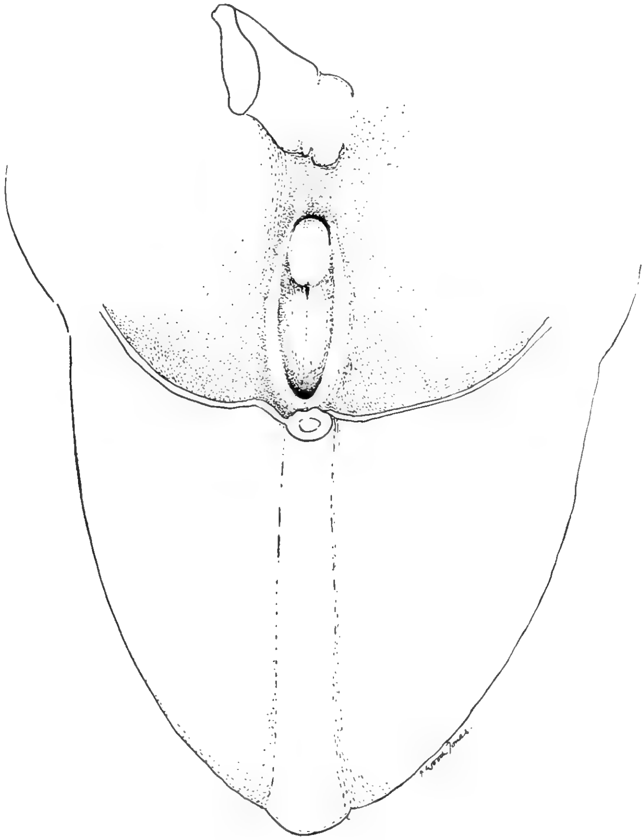

FIG. 7.—*Plecotus auritus*. External genitalia of a male embryo of 9 mm. reconstructed from serial sections.

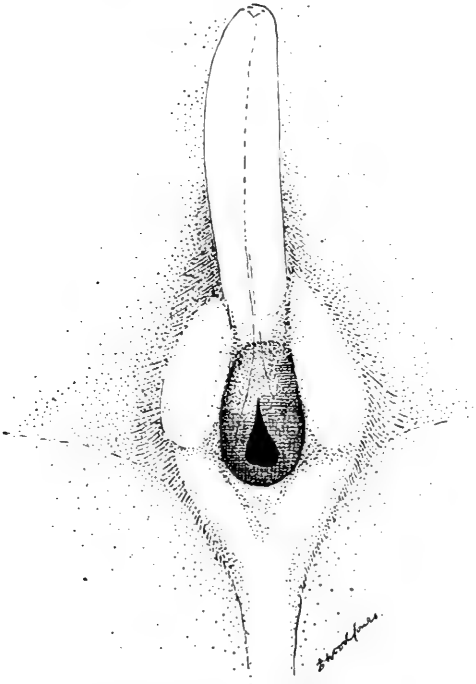

Fig. 8.—*Molossus abrasus.* External genitalia of a male embryo of 28 mm.

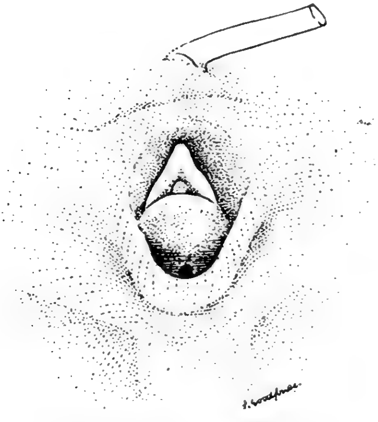

Fig. 9.—*Molossus abrasus.* External genitalia of a female embryo of 24 mm.

embryo of *Molossus abrasus* of 28 mm. the scrotal site in the cloacal margins is already well defined (see fig. 8).

In the case of the females the characters of the external genitalia, peculiar to the two types described are displayed early.

In the female embryo of *Molossus abrasus* of 24 mm. (see fig. 9) the flattened clitoris has already assumed the form so typical of *Galeopithecus* and the Megacheiroptera, and the cloacal margins are still distinctly marked. The embryo of *Brachyphylla cavernarum* is more nearly mature (32 mm.), and in it all the characters of the adult are fully determined (see fig. 10).

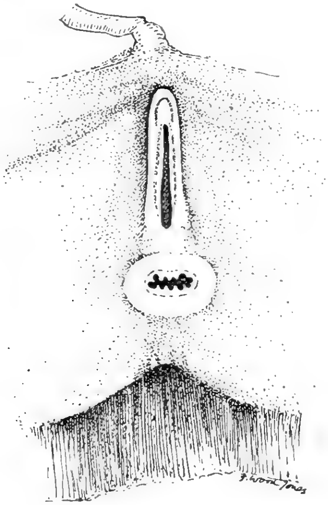

FIG. 10.—*Brachyphylla cavernarum.* External genitalia of a female embryo of 32 mm.

MAMMARY GLANDS.

In all the Microcheiroptera there is a pair of pectoral mammary glands, situated rather laterally upon the enormously broadened chest, and having a very considerable extension of gland tissue upon the dorsal aspect of the trunk. During the time of suckling the whole gland and the nipples are extremely prominent, and the nipples towards the end of the nursing period are usually much elongated. The condition of the adult functional gland is illustrated in *Brachyphylla cavernarum* (see fig. 11).

In the Rhinolophid bats there is an additional pair of nipples situated in the inguinal region. These are, as Rollinat and Trouessart described them, "faux tétons du pubis, faux tétons qui ne sont que des organes de fixation à la disposition du nouveau-né, mais ne lui servent pas à se nourrir car ils ne communiquent avec aucune glande." Elsewhere I have alluded to nipples of this class as "anchoring nipples," since such a term describes their function. These anchoring nipples do not seem to be met with outside the limits of Rhinolophids.

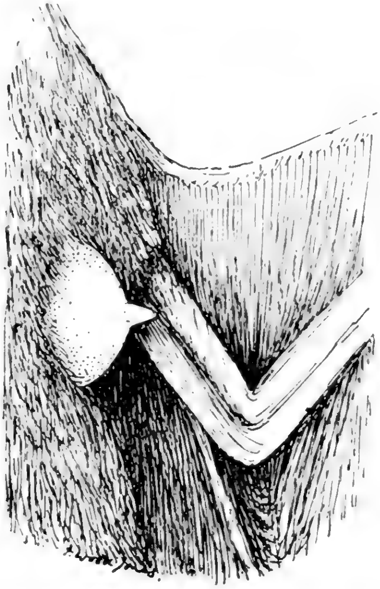

FIG. 11.

PELVIC SYMPHYSIS.

According to Dobson, a ventral meeting of the two sides of the pelvis occurs only in the *Rhinolophidæ*, and this statement appears to be substantiated by the accounts of other authors. So far as my material goes, I have met with it only in *Phyllorhina tridens*, where in both sexes a very short symphysis is present.

In the males of some other species the gap between the two pubic bones appears to be somewhat less than in the females, but even in them a true symphysis does not occur. In *Brachyphylla* the separation in both sexes is extremely wide. This limited distribution of a symphysis pubis in the Microcheiroptera is of the greatest interest, since it is only in those forms in which it is present that any urogenital sinus is found.

In Rhinolophids, where the female symphysis is slightly developed, "le méat urinaire est situé très près de l'extrémité du vagin" (Robin p. 146). In *Phyllorhina tridens* (and, according to Robin, in *P. commersonii*, *P. diadema*, and *P. armigera*) the urogenital sinus is well developed in harmony with the more elongated symphysis. In no other genera is there a urogenital sinus, for the urethra opens directly into the vulval orifice. The Microcheiroptera therefore furnish a good example of symphyseal development, with the presence of a female channel which is common to the urinary and genital systems.

PLACENTATION.

In all the species of which I have had the opportunity of examining the fœtus, and all save one of those described by Robin, the placenta is discoidal. Robin has met with but one exception, and that is in the case of *Miniopterus schreibersii*, in which the placenta is double. Although he likens this to the well-known condition seen among the Primates, there appear to be several important differences, and he himself sums up the situation by saying, "le dédoublement du placenta est un caractère d'ordre secondaire et du peu d'importance au point de vue taxonomique." Harrison Allen has described the embryonic forms of many species, but does not deal with the question of the placentation.

SUMMARY AND CONCLUSIONS.

In a general way the outlines of the genital condition of the Microcheiroptera are clear enough: there has been complete outfolding of the cloaca in all forms. It is only when pressed to an explanation of the varying details seen in the very large number of species that difficulty is encountered. That, judged by the characters of the genitalia, there are two main types embraced within the limits of the group is quite obvious. But it is difficult to know what value to attach to these types in the absence of a very great number of details regarding many species concerning which there is some degree of uncertainty.

It might be suggested that we are dealing with a group which is not truly monophylic, and that more than one primitive mammalian stock may have produced flying members, the finished individuals, derived from whatever stock, having become extraordinarily similar in their general forms by a process of convergent specialisation to their very peculiar mode of life. It is, of course, not impossible, despite the apparent inherent improbability, that this is the actual case. The Phyllostomids may represent the terminal products of a stock which became "bats" in the neotropical region, while the rest of the Microcheiroptera evolved on similar lines, but maybe from a different stock in other parts of the world. The geological record does not assist in confirming or reputing such a supposition. A great deal more work remains to be done in studying the structural details of the group before comparative anatomy can decide the question, and it is impossible to avoid the conclusion that if a tithe of the work that has been lavished on the study of preserved skins and dried skulls had been expended upon investigations with scalpel and forceps, the problem would not now be open for solution. Concerning the zoological position of the two types there can be no doubt, for the Phyllostomids are obviously more Primate-like, or higher, than are the other Microcheiroptera. Indeed it might almost seem that this family had taken to an aerial life after a fair proto-Primate apprenticeship had been served, whereas the remaining members of the group may have had a much more lowly origin.

Connecting forms, not hitherto examined in sufficient detail, may be found uniting the two types and pointing to the Phyllostomids as being the highest evolution within a monophylic group. Or the group may prove not to be a monophylic one, as the work of comparative anatomists upon other systems and organs has hinted, and certainly this study of the genitalia, limited as it is, points in the same direction.

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A NOTE ON THE RETINACULA OF WEITBRECHT.

By THOMAS WALMSLEY, M.B., *Senior Demonstrator in Anatomy, University of Glasgow.*

THE synovial membrane of the hip-joint is in extent and attachment similar to that of other diarthroses, but the retinacula of Weitbrecht (or ligaments of Stanley) lend to it a special interest. These retinacula are readily recognised on the interior of the capsule as flattened bands passing inwards towards the margin of the head of the femur from the attachment of the peripheral capsule. The following description of their constitution may be selected as expressive of current opinion. The retinacula are arranged in three groups, superior, middle, and inferior: structurally, they are synovial covered capsular reflections: morphologically, the inferior set is said to represent the persistent retinaculum of the invaginated ligamentum teres (Keith), while the superior set has been described by Frazer as being entirely due to medially directed reflections of the tendon of the M. pyriformis: functionally, they are developed either to prevent intracapsular fracture of the neck of the femur in the infant (Fawcett) or, if that has already occurred, as a means of fixation of the fragments (Hepburn in Cunningham). These descriptions form the bases of this study of these bands.

The blood-vessels which perforate the capsular attachment and pass along the superficies of the neck of the femur to enter the foramina towards the articular margin of the head may be shown by X-ray photographs of mercury-injected specimens to terminate in the metaphysis of the neck and the epiphysis of the head. From the points where they perforate the capsule these vessels derive and carry inwards indefinite fibrous prolongations of the capsule wall which are covered over or are completely invested by reflections of synovial membrane. These elements constitute the retinacula of Weitbrecht. The fibrous prolongations terminate by fusion with the superficial structures of the neck at varying and indefinite distances from their origin, while the synovial reflections pass onwards to the cartilaginous margin of the head where they form the coverings of the "synovial pads of fat." In Haver's definition the term synovial pad is applied to a mass of vascularised fat invested by synovial membrane locally modified for the production of synovia. In addition, however, to the glandular function of the covering membrane, these masses act as movable pads, which are drawn into and occupy the more obvious peripheral spaces which would otherwise occur between the articular surfaces of organic joints during their action.

This separation of the articular surfaces, as I shall show in a forthcoming publication, is peculiar to organic joints, and to fill the potential intervals movable and yielding structures are required: and such are found in two modifications (Goodsir). If space alone is to be occupied synovial pads fulfil the requirements, and associated with each pad is a synovial mechanism for the regulation of its movements; but if resistance to pressure is an additional function fibrocartilaginous tissue is necessary.

In connection with the hip-joint there are three synovial pads: two are in relation to the articular margin of the head of the femur, and the third is situated in the acetabular fossa. The femoral pads are placed in the superior and inferior concavities of the articular margin of the head at the medial ends of the synovial retinacula. Both are freely movable on the underlying tissues of the neck, so that on semi-flexion of the limb, when the whole peripheral capsule, and therefore the synovial retinacula, are relaxed, these pads react to the suction action generated in the joint within the cotyloid ligament, and move so that the inferior comes to lie on the pubic portion of the acetabular margin and occupies an interval which would otherwise be created between that part of the acetabular surface and the femoral neck adjacent to the receding margin of the head. When the inferior retinacula are stretched, as occurs in the tightening of the capsule in extension or hyperflexion, they pull on the synovial pad and flattening it on the neck of the bone remove it from any possible intervention between the articular surface of the acetabulum and the advancing margin of the femoral head. These pads, then, are placed so as to equalise the uneven articular margin of the head of the femur in its varying position on the uniform margin of the acetabulum, and their synovial mechanisms are the retinacula of Weitbrecht. The acetabular pad is placed in the acetabular fossa superficial to its thin easily detached periosteum, to which it is movably united by weak ligamentous connections and fine vascular channels. The amount of the mass varies in individual cases and may here and there seem to be deficient, especially in the upper part of the fossa, but normally is of volume more than sufficient to fill the acetabular fossa, the excess being necessary in its function. The movements of this pad are such that on semi-flexion of the limb it passes into the acetabulum under the action of the suction force within the joint and controlled by the synovial covering of the lig. teres, and abolishes the interval which would otherwise be produced by the apical displacement of the head of the femur: and this movement is visible from the peripheral aspect of the joint as an "indrawing" of the structures superficial to the "acetabular gap." On extension of the limb the excessive portion of the pad is visibly protruded through the acetabular gap, and reaches that position not by an expulsive action of the advancing apical part of the femoral head but by being actively withdrawn by its peculiar synovial retinaculum attached to the superficial part of the lig. teres.

The suction action generated within the joint is entirely within the cotyloid ligament, and is obtained because of the atmospheric vacuum within that part of the articulation in which the joint surfaces undergo separation from one another. Between the articular surfaces, however, there will be at no time any interval unoccupied by synovial fluid or unobliterated by the movable walls of the containing cavity or of the contained femoral head, since the induction of a vacuum interval by separation of the surfaces would determine the onset of a force active in the re-establishment of surface contact, but detrimental, since in direct opposition, to the working of the contracting muscles. In the lateral movement of the head of the femur which accompanies its rotation to semi-flexion from the extended position the apical interval is avoided by the movement of the acetabular pad, which falls into the acetabulum and diminishes its cubic content. The cotyloid ligament, on the other hand, is expanded by the lateral movement of the head and thus the volume of the cavity is increased, but the movements of the femoral pads avoid the appearance of any marginal interval.

We have determined these facts in the adult human subject, and after consideration of the retinacula in some of the domestic carnivora,[1] certain of the ungulata,[1] and in one of the apes, feel that the following conclusions are justified: That the incidence of the retinacula is coincident with the blood-vessels of the epiphysis of the head and metaphysis of the neck as determined by dissection of the recent specimen or by analysis of the vascular foramina in the macerated bone: that they are reflections of the synovial membrane over the fibrous sheaths of these vessels, and the sheaths are indefinite prolongations of the capsule wall: that they serve as an active mechanism in the function of the femoral synovial pads. Further, we would believe that none of them possesses any peculiar morphological significance, but that they are developed and are retained permanently where they will be free from direct capsular pressure and are associated with the blood-vessels and synovial pads purposively and precisely in those situations.

In denying the morphological significance of the inferior retinaculum it

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[1] In these groups there is no superior retinaculum, nor superior femoral synovial pad, owing to the shape and articular incidence of that area of the femoral head.

seems reasonable to conclude that the view advanced by Keith is in itself insufficient to account for the persistent retention of a structure, of importance only at so remote a stage in phylogeny: nor is it in agreement with the facts of comparative embryology. In the human embryo the lig. teres is completely free at the first appearance of the joint cleft: in the embryo tapir a synovial mesentery binds the ligament *to the capsule wall*, while in the adult the ligament is invested as in the human subject (Welcher): in the walrus, where the limb pertains to the reptilian type, the ligament arises within the joint cavity permanently enfolded in a synovial reflection *from the capsule* (Moser). We believe these facts to indicate that the inferior femoral retinaculum does not represent, in whole at least, the persistent remains of the mesentery of the invaginated lig. teres, but that this mesentery would, and possibly does occur, as the retinaculum of the acetabular pad of fat (also described by Weitbrecht) which arises in relation to the extra-acetabular part of the lig. teres and invests the blood-vessels passing through the acetabular gap to the acetabular synovial pad. As regards the superior group being the direct prolongation of the tendon of the M. pyriformis, we believe this to be the seeming result of the fusion of that tendinous expansion with the capsule, and that it is from the capsule that the fibrous elements of the retinaculum are derived. In the majority of mammalian groups (of all we have examined) the superior retinaculum is absent, and this we have associated with the shape of the articular femoral head.

In the infant the retinacula are of relatively larger size than in the adult, and we would relate the fact to the relatively larger blood-vessels which pass to the head at that period.

A CASE OF CONGENITAL ATRESIA OF THE ILEUM.

By CECIL P. G. WAKELEY, M.R.C.S. Eng., L.R.C.P. Lond., *House Surgeon, King's College Hospital; Assistant Demonstrator of Anatomy at King's College, London.*

THE specimen described in this paper occurred in a female full-term child, which was brought to King's College Hospital on the second day after birth with symptoms of obstruction. The signs pointing to obstruction of the small intestine, the child was operated upon at midnight the same day, an exploratory laparotomy being performed through the upper part of the right rectus muscle. The stomach and proximal part of the small intestine were found to be enormously distended and antiperistalsis could be plainly seen. There was a marked narrowing of the intestine in the upper part of the ileum (fig. 1). The rest of the small intestine beyond the constriction was very small and received its blood supply from a pedicle of mesentery, in which the vessels were dilated and thrombosed. The cæcum and the rest of the large intestine were normal.

As regards treatment, a gastro-enterostomy was contra-indicated on account of the rest of the small intestine having a defective blood supply, its vessels being thrombosed. It would have been useless to have performed a jejunostomy, because the child could not have lived with merely a stomach and at most 20 inches of small intestine; and, besides this, the condition of the jejunum was very bad, it was almost black in colour and covered with flakes of coagulated lymph. Having carefully considered these points, I very reluctantly replaced the intestine and closed the wound. The child died eight hours after the operation.

At the post-mortem examination no other congenital defects were found.

On making a more detailed examination later it was found that the distended part of the gut above the constriction contained meconium. The distal part of the ileum and large intestine were empty. The mesentery opposite the constriction and the part of the intestine beyond this contained numerous enlarged lymphatic glands and the veins were thrombosed. The atresia extended for a distance of about 2 cm. and the greatest diameter here was less than 4 mm.

A transverse section (fig. 2) through the middle of the imperforate part showed that the lumen was blocked by a loose tissue consisting in the centre of detached extremities of the villi and fibrinous strands, external

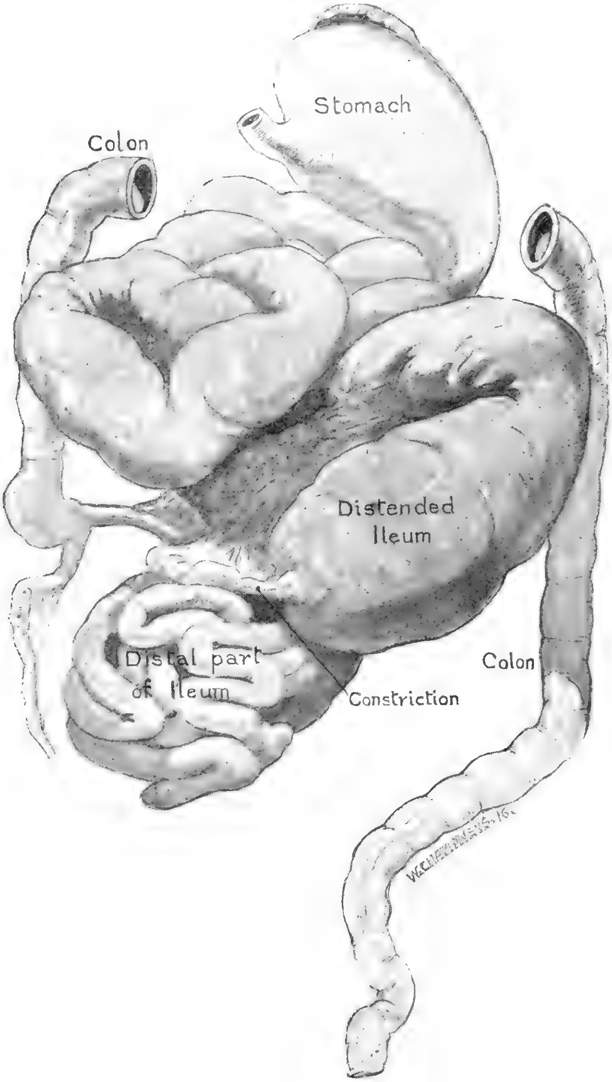

Fig. 1.—Atresia of ileum.

to this was an intermediate zone of connective tissue, continuous with the interglandular tissue surrounding the basis of Lieberkühn's glands. These lay in the third or outer zone. In the intermediate zone the epithelium had degenerated, and was replaced by a granular material and fibrinous bands.

A drawing of a somewhat similar case was kindly sent by Professor P. Thompson for exhibition with my own specimen. The imperforate part of the intestine in his case was, however, much nearer the ileo-cæcal valve, and the intestine was reduced to a fibrous cord running along the free border of the mesentery and joining the proximal and distal parts of the intestine.

FIG. 2.—Transverse section through imperforate part of ileum showing thrombosed vessels in the mesentery.

The interest of these cases lies principally in the possibility of saving life by intestinal anastomosis. Quite recently N. P. Ernst of Copenhagen has published (1) a case in which he succeeded in saving the life of a child by performing a duodeno-enterostomy for an atresia situated below the papilla of Vater. He brought a coil of jejunum 4 inches from the duodeno-jejunal flexure upwards in front of the transverse colon, and united it to the duodenum close to the hepatic flexure.

Another successful case was reported by P. Flockens (2), where atresia was present between the middle and lower thirds of the small intestine. The bowel was reduced to a fibrous cord, at the free edge of the mesentery, which united the blind ends of the bowel. An entero-entero-anastomosis was performed, and the child made a complete recovery.

As regards the etiology of these cases there appears to be no very satisfactory explanation of the cause of the atresia. The view most commonly held is that of Tandler (3) and afterwards confirmed by Forssner (4), viz. that the normal more or less complete obliteration of the lumen of the tube, by proliferation of the intestinal epithelium, persists. This proliferation occurs in human embryos between 5 and 30 mm., and is most marked in the duodenal region. Moreover, it is stated that the gut fails to expand owing to pressure exerted by the mesodermal wall on the enclosed epithelial cord.

Professor Kreuter, on the other hand, though agreeing in certain points with the former, believes that the epithelium degenerates in places, and that here and there rounded cells from the mesodermic wall penetrate it, and thus reach the surface of the mucous membrane and eventually lead to occlusion.

Some cases appear to be due to constrictions from without by bands, while others appear to be associated with twists and bends of the gut, *e.g.* those at the proximal and distal flexures of the umbilical loop of the intestine.

Professor P. Thompson suggests that in his specimen, the atresia lying within the sphere of influence of the vitelline duct, it may have arisen when the duct was separated from the summit of the intestinal loop at the end of the first month.

My specimen and others, in which a considerable length of the intestine is imperforate, suggest that a twist or blocking of the mesenteric vessels resulting in a defective blood supply of part of the intestine may in some cases be the immediate cause of the arrest in its development.

In conclusion, I should like to offer my best thanks to Dr R. J. Gladstone for so kindly helping me with the dissection of the specimen and showing it, in my absence, at the meeting of the Anatomical Society.

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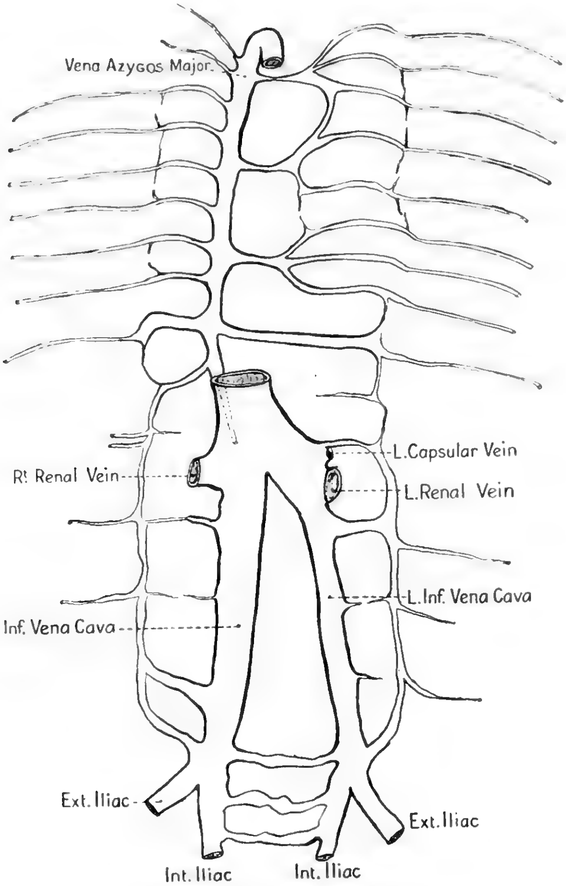
(2) Flockens, P., *Nederland. Tijdschr. f. Geneesk*, 1911, vol. i., No. 18.
(3) *Morphologisches Jahrbuch*, 1902, Bd. xxix.
(4) *Nord. Med. Archiv*, 1905, Afd. i., No. 20.

A CASE OF DOUBLE INFERIOR VENA CAVA. By M. F. Lucas, M.B., B.S., *Lecturer on Embryology, The London School of Medicine for Women.*

THE accompanying diagram illustrates the arrangement of veins on the posterior wall of the trunk of a male subject, æt. 70, dissected in the anatomical department during the present session. The vena cava is double below the entrance of the renal vessels, the left inferior vena cava



A case of double inferior vena cava.

joining the right by a very large connecting trunk at the level of the second lumbar vertebra. The right and left inferior venæ cavæ lie on the anterior aspect of the bodies of the lumbar vertebræ and terminate below in right and left internal and external iliacs, the tributaries of which are quite normal. The vena azygos major on the right side, and the anastomotic loops (venæ azygos minores) on the left side, lie on the bodies of the thoracic vertebræ in a corresponding position to that occupied by the inferior venæ cavæ. The vena azygos major, besides communicating below with the right ascending lumbar veins, also opens into the undivided portion of the inferior vena cava on its posterior surface. The lumbar veins arise from bilateral vessels (of considerable size on the right side) which run vertically on a line joining the roots of the transverse processes of the lumbar vertebræ, and communicate below with the inferior venæ cavæ and above with the venæ azygos. There are a few small veins connecting adjacent intercostal veins across the heads of the ribs, and these are in line with the large vertical veins found in the lumbar region. The symmetrical arrangement of the whole anomalous system of veins is particularly striking.

ON THE PROPORTIONS AND CHARACTERISTICS OF THE MODERN ENGLISH CLAVICLE. By F. G. PARSONS, *Professor of Anatomy in the University of London.*

THE investigations with which this paper is concerned have gradually grown out of the desire to know whether we could form any idea of the shoulder breadth and physique of prehistoric races from a study of their clavicles in the same way that we estimate their height and the muscularity of their lower limbs from their femurs. I was also anxious to know whether the clavicle is of any use in the difficult matter of sexing a skeleton.

I was more happy in clavicular than in femoral measurements, because I was able to examine the bones of 103 males and 80 females, of whose age and sex I was absolutely certain; while in the case of the femur investigators have to content themselves with a few senile bones of known sex or else to guess the sex in a large mass of doubtful bones and then to deduce sex characteristics from the bones thus arbitrarily sexed.

The people on whom these clavicular measurements were made belonged to the English lower and lower-middle classes. They were all full grown, and their average age was 44 years. None were under 18 years, and all cases in which the bones were diseased or the body deformed were excluded.

In the first place the shoulder width was taken with a large sliding scale specially made for the purpose.

At first I took the biacromial breadth recommended in the anthropological text-books, but after using it for some time on both the living and dead subject, I came to the conclusion that it is a thoroughly unpractical and unreliable measurement except in the thinnest bodies.

I have found competent observers differing by two, three, or more centimetres in this measurement, and I have made as great differences myself in remeasuring the same body after a short interval; in fact, I was so disappointed that I left off taking it and contented myself with measuring the shoulder width at the upper part of the deltoid. I know, of course, that the width here depends a good deal on the fatness and muscularity of the body, but it is a measurement on which different observers can agree and, when a large enough number of cases is taken, a much more reliable average established.

I find that, after measuring the biacromial and the total shoulder width of 73 living adults, the total width at the upper part of the deltoid averages 35 mm. more than the biacromial in 21 males and 28 mm. more than the biacromial in 52 females. The total averages were:

	Biacromial.	Total Width.
21 ♂	379 mm.	414 mm.
52 ♀	348 „	376 „

These measurements were taken from young adults at St Thomas's Hospital and the London School of Medicine for Women.

I found it easier to determine the biacromial measurement in living than in dead subjects, but even then it was necessary to take the mean of three separate attempts at measurement in many cases.

My first point, then, was to see what proportion the length of a clavicle bears to the width across the shoulders at the upper part of the deltoid, and here I was at once confronted with the difficulty that the two clavicles are seldom the same length, for 83 left male clavicles gave me an average clavicular length of 153 mm., while 70 right male bones averaged 151 mm. In the females, on the other hand, I found that 64 left and 65 right bones both gave me an average of 138 mm.

But, of course, many of these measurements were made on people from whom I had only been able to secure one clavicle, so I decided to check them with 50 males and 50 females in whom the clavicles of both sides were available. The result of this was that in 50 males the left clavicle averaged 154 mm. and the right 152 mm., while in 50 females the average was 139 mm. on the left and 138 mm. on the right.

I therefore believe that the left bone averages one to two millimetres more than the right in length, but I do not think that this is likely to make any great practical difference in working out the proportion of the shoulder width.

For instance, by dividing the shoulder width into the clavicular length × 1000, I found that with 50 male bodies in which both clavicles were present, the left clavicle averaged ·387 of the shoulder width, while the right averaged ·382. In 49 female bodies with both clavicles available, the left averaged ·383 and the right ·380.

To take a concrete example, let us pick out at random No. 58 from the left female clavicles. The clavicular length of this is 134 mm., and if this is divided by ·383, the average proportion for left female clavicles, we should estimate that the possessor of the bone had a shoulder width of about 35 cm., while, as a matter of fact, she was 34·1 cm. across the shoulders. This, I think, is as near as we have any right to expect to get in practice when we consider the many disturbing influences at work; for this particular individual might have been fat or lean, muscular or attenuated, while the left clavicle, which we are supposing the only clue given us, might in this particular case have been a good deal shorter or a good deal longer than its fellow. I submit that if from a clavicle we can deduce the actual shoulder width of an individual to within a centimetre or two, we are distinctly adding to our power of reconstructing the whole contour of the body from a part.

Of course I am far from claiming that what is true for modern English people must be true for all races, but we can only advance a little at a time and that with great labour.

We have seen that in both sexes the left clavicle seems to average a little more than the right. Is this in spite or because of the fact that the right arm is used more constantly than the left? Unfortunately, I have no means of knowing which of the possessors of the clavicles were left-handed, but I can think of two possible ways in which increased use of a clavicle might lead to shortening: firstly, that it might increase the curvature and thus bring the two ends nearer; and secondly, that it might lead to an earlier bony union of the epiphyses, which would stop further growth. Both these points will be investigated later; but for the present I shall content myself with recording that out of 100 individuals in whom the length of both clavicles was available, the left was the longer in 54 per cent., the right in 34 per cent., while in 12 per cent. the length on the two sides was equal. That the longer clavicle is so comparatively often on the right side makes it unlikely that left-handedness is the cause or, at any rate, the only cause. I would further record that while the left bone averages 2 mm. more in length than the right, the differences between the two may be as much as 9 mm.

It is the occasional presence of these extreme cases that makes it desirable, whenever the chance occurs, to take the mean length of the two clavicles and to divide it by the mean proportion of the clavicle to the shoulder width on the two sides. Even by this method considerable error may arise in individual cases, errors of 3 cm. or even more, though this, of course, would be expected by anyone who realises the great difference which a plentiful supply of subcutaneous fat makes in the breadth of the shoulders; but when a series of ten cases is available the average, for practical purposes, is always reached.

If it is thought advisable to apply the ratio to a single skeleton, it must be understood that the result will be an approach to the actual shoulder width during life, presuming that the individual was moderately supplied with fat and muscle.

THE CURVATURE OF THE CLAVICLE.

After taking the clavicular length and finding its proportion to the shoulder width, I sought a method of estimating the curvature of the clavicle, and at last adopted the following plan.

An accurate contour of the clavicle from above is drawn with the dioptograph, but before this can be done it is necessary to be sure that the bone is properly orientated, and it should be noticed in doing this that the facet for the first rib is not directly below the sternal end but lies below and in front. There is generally a small tubercle for the sterno-mastoid muscle directly above the sternal end, and this I found very useful; but, failing this, as long as the anterior and posterior borders of the acromial third of the bone are in the same horizontal plane, the clavicle is very nearly in the living position.

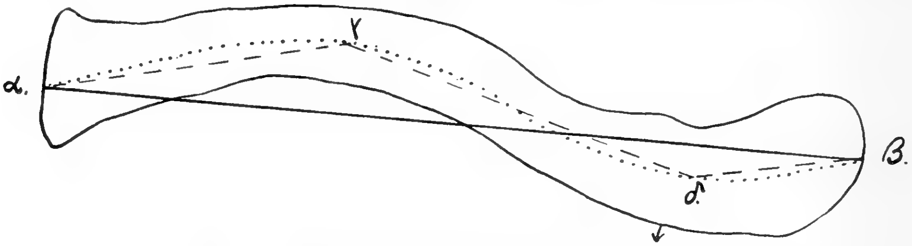


FIG. 1.—Method of estimating the curvature of a clavicle.

When the contour has been drawn the central points of the sternal and acromial ends (α and β, fig. 1) are joined by a straight line, and then the central axis of the bone is drawn as a curved line which is always half-way between the anterior and posterior borders.

The points of greatest anterior and posterior convexity (γ and δ) are then fixed on the curved line, and the four points α, γ, δ, β are joined by straight lines.

In this way two angles are described—an inner one (α, γ, δ), open backwards; and an outer one (γ, δ, β), open forwards. When the size of each of these has been taken by means of a protractor and the two added together, the sum will be the index of curvature; though, of course, the lower the index the more curved is the clavicle and vice versa.

The figures obtained in this way give me the following results:—

In 83 male left clavicles the average index of curvature is 301, while in 70 right males it is the same; but when the corresponding bones of opposite sides of fifty males are taken the left index is 300 and the right 301. In the same way the average index of 64 left female bones is 306 and of 65 right female bones 305; but when fifty actual pairs of bones are dealt with the left is 305 and the right 304.

There is therefore pretty definite evidence that the male bones are more curved than the female, while in both sexes the right bone is a little more curved than the left.

As the difference in the curvature between the two sides only amounts to 1°, it does not look as if it could account for the greater length of the left clavicle; but, in order to test the matter further, I picked out the fourteen cases in which the left bone was 5 or more than 5 mm. longer than the right and added up the indices of curvature, but to my surprise the right bones in these individuals were, on the average, slightly less curved than the left.

A similar experiment on the 12 females in which the left bone was more than 3 mm. longer than the right showed that the right bone was more bent than the left to the extent of an average of 4°. I do not dare to lay any stress on this last, while the result of the male bones is so different, and I cannot think that the greater length of the left clavicle is to be accounted for by the greater curvature of the right.

A casual inspection of a number of clavicles gave me the impression that the bones of old people were more curved than those of young; but on picking out the 25 left male clavicles from subjects between 18 and 35 years of age I find that the average curvature is 300, while the average for all ages is, as we have seen, 301. If, therefore, there is a slight difference, it is evidently so slight as to be of no practical value in determining the age of bones.

THE AVERAGE CONTOUR OF THE CLAVICLE.

The measurements which follow in the tables have been planned with the object of enabling a diagram to be drawn of an average modern English clavicle, of both sexes, from above and from in front.

By putting these together a model of such a clavicle may be constructed, and this may serve as a standard of comparison with those of other people.

Having determined the length and degree of curvature of the clavicle, the next thing is to note the position of the points of maximal curvature. This is done by recording the lengths of the three segments $\alpha\gamma$, $\gamma\delta$, and $\delta\beta$ (fig. 1), which are spoken of in the tables as inner, middle, and outer segments.

When these are known it is possible to draw the framework of a single clavicle or, as in fig. 2, of the average of a series. The next step in the reconstruction of the average clavicle is to put in the central axis as a curved line with its maximal convexities at γ and δ, and on this the contour of the bone may be built up if its width at certain points is known.

I have contented myself with taking the width at five places, and with these I find that a very accurate reconstruction of an individual clavicle is possible; but it is clear that the more measurements there are the greater will be the accuracy and the less left to the fancy of the draughtsman.

The first width (see fig. 3) is that of the inner extremity, and it, like all the other widths, was measured on the dioptographic tracing with a steel tape and then on the actual bone with calipers, thus checking the tracing for this and other purposes.

In the left female clavicles the average measurement is 21 mm.

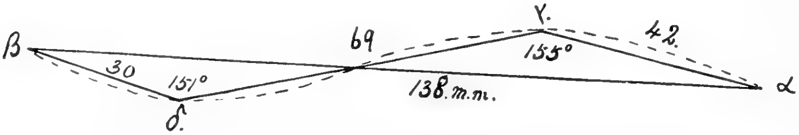


Fig. 2.—Framework for reconstruction of 64 left female clavicles.

The second width is at the inner angle and is 11 mm.

The third width is taken wherever the bone happens to be narrowest, and, in order to fix its average position, its distance from the point a along the line $a\beta$ has to be ascertained. This average distance in the particular group of female bones under study is 52 mm., but its range of variation is very great and varies from 25 to 91 mm.

The fourth width is at the conoid tubercle, which is at or close to the outer angle of the bone, though I have thought it wiser to take its distance from the point a in each case. The average width here is 18 mm., and the average distance from a 104 mm.

The last width is the greatest obtainable in the acromial third of the bone, and averages 21 mm.

With these widths the average contour of the left female clavicle from above may be completed (fig. 3), and in the same way, by taking the proper measurements recorded in the tables, the contours of the male bones (figs. 4 and 6) may be obtained.

The contour of the bone from in front shows so little constant curvature that I have not thought it worth while to estimate; though no doubt it could be done in the same way in which the antero-posterior curves were measured; sometimes there is a distinct convexity upwards of the sternal two-thirds of the bone, while at others the central axis is practically a straight line.

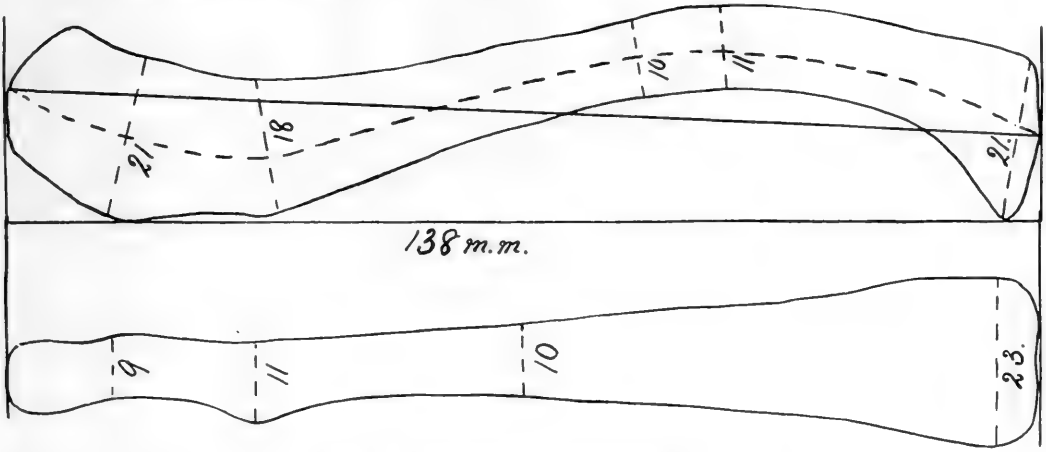


FIG. 3.—Average of 64 left clavicles, ♀.

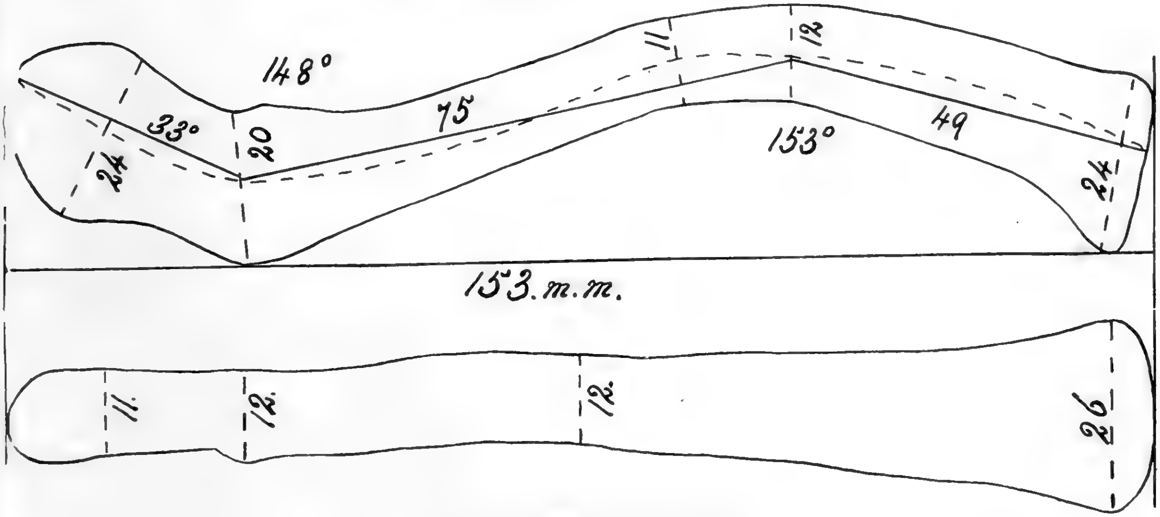


FIG. 4.—Average of 83 left clavicles, ♂.

I have satisfied myself with taking the depth at four places: firstly, the inner end; secondly, the middle of the bone; thirdly, at the conoid tubercle; and fourthly, the least depth of the acromial end. The average depths are recorded on the contours from in front in figs. 3, 4, 5, and 6.

Sex Characteristics of the Clavicle.

Since we are in possession of a fair number of clavicles, the sex of which is known, we can test the value of various possible sex characteristics.

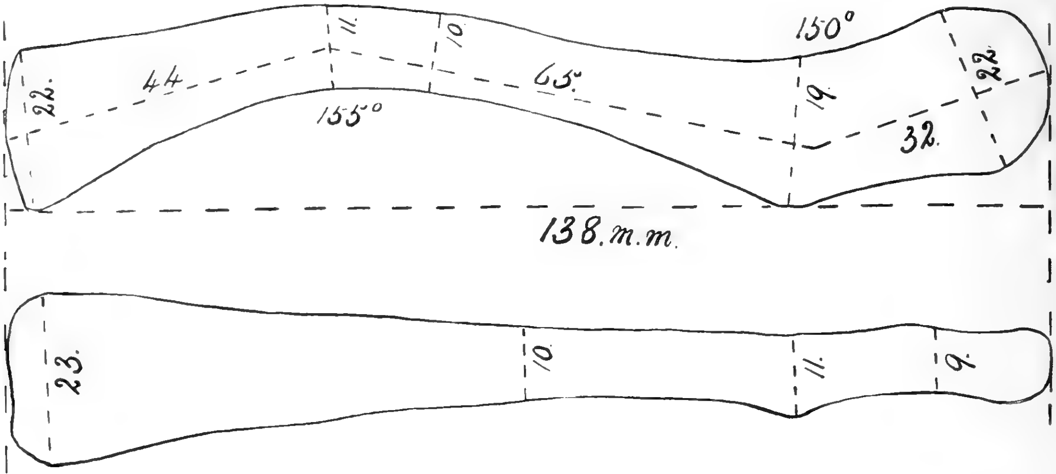


Fig. 5.—Average of 65 right clavicles, ♀.

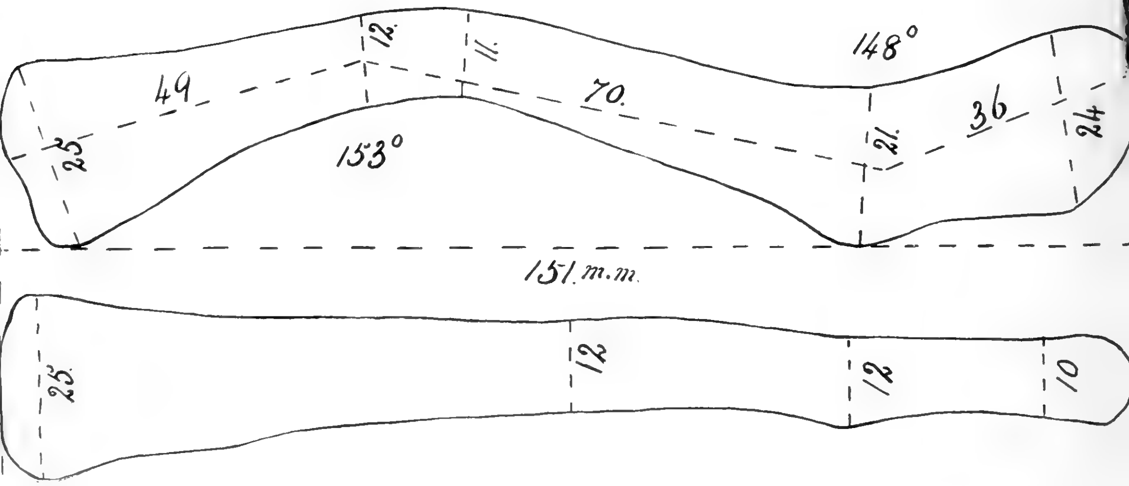
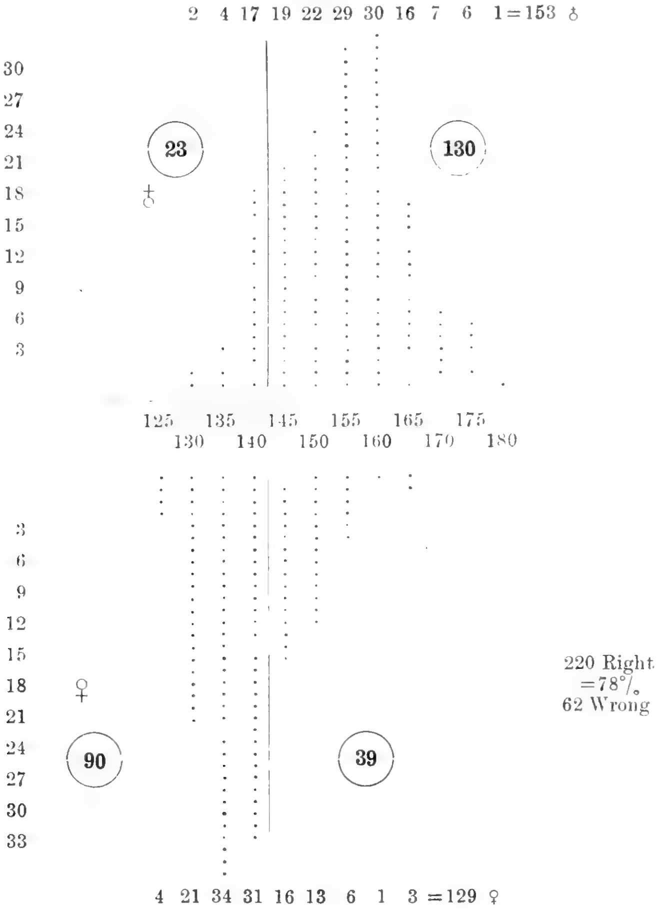


Fig. 6.—Average of 70 right clavicles, ♂.

Length.—As has been stated already, the average length of 70 male right clavicles is 151 mm., and of 83 left 153 mm.; while 64 left and 65 right female bones each averaged 138 mm. We may, therefore, conclude that the average male English clavicle averages 14 mm. more than the female in length, but when the lengths are arranged in a chart (chart 1) it is clear that the overlap is considerable. If we place

CHART NO. 1.—CLAVICULAR LENGTHS.



the dividing line just below 145 mm. it will be seen that 262 of the 282 bones would be rightly, and 62 wrongly sexed. In other words, there would be an error of 22 per cent.

It must, however, be borne in mind that this chart does not give us a true estimate of the chances, because the number of female observations is only 129, while that of the males is 153. To get a just estimate we must add 24—the difference between 153 and 129—to the female side of the chart and must distribute it proportionately to the size of the different columns on that side. When this is done the chances in favour of a bone under 145 mm. being female are as 106 to 23 instead of 90 to 23; that is to say, nearer 5 to 1 than 4 to 1.

On the other hand, a bone of 145 mm. or over is likely to be male in the proportion of less than 3 to 1 (2·6 : 1) instead of rather over 3 to 1.

The important thing to notice is that while the absence of equal numbers of the two sexes is regrettable, the lessons to be learnt from the chart would not be materially altered by the addition of another 24 female clavicles had they been available.

Of course we must take into account the fact that there are 24 fewer female than male bones, and if these are added in their proper proportion on each side of the vertical line the error remains the same.

It is clearly unwise to tie ourselves down to any one point in determining the sex of a bone, and, to me, the most common-sense course seems to take several characteristics and to find out by careful charting what are their relative values in order that, when a bone comes to be sexed, each characteristic may be given its proper numerical value.

Stoutness.—We know that the female clavicle is not only shorter but slighter than that of the male, and I have therefore decided to take the circumference of the bone at its middle, measured with a steel tape, and to plot out a chart in order to see what help in sexing a bone can be expected from it.

Chart No. 2 shows this arrangement, and if we take a line between 35 and 36 mm. as the arbitrary division we find that, of the 281 bones, 234 would be rightly sexed and 47 (16 per cent.) wrongly.

When the missing difference between the sexes of 23 female bones is supplied in its proper proportion the error is increased to 17 per cent., but it is clear that the circumference at the middle is a more valuable test of sex than is the length of the bone.

Size of the Inner End.—In many bones the size of the articular ends is regarded as a test of sex, and I have therefore determined to use the inner end of the clavicle.

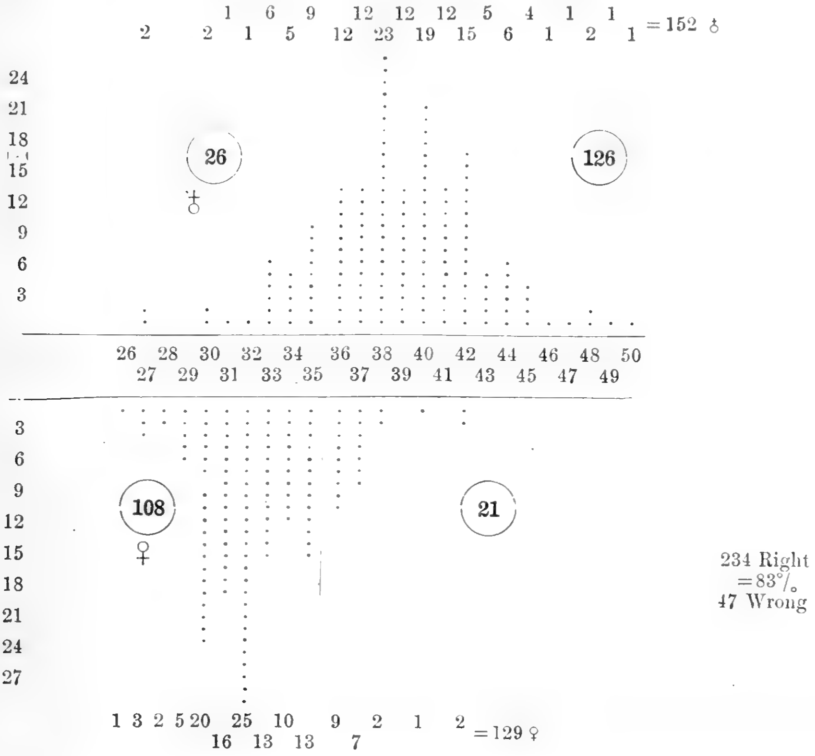
For practical purposes I found it better to add together the height and width of this part of the bone, determined by calipers, than to take its circumference with the steel tape. In the tables I have called this the "index of the inner end."

Chart No. 3 shows these measurements plotted out, and the dividing line has been drawn between 47 and 48.

This shows that 73 out of the 281 bones would have been wrongly sexed—an error of 26 per cent., which remains the same when the total numbers of the sexes are made even.

It is therefore evident that the circumference gives us 83 per cent. of successes, the length 77 per cent., and the inner end 74 per cent., but it is possible that by applying all three we may get better results still.

Chart No. 2.—Circumference at Middle.



My method of doing this will be illustrated best, perhaps, by taking two or three examples.

Suppose we take a bone the length of which is 150 mm., the circumference 44 mm., and the end index 54: there can be no hesitation in presuming that it is male, because every one of the tests falls on the male side of the vertical dividing line in the charts; but if we take another the length of which is 154, the circumference 35, and the end index 40: it is male according to its length, though female both in circumference and end index, but

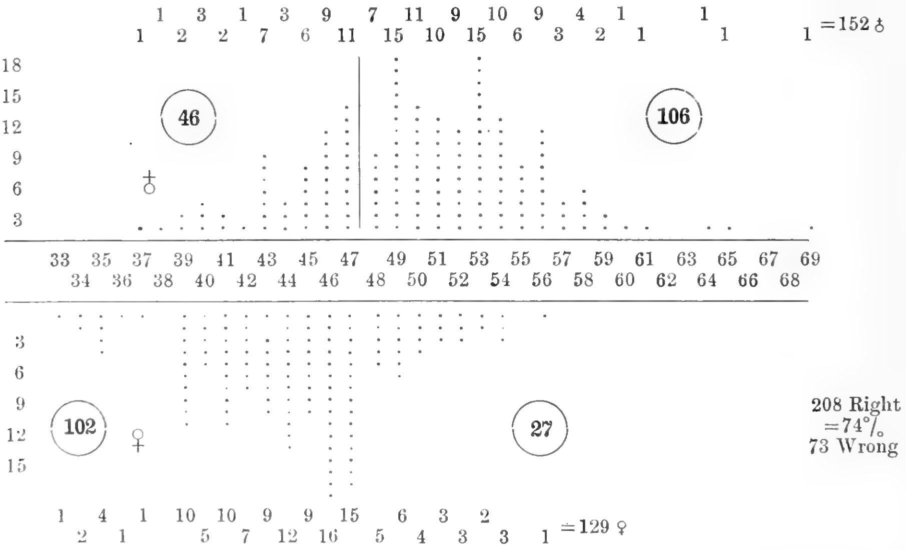
I should not place it among the females without valuing the points on each side. It is 10 points on the male side in length (the dividing line in chart 1 being between 144 and 145); it is one point on the female side in circumference, and eight points on the female side in end index—that is, ten chances of its being male to nine of its being female. But then these chances are not of equal value, and in order to get their true values I propose to divide each by its own coefficient of error, *i.e.*

$$\frac{10}{\cdot 23} = \cdot 44\ \text{♂},\ \frac{1}{17} = \cdot 06\ \text{♀},\ \frac{8}{26} = \cdot 3\ \text{♀}.$$

Adding the female points together we get ·44 in favour of the bone being male and ·36 in favour of its being female, or 0·8 in favour of the male sex altogether.

As a matter of fact this bone really was that of a male, but all cases

CHART NO. 3.—INNER END INDICES.



are not equally happy, for there are a certain number of female bones which are markedly male in all three tests and vice versa.

Of course it is only a very small number of bones which require so careful an investigation as the example just taken, and in most cases a glance at their measurements determines the sex to which they should theoretically belong. When the 282 bones had been sexed in this way I found that I had made 34 mistakes—that I had sexed 88 per cent. correctly and 12 per cent. wrongly. A greater mass of material might alter this, but I do not think greatly, since taking away 50 bones at random, *i.e.* in the order in which I got them, makes very little difference to the results.

Of course this is only an example of what can be done with modern English bones, and another race might need a quite different set of coefficients.

THE SURFACES OF THE CLAVICLE.

Different authors have described the surfaces of the clavicle so differently that there is evidently a good deal of variation, and into this it may, perhaps, be worth while to inquire. Unfortunately, two observers might easily differ as to what surfaces were present in a particular clavicle, since a section through the inner third is often different to one through the middle.

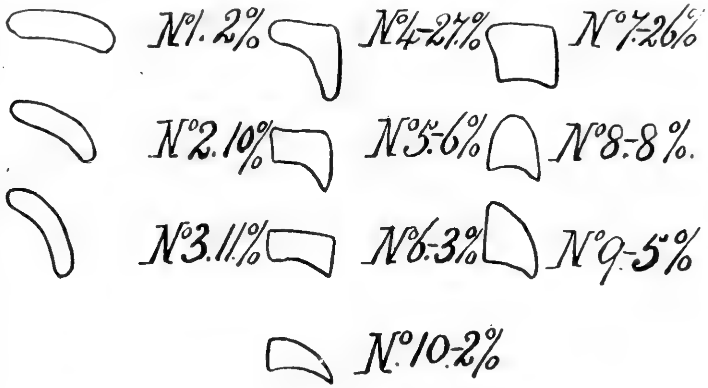


Fig. 7.—Sections of clavicles at middle.

I have therefore contented myself by noting the appearance of the section of the bone at its middle, and find that the 286 bones fall into ten subdivisions which are figured in the accompanying diagram (fig. 7). The first three of these are bones which are flattened, having two surfaces and two borders, but the surfaces may be superior and inferior, anterior and posterior, or intermediate. The fourth variety, which seems the commonest, is three-sided, with a definite superior, anterior, and postero-inferior surface, the latter being concave from above downward. The fifth, sixth, and seventh varieties are quadrilateral; while the eighth, ninth, and tenth are again triangular in section, but the surfaces are anterior, posterior, and inferior. It seems to me that most English clavicles are either triangular with one surface upward or quadrilateral with the posterior and inferior surfaces concave.

THE NUMBER OF NUTRIENT FORAMINA.

It is well known that the clavicle, like the femur, often has two nutrient foramina. In the 286 bones which I examined I found it single in 64 per cent., double in 26 per cent., triple in 5 per cent., quadruple in 7 per cent. (2 specimens), while in 5 per cent. no definite foramen could be seen. In these latter cases, no doubt, the bone is nourished by the numerous small foramina at the sternal and acromial ends.

The position of the foramina is, as is well known, on either the posterior or inferior surface, or the border between them when both are present; but in eleven cases out of the 286 (nearly 4 per cent.) I found a very definite foramen on the anterior surface close to the outer limit of the attachment of the pectoralis major.

When there is more than one foramen a very common place for one of them is close to the trapezoid ridge on the lower surface.

PERFORATIONS IN THE CLAVICLE.

Most museums have specimens of the supraclavicular nerve piercing the clavicle. In the 286 bones which I examined I found seven specimens of this (2·5 per cent.), though, since in two cases the perforation was bilateral, the percentage overstates the frequency of its occurrence.

The curious thing about this perforation is that in every one of the seven cases it has a common opening at the back of the bone with the nutrient foramen. Sometimes it pursues quite a tortuous course through the bone, and almost invariably has a greater mass of bone below than above it.

DEPRESSION FOR THE FIRST RIB.

The frequency of this depression is not fully realised. If it is carefully looked for a more or less distinct concavity where the clavicle presses on the first rib, external to its junction with the cartilage, is present in 43 per cent. of all cases. It is, of course, quite distinct from the portion of the articular extremity which articulates with the first rib and has already been referred to as directed forwards as well as downwards. In order to distinguish the two it will perhaps be better to speak of the one under discussion as the "rhomboid depression," because it is close to the attachment of the rhomboid ligament.

Rhomboid Pit.—In 10 per cent. of my specimens I found a rough irregular depression for the attachment of the rhomboid ligament. In certain cases this pit was a centimetre in depth and penetrated half through the thickness of the bone.

Conoid Facet.—This facet is caused by the clavicle articulating with the coracoid process of the scapula close to its bend. It is not a common abnormality, and I only found four examples of it in my series.

FIG. 8.—Rhomboid pit.

Trapezoid Tubercle.—The outer part of the trapezoid ridge is sometimes so accentuated as to form a very definite tuberosity, greatly increasing the apparent depth of the acromial end of the bone.

[TABLE.

TABLE I.—FEMALE CLAVICLES—LEFT.

No.	No. of Subject.	Age.	Length of Clavicle.	Shoulder Width.	Proportion.	Curvature.			Segments.			Widths.							Depths.				Circumference at Middle.	Index of Inner End.
						Inner Angle.	Outer Angle.	Total Curvature.	Inner.	Middle.	Outer.	At Inner End.	At Inner Angle.	Least Width.	Distance.	At Conoid.	Distance.	At Outer End.	At Inner End.	At Middle.	At Conoid.	Least Outer Depth.		
1	1	...	125	354	353	151°	161°	312	35	60	32	22	11	10	39	18	92	23	23	9	11	9	31	45
2	8	...	150	370	405	149	141	290	49	75	33	21	10	10	48	18	119	20	25	10	13	8	31	46
3	10	36	141	357	395	152	151	303	49	62	35	18	10	9	41	18	107	27	26	10	13	9	32	44
4	14	59	134	336	399	163	158	321	43	57	36	22	11	8	27	16	100	19	22	12	11	10	36	44
5	20	59	135	358	377	160	158	318	40	64	31	23	11	11	40	21	104	24	17	11	9	9	35	40
6	26	38	129	354	364	156	144	300	39	60	34	17	10	10	37	19	95	18	22	11	12	10	31	39
7	36	65	149	358	416	160	135	295	50	81	24	23	13	11	91	16	120	20	22	9	11	11	33	45
8	47	52	129	362	356	154	157	311	33	68	29	23	11	8	65	19	98	21	22	9	10	9	28	45
9	60	69	139	357	389	151	155	306	46	68	28	21	10	9	75	22	105	28	28	10	13	10	32	49
10	64	48	141	362	390	154	158	312	46	72	26	16	11	10	29	19	106	20	23	10	11	8	35	39
11	68	20	130	342	380	158	153	311	40	54	36	20	10	10	40	21	90	23	22	10	11	8	34	42
12	73*	45	142	367	387	154	156	310	41	71	33	23	10	10	45	15	110	20	24	10	12	9	30	47
13	79*	49	149	372	401	146	163	309	53	70	32	23	11	10	67	17	113	25	21	11	11	10	33	44
14	81*	46	134	377	355	152	138	290	45	64	28	21	10	10	55	16	98	15	22	8	10	7	30	43
15	82	28	133	330	403	159	154	313	37	67	30	20	8	8	37	17	95	16	24	10	11	9	32	44
16	83	31	139	385	361	153	159	312	36	71	35	20	11	10	48	24	104	29	24	11	11	11	33	44
17	87*	54	145	385	377	153	153	306	48	65	35	22	11	9	30	21	107	21	25	10	12	7	33	47
18	96*	46	155	351	441	150	145	295	53	75	34	21	11	10	36	16	120	16	22	10	11	6	34	43
19	98*	55	133	333	399	153	152	305	43	63	28	23	11	9	63	23	100	21	25	10	12	9	32	48
20	104*	44	127	348	365	156	143	299	38	60	32	21	9	8	48	18	96	22	20	9	12	11	30	41
21	105	70	133	344	387	141	148	289	45	68	27	22	13	12	71	19	98	19	24	9	11	10	32	46
22	106*	25	138	358	389	153	154	307	48	63	28	26	12	12	50	21	104	22	28	14	10	8	42	54
23	107*	36	134	375	357	157	156	313	44	56	35	25	13	10	68	21	98	25	27	12	15	12	36	52
24	108*	73	139	372	374	157	161	318	47	66	28	23	11	9	57	17	106	17	23	11	11	10	34	46
25	109*	40	149	370	403	153	163	316	53	69	30	22	10	9	80	19	102	18	22	9	10	10	32	44
26	110*	30	128	331	387	151	158	309	49	52	29	20	8	7	35	14	96	15	19	10	10	6	34	39
27	111*	46	136	330	412	152	142	294	38	71	32	21	11	9	57	18	101	17	22	9	11	8	38	43
28	112*	19	132	331	399	156	143	299	40	62	32	20	13	10	73	17	98	23	21	9	12	11	30	41
29	113*	52	139	...	...	156	133	289	39	76	30	17	10	9	83	14	113	18	16	8	10	9	29	33

30	123*	45	135	372	363	156	155	311	39	73	25	27	11	10	55	23	101	24	20	9	11	6	31	47
31	124*	67	142	372	382	156	160	316	47	67	31	23	12	11	37	21	107	25	24	10	9	8	35	47
32	126*	65	138	371	372	156	136	292	42	66	34	22	11	11	42	19	102	21	23	9	12	10	30	45
33	128*	60	133	357	373	147	149	296	44	64	31	20	10	10	42	18	100	20	26	10	10	11	35	46
34	136*	57	148	394	376	153	152	305	45	81	28	19	11	10	63	19	113	22	21	8	9	8	30	40
35	137*	64	136	405	336	147	149	296	45	72	25	20	10	9	33	13	104	16	22	9	10	8	31	42
36	138*	59	128	325	394	155	145	290	35	61	35	20	11	11	37	20	95	22	19	8	10	8	30	39
37	139*	73	140	377	371	156	152	308	35	69	39	23	12	10	60	19	102	23	25	11	11	10	34	48
38	140*	72	137	334	410	157	157	314	30	74	33	21	11	10	35	20	93	27	21	10	11	8	32	42
39	141*	39	136	353	395	156	154	310	35	71	32	20	12	10	53	24	99	25	20	10	9	9	30	40
40	142*	23	131	395	332	163	164	327	44	66	24	24	14	11	81	23	100	24	22	10	11	8	32	46
41	143*	26	134	342	392	157	157	314	45	66	26	20	11	9	35	18	104	22	21	10	12	11	31	41
42	144*	25	141	383	368	152	149	311	51	70	24	20	10	9	30	18	101	11	19	11	10	8	33	39
43	145*	27	128	339	378	153	149	302	40	60	28	20	11	10	25	19	98	20	22	11	10	9	33	42
44	146*	26	139	358	388	158	149	307	35	74	31	19	11	10	88	22	99	24	22	10	9	8	31	41
45	147*	58	140	402	348	154	140	294	44	69	32	27	11	10	75	14	107	23	26	10	11	11	31	53
46	148*	40	130	364	357	149	152	301	32	72	28	19	10	10	28	19	97	23	22	9	11	9	30	41
47	149*	64	150	366	410	156	157	313	46	80	28	23	11	10	36	20	115	27	20	10	11	7	32	43
48	150*	30	130	351	370	166	161	327	34	70	26	20	13	11	69	20	99	26	26	9	10	10	30	46
49	151*	38	154	413	373	151	141	292	53	64	42	26	12	12	67	15	117	14	28	12	11	10	35	54
50	153*	19	142	345	412	152	148	300	46	72	28	22	11	11	63	17	107	26	25	10	12	9	35	47
51	154*	48	129	359	359	159	156	315	39	64	30	21	12	9	77	18	103	21	27	11	9	8	32	48
52	156*	28	134	340	394	151	150	301	38	71	29	22	10	9	80	17	104	23	24	9	12	9	29	46
53	158*	24	162	413	392	159	136	295	50	88	25	23	12	12	73	20	121	25	24	10	12	10	35	47
54	159*	30	135	355	380	157	157	314	47	60	30	17	11	9	24	15	92	19	24	9	11	8	30	41
55	162*	32	137	370	370	164	163	327	42	67	30	20	12	12	68	15	106	25	21	8	9	7	29	41
56	174*	33	135	352	384	144	142	286	39	65	36	18	10	10	27	17	100	16	23	9	10	8	32	41
57	175*	35	162	375	433	154	146	300	45	81	40	20	11	10	64	17	121	19	24	10	12	9	32	44
58	176*	18	134	341	393	161	146	307	32	73	33	17	9	8	43	12	102	18	17	8	9	8	26	34
59	177*	24	121	306	295	161	141	302	25	68	33	18	11	9	63	13	93	15	17	9	11	10	27	35
60	179*	76	146	383	381	153	148	301	46	80	25	21	12	11	33	16	112	21	24	11	11	9	35	45
61	180*	32	149	363	410	155	144	299	39	74	39	22	10	9	53	20	111	21	22	10	12	9	31	44
62	181*	48	141	380	371	162	154	316	46	73	25	23	9	9	42	20	106	33	23	10	11	9	33	46
63	182*	38	141	362	390	162	146	308	45	76	24	17	11	10	30	18	110	22	22	9	15	11	29	39
64	183*	62	138	356	388	153	157	310	48	72	20	24	11	10	38	22	105	24	27	10	9	10	31	51
Average		44	138	361	383	155	151	306	42	69	30	21	11	10	52	18	104	21	23	10	11	9	32	44

indicates that the corresponding bone of the opposite side is recorded in another table.

TABLE II.—FEMALE CLAVICLES—RIGHT

No.	No. of Subject.	Age.	Length of Clavicle.	Shoulder Width.	Proportion.	Curvature.			Segments.			Widths.							Depths.				Circumference at Middle.	Index of Inner End.
						Inner Angle.	Outer Angle.	Curvature.	Inner.	Middle.	Outer.	At Inner End.	At Inner Angle.	Least Width.	Distance.	At Conoid.	Distance.	At Outer End.	At Inner End.	At Middle.	At Conoid.	Least Outer Depth.		
1	10*	36	147	357	412	156°	160°	316	53	63	33	19	10	9	26	24	109	28	27	12	11	9	38	46
2	11	20	135	327	413	156	161	317	47	73	18	22	10	9	68	20	101	21	21	9	10	8	30	43
3	19	29	149	342	436	154	163	317	53	67	31	19	10	10	51	20	111	19	21	9	10	7	32	40
4	23	42	124	347	360	158	142	300	35	57	37	19	9	9	49	18	89	23	20	13	15	8	37	39
5	24	56	137	357	384	145	155	300	49	61	31	23	11	10	72	20	104	21	22	9	11	10	31	45
6	27	35	133	379	351	162	160	322	43	61	31	24	9	9	62	24	96	21	28	9	10	8	32	52
7	39	53	132	372	355	152	156	308	51	58	27	26	11	10	75	20	99	24	28	11	13	11	37	54
8	42	28	126	344	366	159	144	303	40	62	29	23	11	9	51	12	97	18	24	8	9	6	31	47
9	43	50	153	346	442	156	154	310	50	72	33	25	10	10	71	23	115	25	26	13	14	13	37	51
10	45	48	138	372	371	155	145	298	46	63	33	23	10	9	26	21	106	23	26	11	13	10	40	49
11	48	56	145	350	414	150	158	308	44	72	33	24	10	8	70	18	118	23	23	11	10	9	30	47
12	51	40	133	359	370	157	145	302	39	57	39	23	10	10	36	20	95	25	23	10	12	12	35	46
13	53	58	137	368	372	155	157	312	48	59	34	22	9	9	48	19	103	22	25	11	13	11	37	47
14	56	48	151	388	389	158	155	313	47	71	34	23	12	11	83	28	110	30	27	10	13	12	36	50
15	73*	45	143	367	389	152	148	300	42	70	37	25	10	10	74	15	109	20	25	9	12	10	32	50
16	79*	49	144	372	387	148	158	306	51	63	36	23	12	10	71	20	105	23	20	11	11	9	33	43
17	81*	46	135	377	361	152	134	286	49	71	25	21	12	10	73	14	103	16	19	7	10	8	30	40
18	84	48	130	362	359	163	157	320	35	68	29	23	10	8	61	19	100	22	22	10	10	10	30	45
19	87*	54	146	385	379	155	162	317	55	58	37	23	11	10	76	24	110	23	24	11	10	8	36	47
20	96*	46	155	351	442	152	144	296	55	72	31	22	10	10	35	16	116	20	20	11	10	6	34	42
21	98*	55	130	333	390	153	153	306	44	59	30	22	10	9	62	19	95	19	25	11	11	8	32	47
22	104*	44	132	348	379	155	146	301	44	59	34	23	8	7	66	16	99	20	20	10	12	10	30	43
23	106*	25	131	358	366	151	149	300	43	61	30	24	11	11	42	21	95	23	25	12	11	8	42	49
24	107*	36	138	375	368	151	154	305	45	64	34	25	13	10	58	19	104	24	24	11	14	10	36	49
25	108*	73	135	372	363	153	159	312	51	61	27	22	12	11	31	20	102	20	23	11	12	10	34	45
26	109*	40	143	370	386	149	162	311	51	63	30	22	11	9	71	17	108	21	25	11	11	10	32	47
27	110*	30	126	331	381	150	155	305	48	52	31	18	9	9	36	16	95	15	17	11	10	6	34	35
28	111*	46	128	330	388	157	132	289	33	65	32	23	12	12	48	18	96	20	24	9	12	9	31	47
29	112*	19	132	331	400	165	150	315	33	70	30	23	14	9	63	19	99	24	21	9	12	10	30	44

30	113*	52	140	...	...	154	133	287	47	68	33	19	10	9	27	19	110	19	17	8	10	8	29	36
31	123*	45	131	372	252	152	150	302	38	66	31	25	10	10	42	23	97	24	22	11	11	9	35	47
32	124*	67	144	372	387	171	155	326	44	62	39	26	12	11	51	10	106	23	23	11	9	9	37	49
33	126*	65	135	371	364	156	138	294	33	73	31	24	10	9	39	18	100	22	22	9	11	9	30	46
34	128*	60	129	357	362	154	141	295	43	59	32	22	11	11	42	20	93	20	24	11	13	12	36	46
35	136*	57	148	394	376	155	163	318	48	70	36	19	11	11	53	20	110	28	22	9	10	7	32	41
36	137*	64	133	405	328	154	143	297	49	64	25	25	10	9	35	12	101	17	23	10	10	10	32	48
37	138*	56	129	325	397	151	149	300	45	58	30	21	11	11	40	21	99	24	21	9	9	8	32	42
38	139*	73	139	377	369	157	152	309	36	67	39	25	11	10	46	20	105	25	24	11	12	9	36	49
39	140*	72	137	334	410	153	140	293	35	74	30	20	15	11	53	21	99	26	21	10	10	8	32	41
40	141*	39	138	353	391	154	155	309	39	67	35	22	13	10	56	20	99	25	22	10	11	9	33	44
41	142*	23	129	395	327	156	161	317	46	62	24	24	11	11	58	23	97	25	21	10	11	9	33	45
42	143*	26	135	342	395	163	150	313	42	65	30	19	12	11	50	21	105	21	18	11	12	10	34	37
43	144*	25	139	383	363	151	149	300	50	58	34	18	11	9	35	13	105	19	24	12	10	7	35	42
44	145*	27	129	339	381	154	154	308	41	61	30	18	10	10	45	19	99	24	21	11	11	9	33	39
45	146*	26	138	358	386	154	154	308	45	64	32	23	12	11	77	21	98	24	23	10	9	9	32	46
46	147*	58	133	402	331	156	139	295	42	62	27	25	10	8	57	18	103	27	28	10	11	11	30	53
47	148*	40	126	364	346	150	142	292	41	55	35	21	11	9	28	20	95	26	23	9	12	10	32	44
48	150*	30	133	351	379	161	170	331	43	65	26	18	11	10	26	20	103	28	25	10	10	9	31	43
49	151*	38	154	413	373	148	144	292	50	75	36	28	12	12	60	17	117	18	28	11	10	10	36	56
50	153*	19	140	345	406	151	143	294	41	68	36	21	12	12	41	19	107	21	25	10	13	11	37	46
51	154*	48	129	359	359	160	146	306	34	59	39	20	13	10	72	18	100	20	23	11	9	11	33	43
52	156*	28	136	340	400	154	143	297	39	68	32	23	11	10	49	17	104	22	23	10	12	10	30	46
53	158*	24	164	413	397	162	149	311	45	80	43	25	11	11	47	16	121	23	25	12	13	10	36	50
54	159*	30	131	355	369	155	153	308	43	59	28	18	10	9	57	19	99	20	21	9	11	8	28	39
55	162*	32	142	370	384	160	148	308	42	75	25	23	12	12	55	17	104	24	24	8	8	8	32	47
56	174*	33	135	352	384	143	132	275	51	55	36	14	10	11	31	15	102	17	21	12	10	8	37	35
57	175*	35	160	375	427	151	150	301	51	75	40	22	13	12	40	19	117	21	24	10	11	9	32	46
58	176*	18	132	341	387	161	149	310	37	68	31	18	8	8	55	15	102	18	17	8	9	8	27	35
59	177*	24	124	306	405	163	151	314	37	59	30	17	10	9	53	17	96	19	17	8	10	10	27	34
60	178	22	136	344	395	153	132	285	45	68	30	16	12	10	84	16	110	18	23	10	10	9	33	39
61	179*	76	148	383	386	155	156	311	49	68	34	27	11	11	44	20	107	23	24	11	10	9	35	51
62	186*	32	145	363	399	154	145	299	44	69	34	24	11	10	70	20	107	21	24	11	12	9	31	48
63	181*	48	137	380	361	161	148	309	52	63	25	24	11	10	41	17	104	19	26	11	11	10	35	50
64	182*	38	138	362	381	160	146	306	44	65	30	21	12	12	59	19	107	24	23	10	14	11	31	44
65	183*	62	139	356	390	156	160	316	57	57	29	25	10	9	36	22	109	24	27	11	10	9	34	52
Average		43	138	361	382	155	150	305	44	65	32	22	11	10	52	19	104	22	23	10	11	9	33	45

TABLE III.—MALE CLAVICLES—LEFT.

No.	No. of Subject.	Age.	Length of Clavicle.	Shoulder Width.	Proportion.	Curvature.			Segments.			Widths.							Depths.				Circumference.	Index of Inner End.
						Inner Angle.	Outer Angle.	Total Curvature.	Inner.	Middle.	Outer.	At Inner End.	At Inner Angle.	Least Width.	Distance.	At Conoid.	Distance.	At Outer End.	At Inner End.	Middle.	At Conoid.	Least Outer Depth.		
1	3	...	139	365	381	153°	133°	286	34	71	35	21	11	9	61	17	99	17	26	9	10	8	30	47
2	4	...	147	377	390	162	148	310	43	72	30	26	14	13	73	16	112	17	28	13	11	10	42	54
3	5	...	148	385	384	159	155	314	53	69	30	27	13	11	82	22	111	22	27	14	14	11	40	54
4	6	...	152	384	396	154	155	309	52	67	35	21	11	11	65	22	112	23	24	13	13	11	35	45
5	9	...	160	406	394	151	149	300	53	74	31	22	13	11	70	17	116	17	28	10	11	10	33	50
6	12	...	140	363	386	149	148	297	42	68	35	25	14	12	76	19	102	19	21	10	10	8	33	46
7	16	70	165	421	392	157	153	310	47	87	31	28	13	10	73	20	120	27	29	13	10	11	40	57
8	18	48	153	410	373	152	149	301	50	82	24	25	13	12	61	24	112	29	29	13	11	9	40	54
9	21	67	149	387	385	154	139	293	36	80	36	22	13	11	78	21	104	26	27	12	13	9	37	49
10	28	43	165	400	413	151	139	290	50	88	30	29	15	13	83	27	118	27	32	12	13	11	42	61
11	30	58	161	398	405	149	144	293	55	84	29	29	13	12	36	27	120	31	27	15	11	12	42	56
12	32	42	153	402	381	140	156	296	60	69	29	25	15	13	85	20	108	22	27	14	13	13	45	52
13	33	20	153	383	399	159	148	307	40	74	35	28	13	11	72	17	108	29	28	9	11	12	35	56
14	35	21	162	407	398	158	142	300	42	89	31	23	12	11	73	17	122	24	29	12	11	9	37	52
15	37	31	162	449	361	160	162	322	45	79	37	23	11	11	67	20	119	20	26	13	13	12	40	49
16	46	29	159	429	371	156	154	310	51	70	41	27	11	11	70	19	104	27	24	13	13	12	37	51
17	49	30	145	382	380	162	147	309	32	83	33	21	16	12	77	18	104	24	22	15	18	10	41	43
18	50	59	138	353	391	155	152	307	47	60	32	23	11	9	73	19	100	22	24	11	13	11	36	47
19	52	36	149	400	373	166	131	297	38	88	28	28	11	11	37	20	113	25	25	12	15	12	38	53
20	54	47	151	411	367	167	139	306	52	64	37	24	12	11	64	21	113	24	25	15	14	13	39	49
21	55	43	150	418	359	160	136	296	44	77	32	25	13	12	37	19	113	26	30	15	13	12	43	55
22	58	48	154	408	377	149	153	302	54	72	32	26	12	11	48	21	110	24	26	15	16	14	42	52
23	61	32	160	393	407	156	147	303	52	79	32	24	12	10	32	20	123	23	23	12	12	8	38	47
24	62	60	147	377	390	153	154	307	49	70	30	18	13	11	29	20	117	24	24	13	14	12	38	42
25	65	33	155	404	384	152	129	281	49	82	27	29	11	11	70	20	119	29	27	14	14	14	41	56
26	66*	18	130	369	352	158	151	309	46	52	32	21	11	10	60	14	96	20	18	10	11	11	30	39
27	69*	26	159	392	406	150	149	299	52	72	38	22	9	9	52	19	112	19	22	13	13	11	41	44
28	70	50	140	401	349	146	159	305	46	67	32	23	12	10	63	18	101	22	...	...	...	...	...	...
29	71*	31	151	394	388	159	154	313	49	68	33	22	13	11	56	20	110	27	24	12	12	10	39	46
30	72*	56	147	374	393	153	149	302	54	65	30	29	10	9	48	24	106	26	21	14	11	9	39	50
31	74	58	137	378	362	155	150	305	43	63	33	27	11	10	60	22	102	22	26	14	12	10	40	53
32	75*	38	157	364	431	158	156	314	53	70	35	24	10	9	83	15	112	19	22	12	10	10	32	46
33	77	28	162	409	396	154	149	303	46	81	35	24	13	12	68	24	120	24	27	13	11	9	38	51
34	78	43	152	405	375	159	156	315	38	81	33	22	12	12	58	20	112	28	27	13	13	11	40	49
35	80	58	153	423	362	153	146	299	47	73	36	28	11	11	54	18	111	20	27	14	12	11	41	55
36	85*	29	157	414	379	157	144	301	50	74	38	22	13	12	87	17	120	24	27	12	12	9	36	49
37	86*	51	155	419	370	157	151	308	49	76	34	20	12	12	50	20	114	26	26	11	12	11	38	46

38	90*	old	140	410	341	154	146	300	40	68	37	25	11	10	54	17	104	22	24	10	13	9	37	49
39	91*	72	157	392	401	148	141	289	49	75	38	23	12	12	70	23	119	20	22	10	13	10	35	45
40	92*	68	143	407	351	134	144	278	56	63	32	19	12	10	76	19	101	24	21	13	12	12	33	40
41	93	43	151	382	395	147	156	303	56	71	28	27	14	12	85	18	116	23	29	12	12	11	38	56
42	94*	59	165	419	394	163	144	307	42	83	42	28	12	12	65	17	118	25	30	13	16	17	42	58
43	95*	59	140	373	375	148	132	280	45	68	35	27	14	11	80	17	108	26	25	12	14	14	35	52
44	97*	59	167	429	389	161	152	313	49	83	38	29	13	12	72	17	123	23	27	12	12	10	38	56
45	99*	39	156	409	381	150	150	300	60	64	33	23	11	10	33	17	117	27	26	11	13	8	37	49
46	100*	56	145	363	399	151	154	305	47	69	31	25	13	9	70	18	107	24	28	12	12	12	34	53
47	101*	20	151	394	383	155	146	301	43	76	33	25	10	10	53	16	113	20	24	11	9	9	33	49
48	102*	19	158	415	381	154	153	307	55	71	33	25	12	12	70	20	123	26	25	13	12	11	40	50
49	103*	48	156	403	387	145	141	286	57	76	29	26	12	12	65	25	122	28	27	14	14	9	42	53
50	114*	68	149	413	361	154	120	274	39	82	30	34	12	11	83	19	110	23	35	13	13	11	39	69
51	115*	51	140	367	381	150	155	305	45	61	36	20	11	10	70	22	102	20	23	13	13	11	36	43
52	116	50	166	422	393	145	147	292	53	85	36	26	10	9	77	24	123	29	24	12	12	9	35	50
53	117*	43	172	436	394	153	143	296	59	91	25	19	13	12	35	17	134	17	28	10	11	9	38	47
54	118*	71	153	383	399	157	158	315	46	70	42	28	11	11	52	24	113	25	31	13	12	12	40	59
55	119*	65	156	450	347	161	147	308	45	77	40	29	14	10	78	20	122	27	27	14	15	12	41	56
56	120*	27	154	401	384	152	151	303	49	76	31	20	13	10	74	16	119	22	27	10	8	7	34	47
57	121*	60	150	398	377	153	125	278	41	86	25	27	13	11	58	15	113	24	25	13	12	12	40	52
58	122*	55	149	409	364	152	148	300	49	68	35	22	12	11	33	18	111	21	24	12	12	10	39	46
59	125*	57	145	396	366	151	153	304	46	69	34	28	14	13	73	21	103	24	26	12	14	11	41	54
60	127*	28	161	378	426	146	151	297	49	81	35	22	13	11	69	20	120	27	25	13	10	8	37	47
61	129*	52	149	380	392	153	149	302	52	59	41	22	12	11	60	20	106	21	28	12	10	9	37	50
62	130*	50	158	403	370	151	151	302	50	83	29	21	11	10	70	18	115	20	26	12	10	10	36	47
63	131*	23	140	340	412	152	140	292	39	82	25	20	9	9	30	17	111	20	20	8	9	6	27	40
64	132*	54	154	402	383	156	154	310	57	67	31	26	14	13	38	25	111	27	27	12	10	10	43	53
65	133*	42	147	404	364	151	149	300	49	78	22	24	12	11	70	19	112	22	30	11	12	11	38	54
66	134*	49	140	403	347	158	149	307	48	64	30	21	9	9	55	17	110	18	22	12	13	13	34	43
67	135*	30	147	401	367	153	146	299	53	70	25	24	14	12	87	20	107	26	27	10	9	8	38	51
68	152*	52	159	403	395	151	155	306	45	87	29	26	14	13	75	21	110	28	27	13	12	9	42	53
69	155*	30	156	397	393	157	143	300	50	72	37	25	14	14	47	18	118	22	25	12	13	11	46	50
70	157	40	152	371	410	150	155	305	52	74	30	20	12	11	84	20	113	24	23	10	11	8	35	43
71	160*	23	176	427	412	149	152	301	60	81	40	24	13	12	35	22	133	26	26	12	13	10	44	50
72	161*	39	146	373	392	156	142	298	52	66	30	22	13	13	28	20	108	21	29	13	11	9	42	51
73	163*	34	142	365	389	151	153	304	53	57	38	22	12	12	63	15	110	20	21	10	10	9	34	43
74	164*	64	172	455	378	160	145	305	55	83	36	24	12	12	61	20	133	28	30	13	12	10	40	54
75	165*	66	160	420	381	150	149	299	49	88	27	25	14	11	82	19	119	28	31	11	11	9	36	56
76	166*	19	144	380	379	154	160	314	48	75	23	19	13	12	33	23	105	27	22	11	11	9	37	41
77	167*	33	173	420	412	150	144	294	57	85	33	25	16	15	15	22	129	23	28	12	12	11	44	53
78	168*	41	148	360	411	146	142	288	46	74	33	22	13	12	42	18	111	24	29	11	15	10	40	51
79	169*	34	158	405	390	144	151	295	45	81	36	29	16	13	71	19	117	31	29	16	14	12	48	58
80	170*	50	158	401	394	153	150	303	49	79	34	23	11	10	74	20	125	25	32	11	12	10	33	55
81	171*	64	155	394	393	146	132	278	46	81	35	23	14	12	86	17	112	23	25	13	15	11	39	48
82	172*	33	171	402	425	151	161	312	60	70	39	23	12	11	48	21	120	34	22	11	14	10	40	45
83	173*	43	164	392	418	156	153	309	50	76	41	20	12	11	22	20	127	24	24	13	12	10	38	44
Average		45	153	398	385	153	148	301	49	75	33	24	12	11	61	20	113	24	26	12	12	11	38	50

TABLE IV.—MALE CLAVICLES—RIGHT.

No.	No. of Subject.	Age.	Length of Clavicle.	Shoulder Width.	Proportion.	Curvature.			Segments.			Widths.							Depths.				Circumference.	Index of Lower End.
						Inner Angle.	Outer Angle.	Index of Curvature.	Inner.	Middle.	Outer.	At Inner End.	At Inner Angle.	Least Width.	Distance.	At Conoid	Distance.	At Outer End.	At Inner End.	At Middle.	At Conoid.	Least at Outer End.		
1	2	...	156	394	396	151°	154°	305	46	70	42	22	13	11	70	20	113	26	21	13	11	8	40	43
2	7	...	154	385	400	152	154	306	50	70	38	22	12	11	87	22	115	22	25	13	12	11	40	47
3	13	58	154	389	396	141	156	297	47	73	37	25	13	12	81	18	107	25	25	12	12	10	37	50
4	15	52	162	413	392	149	145	294	51	74	43	26	12	12	60	26	118	22	27	12	13	11	39	53
5	17	41	166	431	385	158	144	302	48	90	29	24	13	13	80	22	124	23	25	11	12	11	36	49
6	22	64	143	404	354	155	140	295	44	66	36	24	15	12	65	17	108	22	28	13	12	10	40	52
7	25	47	141	389	362	151	150	301	45	63	32	29	12	11	34	20	115	29	25	15	14	12	44	54
8	31	28	154	424	363	150	171	321	55	68	31	27	12	12	55	26	109	34	27	13	13	12	41	54
9	34	...	139	387	359	147	145	292	44	67	32	22	13	12	32	23	99	27	29	13	14	12	42	51
10	38	22	154	400	385	155	146	301	48	76	33	19	15	12	78	17	118	18	21	11	11	11	35	40
11	40	48	141	382	369	156	153	309	47	59	37	25	12	12	45	26	98	28	28	13	10	10	41	53
12	41	68	148	402	368	153	150	303	52	59	39	30	14	13	60	22	106	25	26	15	15	12	45	56
13	44	36	148	392	378	137	150	287	48	63	40	25	14	12	70	23	104	25	23	13	13	10	41	48
14	57	26	162	428	379	158	170	328	55	70	39	22	12	10	66	23	125	34	29	12	13	10	39	51
15	59	56	155	419	370	155	156	311	46	72	35	21	12	11	67	19	118	23	25	12	14	12	40	46
16	63	49	140	356	393	148	163	311	47	63	30	25	13	13	52	24	98	24	24	14	11	8	42	49
17	66*	18	126	369	341	149	150	299	44	50	35	20	11	10	60	15	95	19	18	10	10	10	31	38
18	67	60	161	425	397	153	141	294	60	63	40	30	17	15	40	32	115	30	28	13	15	14	47	58
19	69*	26	158	392	403	150	152	302	58	64	42	28	9	9	52	19	115	19	22	14	12	11	42	50
20	71*	31	153	394	388	154	153	307	54	73	29	25	13	12	41	23	113	29	27	14	12	9	39	52
21	72*	56	145	374	388	155	161	316	58	51	36	28	11	11	55	22	102	29	25	11	11	9	38	53
22	75*	38	160	364	439	158	161	319	58	75	30	24	10	9	69	18	118	20	26	12	10	9	33	50
23	76	50	152	398	382	156	137	293	43	78	31	26	13	12	65	23	118	20	26	11	14	10	35	52
24	85*	29	160	414	386	156	152	308	47	80	36	23	11	10	53	19	119	25	26	12	11	9	38	49
25	86*	51	155	419	370	157	141	298	48	76	35	22	11	10	37	19	124	25	24	13	13	11	38	46
26	88	34	140	377	371	150	139	289	40	81	23	19	15	12	62	17	116	18	20	9	10	10	33	39
27	89	36	132	370	357	161	148	309	48	52	34	20	9	9	49	16	100	20	23	12	14	11	35	43
28	90*	old	140	410	341	145	143	288	48	59	40	25	12	11	69	21	102	23	20	12	13	11	41	45
29	91*	72	153	392	390	154	145	299	51	61	43	28	12	11	38	23	110	20	25	15	13	11	36	53
30	92*	68	143	407	351	139	147	286	54	59	35	24	12	11	72	18	117	23	23	14	17	11	38	47
31	94*	59	160	419	382	159	145	304	42	73	48	27	13	12	65	23	114	25	30	14	15	16	45	75

32	95*	59	135	373	362	149	133	282	41	65	37	26	13	11	70	17	107	25	25	13	17	13	38	51
33	97*	59	167	429	389	159	156	315	57	69	42	30	12	12	68	18	121	27	25	13	13	11	43	55
34	99*	39	149	409	364	161	146	307	56	61	31	25	12	11	50	18	112	22	27	12	16	9	36	52
35	100*	56	140	363	386	151	153	304	42	57	37	27	12	10	65	20	105	26	26	14	13	11	39	53
36	101*	20	144	394	365	156	149	305	50	62	33	24	11	11	50	20	105	20	23	12	9	10	38	47
37	102*	19	160	415	386	157	150	307	53	74	49	28	12	11	44	20	119	22	26	11	12	11	43	54
38	103*	48	149	403	370	153	161	314	61	67	35	24	13	12	73	24	123	26	27	18	13	10	50	51
39	114*	68	156	413	378	158	128	286	48	76	31	32	12	10	80	17	115	23	33	11	15	11	38	65
40	115*	51	145	367	395	152	148	300	40	71	36	24	13	12	58	23	106	25	22	12	13	10	37	46
41	117*	43	168	436	385	152	144	296	57	80	36	23	14	14	63	18	132	16	26	11	11	9	40	49
42	118*	71	154	383	402	160	158	318	46	68	42	27	12	11	55	22	115	27	31	13	13	11	42	58
43	119*	65	161	450	358	164	148	312	32	90	42	27	15	11	51	20	122	25	30	12	13	12	42	57
44	120*	27	146	401	364	148	145	293	46	70	33	20	11	10	64	18	110	23	24	12	8	8	37	44
45	121*	60	142	398	357	143	136	279	38	81	31	20	13	10	73	16	109	22	25	11	12	10	39	51
46	122*	55	145	409	355	156	141	297	40	70	39	26	12	11	75	16	106	19	23	10	12	11	36	49
47	125*	57	143	396	361	158	157	315	47	59	40	28	11	11	51	21	103	23	25	15	11	10	43	53
48	127*	28	160	378	423	158	145	303	45	85	33	22	11	10	52	26	118	27	26	13	11	8	38	48
49	129*	52	143	380	376	155	139	294	49	53	40	26	13	13	62	18	99	23	29	12	11	9	38	55
50	130*	50	157	403	390	155	144	299	53	74	33	23	11	11	70	17	118	19	25	13	11	10	38	48
51	131*	23	139	340	409	154	144	298	46	66	33	16	9	7	29	17	108	21	21	8	9	7	27	37
52	132*	54	151	402	376	153	146	299	58	56	40	30	14	13	50	26	106	26	26	11	12	11	45	56
53	133*	42	148	404	366	151	143	294	51	72	30	24	12	10	68	19	109	23	29	11	12	10	36	53
54	134*	49	132	403	328	156	143	299	50	55	30	25	11	10	42	17	100	21	24	11	14	14	36	49
55	135*	30	138	401	344	156	153	309	48	59	30	25	13	13	52	25	106	29	28	11	12	9	38	53
56	152*	52	157	403	390	155	156	311	45	83	32	28	15	13	66	24	117	27	26	14	12	9	44	54
57	155*	30	157	397	395	154	148	302	51	68	40	23	14	13	34	21	121	23	24	13	14	11	48	47
58	160*	23	175	427	410	151	150	301	59	84	37	24	13	12	40	20	131	23	24	13	14	9	39	48
59	161*	39	144	373	386	153	148	301	50	67	30	21	13	11	37	23	107	27	27	11	12	9	44	48
60	163*	34	134	365	367	155	146	301	38	63	35	24	11	11	45	16	102	28	21	10	12	10	34	45
61	164*	64	167	455	367	162	144	306	51	81	38	31	12	12	48	21	124	27	29	12	12	10	44	60
62	165*	66	161	420	383	152	152	304	56	79	30	30	14	13	84	23	121	32	29	13	10	10	42	59
63	166*	19	142	380	374	152	153	305	46	68	32	21	13	12	70	21	109	24	20	10	10	9	36	41
64	167*	33	167	420	398	152	137	289	55	87	30	25	16	16	71	22	127	29	25	13	13	10	41	50
65	168*	41	148	360	411	147	139	286	56	69	28	21	13	13	49	21	113	24	24	12	15	10	42	45
66	169*	34	156	405	385	153	144	297	52	71	39	31	11	10	35	23	117	29	33	13	15	13	49	64
67	170*	50	161	401	401	153	144	297	48	83	36	25	13	12	63	22	125	27	30	12	11	10	37	55
68	171*	64	156	394	396	152	152	304	48	68	44	23	12	11	78	20	113	23	23	13	14	11	40	46
69	172*	33	173	402	430	152	146	298	51	83	42	21	12	12	52	21	127	29	27	12	13	11	41	48
70	173*	43	164	392	418	158	148	296	47	83	39	24	13	11	35	22	127	25	25	12	11	9	40	49
Average		45	151	398	381	153	148	301	49	70	36	25	12	11	58	21	113	24	25	12	12	10	40	50

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NEOPALLIAL MORPHOLOGY OF FOSSIL MEN AS STUDIED FROM ENDOCRANIAL CASTS. By Professor M. BOULE (*Muséum d'Histoire Naturelle, Paris*) and Professor R. ANTHONY (*École d'Anthropologie, Paris*).

THE very accurate researches of Professor J. Symington, as to what might be learned of human cerebral morphology from the observation of the endocranial cast,[1] have led him to confirm an anatomical fact which has long been considered by everyone as a commonplace, and upon which we have very particularly insisted at the beginning of our paper concerning the encephalon of the La Chapelle aux Saints Man,[2] namely, that *an endocranial cast can afford but incomplete and conditional information about the morphology of the neopallial foldings.*[3]

Having considered, nevertheless, that such conditions did not render a study of endocranial casts fruitless and ineffectual, we were deeply surprised that Professor Symington's researches should have led him to the following conclusions:—

"1. That the simplicity or complexity of the cerebral fissures and convolutions cannot be determined with any degree of accuracy from endocranial casts, even from complete skulls, much less from reconstructions from imperfect skulls.

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[1] J. Symington, "On the Relations of the Inner Surface of the Cranium to the Cranial Aspect of the Brain": The Sir John Struthers Anatomical Lecture, delivered at the Royal College of Surgeons of Edinburgh on 16th December 1914: *Edinburgh Medical Journal*, Feb. 1915. The author also presented the results of that study to the Anatomical Society of Great Britain and Ireland (see *Proceedings*, 1916).

Id., "Endocranial Casts and Brain Form: a Criticism of some recent Speculations," *Journal of Anatomy and Physiology*, Jan. 1916.

[2] M. Boule et R. Anthony, "L'encéphale de l'homme fossile de La Chapelle aux Saints," *L'Anthropologie*, mars-avril 1911.

[3] G. Elliot Smith says: "The beautiful series of casts which Professor Symington has shown do not demonstrate anything that anatomists have not been familiar with for a century at least; for every time one removes a carefully hardened brain from the cranium, all the points mentioned by Professor Symington obtrude themselves on the attention." ("An Answer to Professor Symington," *Proc. Anat. Soc. of Great Britain and Ireland*, Jan. 1916.)

"2. That it is not possible to estimate, even approximately, from the La Chapelle or Piltdown endocranial cast the relative degree of development of the various sensory and association centres in the cortex.

"3. That the various deductions made by Boule, Anthony, Elliot Smith, and others, with reference to the primitive and simian features of the brain of certain prehistoric men, from an examination of their endocranial casts, are highly speculative and fallacious."[1]

First, we might note with Professor G. Elliot Smith that "because many specimens afford negative evidence is surely no reason for refusing to recognise positive information of the most definite character when it occurs."[2]

It would be regrettable in every respect if we should refuse to avail ourselves in palæontology of the endocranial casts which are able to give us, on the one hand, positive information on all that relates to the general shape of the encephalon, and, on the other, valuable indications on the morphology of the dura mater sinuses, the meningeal vessels, and even, as admitted indeed by Professor Symington[3] himself, on the shape and position of the Sylvian complex at its opening, as well as, generally speaking, of the neopallial foldings that lie in the orbital region, along the lower external edge of the hemispheres, at the anterior end of the temporal lobe.

The identification of the other convolutions is, of course, much less certain, but must we refrain from starting any discussion about them and from presenting hypotheses even supported by arguments?

We shall first examine the broad question how far and in what measure the results of Professor Symington's researches, applicable indeed to modern Man, are so for fossil men; and secondly, we shall review those of our own conclusions which the author has thought fit to reject.

It is well known that if there are Mammals, such as modern Man and Cetaceans, concerning the neopallial foldings of which the study of endocranial casts can afford but incomplete information, there are others, such as Carnivores and Ungulates, in which the neopallial foldings are so plainly printed on the endocranial cast, as well on the roof as on the sides

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[1] J. Symington, *Journal of Anatomy and Physiology*, 1916, *loc. cit.*, p. 130.

[2] G. Elliot Smith, "An Answer to Professor Symington," *Proc. Anat. Soc. of Great Britain and Ireland*, Jan. 1916.

[3] J. Symington, *Edinburgh Medical Journal*, *loc. cit.*, pp. 98 and 99. In his address to the British Association in 1903 (see *Report*, p. 794), Professor Symington himself urged the importance of making such use of endocranial casts as we have done.

and the base, that they can be read on a cast nearly as easily and with as much exactitude and precision as on the surface of the brain itself. G. Schwalbe[1] in 1904, and one of us[2] in 1903, drew attention to that important fact, which many former works, more particularly those of P. Gervais, had already disclosed. Moreover, both R. Anthony and G. Schwalbe proved that in some members of the Mustelidæ group, for instance, a certain number of neopallial foldings are recognisable on the surface of the endocranial cast.[3]

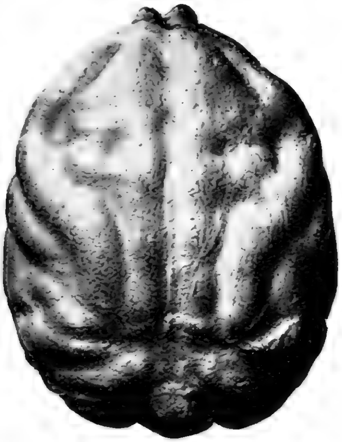

FIG. 1.—Endocranial cast of *Indris brevicaudatus* E. Geoffr. (Anatomie comparée, Muséum d'Histoire naturelle, Paris, No. A 10,595). Norma verticalis, showing the clearness and the precision of the neopallial impressions.

While in modern Man, as Professor Symington[4] has remarked, the foldings, plainly visible at the base of an endocranial cast, become less and less so as you draw nearer to the vertex, it is otherwise in some Primates—Lemurs, for instance,—in which the distinctness and extent of

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[1] G. Schwalbe, "Über die Beziehungen zwischen Innenform und Aussenform des Schädels," *Deutsches Archiv f. klinische Medizin*, Bd. lxxiii., 1904.

Id., "Über das Gehirnrelief des Schädels bei Saügetieren," *Zeitschr. f. Morphol. und Anthrop.*, Bd. vii., 1904.

Id., "Über das Gehirnrelief des Schläfengegend des menschlichen Schadels," *Zeitschr. f. Morphol. und Anthrop.*, Bd. x., 1907.

[2] R. Anthony, "Introd. à l'étude expérim. de la Morphogénie. Modifications craniennes consécutives à l'ablation d'un crotaphyte chez le chien, et considér. sur le rôle morphogénétique de ce muscle," *Bull. et Mém. Soc. Anthrop. de Paris*, 1903.

[3] R. Anthony et G. Schwalbe, *loc. cit.* In his 1907 memoirs Schwalbe showed that even in human endocranial casts the prominence of the convolutions is visible on the surface of the fossa temporalis.

[4] J. Symington, *Edinburgh Medical Journal*, *loc. cit.*, pp. 98–99.

their cerebral endocranial impressions are similar to those seen in Carnivores and Ungulates.

Everyone is acquainted with Professor G. Elliot Smith's[1] remarkable studies on the endocranial casts of the extinct Lemurs of Madagascar (not to mention the series of memoirs on the endocranial casts of other mammals—see *Transactions of the Linnean Society*, 1899 and 1903, and the Catalogue of the brains and cranial casts in the Museum of the Royal College of Surgeons, 1902).

Monkeys and Apes, considered from that standpoint, are not exactly similar to Man, nor to Carnivores, Ungulates, and Lemurs. If the endocranial casts of Chimpanzees, Gorillas, Orang-outangs are particularly akin, with respect to the vagueness and extent of their impressions, to those of human skulls, those of Cercopithecinæ and the Gibbon still retain on their whole surface neopallial impressions which, although not sharply defined in some cases, are yet always unmistakable. Therefore the value of the information that the study of endocranial casts may afford about neopallial morphology is very different according to the types considered.

Fig. 2.—Endocranial cast of *Hylobates leuciscus* Schreb. (Anatomie comparée, Muséum d'Histoire naturelle, Paris, No. A 8102). Left norma lateralis, showing sufficiently precise and clear neopallial impressions.

The question to be decided is this: What definite inferences may we draw from a study of fossil men's endocranial casts?

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[1] G. Elliot Smith, "On the Form of the Brain of the Extinct Lemurs of Madagascar, with some Remarks on the Affinities of the Indrisinæ," *Trans. of the Zool, Soc. of London*, vol. xviii. part ii., May 1908.

An examination of the endocranial casts of La Chapelle, La Quina, and Neanderthal justifies the conclusion that the region in which neopallial foldings are plainly demonstrated extends further forwards and backwards in them than in those of modern Man. These fossil men, viewed from that standpoint, would be, as it were, the link between the latter and the Gibbon.

The clearness and extent of neopallial impressions on the endocranial cast of an animal depend of course on many factors, all of which it would be difficult to enumerate.[1] But it seems that platycephaly is certainly to be considered as one cause, for we notice that, whereas in the Gibbon, the most platycephalic among Anthropoid Apes, foldings are to be seen imprinted on the whole endocranial surface, in modern Man they persist only at the base—by reason, probably, as previously said, of the force of gravity. In Neanderthalians, endocranial impressions of the furrows are more plainly perceivable, being usually apparent on the surface of the frontal and occipital regions. The following figures clearly express the great platycephaly of the Neanderthalians compared with modern men:—

Fig. 3.—Endocranial cast of Gorilla (Anatomie comparée, Muséum d'Histoire naturelle, Paris, No. A 8026). Left norma lateralis on which neopallial impressions are neither clear nor precise.

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[1] *Cf.* about that question, R. Anthony, "Introd. à l'étude expérimentale de la Morphogénie, etc.," *Bull. et Mém. Soc. Anthrop. de Paris*, 1903.

1. *Vertical longitudinal cranial index of Schwalbe.*

Neanderthalians	La Quina	39·09[1]
	Neanderthal	40·4[2]
	La Chapelle	40·5[3]
Minimum in modern Man		45[4] (an Australian)

2. *Frontal angle of Schwalbe.*

Neanderthalians	Neanderthal	44°[5]
	La Quina	45°[6]
	La Chapelle	45·5°[7]
Minimum in modern Man		50°[8] (a South Australian)

Moreover, the following observation may be accepted as supporting our contention:—the vertical longitudinal cranial index of Pithecanthropus is 34·2, the frontal angle is 34°,[9] and Dubois, speaking of its endocranial cast, says: "In the frontal region of the hemispheres the convolutions are most perfectly distinct."[10]

The fact, however, that the Chimpanzee, the Gorilla, and the Orang, still more platycephalic than Neanderthalians, afford, in most cases, a nearly smooth endocranial cast, shows that cranial flatness is not the only condition to be taken into account in this matter.

Professor Symington's mistake lies, we think, in assuming implicitly and without question—in spite of the researches of one of us,[11] as well as of Henri Martin[12] and others, concerning the various parts of the skeleton—that what is true of modern Man must also necessarily be true of a Neanderthalian.

But, if we admit that on the endocranial cast of a modern Man there is

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[1] H. Martin, *Bull. Soc. préhistorique française*, 1912, p. 32.

[2] G. Schwalbe, *Verhandl. d. anat. Gesells.*, 1901, p. 49.

[3] M. Boule, *Ann. de Paléontologie*, 1911, p. 36. The impressions of the frontal and occipital furrows are somewhat plainer in La Quina than in La Chapelle Man, and R. Anthony's remarks concerning the former have corroborated those previously made concerning the latter. It is regrettable that Professor Symington did not take them into account. . . . R. Anthony, "L'encéphale de l'homme fossile de La Quina," *Bull. et Mém. Soc. Anthrop. de Paris*, 6 mars 1913.

[4] Sollas, *Phil. Trans.*, 1907, p. 285.

[5] G. Schwalbe, *Verhandl. d. anat. Gesells.*, 1901, p. 46.

[6] H. Martin, *Bull. Soc. préhistorique française*, 1912, p. 32.

[7] M. Boule, *Ann. de Paléontologie*, 1911, p. 41.

[8] G. Schwalbe, *Zeitsch. f. Morph. und Anthrop.*, 1899, p. 149.

[9] *Ibid.*, 1899.

[10] Eugène Dubois, "Remarks upon the Brain Cast of *Pithecanthropus erectus*," *Proceedings of the Fourth International Congress of Zoology*, held in Cambridge in 1898.

[11] M. Boule, *Annales de Paléontologie*, 1911.

[12] H. Martin, *Bull. Soc. préhistorique française*, 1912.

a certain region in which neopallial foldings may be identified almost with certainty, it will be found that this region will be extended both further forwards and further backwards on a Neanderthalian cast (fig. 4).

From re-perusal of the papers relating to the endocranial casts of the La Chapelle aux Saints,[1] La Quina,[2] and Neanderthal[3] crania, it seems clear to us:—

Firstly, that we sufficiently emphasised the fact of the hypothetical character of some of our suggestions in reference to neopallial morphology;[4] and

Fig. 4.—Scheme showing the regions of an endocranial cast in the highest Primates, where the neopallial impressions are usually sufficiently clear and precise.

Black-tinted = modern Man.
Black-tinted and grey-tinted = Neanderthalian Man.
The whole norma lateralis = Gibbon.

Secondly, that we laid special stress upon the lack of clear indications of the neopallial features upon the upper surface of the cast, as is the case in most human and anthropoid specimens. Does not our tediously long discussion of the probable place and general direction of the central sulcus[5] afford positive proof of the fact that we refrained from assuming the presence of features of which no trace could be detected?

Consequently, Professor Symington's arguments and criticism are wholly irrelevant.[6]

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[1] M. Boule et R. Anthony, *loc. cit.*, *L'Anthropologie*, mars-avril 1911.

[2] R. Anthony, *loc. cit.*, *Bull. et Mém. Soc. Anthrop. de Paris*, 6 mars 1913.

[3] *Ibid.*

[4] See M. Boule et R. Anthony, *loc. cit.*, *L'Anthropologie*, mars-avril 1911.

[5] *Ibid.*; and also R. Anthony, *loc. cit.*, *Bull. et Mém. Soc. Anthrop. de Paris*, 6 mars 1913.

[6] J. Symington, *loc. cit.*, *Journal of Anatomy and Physiology*, Jan. 1916, pp. 117–122.

With reference to the probable position of the Sylvian fissure and its anterior and posterior pre-Sylvian branches, which we tried to determine, there is no doubt indeed that in modern Man (as Professor Symington says) most frequently no groove is found on the endocranial cast corresponding to the two pre-Sylvian branches, and the important groove (very often well marked) crossing the lateral boundary of the orbital surface corresponds to lateral offshoots of the sulcus orbitalis.

But in the La Chapelle aux Saints Man the aspect of the same region is very different (perhaps because of the great importance of its platycephaly). The aspect of this region of the La Chapelle aux Saints endocranial cast is also found in the specimen from La Quina. But we have said enough to expound the arguments in justification of our interpretations. "If any such arrangement of parts (the arrangement supposed by M. Boule and R. Anthony) actually existed in the Chapelle brain, it would form an interesting comparison with a fœtal brain of about the seventh month."[1] This is precisely our opinion. We are supposing that if Professor Symington had examined the paper on the interpretation of the La Quina endocranial cast, and had glanced over the figures contained therein, especially figure 20,[2] he would be satisfied with the probability of our interpretation.

Recalling the want of details figured on the roof of the endocranial cast, we are surprised that in his representation of the norma verticalis (fig. 7 according to Boule and Anthony, as he says) Professor Symington indicated the upper part of the central fissure (C.F.), which is not indicated in our figure 8.[3]

It is clear also that if in the same figure the beginning of the depression *Spo* is considered as the very probable point of emergence of the incisura parieto-occipitalis, the whole depression does not represent this incisura.

As a general conclusion we are venturing to assert—

That the results of Professor Symington's researches, though of value for modern Man, are not necessarily valid for the interpretation of a fossil Neanderthal Man, where the shape of the cranium is so different.

Therefore it is not only permissible, but we think highly desirable, to endeavour in the case of this fossil Man, as well as for any fossil Primate, to determine what positive information can be obtained from the endocranial cast, the only material available for such a purpose.

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[1] J. Symington, *loc. cit.*, *Journal of Anatomy and Physiology*, Jan. 1916, pp. 119–120.

[2] R. Anthony, *loc. cit.*, *Bull. et Mém. Soc. Anthrop. de Paris*, 6 mars 1913.

[3] Compare fig. 7 in Symington, *Journal of Anatomy and Physiology*, Jan. 1916, with fig. 8 in M. Boule et R. Anthony, *L'Anthropologie*, mars-avril 1911.

THE INTRINSIC ANATOMY OF THE LARGE NERVE TRUNKS OF LIMBS. By Alwyne T. Compton.

The surgery of the nervous system has received a considerable impetus during the past few months; and the results of improved technique in primary and secondary nerve-suture, nerve-implantation, and nerve-grafting are becoming definitely known. Operations of this kind are increasingly frequent. It is therefore a matter of interest and importance to gain a knowledge of the finer macroscopic structure of the chief nerve-trunks, more especially in the limbs, in order that, where a choice exists, the surgeon may select that method by which the normal anatomical and physiological conditions may be restored as completely as possible.

With a view to throwing light upon this subject, the conditions of several nerves are being investigated in the adult as well as in the fœtus. In this paper the results of the study of six fœtal and as many adult sciatic nerves are recorded.

The objects of the investigation are four: to ascertain whether it is possible to trace the course of the various nerve-bundles within the trunk of the great sciatic; to determine the relative positions of these bundles; to discover, if possible, some trustworthy marks upon the sheath or surface of the nerve-trunk, which may serve as guides to the position of subjacent nerve-bundles; and, lastly, to note the levels at which the several branches leave the nerve-trunk.

A brief summary of the results of the investigation will be found at the end of the paper. But it will be well to state here, firstly, that it is fairly easy, especially in the fœtal nerve-trunk, to isolate the bundles without injuring them. The whole trunk is enclosed in a tough connective-tissue sheath. From the deep surface of this sheath a number of septa pass inwards among the nerve-bundles, investing each bundle with a tubular sheath. Some of these septa are firmly adherent to the outer sheath, while others are looser and more delicate, and therefore more easily separated from the adjacent nerve-bundles. Some bundles are very easily isolated, while others need the most careful manipulation to free them from their sheath. The posterior tibial nerve was easy to isolate on account of the looseness of its sheath. Incidentally it may be mentioned that the sheath of this nerve was distinguished in most of the cases examined by being more vascular than the others. With regard to the possibility of determining the relative positions of the bundles in the sciatic trunk, it may be said that as a rule this point presented no difficulties, and that it has been possible to map out the position of each bundle fairly accurately. Unfortunately, no landmarks of any value could be found upon the sheath of the sciatic trunk which might be used as guides to determine the position of the various nerve-bundles. It was hoped at the outset that such landmarks might be furnished by the blood-vessels which pierced the sheath or were distributed upon its surface.

The exact points at which the branches leave the trunk are not quite constant. It is difficult to avoid stripping up a nerve a little too far when cleaning it. It then has the appearance of coming off the trunk at a higher level than is actually the case. The nerve to the femoral head of the biceps leaves the actual nerve-trunk above the level of the ischial tuberosity; but the point at which it emerges from the sheath of the trunk may be two or three inches below the tuberosity. The same applies to several other branches.

The methods employed in this investigation were dissection of hardened and fresh nerves, and the examination of transverse sections made through fœtal limbs showing the sciatic nerve *in situ*. The dissections were carried out with the aid of a lens. Each nerve was traced into the trunk, a note being made of its point of exit. The nerve was then followed upwards upon the surface of the trunk or through its substance, as the case might be. In the hardened nerves it was possible, by avoiding all unnecessary displacement of parent trunk or branch, to determine the position and course of each nerve-bundle. The shape of the transverse section of each larger bundle could also be made out, and how its shape was influenced by the pressure of neighbouring bundles. Each bundle was isolated for a short distance at first, so as not to alter its relation to the surrounding nerves. The bundle next to it was then treated in the same way, and the process repeated until, little by little, the whole sciatic trunk had been examined. During the dissection, measurements were constantly taken, and drawings were made both of the surface of the sciatic trunk and of transverse sections.

The portion of the great sciatic nerve which has been investigated is that which lies below the lower margin of the gluteus maximus muscle.

The sciatic trunk is usually more than half an inch broad, oval in section, its surfaces looking antero-posteriorly, except where it lies to the outer side of the ischial tuberosity. In this region the trunk is slightly twisted round its long axis, its posterior surface looking outwards as well as backwards.

BRANCHES OF THE GREAT SCIATIC NERVE.

The exact levels at which the branches are given off vary somewhat. The nerve to the femoral head of the biceps pierces the sheath of the sciatic trunk two to three inches below the tuber ischii. It is derived from the peroneal division, and enters the muscle close to the upper part of its posterior free border. The nerves to the ischial head of the biceps, the semitendinosus, the semimembranosus and adductor magnus muscles come off either separately or by a common trunk from the inner side of the tibial division of the great sciatic. In either case they leave the tibial one to two inches below the ischial tuberosity. The nerve to the ischial head of the biceps passes downwards and, inclining slightly outwards, crosses the main trunk posteriorly and enters the biceps upon its inner and deep surface three to four inches below the tuberosity. The nerves to the semitendinosus are two in number. They enter the deep surface of the muscle, one above and the other below the tendinous intersection. The upper branch reaches the muscle about three inches below the tuberosity, the lower branch about the middle of the thigh. The nerve to the semimembranosus is long and rather slender. It enters the cleft between that muscle and the adductor magnus and sinks into the deep surface of the semimembranosus below the middle of the thigh. The branches to the adductor magnus enter the muscle at various points in the middle third of the thigh. The disposition of the nerve-bundles in the trunk is correlated with the anatomical disposition of the structures to which they are distributed. That is to say, the sensory bundles occupy the more superficial (posterior) position, while of the more deeply situated motor bundles the nerves eventually distributed to the deeper limb-muscles occupy a deep (anterior) position relatively to those distributed to the more superficial muscles. The same rule applies to the branches given off from the tibial division in the popliteal space. The most superficial nerve here is the tibial communicating (posterior cutaneous nerve of the calf). This nerve not only occupies the central and most posterior position in the popliteal space, but it preserves this position when traced into the tibial trunk. Next in order from the surface towards the back of the knee-joint follow the nerves to the two heads of the gastrocnemius and the plantaris. These three are practically equidistant from the surface of the limb, and in the tibial trunk their corresponding bundles have the same relative position to each other. Next follows the nerve to the soleus, only very slightly

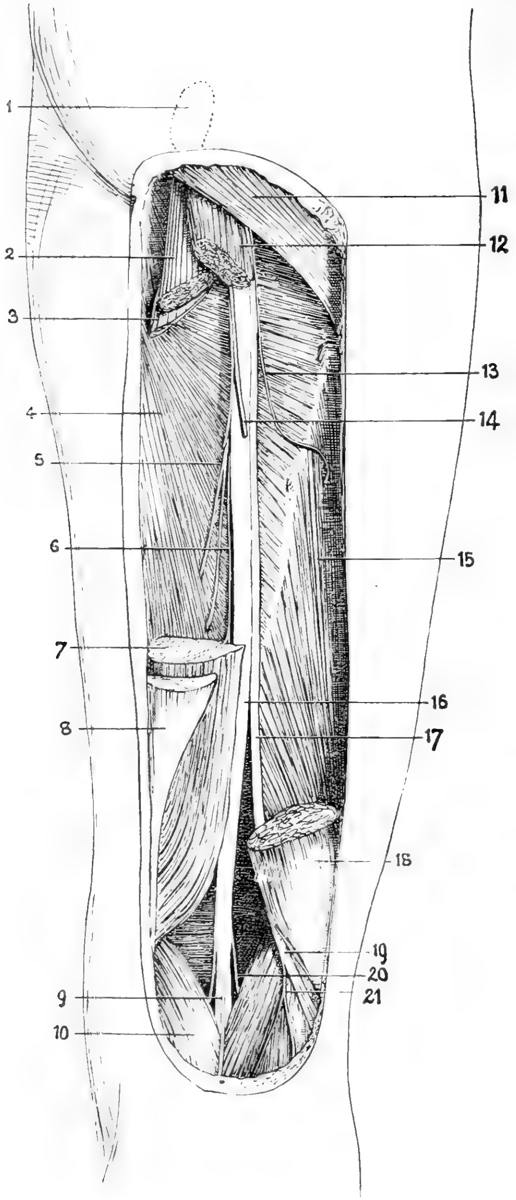

Fig. 1.—General view of the sciatic trunk. Hamstring muscles partly removed.

1, Tuber ischii; 2, semitendinosus; 3, semimembranosus; 4, adductor magnus; 5, nerve to the adductor magnus, partly covered by the nerve to the semitendinosus which has been cut short; 6, nerve to the semimembranosus; 7, semimembranosus; 8, semitendinosus; 9, tibial communicating nerve (posterior cutaneous nerve of the calf); 10, inner head of gastrocnemius; 11, gluteus maximus; 12, biceps femoris, ischial head; 13, nerve to femoral head of biceps; 14, nerve to ischial head of biceps; 15, femoral head of biceps; 16, tibial trunk; 17, common peroneal trunk; 18, biceps; 19, common peroneal trunk lying upon plantaris and outer head of gastrocnemius; 20, plantaris; 21, lateral cutaneous nerve of the calf.

deeper than the nerve to the outer head of the gastrocnemius (fig. 2). To the inner side of the nerve to the popliteus and almost the same distance from the surface is the posterior tibial nerve. It will be shown later that the bundles as seen upon a cross-section of the tibial trunk are approximately in the same relative position as the nerves derived from these bundles. In the case of the common peroneal nerve this applies also, but in a modified degree. As the nerve passes round the neck of the fibula, it has the form of a flattened band. This band can be seen to consist of two parts, antero-superior and postero-inferior. The former is the anterior tibial nerve (deep peroneal), the latter is the musculo-cutaneous (superficial peroneal). Lying between the two is the nerve to the peroneus longus. In some cases the small articular branch to the knee-joint can also be seen lying in front of the anterior tibial. Further proximally, in the outer part of the popliteal space, the common peroneal nerve gives off its cutaneous branches, the lateral cutaneous and peroneal communicating.

NAKED-EYE APPEARANCE OF THE SCIATIC TRUNK.

The trunk is enclosed in a firm sheath which varies in thickness and transparency in different subjects. Loose areolar tissue fills the space between the surrounding muscles and the nerve-trunk. In this tissue ramify vessels derived from the perforating branches of the profunda femoris artery. In the upper part of the posterior region of the thigh, several other branches derived from the inferior gluteal artery pass downwards in relation to the sheath of the sciatic trunk; and a few twigs from the internal circumflex artery reach the nerve. Of these vessels only two appear to have any fairly constant relation to the sciatic sheath. These are branches of the sciatic (inferior gluteal) artery. In several of the subjects examined, these two vessels were found to leave the sciatic artery immediately below the pyriformis and to proceed downwards upon the sheath as it covers the posterior surface of the sciatic trunk. The two arteries run parallel with each other, and parallel also with the inner and outer borders of the nerve-trunk, in such a manner as to divide the posterior surface of the trunk into three equal columns.

In cases where the tibial and common peroneal trunks are enclosed in a common sheath, the posterior surface of the sciatic trunk is divided into a large median and a smaller lateral column by a furrow. This furrow represents the line of division between the tibial and common peroneal trunks. It is occupied by an antero-posterior septum which blends in front and behind with the common fibrous sheath. The furrow is usually distinct enough to be visible through the sheath. In some cases the furrow

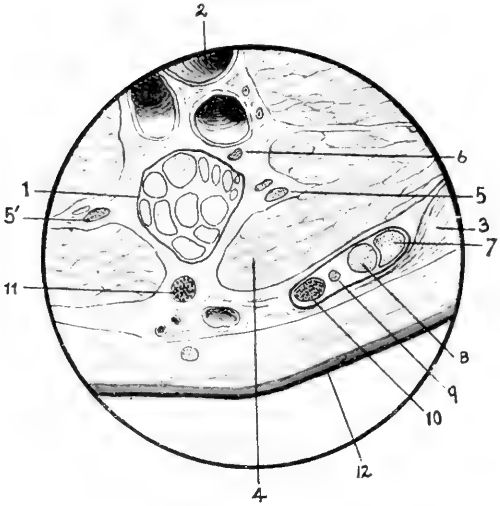

FIG. 2.—Transverse section through right fœtal leg at level of upper end of tibial diaphysis.

1, Tibial trunk ; 2, popliteal vessels ; 3, biceps ; 4, gastrocnemius, outer head ; 5, nerve to outer head of gastrocnemius ; 5′, nerve to inner head ; 6, nerve to popliteus—between this and the nerve to the outer head of gastrocnemius is seen the nerve to the soleus ; 7, anterior tibial bundle (deep peroneal) ; 8, musculo-cutaneous bundle (superficial peroneal) ; 9, branch to peroneus longus ; 10, peroneal cutaneous bundle ; 11, tibial cutaneous bundle (posterior cutaneous nerve of the calf) ; 12, skin.

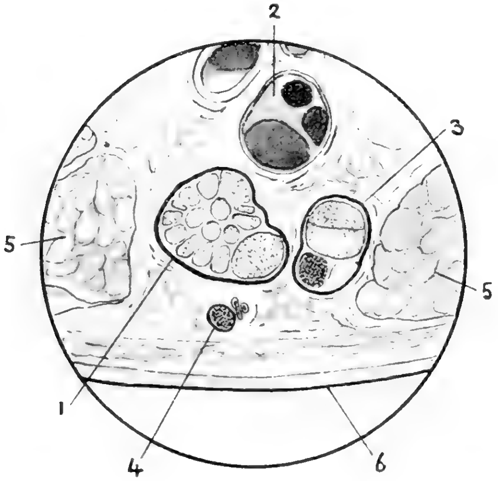

FIG. 3.—Section through middle of popliteal space. Same limb as fig. 2.

1, Tibial trunk ; 2, popliteal vessels ; 3, common peroneal trunk, showing peroneal cutaneous bundle (dark) postero-internally, anterior tibial anteriorly, and musculo-cutaneous bundle between the two ; 4, tibial cutaneous bundle ; 5, gastrocnemius ; 6, skin.

is filled up with fat, and a yellowish line is then seen marking the cleft between the two nerve-trunks. Distally the furrow lies at the junction of the outer with the middle third of the sciatic trunk. At the proximal end it is situated rather nearer the outer border; and it will be observed that the outer one of the two longitudinal arteries above mentioned lies either in the furrow itself or immediately to the inner side of it. Occasionally one or two other blood-vessels are found passing obliquely through the interval between the tibial and common peroneal trunks, thereby helping further to distinguish the one from the other. When the whole trunk lies exposed in a dissection, it is easy to split the sciatic trunk into its two main divisions by pulling apart the tibial and peroneal trunks from below upwards. But it is by no means always easy to find the exact plane of division if only a short piece of the nerve is seen at the bottom of an operation wound. The surface of the nerve may present such a perfectly uniform appearance, especially in its proximal part, that measurement must be relied upon. Distally the inner two-thirds and proximally the inner five-eighths of the posterior surface of the sciatic trunk may be regarded as belonging to the tibial, the remainder to the common peroneal trunk. Unfortunately, the two longitudinal vessels are only traceable for three or four inches, and by the time the sciatic trunk has emerged from beneath the gluteus maximus they are so much reduced in size as to be practically useless as guides. These vessels are shown in section in figs. 4 and 5.

Not until the enveloping fibrous sheath is opened can the nerve-bundles be distinctly seen. It then becomes evident that both divisions of the sciatic trunk show several parallel longitudinal markings which represent the various nerve-bundles separated from each other by the perineurium. Distally the bundles become directly continuous with the branches given off from the sciatic trunk. Here also the perineurial sheaths appear to be less firmly connected with each other than they are in the trunk higher up. For an inch or two the nerves can be readily followed upwards into the trunk. More proximally the process of splitting becomes difficult. The difficulty is partly due to the more intimate connection between the perineurium of one bundle and that of its neighbours, partly because branching takes place. It will be useful here to anticipate by stating that the central parts of both tibial and peroneal trunks are in part occupied by a plexus. The plexus nowhere comes to the surface, being everywhere covered by the longitudinal bundles seen upon the surface. The fibres which form the plexus are derived from branches split off from the deeper aspects of many of the bundles. The plexus is not equally well marked throughout the trunk. It occupies chiefly the middle third. The distal

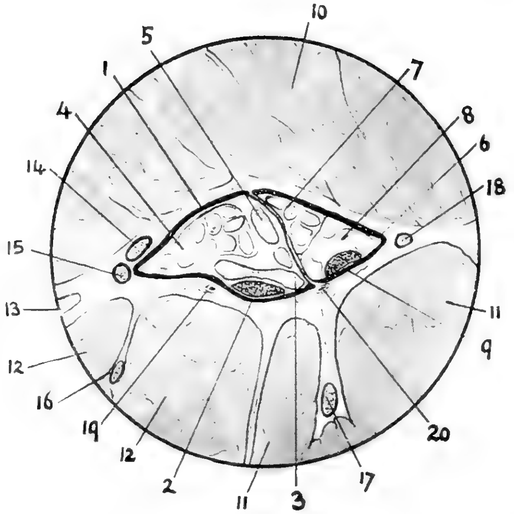

FIG. 4.—Transverse section through middle of thigh. Same limb as the foregoing figure.

1, Tibial trunk; 2, tibial cutaneous bundle; 3, gastrocnemius and soleus bundle; 4, posterior tibial bundle; 5, popliteus and plantaris bundles; 6, common peroneal trunk; 7, anterior tibial bundle; 8, musculo-cutaneous bundle; 9, peroneal cutaneous bundle; 10, adductor magnus; 11, biceps; 12, semitendinosus; 13, semimembranosus tendon; 14, 15, 16, 17, 18, nerves to adductor magnus, semimembranosus, semitendinosus, biceps (ischial head), and biceps (femoral head) respectively; 19, 20, branches of sciatic artery descending upon the sheath of the sciatic trunk.

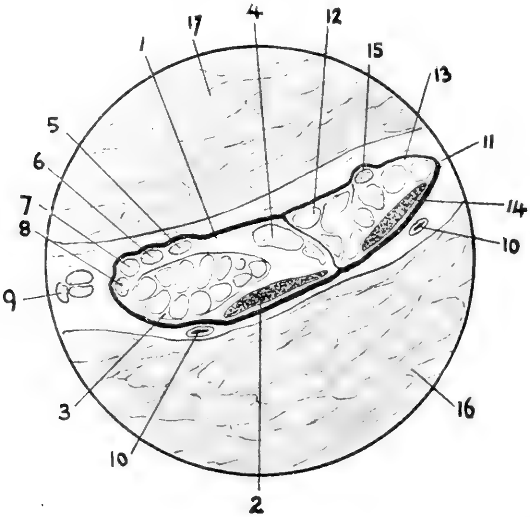

FIG. 5.—Transverse section through proximal part of thigh. Same subject as foregoing sections.

1, Tibial trunk; 2, tibial cutaneous bundle, flattened; 3, posterior tibial bundle; 4, popliteus and plantaris bundle; 5, nerve to adductor magnus; 6, nerve to semimembranosus; 7, nerve to semitendinosus; 8, nerve to biceps (ischial head)—these four nerves here lie within the sheath of the tibial trunk, upon the anterior (deep) surface of the posterior tibial bundle; 9, small sciatic nerve (posterior cutaneous nerve of the thigh); 10, branches of sciatic artery; 11, common peroneal trunk; 12, anterior tibial bundle; 13, musculo-cutaneous bundle; 14, peroneal cutaneous bundle flattened; 15, nerve to the femoral head of biceps within the sheath of common peroneal trunk; 16, adductor magnus; 17, gluteus maximus.

third is altogether free from branchings, the proximal third almost free. If the trunk be dissected without injuring any of the bundles, it is easy to split up the whole thickness of the distal third into its component bundles. The proximal third can be treated in the same way with almost equal ease. But in the middle third only the superficial bundles can be readily lifted out of their beds. When this is done, the branching fibres will be seen leaving the deep surface of each bundle. To display the plexus it is necessary to free all these branches from surrounding connective tissue. It will then be seen that the plexus is most complicated in the centre, less so at either end. At the proximal end the network becomes simplified by the reunion of fibres emerging from and entering into the plexus. The finer meshes of the plexus are gradually gathered up into strands which become continuous with the superficial bundles above the proximal end of the plexus. The plexus affords numerous facilities for the rearrangement of fibres, and the elements composing any given bundle are by no means necessarily the same below the plexus as they are above it. It is probable that most of the fibres composing a bundle pass over to other bundles and that they are replaced by fibres entering the bundle from elsewhere. Some bundles give off a larger number of fibres than they receive, and these diminish in size from above downwards. Other bundles show the opposite arrangement. The tibial communicating and peroneal communicating bundles probably undergo least change in composition. Their upward prolongations certainly show least tendency to branching. In ten out of the twelve cases examined, no branches at all were found. In the other two cases the tibial communicating bundle sent two branches upwards into the gastrocnemius bundle.

ARRANGEMENT AND POSITION OF THE NERVE-BUNDLES.

It will be convenient to trace first the course of the *cutaneous bundles* derived from the tibial communicating, peroneal communicating, and lateral cutaneous nerves of the calf.

The tibial communicating nerve (posterior cutaneous nerve of the calf).—The part of this nerve which lies free in the popliteal space is circular on section. The bundle belonging to it lies as a somewhat flattened band upon the centre of the posterior surface of the tibial trunk, and covers rather less than the middle third of the latter. When traced upwards, the bundle very gradually inclines outwards towards the lateral border of the tibial trunk, which, however, it does not actually reach. In the lowest part of the trunk this bundle therefore lies equidistant between the two borders of the trunk. At the proximal end it covers the outer third or a little more of the trunk, with a narrow bundle just visible to its outer side, lying in touch with the septum between the tibial and common peroneal trunks. This condition existed in all the cases examined except two fœtal ones, in which the tibial and peroneal cutaneous bundles approached each other centripetally, and in the proximal third were only separated by the septum. The tibial communicating bundle broadens slightly as it approaches the proximal end of the sciatic trunk, so that more surface is here covered by it than is the case distally. This broadening is not due to an addition of fibres. None enter or leave the bundle, and it is easy to separate the bundle from the trunk. This was impossible only in the two cases just mentioned, in which there were two slender branches running upwards and outwards from the tibial communicating nerve to join the outer gastrocnemius bundle.

The peroneal cutaneous bundle. — In this are included the lateral cutaneous nerve of the leg and the peroneal communicating nerve. These nerves leave the common peroneal trunk on its postero-internal aspect. When traced upwards upon the peroneal trunk, this bundle is seen to incline gradually outwards in the same way and almost to the same degree as the tibial communicating nerve. In most of the cases examined, the peroneal cutaneous bundle also became flatter and broader proximally, and covered rather less than the outer half of the common peroneal trunk at its proximal end. This bundle therefore crosses the posterior surface of the common peroneal trunk diagonally from the inner side below to the outer side above.

Having traced the two cutaneous bundles, and bearing in mind the areas which lie on either side of them, it will be easier to follow the course of the other bundles found in these areas.

COMMON PERONEAL TRUNK.

This trunk can be divided up into four bundles. Besides the peroneal cutaneous bundle just described, there are anterior tibial (deep peroneal), musculo-cutaneous (superficial peroneal), and the bundle formed by the branch to the peroneus longus muscle. In the popliteal space the trunk is oblong on section, and these bundles lie side by side. The anterior tibial lies outermost, the musculo-cutaneous next, then the small nerve to the peroneus longus, and, most internally, the peroneal cutaneous bundle. A short distance below the point at which the tibial and common peroneal trunks come in contact, the peroneal trunk is no longer oblong, but becomes circular on section. More proximally still, the inner side of the peroneal trunk becomes flattened against the outer side of the tibial trunk. But the septum runs forwards and inwards, not directly forwards. Therefore the innermost part of the common peroneal comes to lie anterior (deep) to the outermost part of the tibial trunk. In this region the common peroneal trunk has a roughly triangular outline on transverse section (figs. 4 and 5). A section through the upper part of the popliteal space (fig. 3) shows the common peroneal trunk circular on section. The bundles have undergone a slight change in position. The anterior tibial bundle is now in front, the musculo-cutaneous bundle lies immediately behind it, and posteriorly are the peroneal cutaneous bundle and the nerve to the peroneus longus side by side, the muscular bundle to the outer side of the sensory. More proximally where the trunk is triangular on section (figs. 4 and 5) the antero-internal angle is occupied by the anterior tibial bundle, the outer angle by the musculo-cutaneous bundle, the postero-internal angle also by that part of the musculo-cutaneous bundle which is not covered by the peroneal cutaneous bundle. In other words, all the bundles composing the common peroneal trunk are spirally arranged. It may be observed that the nerve to the femoral head of the biceps has a similar disposition. This nerve emerges from the common peroneal trunk upon its anterior surface near the groove between the anterior tibial and musculo-cutaneous bundles. Followed distally the nerve winds round to the outer side of the trunk and finally pierces the sheath at the lateral edge (fig. 4). This nerve leaves the trunk in the region of the tuber ischii, but remains within the sheath till it reaches a point about two inches further down.

THE TIBIAL TRUNK.

The most superficial (posterior) branch of the tibial trunk in the popliteal space is the tibial communicating nerve. The bundle of this nerve has been described lying upon the posterior surface of the trunk. Next in order come the nerves to the two heads of the gastrocnemius, and the nerves to the plantaris and soleus. The nerve to the soleus is large, and is given off from the outer side of the tibial trunk a little below the level of the knee-joint. The other three nerves leave the trunk at a slightly higher level. The nerves to the outer head of the gastrocnemius and plantaris come off from the outer side, the nerve to the inner head of the gastrocnemius from the inner side of the trunk. Followed upwards, these nerves are seen to spring from a common bundle, which is situated immediately anterior (deep) to the tibial communicating bundle. In transverse section this bundle for the supply of the calf-muscles is at first dumb-bell shaped, its two thickened borders being occupied by most of the fibres. At a somewhat higher level the section becomes crescentic. In the crescent the fibres are evenly distributed. The concavity of the crescent faces backwards and is filled by the tibial communicating nerve (fig. 4). This relation remains unchanged throughout the lower half of the trunk. Above this level the motor bundle gradually dwindles, its fibres passing into the plexus. The gastrocnemius and soleus bundle is slightly broader than the overlying sensory bundle, a narrow strip being visible on either side of the sensory bundle. The outer strip (outer gastrocnemius, soleus and plantaris fibres) lies along the septum dividing tibial and common peroneal trunks. Lying also in touch with the septum, but anterior (deep) to the gastrocnemius and soleus bundle, is the nerve to the popliteus. This nerve leaves the tibial trunk upon its antero-external aspect; and the corresponding bundle is seen on transverse section in the antero-external angle of the tibial trunk (figs. 4 and 5). This bundle can be traced upwards into the proximal third of the trunk. The slender plantaris bundle intervenes between it and the gastrocnemius-soleus bundle. The internal two-thirds of the tibial trunk are occupied by the upward extension of the posterior tibial nerve. Transverse sections through various regions show that this large bundle is oblong on section, and that internally it reaches to the inner border of the trunk, while externally it occupies the angle between the popliteal and gastrocnemius-soleus bundles. Proximally, however, the antero-internal part of the posterior tibial bundle is covered by the nerves to the hamstring muscles.

NERVES TO THE HAMSTRING MUSCLES.

These nerves, with the exception of the nerve to the femoral head of the biceps, are given off from the inner side of the tibial trunk. In sections across the proximal end of the trunk four nerves are visible upon the antero-internal surface of the trunk, between the sheath and the posterior tibial bundle. The outermost of these is the nerve to the adductor magnus. Next in order comes the nerve to the semimembranosus, then the nerve to the semitendinosus, and most internal the nerve to the ischial head of the biceps. When traced distally these nerves are seen winding spirally round the inner side of the tibial trunk. The first to appear upon the posterior aspect is the nerve to the biceps. Then follows the nerve to the semitendinosus. The nerve to the semimembranosus remains upon the inner side of the tibial trunk. The nerve to the adductor magnus remains in front of the tibial trunk, but inclines to its inner side. The posterior tibial bundle is therefore in contact both with the anterior and with the posterior part of the sheath, except postero-externally, where it is overlapped by the tibial communicating and gastrocnemius-soleus bundles;

and antero-internally, where its proximal part is overlaid by the nerves to the hamstring muscles and the adductor magnus. It has already been mentioned that the posterior tibial bundle is easy to isolate, being connected only loosely with its neighbours. In several of the cases it was also found that a few blood-vessels lay in the loose areolar tissue surrounding this bundle. These vessels may be of use in locating the posterior tibial bundle.

SUMMARY.

1. In the upper part of the thigh the tibial and common peroneal trunks are applied so closely to each other, that the line of division may escape detection. Yet each trunk is completely separated from the other, enclosed in its own fibrous sheath. The adjacent parts of the two sheaths adhere to each other and form a septum. The septum does not occupy an antero-posterior plane, but passes forwards and inwards between the two trunks, beginning behind at the junction of the outer with the middle third of the posterior surface of the sciatic trunk, and ending in front near the middle line of the anterior surface. In other words, the common peroneal trunk lies along the outer side and rather in front of the tibial.

2. There are no reliable landmarks upon the sheath indicating the position of subjacent nerve-bundles. There are several blood-vessels running upon the sheath, but they are not constant enough to be of service. The sciatic artery sends down a branch to the sciatic trunk. This vessel divides into two branches which run downwards upon the posterior aspect of the sheath. The outer one usually lies in the groove between peroneal and tibial trunks—that is, at the junction of the outer with the middle third. The inner branch of the artery bisects the posterior surface of the tibial trunk. These vessels are only two or three inches long, and do not reach further than the lower edge of the gluteus maximus. One or two vessels may sometimes be seen piercing the sciatic trunk along the line of the septum.

3. The level at which each nerve leaves the trunk varies to some extent. The nerves to the hamstring muscles emerge from the sheath one or two inches distal to the ischial tuberosity. The nerves to the gastrocnemius, soleus, and plantaris arise near the centre of the popliteal space, the nerve to the popliteus more distally, and the branches to the flexor longus digitorum, flexor longus hallucis, and tibialis posticus at the lower end of the popliteal space. It is not possible to recognise each nerve merely by the level at which it leaves the trunk. More constant than its origin is the relation which each nerve has to neighbouring nerves and to the trunk from which it arises. There is no haphazard grouping of the nerves or

their bundles in the trunks, but a definite arrangement depending upon the relative position of the soft parts. In the case of muscular branches the nerves run as directly as possible from the points of exit from the nerve-trunk to the points of entrance into their respective muscles.

4. Both tibial and common peroneal trunks contain a plexus involving in each case the central part of the middle third. Distal to the plexuses the trunks are made up of unbranched bundles. In the proximal third there is little or no plexiform arrangement. The plexuses are overlaid by a layer of longitudinal bundles forming the direct, unbranched upward prolongations of the several nerves given off from the trunks below the plexuses. On the surface there is no indication of a plexus. Distal to the plexus the bundles are identical with the nerves emanating from them. Proximal to the plexus these bundles, although superficially continuous with the nerves below, have partly lost their identity through interchange of fibres. The posterior tibial bundle appears to be only slightly connected with the plexus of the tibial trunk. The other bundles, with the exception of the two sensory ones, are extensively involved in the plexuses. The plexuses may be supposed to be largely, if not entirely, composed of motor fibres. The purely cutaneous bundles have little or no connexion with the plexuses. What relation the mixed nerves have to the plexuses it is impossible to say until the sensory have been separated from the motor bundles. One of the functions of the plexuses in the nerve trunks may be to supply to each muscle several routes by which impulses may reach it. In case one route becomes blocked, several others are still available. There is no doubt that a nerve trunk may be partly divided without producing any perceptible disturbance of function in the motor nerves arising from the nerve trunk distal to the seat of injury.

5. A variable but considerable portion of the posterior surfaces of the tibial and common peroneal trunks is covered by sensory fibres. These are grouped in two bundles, one associated with each division of the sciatic trunk. These bundles are superficial throughout. They are not connected with the plexuses, or only to a slight extent. In one instance it was found that the tibial sensory bundle sent two fine branches upwards and outwards into the outer gastrocnemius bundle. The tibial sensory bundle lies in the middle line of the tibial trunk distally. Proximally it inclines slightly outwards. The same course is pursued by the peroneal sensory bundle. Distally this bundle is situated upon the posterior surface of the common peroneal trunk, and slightly to the inner side. Proximally the bundle is still behind, but has gradually gained the outer aspect of the trunk. This change of position on the part of the peroneal sensory bundle is associated with the general spiral arrangement of the other

peroneal bundles. In the tibial trunk the slightly oblique course of the tibial sensory bundle is independent of the direction of the other tibial bundles. The latter are practically vertical throughout.

6. The twisting of the nerve trunks, shown decidedly in the peroneal trunk, less so in the tibial, points probably—but not absolutely—to the twisting which the limb is believed to undergo during development. Of all the structures of the limbs which might be expected to show evidence of such rotation, none would be more likely to do so than the nerves.

7. The origin of the nerve to the femoral head of the biceps from the anterior (deep) surface of the common peroneal trunk is consistent with the generally accepted view that this muscle is an extensor derivative functioning as a flexor.

8. The relative position of the tibial and common peroneal trunks is correlated with their flexor and extensor distributions, *i.e.* the tibial towards the ventral side of the limb, the peroneal towards the dorsal side. The common peroneal trunk tends to lie upon the anterior as well as upon the outer side of the tibial.

9. The nerves to the hamstring muscles leave the sciatic trunk proximal to the plexuses described above. None of these nerves are connected with the plexuses. The dissection of the proximal parts of the sciatic trunks was not completed. As far as it went, the examination of this part of the trunk suggested the presence of a smaller plexus formed by a branching of the nerves supplying the hamstring muscles.

10. The vascularity of the sheath of the posterior tibial bundle may be of service in differentiating this bundle from neighbouring ones. The fact that this bundle survives injuries more readily than some of the others may be taken as clinical evidence of its richer blood supply, and also, perhaps, of its looser sheath.

I cannot close this part of the work without expressing my sincere thanks to Professor Barclay Smith for his kindness in supplying me with material from the Anatomical Department at King's College; for many most interesting and valuable suggestions; and, most of all, for his unlimited care and patience in repeatedly going over the subject of this paper with me.

THE GENITALIA OF TUPAIA. By FREDERIC WOOD JONES, *Professor of Anatomy in the University of London; The London School of Medicine for Women.*

MATERIAL.

THE species that I have dissected is *Tupaia ferruginea*; it is the one that is especially entitled to the native name "tupai tanah" in the Straits Settlements.

I have had the opportunity of dissecting two specimens, a male and a female, both of them fully adult. The condition of these two examples, which were preserved in spirit, is such that every confidence may be placed in the normal appearance of the parts described. The preservation rendered histological examination of the tissues quite satisfactory. For the use of this material I am indebted to the kindness of Dr Foster Cooper and Professor G. Elliot Smith. The specimens formed part of the collection of the Survey of the Vertebrate Fauna of the Malay Peninsula undertaken by the Federated Malay States Museum, and they were taken at Kuala Lumpur.

REPRODUCTION.

Tupaia ferruginea lives as a rule in pairs or as solitary individuals (Cantor); it does not associate in groups, a family party being the limit of community.

From one to three young are produced at a birth. Cantor describes the birth of a single offspring as the most usual occurrence with *T. ferruginea*; but Boden Kloss regards two as constituting a normal litter. Lyon gives a list of embryos examined in pregnant females, and in one case there were three present, but in others only one or two.

The birth of two young would seem to be the rule with *T. belangeri*, one with *T. nicobarica*, and as many as four with *T. chinensis* (Lyon).

The nesting habits of the Tupaiadæ have been described by a few observers. Boden Kloss has described the nest of *T. ferruginea*, which is placed in holes in trees or even in fallen stumps.

The nest of *T. chinensis* has been found in a hollow bamboo (Lyon).

Charles Hose has recorded the nesting of *T. minor* in Borneo: "It breeds in a nest in an old stump covered with creepers, but I am not sure whether it makes the nest itself or occupies the nest of a bird. I have found two of these nests, but the material used was different."

I know of no observations upon the condition of the young at birth, nor upon the length of stay in the nest and the period of suckling. Breeding seems to take place throughout the year, but no observations appear to have been recorded upon the duration of gestation.

REPRODUCTIVE SYSTEM.

In a paper entitled "The Anatomy of *Tupaia*," Garrod made some slight notes upon the internal genitalia of the male *T. belangeri* in 1878. In 1914, Pehrson, in describing the ossicle in the clitoris of some Primates and Insectivores, makes brief mention of the condition of this structure in the female *T. javanica*. With the exception of these papers, I have, so far, encountered no published work upon the reproductive system of the Tupaias.

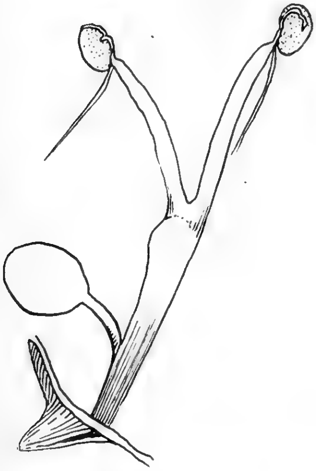

FIG. 1.—*Tupaia ferruginea.* Internal genitalia of adult female.

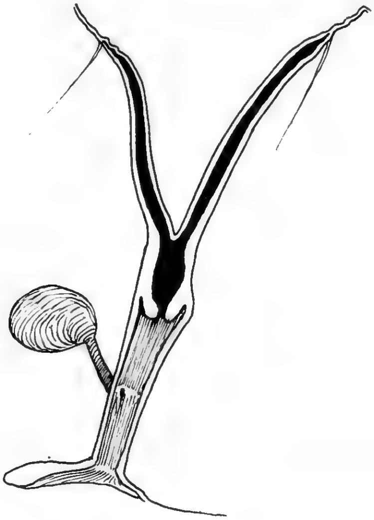

FIG. 2.—*Tupaia ferruginea.* Internal genitalia of adult female seen in section.

Female (see figs. 1 and 2).—The ovary was extremely small in my specimen; it was surrounded by a partial bursa. The cephalic ovarian ligament is but poorly developed; but the caudal ligament is well defined. The Falloppian tubes are narrow-bored and tortuous, and closely applied to the ovary, the ostium abdominale being within the ovarian capsule. The cornua of the uterus are elongated, and the body of the uterus is comparatively small. Lyon, who records the number of embryos present in several pregnant females, does not state in what part of the uterus the pregnancy occurs, and it would be interesting to know if there is any specific variation in the site of fœtal lodgment. A well-marked os uteri marks off the lower limits of the uterine cavity from the vagina. The vagina is a roomy thin-walled chamber, and measures 7 mm. from os uteri to urogenital sinus The urogenital sinus is longer than the vagina, and measures 9 mm.: it is distinctly marked off from the vagina above, but in my specimen no structure which can definitely be named a hymen is present below.

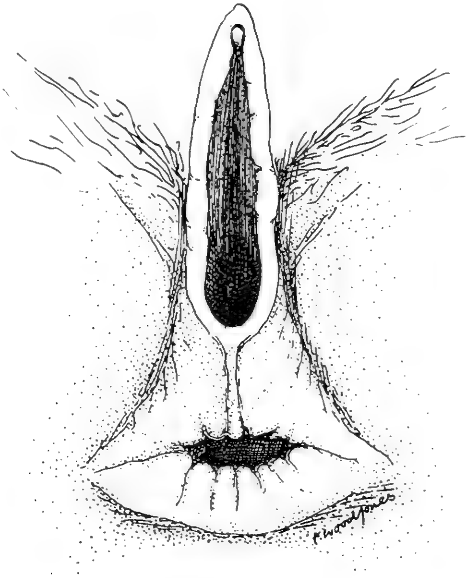

Fig. 3.—*Tupaia ferruginea.* External genitalia of adult female.

The whole urogenital sinus is smooth-walled, and covered with a shining mucous membrane. The urogenital sinus lies behind the elongated pubic symphysis.

The external genitalia of the female (see fig. 3) show several features which are worthy of note. The genital outlet is elongated in an antero-posterior direction, the total length of the orifice being 7 mm. The external genitalia can only be described as prominent. The very considerable extent of the vulval orifice is brought about by the prominence of the genital tubercle, and the structures embryologically associated with it.

The clitoris is free at its extremity, which is small and appears as a median elevation between the two prominent folds (inner genital folds) which, running from it, bound the sides of the vulval orifice and lead to the prominence of the part.

Behind the vulval orifice these inner genital folds meet in a definite commissure and thence proceed across the perineum as a median raphé (4 mm. in length) which terminates at the anal margin. Within the vulva, the mucous membrane is slightly folded in a radiating manner, the ridges upon the surface all converging upon the mouth of the urogenital sinus, which is situated at the extreme posterior limit of the vulva. The urogenital orifice is situated, therefore, very near to the anus, and the perineum is extremely short.

The region around the anus, and upon either side of the inner genital folds, is devoid of the general body hairs; there is, in the spirit specimen, no distinct trace of pigmentation, but sparse specialised sexual hairs are scattered over the whole region.

Male.—The general disposition of the internal genitalia of the male is shown in figs. 4 and 5, and but few points require further emphasis.

The entrance of the genital ducts into the urogenital tract is effected at the very considerable distance of 7 mm. from the site of opening of the ureters. For some considerable distance before they pierce the urethral wall, the genital ducts are in close contact with each other, but although their union is anatomically a very intimate one the tubes remain entirely separate until they open into the urethra.

In this part of their course they have placed upon either side of them, and behind them, bulky bilateral masses, which appear to the naked eye to be faintly subdivided into upper and lower portions. The line of demarcation is, however, but feebly delineated. Upon histological examination the upper portions of these masses prove to be complex vesiculæ seminales, while the lower portions compose the prostate. The prostate is strictly limited to these two postero-lateral masses, there being no gland tissue upon the anterior wall of the urethra, and none corresponding to the human third lobe. The common ejaculatory ducts open into the urethra, entirely separately, upon a slightly marked colliculus seminis, there being no common chamber, or uterus masculinus. The portion of urethra intervening between the site of opening of the genital ducts and the bulb is elongated: it runs behind the symphysis pubis, and measures 13 mm. in my specimen. It is wrapped round by an uninterrupted muscular coat (m. constrictor urethræ), and is enclosed in its entire extent between the two levator ani muscles, which form a muscle sheath common to it and to the lower part of the rectum.

The bulb of the urethra is prominent, the bulbar muscles constituting an exceptionally bulky mass. Two glandular bodies are placed upon either side of the bulbar muscles. The larger mass, situated cephalad, is 7 mm. in its long axis, and is dark yellow in colour. It presents all the histological features of the glandulæ bulbo-urethrales, its ducts open into the bulbar portion of the urethra, and these two bodies are therefore regarded as true Cowper's glands. The smaller mass measures 4 mm. in its long axis; it is pale yellow, and is bound but loosely to the bulb, it being situated, in the undisturbed condition of the parts, in the interval between the rectum and the bulbar musculature. No duct opening of these glands into the urethra could be found in serial sections, and it is therefore most probable that they belong to the class of circumanal scent glands.

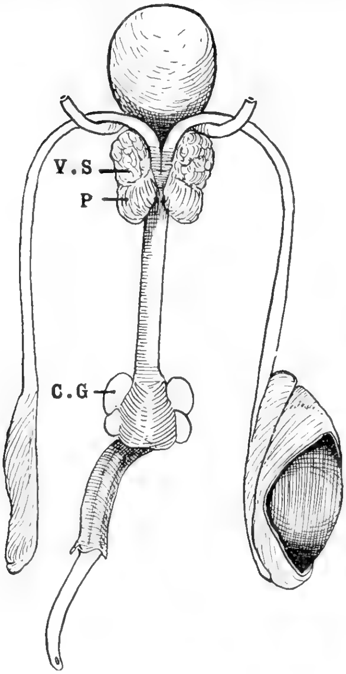

FIG. 4.—*Tupaia ferruginea.* Genitalia of the male viewed from behind.

V.S., vesiculæ seminales; P., prostate; C.G., Cowper's glands.

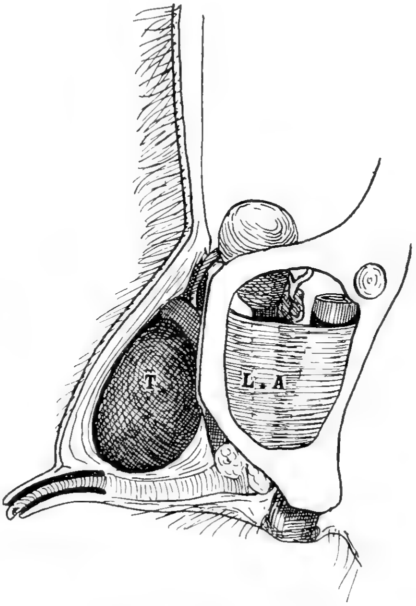

FIG. 5.—*Tupaia ferruginea.* Dissection of the male pelvis from the left side to show the relation of the scrotal pouch to the body of the penis.

T., right testes; L.A., levator ani.

In my male specimen there was a very curious disproportion in the relative sizes of the two testes, for while that of the right side was large, measuring 15 mm. in its long axis and 9 mm. in breadth, the left one was a mere fusiform mass of tissue. Histologically, the left testis appeared to be in a functionless condition, the testicular structure being extremely rudimentary; if this is a pathological feature, or merely a functional phase, I am unable to determine.

The epididymis is well developed. The total length of the right testis including the epididymis was 19 mm.

The tunica vaginalis extended no further than the upper pole of the testis, and no trace of a funicular process could be found, the isolation of the tunica vaginalis being as complete as in Man.

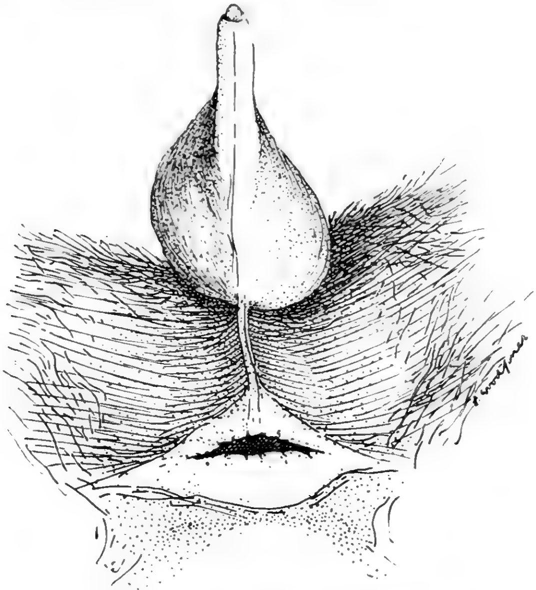

FIG. 6.—*Tupaia ferruginea.* Perineal view of the external genitalia of adult male.

The external genitalia of the male are of the greatest interest (see figs. 6 and 7). The penis is elongated, its total extra-pelvic course being 30 mm., and of this length 10 mm. consists of the fusiform glans. In the undisturbed condition of the parts, the tip of the glans protruded very slightly from the prepuce, the skin of which is finely wrinkled, and of a colour markedly lighter than the skin of the scrotal areas. A few fine down hairs arise from the base of the external surface of the prepuce. Owing to the curious disposition of the scrotal area, the penis, as it appears upon the external surface of the body, is abbreviated: the external surface of the prepuce measuring no more than 5 mm., whilst its internal surface is double that length.

The glans penis is thin and tapering; in the spirit-preserved specimen it is of a pale yellow colour, and is marked by fine transverse wrinkles. There are no projections from its surface, nor are there any visible glandular elevations or orifices. The opening of the urethra is sub-terminal and is situated upon the lower surface of the glans, presenting very much the appearance of the eyelet of a catheter. In my specimen no ossicle was present on the penis.

The most striking feature of the external genitalia of the male is the curious cephalic position of the scrotal pouches. Such a site of the scrotal area is unique among Eutherian Mammals. The testes are obviously permanently descended, and they are lodged beneath skin pouches, having the well-defined characters of the area scroti, which are situated cephalic to the root of the penis. The site of testicular lodgment is not so far forward as it is in the Metatheria; but it occupies a strange position upon the cephalic aspect, and to the sides, of the body of the penis. Perhaps the best description of this peculiarity could be given by likening the scrotal area of the male to the position of the Mons Veneris in the female. In the Metatheria the testes are herniated into scrotal sacs situated cephalic to the site of the Mons Veneris area; in Eutheria, as a rule, into some site caudad of this area; but in *Tupaia* they have lodged within the area, and have depended slightly upon either side of the genital tubercle.

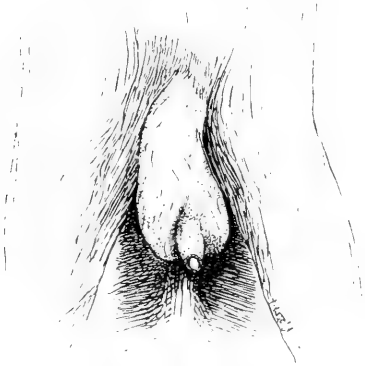

Fig. 7.—*Tupaia ferruginea.* Ventral view of external genitalia of adult male.

The skin of the scrotum is pigmented, and is considerably darker in colour than the skin of the surrounding districts. It gives rise to scattered hairs which are distinct from the body hair, and it is fine—almost shining—

in texture. There is a well-marked median raphé which extends along the body of the penis across the perineum and to the anal orifice.

MAMMARY GLANDS.

The female of *Tupaia ferruginea* possesses four nipples and mammary glands which, in my specimen, are all small and equal in development. They are situated upon the sides of the chest and abdomen as an anterior and a posterior pair. The anterior pair is separated by some 20 mm. from the axilla, and the posterior pair is 20 mm. behind the anterior pair, a slightly smaller interval separating the posterior pair from the region of the groin.

In *T. belangeri* there are three pairs, the additional pair being situated apparently between the thoracic and preinguinal pair of *T. ferruginea*. In *T. nicobarica* there is but one pair, which would appear to occupy the site of the thoracic pair of the other species. I have not examined these species, and I take the statements concerning the number of mammary glands from the paper by Lyon which has been quoted previously.

THE PELVIC SYMPHYSIS.

The ventral contact area between the two sides of the pelvis extends for a length of 7 mm., and so can only be described as long when the whole proportions of the pelvis are considered. This length of symphysis in so small an arboreal animal, at first sight, seems somewhat anomalous. But it must be remembered that *T. ferruginea* is best described as a bush animal rather than as a thoroughly arboreal one—and by this is implied that it is a haunter of undergrowth rather than of forest trees. The native name "tupai tanah" has regard to this habit, for it means ground squirrel, and is used to distinguish the animal from the true Squirrels, which live in the tree tops. There is a characteristic of this species which I observed in Singapore, that if Squirrels and Tupaias are met in undergrowth, the Squirrels take to the trees when alarmed, but the Tree Shrews make for the ground. Their arboreal activities are well developed, but the tree tops are not their home, nor even the retreat to which they betake themselves in danger. *Tupaia ferruginea* is an arboreal adventurer rather than an elaborated arboreal animal; but it appears, from written accounts, that other Tree Shrews, and especially *Ptilocercus*, have advanced further than this in arboreal life, and I should imagine that in them the area of symphysis would be shorter, and that corresponding differences would be present in the internal genitalia; but I know of no account by which to confirm, or disprove, this supposition.

PLACENTATION.

I have not been able to find any description of the placentation of *Tupaia*, but it seems reasonable to assume, as apparently zoological authorities do, that it is of the type usual among the Insectivora. This assumption is the more justified since Lyon records the condition of several pregnant females without making any note upon the embryo, membranes, or placenta.

SUMMARY AND CONCLUSIONS.

The genitalia of this animal exhibit an extraordinary blend of characters, since combined with features which are distinctly reminiscent of the Metatheria are conditions which find their exact parallels in the Primates.

In the internal genitalia, the length of the urogenital sinus in the female is correlated with the length of the wrongly-named "membranous portion of the urethra" in the male; and both features, I imagine, are the direct result of the length of the ventral pelvic symphysis.

Concerning the external genitalia, there can be no doubt that development has taken place by cloacal outfolding. The main features of the external genitalia may be summed up by saying that the female condition is singularly like that seen in many Primates, and that the male has several features which are found again in the higher Primates, combined with a scrotal disposition which seems obviously a transition phase from a Metatherian stage.

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THE INTERNAL STRUCTURE OF THE SPHENOIDAL SINUS.

By V. ZACHARY COPE, B.A., M.D., M.S., F.R.C.S., *Surgeon to Outpatients, St Mary's Hospital, London.*

THE internal structure of the sphenoidal sinus varies greatly in different skulls and on opposite sides of the same skull, and the great differences observed may be responsible for the total lack of any previous attempt to determine the arrangement and significance of the ridges and septa which are frequently found therein. Examination of a large number of sinuses (292 belonging to 180 skulls) reveals the fact that, though it is rare to find two sinuses exactly alike, there are certain features which recur with such regularity as to enable us to bring a certain amount of order out of seeming disorderly chance-variations.

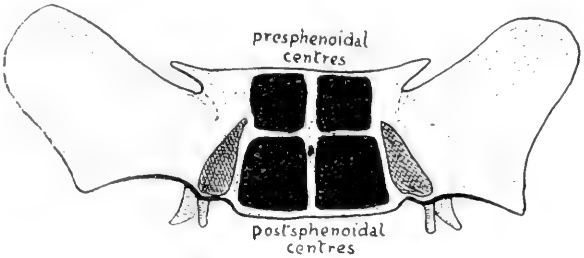

FIG. 1.—A scheme to show the centres concerned in the formation of the sphenoidal sinus. Body centres black, centres for lingulæ cross-hatched.

Before indicating these features we must prepare the way by a brief consideration of a few points relative to the development of the sinus.

The body of the sphenoid is developed from four symmetrically placed bony nuclei, two pre-sphenoidal centres in front and two basi- or post-sphenoidal centres behind. The cartilage between the pre- and post-sphenoidal portions disappears either shortly before or soon after birth; in a sagittal section the line representing its position begins above near the olivary eminence and extends obliquely downwards so that the section of the pre-sphenoidal area approaches the triangular rather than the quadrilateral shape. Along each side of the post-sphenoid area the bone is formed from the lingual centres. Each lingual centre leads to the formation of a triangular portion of bone with a small base posteriorly (corresponding to groove for the internal carotid artery) and a thin tapering portion which ends in an acute angle opposite the posterior end of the pre-sphenoid. The major part of the lateral aspect of the pre-sphenoid is in contact with the bone formed from the great wing of the sphenoid. The lingulal area unites with the body of the sphenoid before birth, but the fusion takes place from above downwards, and for some little time after birth indications of the groove between body and lingula can be seen (see fig. 2). The lingula unites with the great wing at a later date after birth.

The sphenoidal sinus is developed primarily at the expense of that portion of the bone formed from the pre-sphenoidal nucleus. During childhood this area becomes almost completely hollowed out, but an antero-posterior septum remains between the two sinuses, and the burrowing air-cavity still respects the boundaries of the areas developed from the nuclei of the post-sphenoid, the lingula, and the great wing. This condition may persist until adult life, but as a rule some time between puberty and adult age the sinus extends backwards or sideways or in both directions. Now there is evidence to show that the bone formed at the line of fusion of two bony centres may be, and often is, of a denser and more resistant nature than the tissue on either side of that line. This fact would account for the restriction of the sinus to the pre-sphenoid during childhood, and would offer an explanation for the frequent incomplete destruction of some of these fusion-barriers by the increased growth-activity of puberty. We hope to show that there are often present in the sinus ridges, crests, or partial septa indicating the position of the lines of fusion between the areas

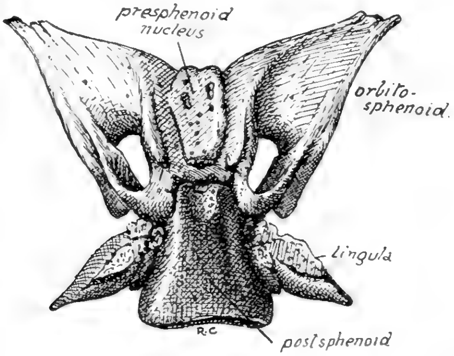

Fig. 2.—Under surface of sphenoid at birth (alisphenoid not present), to show incomplete fusion between lingulæ and body centres.

of bone formed from the nuclei of the pre-sphenoid, post-sphenoid, the lingula and great wing.

When once the barrier between the pre- and post-sphenoid is penetrated, growth is rapid, so that the sinus which first penetrates has the advantage over that of the opposite side, and usurps some of the space which by right should belong to its neighbour. Sometimes, indeed, the sinus of one side fails to break into the post-sphenoidal area, and the other sinus may then occupy three parts of the sphenoidal body. More commonly the struggle for the possession of the post-sphenoid results in the deviation of the posterior part of the main inter-sphenoidal septum to one or other side of the mid-line.

FIG. 3.—Sagittal section of skull of pig, to show synarthrodial joint between pre- and post-sphenoid. (Specimen in R.C.S. Museum, London.)

If we examine the skull of a pig we gain some help towards understanding the structure and development of the sphenoidal sinus. In the pig there is a synarthrodial joint between the pre-sphenoid and the post-sphenoid. The sinus pushes back through this joint, but the opening made is small, and even after the post-sphenoid has been excavated there remain well-marked medial and lateral elements of the septum between the pre- and post-sphenoid.

Consideration of the mode of development will show that for the sinus to extend laterally to any appreciable extent it must break through either the fusion-barrier between the body and great wing in front or that between the body and lingula behind. But lateral extension is more difficult behind because of the additional fusion-barrier between the lingula and great wing. We should therefore expect that the sinus would more frequently break through into the great wing anteriorly. Observation shows this to be the case, for, though the sinus in a considerable number of cases never bursts out of the body of the sphenoid, when a lateral recess is present it communicates with the main part of the sinus through an opening corresponding to the lateral aspect of the pre-sphenoid, and is separated from the posterior part of the sinus by an incomplete antero-posterior septum corresponding to the fusion-line between the post-sphenoid and lingula or the lingula and great wing.

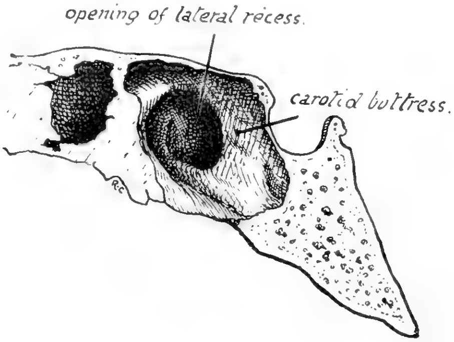

Fig. 4.—Sagittal section of sphenoid, showing opening into lateral recess in front of carotid buttress.

Sometimes the posterior ethmoidal cells push back into the pre-sphenoidal area and overlap the sphenoidal sinus, but I have never yet seen a specimen in which the ethmoidal cell had succeeded in penetrating the post-sphenoid area; the septum of bone separating the ethmoid and sphenoidal sinuses in these cases corresponds in position to the pre-post-sphenoidal fusion-line.

Sphenoidal sinuses may usefully be classified, according to the amount of their extension backwards, into (*a*) pre-sphenoidal sinuses which are confined to the pre-sphenoid; (*b*) post-sphenoidal sinuses which extend back almost to the clivus; and (*c*) sinuses of an intermediate size in which the post-sphenoid is only slightly encroached upon. Of the 292 sinuses which I examined, 155 were post-sphenoidal, 72 pre-sphenoidal, and 65 intermediate in type. It is quite clear that in a sinus confined to the pre-sphenoid there are not likely to be any septa apart from the lamella which separates the right sinus from the left, so that the following account of the internal structure refers for the most part to the sinuses of the post-sphenoidal and intermediate types.

We will consider the internal structure of the sinus under the following heads:—

1. Inter-sphenoidal septum.
2. Transverse sphenoidal septum (trans-sphenoidal).
3. Carotid buttress.
4. Recesses from the main sinus.
5. Bulges into the sinus.

Fig. 5.—Sphenoidal sinus, showing trans-sphenoidal septum.

1. The pre-sphenoidal portion of the inter-sphenoidal septum is usually median in position and antero-posterior in direction. It is not uncommon, however, for it to be slightly to one or other side of the median line. The post-sphenoidal portion of the septum more commonly deviates from the middle line, and sometimes bends almost at right angles to the anterior part so as to form the posterior wall of the opposite sinus. Quite a common attachment posteriorly is to a point corresponding to the situation of the internal carotid artery, so that if the surgeon relied on the septum to guide him to the pituitary fossa he would frequently make a serious mistake.

2. The "trans-sphenoidal septum" is the name best suited to express the

remaining portion of the barrier between the pre- and post-sphenoid. If the element is small, the term "trans-sphenoidal crest" or "ridge" may be used. The common position for this ridge is in the roof of the sinus just behind the level of the olivary eminence or tuberculum sellæ. More rarely the ridge will be found on the floor of the sinus. When the unabsorbed part of the septum is that section attached to the lateral wall, it forms a buttress for the carotid artery, and will be described under that heading. The crest on the roof of the sinus is to be found in about a fourth or a fifth of all sinuses. Much more rarely that part of the septum attached to the floor of the sinus persists, so that we have some ground for concluding that the growing air-cell penetrates first into the lower part of the post-sphenoid. Sometimes the crest is present on both sides, but quite commonly only in the sinus of one side.

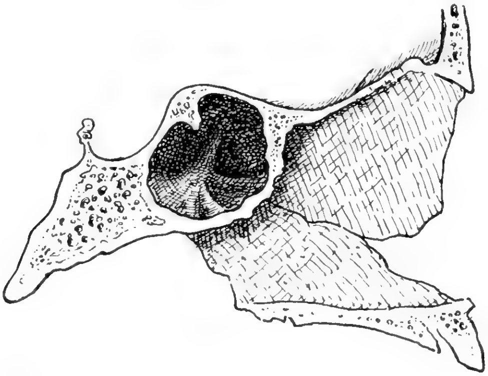

Fig. 6.—Sphenoidal sinus, showing trans-sphenoidal ridge and carotid buttress formed by lateral part of trans-sphenoidal element.

3. In skulls in which the sinus does not extend so far laterally the internal carotid artery is supported by the lingula and the lateral wall of the sphenoidal body; but in addition it may have other supports, and when lateral extension takes place there is need of some supporting process if the artery is not to encroach on the sinus. I have applied the term "carotid buttress" to the various special supports which prop up the roof of the sinus in the region of the carotid bulge. The carotid buttress may be derived from different elements:—

(*a*) It may be formed by the lateral portion of the trans-sphenoidal septum. In this case it will be found as a vertical ridge or partial septum with the free edge directed transversely towards the inter-sphenoidal septum.

(*b*) The buttress may be derived from the median part of the trans-sphenoidal septum. In such a case, which is much rarer than the first variety, it is attached to the inter-sphenoidal septum, and the free crescentic edge extends across the sinus like part of a Gothic arch.

(*c*) The third type of buttress is found in those sinuses with a lateral extension into the lingula and great wing. It consists in an antero-posterior septum attached posteriorly and with a free crescentic edge in front. It corresponds in position with the line of junction of the body of the sphenoid and the lingula, or in some cases possibly with the line between the lingula and great wing. External to this buttress is the lateral recess.

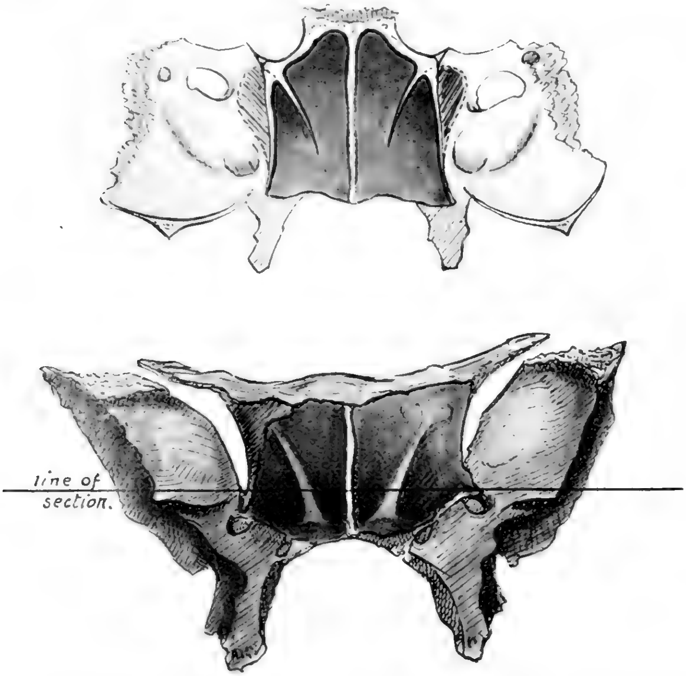

Fig. 7.—Sphenoid opened from the front to show antero-posterior type of carotid buttress. The upper figure is the upper aspect of lower part of bone divided at level of line.

(*d*) Sometimes the posterior attachment of the inter-sphenoid septum is opposite the carotid bulge, and therefore a deviated septum should be regarded as an occasional carotid support or buttress.

In the pre-sphenoidal type of sinus one may often see a posterior ridge indicating the anterior end of the fusion-line between the body of the sphenoid and the lingula.

4. *Recesses from the main sinus.*—The fully developed sinus may confine itself to the body of the sphenoid, but more frequently there are extensions laterally, forwards or backwards.

The lateral recess extends outwards from the side of the body of the sphenoid into the great wing and lingula. I found a well-marked lateral recess in 72 cases out of 292 sinuses examined. Many others in which the septum between the body and lingula was not present should be included if we wish to estimate the relative frequency with which the sinus extends laterally from the body. The lateral recess is bounded medially by the antero-posterior carotid buttress when present, and laterally reaches out to a variable extent, frequently as far as the maxillary nerve, and rarely travelling through the pterygoid process to the surface of the skull below the infra-temporal crest. I have seen several specimens of the last-mentioned variety in human skulls—a fact of interest in that it is the normal condition in the gorilla and chimpanzee. Under the floor of the lateral recess lies the Vidian nerve, and above its roof are the carotid artery and cavernous sinus.

The anterior recess is not so frequently present. It was noted in 13 cases of the series examined, *i.e.* 5 per cent. It extends forwards, outwards, and slightly downwards from the region below the optic nerve, and usurps the position usually occupied by the posterior ethmoidal cells and cell of orbital process of palate, with which it has no communication. In 2 or 3 per cent. of all sinuses the anterior recess is in relationship with the postero-superior wall of the maxillary antrum, from which it may be separated by a transparent shell of bone.

Very rarely a backward prolongation of the sinus into the basi-occipital may merit the name of a posterior recess. There is sometimes a shallow sub-optic recess beneath the prominence caused by the optic nerve, and more rarely an extension into the lesser wing and anterior clinoid process above the optic nerve constituting a supra-optic recess.

We may here with advantage enumerate the various forms which the ground-plan of the sinus assumes. The accompanying diagrams (fig. 8) represent sections through the sinus parallel to its floor. Dotted lines indicate the junction between pre-sphenoid, post-sphenoid, lingula, and great wing; the outline of the triangular lingulal area is thus clearly indicated.

1 and 2 show simple pre-sphenoidal and post-sphenoidal types respectively. 3 shows pre-sphenoidal sinuses with small lateral recesses. In 4 the lateral recess is well marked, and the antero-posterior carotid buttress is shown. 5 indicates a common type, in which the sinus of one side occupies the whole of the post-sphenoid. 6 is a rare form, which I have only seen once or twice, in which the sinus of one side has extended so far across as to

form a lateral recess on the opposite side; ridges corresponding to the post-sphenoid-lingula line were clearly seen in this case. 7 is the ground-plan of a pair of sinuses with lateral and anterior recesses. 8 shows a condition which is unique in the series I have examined; in it the sinus apparently was unable to break through the region of the trans-sphenoidal septum, and so on the right side it forced its way from the pre-sphenoid out into the great wing and then entered and hollowed out the post-sphenoid from its lateral aspect. The front part of this specimen was missing.

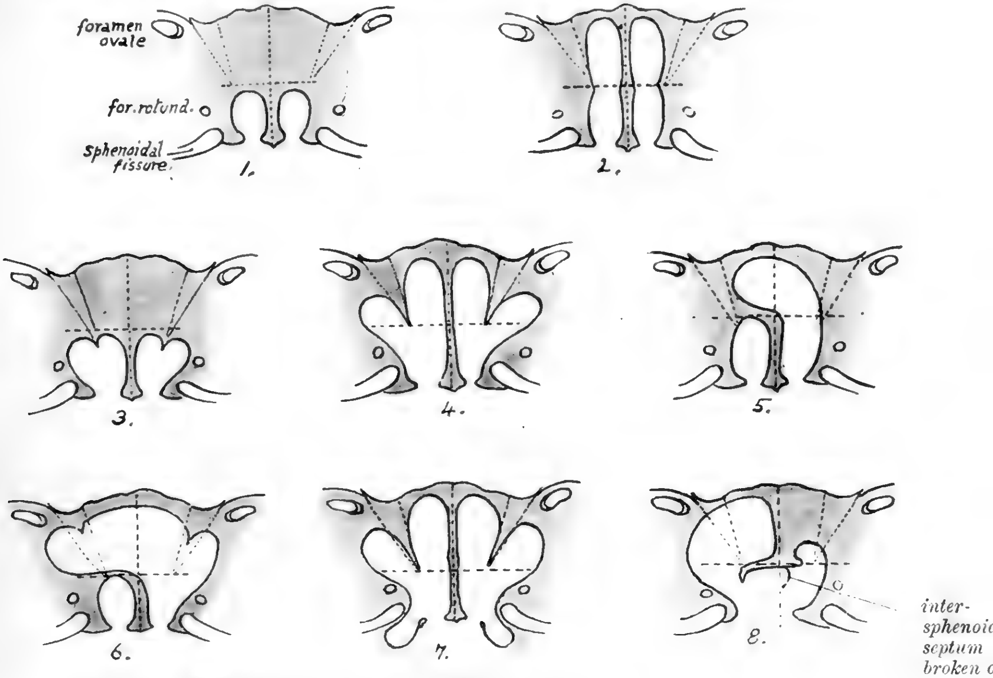

FIG. 8.—Diagram of ground-plan of different types of sinus. The cavities are as they would be seen from above.

5. *Bulges into the sinus.*—The following bulges, caused for the most part by vessels and nerves, may be seen in the walls of the sphenoidal air sinuses:—

(1) Pituitary.
(2) Carotid.
(3) Optic.
(4) Vidian
(5) Maxillary } in the lateral recess.
(6) Spheno-palatine—in the anterior recess.

(1) The varying relations of the pituitary fossa to the sphenoidal sinus may be shown by diagram. The bulge is absent in the pre-sphenoidal type, slight in the intermediate form, and well marked in a fair proportion of the post-sphenoidal sinuses. When a trans-sphenoidal crest is present it may mask the pituitary bulge, but at the same time indicate accurately the antero-inferior part of the fossa. The pituitary bulge is frequently not so marked as the carotid bulge with which it is continuous, and it is sometimes a little difficult to say from an internal inspection of the sinus where one ends and the other begins.

(2) The most constant part of the carotid bulge is that corresponding to the bend under the anterior clinoid process. This frequently causes a prominence even in sinuses of the pre-sphenoidal type. In sinuses of the post-sphenoidal type the artery may cause a sinuous convexity along the lateral aspect of the wall of the cavity. The carotid bulge is frequently partly hidden by the bony buttresses which support it. When there is a well-developed lateral recess the artery lies wholly on the roof of the sinus.

(3) The optic nerve frequently causes a bulge into the antero-superior part of the sinus, and, according to the degree of its projection into the cavity, there may be developed supra- or infra-optic recesses.

(4) When the lateral recess extends sufficiently far out, there may be slight or even well-marked bulging caused by the maxillary division of the fifth cranial nerve. When the sinus extends beyond the foramen rotundum the nerve will sometimes bulge into the roof of the cavity. In 50 cases of this series there was a maxillary bulge.

(5) The Vidian nerve may also cause a bulge, or, strictly speaking, a ridge, on the floor of the lateral recess. In two or three specimens part of this ridge has been wanting in the dried bone, and clearly the nerve must have been separated from the interior of the cavity by a thin layer of soft tissues. The Vidian ridge or bulge was seen in 25 cases in this series.

(6) When the anterior recess is well marked, a vertical bony pillar will be seen leading down from the spheno-palatine foramen and marking the lateral boundary between the main cavity and the anterior recess. This bulge could appropriately be called the spheno-palatine pillar. It is caused by the vessels and nerves descending from the spheno-maxillary fossa.

A NOTE ON THE DUCTUS CAROTICUS AND DUCTUS ARTERIOSUS AND THEIR DISTRIBUTION IN THE REPTILIA.

By CHAS. H. O'DONOGHUE, D.Sc., F.Z.S., *Senior Assistant in the Zoological Department, University College London.*

OWING to the kindness of Professor A. Dendy, F.R.S., I have been able to examine the vascular system of the New Zealand Tuatera (*Sphenodon punctatus*), and I wish to express my thanks for the opportunity of so doing. When dealing with the main arterial roots in the course of this examination it soon became evident that a certain amount of confusion exists in literature concerning the nomenclature of portions of the embryonic arterial system usually fated to disappear but which may remain in a functional or vestigial condition in the adult. It seemed worth while calling attention to this matter in order that the muddle should not be perpetuated.

The foundation of our modern knowledge of the transformation of the arterial arches in the Amniota was laid by Rathke (35) in 1857 in his masterly paper on the aortic roots in Saurians. He pointed out that in the embryo five pairs of arterial arches were present on each side joining the ventral to the dorsal aortæ, Van Bemmelen (5) in 1886 described a transitory arch between the 4th and 5th in Rathke's series. This transitory arch was recorded in man, the rabbit, and the sheep by Zimmerman (40 and 41), and later by Tandler (38) in rat and man,[1] and Lehman (28 and 29) in rabbit and pig. Lewis (30) threw some doubt on the presence of this vessel, and suggested that comparative anatomical considerations had led observers to describe as a vessel what was in reality an indefinite meshwork of small vessels. However, more recent workers have reported the presence of this vessel in other mammals, viz.: in the mole, Soulié and Bonne (37); in the cat, Coulter (19); and in the pig, Reinke (36). There can be little doubt, then, that in the embryos of Amniotes in general six arterial arches make their appearance; the fifth, counting from before backwards, was overlooked by Rathke, is transitory and not so well developed as the remainder, and often apparently runs into the sixth on

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[1] A good review of these changes as they apply to the condition in man will be found in Evans's article (21) in Keibel and Mall's *Manual.*

the dorsal side instead of into the dorsal aorta. In the transformation to the adult condition, as is well known, the first two and the fifth arches disappear, leaving the third, fourth, and part of the sixth as the carotid, systemic, and pulmonary arches respectively. From the third arch the continuation forward of the dorsal aorta constitutes the internal carotid, and the prolongation of the ventral aorta the external carotid. It is probable that the dorsal portions of the first and second arches remain to form the roots of the supra- and infra-orbital arteries respectively. The fourth arch forms the systemic stem, and in reptiles persists on both sides, in birds on the right only, and in mammals on the left only. A branch from the sixth arch on each side constitutes the pulmonary trunk. Certain other parts of the embryonic vessels may remain in a more or less well-developed condition in the adult, and it is respecting the nomenclature of these that the confusion exists.

I. The Ductus Caroticus.

This is a connection in the adult joining the carotid and systemic arches, and usually situated somewhat laterally where both these arteries are bending round the œsophagus. It is actually a persistent portion of the embryonic dorsal aorta, and may be represented merely by a thin strand of

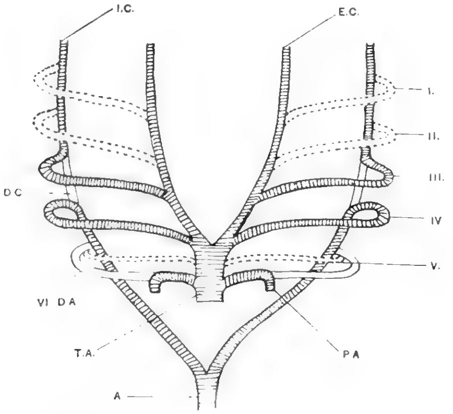

Fig. 1.—Diagram of the arterial arches of an Amniote embryo, to indicate vessels remaining in adult reptiles.

Dotted lines indicate vessels that disappear. Plain lines indicate vessels that may persist as ductus or ligamenta. Shaded portions indicate vessels that persist in the adult. I.–VI., the six embryonic arches; III., the carotid; IV., the systemic; A., dorsal aorta; D.A., ductus arteriosus (Botalli); D.C., ductus caroticus; E.C., continuation of the ventral aorta to form the external carotid artery; I.C., continuation of the dorsal aorta to form the internal carotid artery; P.A., pulmonary artery; T.A., truncus arteriosus.

tissue with no lumen, as for example in *Rana*, in which condition it may perhaps be termed more strictly a ligamentum caroticum, or as a widely open vessel, a ductus, as in *Sphenodon*. In this form, too, it gives off a fair-sized artery, the arteria muscularis cervicis.

II. THE DUCTUS ARTERIOSUS OR DUCTUS BOTALLI.

This structure, usually closer to the heart than the former, represents the continuation of the pulmonary arch from the point of origin of the pulmonary artery to the dorsal aorta. It is not part of the embryonic dorsal aorta like the foregoing, but, like it, may be present in the adult as a solid strand or as an open vessel. Van Bemmelen (5) found it in the larger of the two examples of *Sphenodon* he examined, and in the same species I have found it to be present generally in the form of a small but definite artery joining the two trunks. It is subject to more variation among the Reptilia than the ductus caroticus. Sometimes it remains open, *i.e.* a ductus, but is never so large as the former structure; it may be simply a strand of tissue or ligamentum: or yet again it may be partly open and partly solid, as is frequently the case in the Ophidia. There is also a certain amount of evidence to show that it may gradually close up during the life of the individual after it has reached the adult condition.

In this country the confusion has arisen since either of these vessels indiscriminately has been termed the ductus Botalli, whereas the two structures are distinct and of different morphological value. It has become almost general to describe the ductus caroticus as the ductus Botalli. Bourne (13, vol. ii. p. 275) states that the connexion between the first and second aortic arches in *Rana* persists in the adult as the ductus Botalli; Thomson (39, p. 626) refers to the ductus Botallii (*sic*) in *Lacerta* as joining carotid and systemic arches; and Marshall (32, p. 30) gives the same account for *Rana*. Beddard, whose papers have added so greatly to our knowledge of the vascular system in the Reptilia, also adopts the same terminology. In a diagram of the principal arteries of *Sphenodon* (4, p. 463) he figures this vessel quite accurately, but terms it the ductus Botalli; again in *Tupinambis* and *Iguana* (2, p. 466) he portrays the same artery; and lastly (3, p. 609), he states that no ductus Botalli joins the systemic and carotid arch in *Heloderma*, *Varanus*, and *Amphisbæna*. He uses the term again in the same sense (1, p. 331) in reference to a paper of Brandt's. In all these cases it is the ductus caroticus that is being dealt with.[1]

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[1] The same misuse of the term ductus Botalli, only in the case of birds, is met with in a note by Finn, "On a Functional Ductus Botalli in *Nycticorax violaceus* and *Dafila spinicauda*," *Proc. Zool. Soc.*, Feb. 1891.

Parker and Haswell (34, vol. ii. p. 306) describe a true ductus Botalli in the Urodele *Salamandra*, but a few pages further on (p. 326) apply the same term in *Lacerta* to the connection between carotid and systemic arches. All authors apply the term correctly in the mammals, in which, of course, a ductus caroticus is not present.

There is no doubt whatever as to what structure Botallus himself meant, for he was dealing with a mammal, man, in which there is no ductus caroticus. In his *Opera Omnia* (11) the vessel is dealt with in Observatio III.: "Vena arteriarum nutrix a nulla antea notata" (p. 66). It is figured on p. 68 in a not very clear drawing, but described there under "Figuræ tertiæ Explicatio" as 'F.F. Canalis a pulmonali arteria tendens in aortam." This is the true ductus Botalli, or, as it has been subsequently named, the ductus arteriosus. The other vessel is the ductus caroticus, as it was first termed by Brandt (14).

Both these vessels are present in the embryo, and, as Boas (7) has recorded, present in the young frog and in the salamander at the time of metamorphosis. The same author describes them in the adult *Menopoma* and *Amphiuma* (8), and figures them also in a scheme of the vessels in the adult Triton (9). Fritsch (22) gives a diagram of *Cryptobranchus* in which not only are both these connections present, but also the fifth arch between the systemic and the pulmonary. From these facts we may justifiably conclude that the presence of both structures indicates a lack of specialisation in these regions, and a consequent retention of a fairly primitive condition.

It does not appear out of place here to glance briefly at the distribution of these two vessels or their vestiges in the Reptilia, and for convenience the orders of the class will be the same as those given by Boulenger (12).

RHYNCHOCEPHALIA.

The sole living representative of this order is *Sphenodon punctatus*. In this form the ductus caroticus is well developed on both sides, as recorded also by van Bemmelen (5) and Beddard (4), and has a diameter as large as that of the external carotid. From it is given off a moderate-sized vessel, the arteria muscularis cervicis. The ductus arteriosus is also present, as pointed out above, as a distinct though small artery on each side. Thus the vessels in this form retain on both sides the connecting trunks found in the embryo. It might be suggested, of course, that this arrangement has been reacquired in a secondary way by the retention of larval structures that had disappeared phylogenetically; but taking into consideration various other points in the vascular system, it is much

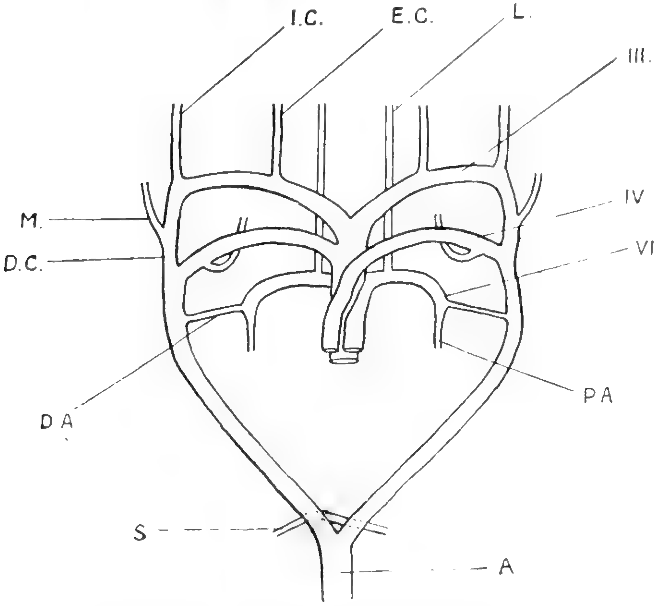

FIG. 2.—Diagram of the arterial arches in *Sphenodon punctatus*.

L., laryngeal artery; M., arteria muscularis cervicis; S., subclavian artery. Other letters as in fig. 1.

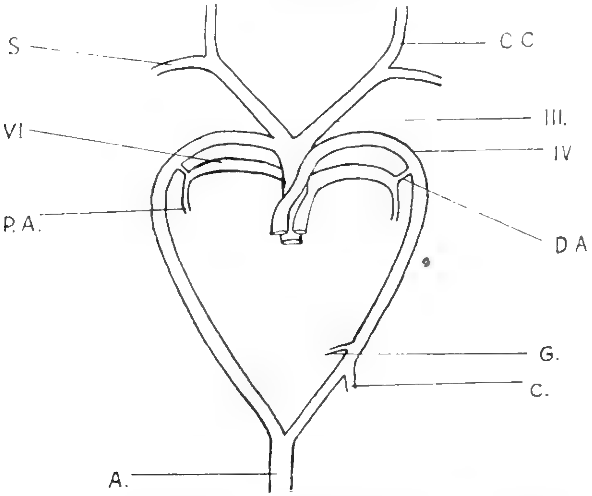

FIG. 3.—Diagram of the arterial arches in *Testudo græca*.

C.C., common carotid artery; G., gastric artery; C., cœliaco-mesenteric artery. Other letters as before.

safer to regard the arrangement met with in *Sphenodon* as a primitive one. In this respect, as far as is known, *Sphenodon* is more primitive than any other living reptile.

CHELONIA.

In his exact account of the anatomy of the tortoise, *Testudo europæa*, Bojanus (10) figures and describes a ductus arteriosus—ductus arteriosus Botalli, as he terms it—on both sides. He does not mention the presence of a ductus caroticus, and in such a careful, detailed piece of work as this is, it does not seem probable that he overlooked it. Gegenbaur (23, vol. ii. p. 385) records the persistence of a small open ductus Botalli on both sides in Chelydra, but makes no mention of the ductus caroticus. Fritsch (22, p. 701) gives a diagram of the heart and vessels in one of the "Schildkröten" (*Chelydra serpentina* ?), in which a ductus Botalli is shown on both sides, but no indication of the other connection. Mackay (31) is still more definite, and asserts that in a number of Chelonia (species not given) that he has dissected he has not found a ductus caroticus. Brenner (17) states that in *Testudo græca* the pulmonary artery undergoes a sudden reduction in diameter at the point where the ductus Botalli should be given off, but was unable to find a trace of that structure on either side. This is an interesting point, as a similar reduction occurs in many forms, particularly in the Ophidia. Hochstetter (25), however, in the same form figures (pl. xxiv. fig. 9) a ligamentum on both sides, states that he has found it in various species of the order, and provides the following interesting footnote: "Auch van Bemmelen [6] spricht von einem Erhaltenbleiben des Ductus Botalli bei Hatteria und einer Reihe von ihm untersuchter Schildkröten. Eine briefliche Anfrage an diesen Autor ergab jedoch, dass er mit seiner Angabe nur hervorheben wollte das Reste der Ductus Botalli bei diesen Formen regelmässig erhalten bleiben dass er diese Reste aber auf ihre Wegsamkeit hin nicht untersucht habe." No mention is made of either vessel in Jacquart's memoir (26) on the heart of *Chelone midas*, but it is not improbable, in the face of the above evidence, that they were overlooked, although he has a note on the ductus Botalli in the human heart in the same paper.

From the foregoing, then, it would appear as if in the Chelonia the ductus caroticus is normally absent, while the ductus arteriosus is represented on both sides.

CROCODILIA.

Rathke (*l.c.*) did not find a ductus caroticus in the following forms:—*Alligator lucius*, *A. sclerops*, *A. palpebrosus*, *A. trigonatus*, *A. cynocephalus*, *A. punctulatus, Crocodilus vulgaris, C. piboreatus, C. rhombifer, C. acutus, Gavialis gangeticus* and *G. Schlegelli.* This vessel has been found in certain forms, however; *e.g.* it is recorded as present but almost closed on both sides in *Alligator mississippensis* by Brandt (16), and in spite of the poor description and very schematic drawing it seems as if he was probably right. Greil (24) also records a left ductus in the crocodile. Hochstetter (25) has recorded ligamenta in one specimen of *A. lucius* 1·5 metres long, but apparently did not find it in three others: and Mackay (31) in a small *Crocodilus niloticus* 29 inches long found a ductus on both sides. It is by no means certain, however, that such cases are not either young animals or exceptional examples, and probably the ductus caroticus is not usually present in the full-grown members of this order.

Not much is known of the ductus arteriosus, although Hochstetter (*l.c.*) has found ligamenta in four separate old specimens of *A. lucius*, while Davenport (20) in two examples, whose age is not given, found open ductus.

Further work is needed on the Crocodilia before it is possible to give a generalised statement of the condition of these vessels; but, as will be seen, both structures may be represented, but the ductus caroticus is probably absent as a rule.

LACERTILIA.

Much more is known about the vessels in the Lacertilia, owing mainly to the pioneer work of Rathke (*l.c.*). Under the name of the "Absteigender Schenkel des Carotidenbogen" this author has recorded the presence of a ductus or ligamentum caroticum in the following species:—*Acontias meleagris, Anguis fragilis, Chamæasaura anguina, Lacerta ocellata, Ameivà vulgaris, Draco viridis, Lacerta agilis, Lophyrus giganteus, Agama mutabilis, Phrynosoma Harlænii, Uromastix spinipes, Cuprepis Merremii, Gongylus ocellatus, Cyclodus nigroluteus, Platydactylus ægyptiacus, Ophisaurus ventralis, Pseudopus Pallasii, Iguana tuberculata, Lyriocephalus margaritaceus, Agama colonorum, Grammatophora barbata, Zonurus cordylus, Platydactylus guttatus, Istiurus amboinensis, Tejus Teguixin,* and *Basiliscus mitratus.* It is found in all stages of development, and in the above list the species are placed approximately in order, the best-developed first, and in the case of the last three it becomes practically obliterated, being represented merely as a strand. Indeed, in *Tejus Teguixin* Brücke (18) has reported a case in which they are entirely absent.

No trace of it is to be found in *Chamæleo vulgaris, C. pumilus, C. verrucosus,* and *C. tigris,* but it is present in *C. planiceps* as a tiny ligamentum visible with the aid of a hand lens. It appears to be lacking in *Varanus ornatus*, *V. bivitattus*, and *V. niloticus*, and also in *Amphisbæna alba*, *A. fuliginosa*, *A vermicularis*, and *Lepidosternon microcephalum*.

Kükenthal figures ductus carotici in *Lacerta agilis* (27), and Brandt (15) records them in *L. crocea* (*Zootoca vivipara*)

Beddard, as pointed out above, has found ductus in *Tupinambis nigropunctatus* and *Iguana tuberculata*, while he reports them as missing in several species of *Varanus* and *Amphisbæna* and in *Heloderma suspectum*.

It will be seen that in general there is a fair correspondence between the position of the heart and the persistence of the ductus caroticus. In the forms in which the heart is far removed from the head the ductus disappears, and in these forms too a carotis primaria is often developed, and *vice versa*. One striking exception is *H. suspectum*, where, as Beddard has pointed out, there seems to be no reason why a ductus should not be present; it is nevertheless absent.

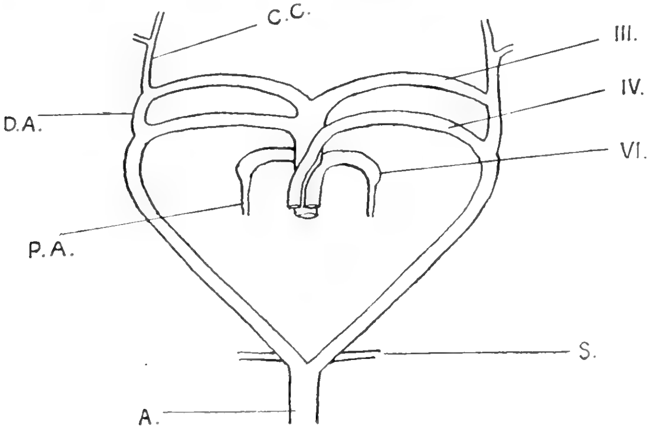

FIG. 4.—Diagram of the arterial arches in *Lacerta viridis*. Lettering as before.[1]

Hochstetter (*l.c.*) states that he has found ligamenta Botalli in all the large Lacertilia in which he has sought it, viz.: *Varanus griseus*, *V. varius*, *V. niloticus*, *Hydrosaurus salvator*, *Uromastix spinipes*, *U. Hardwickii*, *Pseudopus Pallasii*, and others Sometimes it is represented only by a small stump on each side in *H. salvator*, and on the right side only in *Platydactylus annularis*. Brenner (17) points out that in *Lacerta* he

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[1] It will be noticed that the term "common carotid artery" (C.C.) is applied in this form to a vessel that appears to be the morphological equivalent of the internal carotid artery.

has found no ligamentum, but a reduction in the diameter of the pulmonary artery marking its position. The same condition apparently exists in *L. agilis* and *L. viridis*.

In the Lacertilia, then, a ductus caroticus is present in a number of cases, though only in a few is it as well developed as in *Sphenodon*; in most it shows a certain amount of reduction, and in others is absent altogether. The ductus arteriosus when present is in the form of a ligamentum or reduced to a small stump, or when absent its former position may be marked by a reduction in the calibre of the pulmonary artery.

OPHIDIA.

The last and in some ways the most specialised order of reptiles is the Ophidia. According to Brandt (14) the grass snake, *Tropidonotus natrix*, possesses a solid strand of tissue joining the transverse part of the left aortic arch to the carotis primaria, and so representing a ligamentum caroticum. He states that it is a vestigial structure in some ways resembling the ductus Botalli, and homologises it with the "Absteigender Schenkel des Carotidenbogens" of Rathke, proposing for it the name of "ductus caroticus." I have had occasion to point out previously (33) the doubtful nature of this vessel. No connexion exists in this position in the

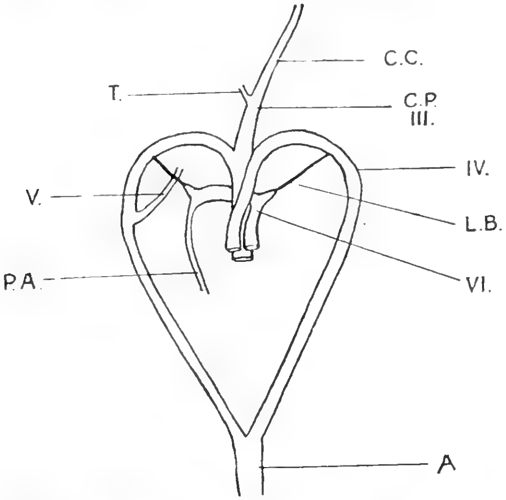

Fig. 5.—Diagram of the arterial arches in *Vipera berus*.

C.P., carotis primaria; L.B., ligamentum arteriosus (Botalli); T., thyroid artery; V., vertebral artery. Other letters as before.

course of embryonic development. From its very nature as a remnant of the dorsal aorta of the embryo this vessel must be considerably dorsal to the external carotid, and, indeed, in a line with the internal carotid, whereas the strand described by Brandt was not only ventral, but considerably posterior to the external carotid. Moreover, I was unable to find any trace of it in the snakes then examined, and have also been unsuccessful in a number of specimens since dissected. Brandt (*l.c.*) also describes a strand in a similar extraordinary position in *Pelias berus*, and adds that he found it hollow in three out of twenty full-grown examples, and also in some young ones. Hochstetter, in mentioning this, points out that he dissected very carefully three injected examples of *P. berus* and numerous examples of *T. natrix*, and other snakes, paying particular attention to this point, but found no trace of such a vessel. In the two adult specimens of *Pelias* (*Vipera*) *berus* that I examined to check the matter the result was the same as Hochstetter's—no ductus or ligamentum was found.

Ductus Botalli are frequently represented on both sides in snakes, although, as is well known, the right lung and pulmonary artery are generally suppressed, with some exceptions, *e.g.* the Uropeltidæ, where it is the left lung and artery. Not only is a ligamentum present, but the most posterior portion often remains open as a small conical sac. In those forms having only one lung and yet having two ductus, the pulmonary arch on the side on which the lung has gone persists up to a point where it is joined by a ligamentum. Frequently, also, a reduction in the diameter of the pulmonary artery occurs just posterior to this point; this has been noticed by Fritsch (22) in *Boa* and *Python*, and Hochstetter (25) in *Boa constrictor*. In the same paper the latter author records the presence of two ductus in *Tropidonatus natrix*, *T. tesselatus*, *Coluber æsculapii*, *Coronella lævis*, *Vipera berus*, *Dryophis mycterigans*, and *Cerastes vipera*. I have also found them in *V. berus*, while I find myself in agreement with Brenner (17) in being unable to find a right ligamentum in *T. natrix* in any of the many examples I have dissected. Certain variations in these structures may occur, for Hochstetter (*l.c.*) describes a *B. constrictor* $2\frac{3}{4}$ metres long in which the ductus remained open on the left but was absent on the right, and a full-grown *C. lævis* in which the right ductus remained open.

As far as can be ascertained, the ductus caroticus does not persist in any adult Ophidian, but the ductus arteriosus is represented by a ligamentum the posterior part of which may remain open as a short conical sac. Generally, two ligamenta are present one on each side, even though the lung and its artery may be suppressed on one side.

SUMMARY.

Three of the six embryonic arches persist in the adult reptile, and of their connecting vessels both ductus carotici and ductus arteriosi may persist or be represented by ligamenta.

In *Sphenodon* both ductus are to be found on each side.

In Chelonia the ductus carotici are usually absent, while the ductus Botalli remain.

In Crocodilia the ductus carotici are probably not usually present, and the ductus Botalli may probably remain.

In Lacertilia the ductus carotici are present very generally, although in a number of species they are reduced or absent, and the ductus Botalli are always reduced and very often absent.

In Ophidia the ductus carotici are normally absent, but the ductus Botalli persist, and often on both sides, in spite of the suppression of one lung and pulmonary artery.

There seems to be little doubt that the main factor affecting the persistence or loss of these structures is the change undergone in the relative positions of the heart and arterial arches in the course of development and subsequent growth. Thus where little relative change takes place, as in *Sphenodon,* all connections are retained. In certain lizards that become relatively broad across the anterior thoracic region the ductus Botalli disappear, and in yet others, like the Varanidæ, where the development of a long neck is accompanied by the separation of the carotid arch from the remaining arches, the ductus carotici also go to the ground. This latter point is well illustrated in the Ophidia; where the carotid arch in the adult is widely removed from the others, the ductus carotici disappear. In the same group, also, owing to the marked lateral compression of the body, the systemic arch is kept in close proximity to the pulmonary, and as a result the ductus arteriosi are practically always represented.

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THE HUMAN PISIFORM. By R. H. Robbins, M.D. Cantab., *Senior Demonstrator of Anatomy, St Mary's Hospital Medical School.*

The few remarks I have to make on the human pisiform are intended as a preliminary to a communication on the condition in certain lower animals. The bone has suffered from the descriptive standpoint, being very small and irregular, and under suspicion of being a sesamoid. The descriptions even in the larger text-books are so lacking in detail, and apparently in accuracy also, that they hardly form a safe guide even to the side to which a given bone belongs; in about 50 per cent. of prepared skeletons the bone is incorrectly placed. I have examined a number of dry specimens, and have also dissected several fresh ones, and have endeavoured to arrive at its more prominent features, and the relation they bear to the soft parts.

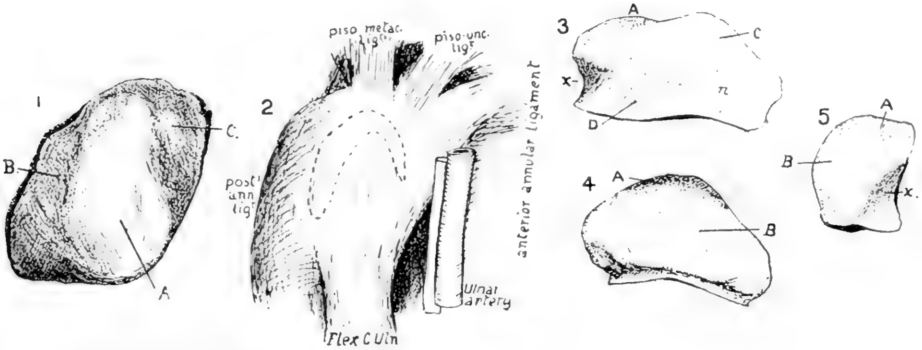
The dorsal aspect of the bone requires no special description. It shows an oval facet, generally slightly concave, for articulation with the cuneiform. The long axis of the facet is directed distally and radially.

No. 1 in the figure represents a pisiform from the anterior aspect. Three surfaces are visible—an anterior, A; an internal or ulnar, B; and an antero-external, C. The surface A constitutes the main attachment of the tendon of flexor carpi ulnaris, as seen in the next figure. Many of its fibres, however, pass beyond to the surface C, to be attached there in a manner to be described presently.

The ulnar surface, B, receives, over a considerable area, fibres of the posterior annular ligament, and, at its distal end, of the piso-metacarpal ligament. Beyond the attachment of these fibres this surface gives direct origin to abductor minimi digiti, the muscle elsewhere arising from the ligaments only. This origin is shown as a dotted line in the figure.

No. 3 shows the bone from what is generally described as the radial aspect. It should be borne in mind, however, that, owing to the longitudinal axis of the bone having a distinctly oblique direction, this aspect is really proximo-radial. An oblique line can be seen clearly, running distally and dorsalwards on this aspect. The line varies from a roughened linear area to a prominent ridge. Its obliquity also varies considerably. It separates two surfaces, the anterior of which is the antero-external surface, C, already mentioned. The more dorsal of the two, D, becomes concave when traced proximally, until it forms a well-marked hollow, *x*, at the proximal end of the bone. In the fresh specimen the distal part of the oblique line is seen to correspond to the attachment of the anterior annular ligament, which presents in this situation a free edge looking radially (see figure). The proximal part of the oblique line corresponds to the radial edge of the flexor carpi ulnaris tendon, the fibres of which have the appearance of being continued, along this line, into the free edge of the ligament. Actually, the bulk of the fibres are interrupted on the bone, but a few can generally be traced through.

Both the tendon and the ligament have other fibres spreading on to the surface C, forming a continuous attachment on this surface, but not presenting many continuous fibres. The abductor minimi digiti will generally extend its attachment on to the portion of the surface C which adjoins the surface A: the origin in such case being from fibres of the anterior annular ligament.



1. Right pisiform from the palmar aspect.
   A, anterior surface; B, ulnar or internal surface; C, antero-external surface.
2. Same, with soft parts in position.
   Dotted line represents attachment of abd. min. dig.
3. Radial aspect, showing oblique line separating surface C, placed antero-distal to it, from D, lying postero-proximal.
   x, hollow at proximal end; *n*, point where ulnar nerve comes first into close relation.
4. Ulnar aspect.
5. Proximal aspect.

The more proximal surface, D, is in relation with the ulnar aspect of the common flexor sheath, except at the proximal end, where the well-marked hollow, *x*, here presented, lies under cover of the flexor carpi ulnaris tendon, and is occupied by a mass of areolar tissue connecting the common flexor sheath with the fascia on the dorsum of the wrist.

Of the two extremities of the bone, the proximal exhibits the hollow, *x*, mentioned above. The curved edge bounding this, and formed by the proximal limits of the surfaces B and A, gives this end of the bone a characteristic appearance.

The distal extremity projects beyond the articular surface, and has a tubercle, often prominent, for the attachment of the piso-uncinate ligament.

These markings that I have described can be identified in all specimens, however apparently dissimilar. The ulnar nerve, if it comes into contact at all, is confined to the distal portion, where it lies palmar to the ridge for the attachment of the annular ligament. Moreover, even in adduction the nerve does not have a close relation with the groove which it has been generally credited with forming.

The other markings on the bone are caused secondarily as the result of the bone coming into relation with the deep aspect of the covering structures. The early position of the developing pisiform can be seen in reconstructions of the successive stages. In this lies the probable explanation of the varying appearances presented by the bone. These, however, can be more conveniently dealt with subsequently in considering the bone from the comparative standpoint.

OBSERVATIONS ON METOPISM. By Professor THOMAS H. BRYCE, University of Glasgow, and MATTHEW YOUNG, M.D., Statistical Department, National Research Laboratory.

THE excellent summary given by Le Double[1] of the statistics of metopism shows that the condition occurs in from 9 per cent. to 10 per cent. of all European crania irrespective of race, of skull form, or of mental condition. Metopism is certainly more frequent in the white races, rarer in the lower races of mankind. It has not so far been observed in the anthropoid apes. More than forty years ago Welcker[2] furnished statistics which seemed to show that metopism occurred more frequently in brachycephalic than in dolichocephalic races, and the generalisation found some support from the observations of Papillaut.[2] Parsons[3] found a metopic suture persistent in the adult in 52 out of 590 specimens (*i.e.* 9 per cent. approx.) in the Hythe series of skulls, which are remarkable for their shortness, being practically equal to the South German in that measurement. He states that the number of metopic skulls occurring in the two sexes shows no appreciable difference, although, according to the figures supplied, there would appear to be some relationship between the frequency of the anomaly and age incidence. Under the age of twenty years the frequency was 20·8 per cent.; in the specimens between twenty and forty it was 9·8 per cent.; and in those over forty, 6·4 per cent. In Macdonnell's Whitechapel English series,[4] dolichocephalic in form, the frequency of the anomaly was 8·2 per cent. Turner in his *Challenger Report* (part xxiv., 1884) says of his 143 crania of aboriginal races from South Africa, South America, Australia, and the Pacific Islands that "the absence of the metopic condition was remarked in the aboriginal series," though he had seen it in the skulls of a Veddah and of an Andaman Islander. Flower observed metopism in six Andamanese crania. Statistics furnished by Le Double's article serve also to prove the greater rarity of the condition in the lower races of mankind.

In the long series of West Scottish skulls preserved in the Anatomy Department of the University of Glasgow, and described recently in a

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[1] *Variations des os du crane de l'homme, etc.*, Paris, Vigot Frères, 1903.

[2] For references see Le Double.

[3] *Journ. Roy. Anthropol. Institute*, vol. xxxviii., 1908.

[4] *Biometrika*, vol. iii. p. 1412.

memoir Dr Young published in the *Transactions of the Royal Society of Edinburgh*[1], metopism occurs in 9·5 per cent. of the crania. The series is remarkably uniform in character, dolichocephalic in type, yet the percentage closely approximates to that in the Hythe series. From the series of 75 metopic skulls two groups were selected—consisting of 45 and 20 specimens respectively. The first group was attributed to the male sex, the second to the female, while the remaining specimens have been noted as doubtful. The determination of sex, difficult in all circumstances, is specially difficult and uncertain in the case of metopic skulls, because, as will afterwards appear, the frontal bone has in the majority of cases an upright character. We do not, therefore, lay emphasis on the sex characters, and in consequence the series are named A and B. A is preponderantly male, B preponderantly female.

CRANIAL MEASUREMENTS.

Table I. shows the mean values for the measurements and indices of the cranial box of the metopic skulls in apposition to the mean values for the same measurements shown by the complete male non-metopic series of 405 skulls and the female series of 100.

The comparison is not without interest. Considering the absolute measurements first of all, we observe that, while the mean capacity of the metopic group A is slightly less than that, in the male non-metopic group, the opposite holds for the B series as compared with the female non-metopic.

The mean length in the A metopic group is about 3 mm. less than that shown in the male non-metopic group, while, though the mean length in series B is less than the normal female, there is less than one millimetre of difference in the values.

It is frequently stated that there is an increase in the mean maximum breadth of the metopic skulls in a series over the general value for maximum breadth. In the A series and the non-metopic male group the mean maximum breadths are practically identical, while in the B group the metopic mean is 1·29 mm. in excess of the female non-metopic mean. Parsons found the increase in the Hythe crania to equal about 1·3 mm.

In the Whitechapel series Macdonnell found the mean values identical in the metopic and non-metopic female crania, while in the male series the metopic group had a mean value 1 mm. in excess of that in the non-metopic group. These data go to show that if there is any increase in maximum breadth in metopic skulls over the normal members of a series it is very slight in degree.

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[1] Vol. li. part ii. (No. 9).

TABLE I.

	Male.	Series A.	Female.	Series B.
Character	Non-metopic (405).	Metopic (45).	Non-metopic (100).	Metopic (20).
(C) Capacity	1459·43 ± 4·11	1444·32	1314·5 ± 6·30	1354·5
(L) Length	187·52 ± ·20	184·71	177·97 ± ·20	177·15
(B) Breadth (maximum)	139·56 ± ·16	139·46	135·16 ± ·29	136·45
(B′) Breadth (minimum frontal)	96·42 ± ·15	99·82	92·66 ± ·25	96·8
(H) Height	132·72 ± ·17	129·75	125·01 ± ·31	126·75
(LB) Basi-nasal length	100·37 ± ·13	98·2	93·82 ± ·20	93·90
(U$_2$) Horizontal circumference (Turner)	526·60 ± ·47	523·84	503·61 ± ·71	505·9
(S) Sagittal arc	378·60 ± ·43	372·02	363·15 ± ·68	364·9
(Q) Transverse arc	311·10 ± ·36	309·8	299·21 ± ·60	302·35
(J) Zygomatic breadth	127·16 ± ·18	125·5	118·16 ± ·26	119·2
100 B/L	74·36 ± ·08	75·53	76·03 ± ·19	77·06
100 H/L	70·81 ± ·09	70·28	70·31 ± ·20	71·79
100 H/B	95·14 ± ·14	93·04	92·53 ± ·29	92·88
Frontal arc	131·73	128·26	126·96	126·5
Parietal arc	127·00	124·68	121·4	121·05
Occipital arc	119·88	119·06	114·76	117·35
Interstephanic diameter	117·93	120·42	114·91	119·85
Asterionic diameter	109·68	108·57	105·44	106·3
Transverse base	115·13	114·02	108·89	109·4

A glance at the table will show that the mean value of the other measurements is slightly greater in the male non-metopic group than in the metopic series A, while the reverse holds for the B series as compared with the female non-metopic group.

Two exceptions to the general rule exist in the greater frontal breadth in both series. This holds for both the frontal and interstephanic diameters.

It has long been known that the minimum frontal breadth is greater in metopic skulls. Cleland refers to the point in his memoir[1] on the skull. The late closure of the suture apparently permits the forehead to broaden. Parsons states the increase to be 6 mm. over the normal in the Hythe series, while in Macdonnell's series the excess was 2·3 mm. in value.

In the present series the mean increase, over the non-metopic groups, in minimum frontal breadth is 3·5 mm. in series A and 4 mm. in series B; the mean increase of the interstephanic diameter is 2·5 mm. for series A, 5 mm. for series B.

The cephalic index is higher by one point in the metopic group than

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[1] *Phil. Trans. Roy. Soc. London*, vol. clx., 1870.

in the normal skull, the difference being due, as the mean breadths are practically equal, to the diminution in mean glabello-occipital length.

This greater metopic cephalic index is also shown by the Whitechapel English series, the Moorfields English series, and the Hythe English series of crania, and is evidence of the fact that within the same series the metopic representatives are on the average more brachycephalic than the normal skulls.

The vertical index is little altered, as height and length are apparently proportionately diminished, while the height-breadth index is slightly reduced owing to the fact that the height is diminished while the breadth remains the same. A reference to the absolute measurements will in the same way explain the differences in the indices in the B series as compared with the non-metopic female group.

While there are notable differences in the relations of the values in the two types of skull to which reference will be made presently, the measurements for minimum frontal breadth and interstephanic breadth stand out from the others as showing a very appreciable change in value in the same direction in passing from the metopic to the non-metopic skull.

An analysis of the values in the A series might incline one at first sight to suggest that, as length and height are reduced in the metopic form while the capacity is not correspondingly diminished, the greater frontal breadth, and consequently the persistence of the suture, might have been necessitated by what may be termed a "compensatory increase" in the frontal region. This has been suggested by various writers. The explanation is rejected by Le Double, and the B series does not tend to support it. The frontal breadth shows a greater divarication than in the A series in favour of the metopic form, while the other measurements remain very slightly in excess of those of the normal group of female skulls.

Here we have an increase in cranial capacity associated with an *absolute* not a *compensatory* expansion of the frontal region of the skull. Had the mean capacity in series B fallen, as in series A, below that of the group compared, there would have been the same diminution in length and height and related dimensions as in series A. The two series taken together rather point to metopism, when not due to pathological conditions, being a progressive manifestation. The fact that metopism is rare in the lower races of mankind lends support to this conclusion.

CORRELATION.

As the frontal breadth is the character found to exhibit a distinct difference in magnitude in the metopic and normal groups, with the excess in favour of the metopic form, we have made the necessary calculations to determine the correlation existing between this and other measurements of the skulls in the series in order to compare the values found with those for the normal group, hoping that by this means some causal factor for the persistence of the suture would be revealed. The great uniformity of the West Scottish series favours such an inquiry. The coefficients calculated are shown in Table II.

TABLE II.—COEFFICIENTS OF CORRELATION IN MALE SEX.

Pair of characters.	Metopic group.	Non-metopic group.
B′ and L	·45 ± ·080	·37 ± ·029
B′ and B	·59 ± ·065	·39 ± ·029
B′ and H	·47 ± ·080	·28 ± ·031
B′ and C	·52 ± ·073	·42 ± ·027
B and L	·55	·454 ± ·026
L and H	·45	·356 ± ·029
B and H	·45	·264 ± ·031
B and C	·72	·73 ± ·017
L and C	·74	·69 ± ·017
H and C	·66	·56 ± ·024
C and U	·83	·78 ± ·013
C and Q	·76	·76 ± ·014
Frontal segment and total sagittal arc	·665	·73 ± ·017
Parietal segment and total arc	·58	·53 ± ·025
Occipital segment and total arc	·54	·77 ± ·013

B = Maximum breadth.
B′ = Minimum frontal breadth.
L = Maximum length.
H = Basibregmatic height.
C = Capacity.
U = Horizontal circumference.
Q = Transverse arc.

The coefficient of correlation between the minimum frontal breadth and the absolute measurements for length, breadth, and height respectively, is in both series—metopic and non-metopic—greater for breadth than for the other two, so that the minimum frontal breadth shows a greater tendency to increase where the maximum breadth increases than when length and height increase, although it also shows a well-marked and almost similar tendency to do so in the last two cases in the metopic group.

While the correlation between maximum breadth and capacity shows practically identical values in the two series, indicating that these characters have similar tendencies to vary in metopic and non-metopic forms, the correlation between minimum frontal breadth and capacity is definitely greater in the metopic than in the normal series, a fact which points to a closer relationship between these dimensions in the former than in the latter group.

An increase in capacity may be obtained by one or more of the dimensions becoming greater in value. In the normal series it was proved that all three chief diameters tend to increase proportionately as the brain-case expands. It would appear that in the metopic series increase in capacity is obtained more frequently, and to a greater extent, by increase of the minimum frontal diameter than in the normal series.

From the evidence here supplied it appears that within a uniform series an approximation to a certain capacity is attained by at least two methods—one in which development goes on in what we regard as the normal way with the closure of the metopic suture at an early stage and expansion more particularly in the hinder part of the vault; another in which there is greater growth in the frontal region, associated with the persistence of the suture for a longer period, or till a later age, than normally to permit of such an increase.

THE CLOSURE OF THE SUTURES.

It is frequently stated that the metopic suture, having persisted till adult life, shows less tendency to fuse than the other sutures, and that it is the last to undergo synostosis. Parsons and Box found no evidence in favour of such a view in the skulls examined by them.

In the present series of 70 skulls three groups may be taken as follows:—

A group A of 29 skulls in which the basal suture has completely fused, and the 3rd molars have either erupted or appear in the cavities of their alveoli, or have failed to erupt. In these 29 skulls all the sutures are open.

Group B of 10 skulls, many edentulous, showing very advanced stages of suture obliteration.

Group C, a middle group of 39 skulls showing various degrees of synostosis, from the very commencement of the process to a fairly advanced stage in some cases.

Groups A and B cannot, obviously, throw any light on the condition of metopism, but it seemed possible that the details in the middle group might provide some further information. The results are shown in Table III.

A consideration of the table brings out the fact, already well known, that synostosis, so far as the outer aspect of the sutures is concerned, begins either in the inferior part of the coronal suture or in the sagittal suture in the region of the obelion.

In this series it is obvious that the closure of the sagittal suture precedes that of the coronal suture, and, what is more interesting, that in

TABLE III.

B = bregmatic part.
V = vertex.
O = obelion.
L = lambda

B = bregmatic part.
C = complex part.
T = temporal part.

L = lambdoid part.
M = middle part.
A = asterionic part.

S = superior part.
M = middle part.
I = inferior part.

S = superior part.
I = inferior part.

Series No.	S. sagittalis.				S. coronalis.			S. spheno-frontalis.	S. lambdoidea.			S. spheno-parietal.	S. masto-occipit.			S. spheno-temp.		
	B.	V.	O.	L.	B.	C.	T.		L.	M.	A.		S.	M.	I.	S.	I.	
A_2	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	
A_3	–	+	+	+	–	–	+	+ : –	+	–	–	–	–	–	–	–	–	Edentulous.
A_4	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_5	+	+	+	+	–	–	–	+ : –	+	×	–	–	–	+	+	–	–	Edentulous.
A_6	+	+	+	+	–	–	–	–	+	+	–	–	–	–	–	–	–	3rd molars in alveoli.
A_7	+	+	+	+	–	–	–	–	+	+	–	–	–	–	–	–	–	"crane en toit."
A_8	–	–	+	–	–	–	–	+ : –	–	–	–	–	–	–	–	–	–	
A_{10}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_{11}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_{12}	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	Edentulous.
A_{13}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_{14}	–	×	+	×	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_{15}	–	–	+	–	–	–	+	+ : ×	+	–	–	+ : –	–	–	–	–	–	
A_{16}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3rd molars failed.
A_{18}	–	+	×	–	–	–	+	+	–	–	–	×	–	–	–	–	–	Edentulous.
A_{20}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3rd molars in alveoli.
A_{22}	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	Edentulous.
A_{24}	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
A_{25}	–	×	+	+	–	–	–	–	+	×	–	–	–	–	–	–	–	
H_1	–	–	+	–	–	–	+	–	+	+	–	–	–	–	–	–	–	Edentulous.
H_2	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3rd molars unerupted.
H_4	–	+	+	+	–	–	×	–	–	–	–	–	–	–	–	–	–	
H_6	×	+	+	+	–	–	+	×	+	×	–	–	–	–	–	–	–	
H_8	–	+	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–	
H_{11}	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
H_{13}	–	–	+	–	–	–	–	–	×	–	–	–	–	–	–	–	–	
H_{14}	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	
H_{15}	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
H_{21}	–	–	+	×	–	–	×	–	×	–	–	–	–	–	–	–	–	
B_3	–	×	+	×	–	–	+	–	+	×	–	–	–	+	+	–	–	Edentulous.
B_{10}	–	–	–	–	–	–	+	+ : –	–	–	–	–	–	–	–	–	–	
B_{12}	–	–	–	–	–	–	×	– : ×	–	–	–	–	–	–	–	–	–	
B_{14}	–	–	+	–	–	–	–	× : –	–	–	–	–	–	–	–	–	–	
B_{15}	–	+	+	+	–	–	×	–	+	+	–	–	–	–	–	–	–	
B_{16}	–	–	+	×	–	–	–	–	–	–	–	–	–	–	–	–	–	
B_{18}	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	
B_{19}	–	–	+	×	–	–	+	+	–	+	–	+	–	–	–	–	–	Edentulous.
B_{25}	–	–	+	×	–	–	–	–	–	–	–	–	–	–	–	–	–	
Y_1	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	

– = open ; + = closed ; × = closing.

In case of difference on two sides, facts represented thus, left right + : –

a number of cases there is considerable fusion both in the sagittal and lambdoid sutures without any signs of synostosis in either the coronal or spheno-frontal sutures. If Parsons and Box[1] are correct in fixing the inferior part of the coronal suture as the first situation to show signs of closure in the majority of cases, then this metopic series is exceptional and agrees with Frederic's[2] series of middle-European crania, broad in type. The condition of metopism is of course established at a time when the question of suture closure does not arise, but the facts may have some significance, viz.—first, that in this metopic series all the frontal sutures show a tendency to remain open, while the sutures in the region of the lambda reveal a tendency to close earlier than the anterior sutures; and, second, that in this respect the skulls agree with a series of skulls brachycephalic in form.

A feature of this series which seems more than a mere coincidence is the frequency with which the upper end of the interfrontal suture becomes confluent with the coronal to the right side of the anterior extremity of the sagittal suture. Out of 72 skulls the confluence was to the right of the sagittal suture in 53 per cent., while in 36 per cent. the two sutures enter the coronal exactly opposite one another. In only 11 per cent. did the confluence lie to the left of the sagittal suture. Perhaps this is to be regarded as further evidence of the asymmetry due to greater development of the left side of the brain in association with the prevalence of right- over left-handedness.

Stieda[3] suggested that the change in the position of the confluence is due to variation in the mode in which a variably developed fontanelle bone present at an early stage becomes fused with the adjacent frontal. One juvenile metopic skull in the series proves the possibility of this explanation, but otherwise we can neither deny nor affirm the theory.

MORPHOLOGICAL FEATURES.

It is known, as stated above, that the metopic suture persists with greater frequency in the white races of mankind. It has also been proved afresh that although metopism occurs with equal frequency in both dolichocephalic and brachycephalic races, the individual specimens in which it is present are more brachycephalic on the average than the others in the series. By comparison of the West Scottish with the Australian and Tasmanian skull it has already been proved that the greater capacity is due to a certain increase in breadth, a slight increase in length, and a marked increase of depth behind. Both by correlation and morphological

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[1] *Jour. Roy. Anthropol. Institute*, vol. xxxv., 1912.

[2] *Zeitschr. f. Morphol. u. Anthropol.*, Bd. ix., 1906.

[3] *Anat. Anzeiger*, Bd. xvi, 1897, p. 226.

analysis the proof was furnished that in the series studied the occipital region of the skull was chiefly responsible for the increase in calvarial height, and therefore an important factor in the cranial expansion. In the present paper it has been proved both by measurement and correlation that there is an absolute lateral expansion of the frontal region in the metopic skull. We therefore proceeded to determine by more detailed analysis what other morphological changes were associated with this expansion, and a series of sagittal outlines of 50 metopic skulls comprising series A and a few others was prepared. The necessary measurements were made and indices calculated from those in order to obtain the data for comparison with those already obtained in a normal series of skulls of the same type. Another motive here entered, viz. that, apart from establishing certain facts for the metopic series, there was the possibility that, by determining any distinguishing morphological features in the metopic as compared with the non-metopic group, some information might be obtained which would throw light on the wider question of the meaning of differences in skull forms.

Before proceeding to an analysis of the measurements and indices, there are certain general morphological features which may be described.

An examination of the individual members of the series conveys the impression that the frontal bone, in addition to being wider, is more vertical and more curved. This is not always the case in the older specimens, but in the younger skulls it is a very marked feature, and the infantile character of the frontal is retained.

In many specimens there is a more or less well-marked post-coronal constriction. Out of 76 skulls examined this was well marked in 31 specimens, slightly marked in another 33, and totally absent in only 12 cases. This character, however, is not peculiar to the metopic skulls of the West Scottish series, although it seems to occur more frequently in them. In a very considerable number of non-metopic skulls a dip occurs in the vault behind the bregma associated with a flattening on each side behind the coronal suture. In certain cases this is so marked that the appearance is as if the skull had been compressed by a tight band carried across the vault. It is further interesting to note that the lateral flattening over the fore and upper part of the parietal bone is frequently unilateral, and, when on one side only, is almost invariably on the right side. The nature and significance of this feature—post-coronal flattening, depression, or constriction, as it may be termed according to its degree—cannot be discussed here. It demands further analysis than we have yet been able to give it. It suffices to record the frequency of its occurrence in the metopic skulls of the series.

In two of the 12 metopic skulls in which there was no post-coronal depression there was a frontal crest, in one of them almost a keel—a condition usually ascribed to precocious fusion of the suture. Again, in some examples there was that conical bulging of the occipital squama which has frequently been described, with a sharp step from the parietal to the occipital bone along the lambdoid suture. We cannot speak as to the relative frequency of this feature, but the impression is left that it is more frequent in the metopic than the non-metopic group.

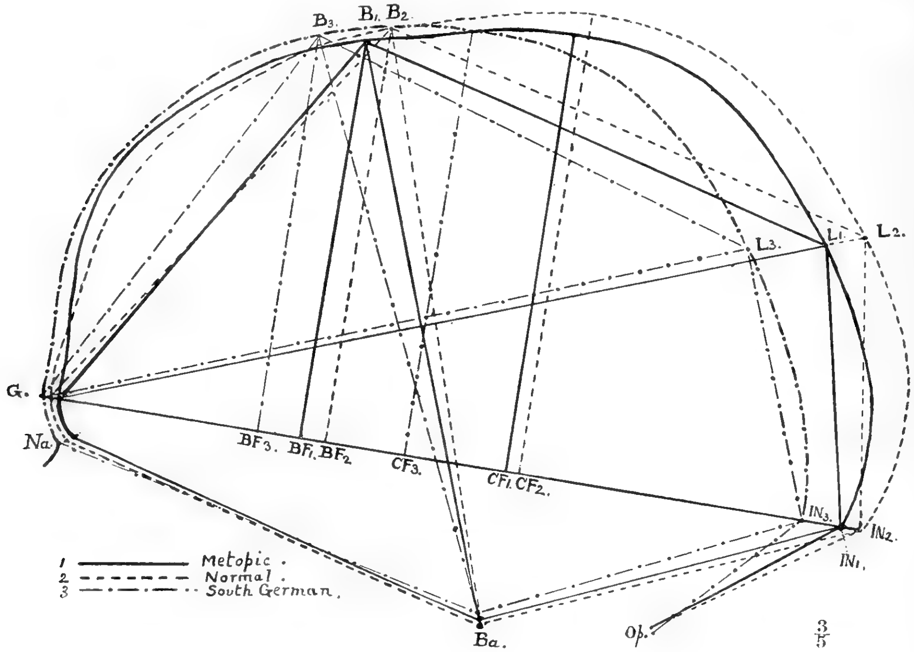
TABLE IV.

	Metopic series (50)			Normal series (100).		
	Min.	Max.	Mean.	Mean.	Min.	Max.
Glabella-inion length	166	189	176·12 (49) one omitted.	182·37	167	196
	(166)	(194)	(176·54)			
Glabella-lambda length	160	190	175·16	184·75	172	198
Calvarial height	84	111	99·5	103·37	94	117
Calvarial-height index	50·60	63·42	56·39	56·68	50	67·5
Maximum breadth	126	150	138·82	140·7	131	152
Calvarial height-breadth index	65·54	77·37	71·67	73·46	65	83
Calvarial height foot-point distance from glabella.	88	113	100·12	105·73	91	123
Calvarial height foot-point positional index.	51·76	63·22	56·70	57·93	50	66
Bregma foot-point distance from glabella.	45	66	54·96	61·96	51	78
Bregma foot-point positional index.	26·79	36·74	31·10	33·89	27·5	42
Length of frontal chord	103	120	109·50	116·49	105	132
Glabella-bregma chord	95	115	104·78	111·62	101	126
Frontal arc length	118	143	128·06	133·54	120	152
Frontal arc height	22	33	27·94	27·32	20	34
Glabella-bregma arc height	18	28	23·1	21·69	15	30
Curvature index of os frontale	19·29	30·84	25·48	23·42	17·54	27·64
Glabella-bregma arc index	16·96	27·27	21·96	19·57		
Length of parietal chord	96	127	112·38	115·15	104	126
Parietal arc length	111	146	123·82	127·83	112	143
Parietal arc height	19	31	24·4	23·49	16	30
Curvature index of os parietale	16·81	24·40	20·79	20·36		
Parietal frontal arc index	87·50	114·06	96·79	95·97	80	101·5
Lambda-inion chord	50	78	62·68	65·19		
Lambda-inion arc	51	83	66·80	69·76	50	95
Occipital arc height	4	16	9·42	9·76	3	19
Curvature index of os occipitale	7·27	24·24	14·83	14·81		
Basi-bregmatic height	120	145	130·20	133·71	123	147
Basi-nasal length	88	108	97·76	100·96		
Inion-basion length	71	95	83·32	86·44	68	97
Bregma angle	53°	64°	58·28°	56·33°	50°	63°
Lambda angle	68°	90°	78·23°	81·95°	70°	88°
Opisthionic angle	31°	47°	37·22°	35·13°	22°	41°

The absolute measurements and indices utilised for the detailed analysis of the characters of the vault are shown in Table IV. side by side with the corresponding values for a normal male series of 100 skulls.

In accordance with the smaller average size of the metopic as compared with the normal skull, there is a general decrease in the mean values of the absolute linear measurements; the only exceptions among those recorded being the heights of the frontal, parietal, and occipital arcs, which are approximately equal severally in the two series. When attention is directed to the indices and angles, however, differences in the mean values in the two series become evident in some cases. The glabella-inion length and calvarial height are correspondingly diminished in the metopic group, with the result that the mean calvarial-height index remains practically unchanged. The calvarial height being diminished to a greater extent relatively than the maximum breadth, the mean calvarial height-breadth index is less in the metopic series than in the normal series to the extent of about two points. The bregma foot-point, or point of intersection of a perpendicular from the bregma on the glabella-inion line, and calvarial-height foot-point, or point of intersection of the perpendicular from the highest point of the vault on this same line, are on the average less distant from the glabella in the metopic than the corresponding points in the normal skull. When the positional indices of these points are compared in the two series it is evident that these points of intersection are relatively and proportionally as well as absolutely further forward, and this is more evident in the former than the latter. The frontal bone is shorter on the average in the metopic than in the normal skull, as is evident from a comparison of the mean frontal arcs and also the frontal chords in the two types. The forward position, however, of the bregma foot-point is also in part accounted for by the more vertical position of the frontal bone in the metopic group. This is shown by the appreciable increase in the size of the bregma angle. On the average this angle is greater in the metopic type than the non-metopic by two degrees. The lambda angle, on the other hand, shows a distinct increase on the average in the normal compared with the metopic skull, so that, while there appears to be an elevation of, or more vertical disposition of, the vault of the metopic skull in front, there seems to be a distinct tendency to flattening in the posterior section above the glabella-inion plane, with a partly compensatory increase below that plane, as is shown by the mean values of the opisthionic angles. While the mean curvature of the parietal and occipital arcs is very similar in both metopic and non-metopic skulls, as is evident from the practically identical mean curvature indices of the parietal and occipital bones, in the case of the whole frontal arc, and to an almost equal degree in the glabella-bregma portion of the arc, the curvature is distinctly more marked in the metopic than in the non-metopic skull, there being a difference of fully two units in the indices.

There is no marked difference in the mean relation of the parietal to the frontal arc in the two types. This is shown by the slight difference, less than one unit, in the mean parietal-frontal-arc indices in the two groups. There is only a difference of about two units in the mean lengths of the lambda-inion chords and about three units in the lambda-inion arcs in favour of the non-metopic group in each instance, so that, while there is present, posteriorly the flattening above the glabella-inion plane already referred to, it is evident that the morphological changes incidental to the persistence of the suture are more marked in the forward portion of the skull.



The method of analysis adopted permits of a reconstruction, from the data, of an ideal outline representing the means of the series compared. Owing to the uniformity of the series these means are not mere abstractions, but represent the type with minor variations eliminated. If now the outlines with their inscribed lines be superimposed, we obtain a graphic representation of the facts detailed above (fig.). The outlines are erected on Schwalbe's base line—glabella-inion,—and so adjusted that the points representing the basion in each as nearly as possible coincide. Examination of the figure shows that the glabella-lambda lines exactly coincide. The same relative proportions are maintained in the occipital region in both metopic and non-metopic skulls, and the glabella-lambda and glabella-inion planes bear the same relative position to one another. It will be observed, however, that the lambda points (L_1, L_2) are further removed from one another than the inion points ($In._1$, $In._2$). This accounts for the diminution of the lambda angle in the metopic outline, and for the flattening of the hinder part of the vault referred to above. This flattening in a more pronounced degree is characteristic of brachycephalic skulls, and the outline of a South German metopic skull with an index of 88 has been introduced into the figure for comparison. It will be noticed that the flattening is here associated with a still more acute lambda angle, the glabella-lambda diameter being reduced relatively more than the glabella-inion diameter. The figure brings out clearly the reasons for the forward position of the bregma and the increase in the bregma angle in the metopic skull. The approach to the brachycephalic characters of the frontal region is shown by the comparison with the South German contour, in which the relative forward shifting of the bregma is a marked feature.

As a result of the above analysis it thus appears that the greater brachycephaly of the metopic specimens in a series is not merely a matter of relative proportions of the diameters, but is associated with changes in the characters of the vault.

SUMMARY AND CONCLUSIONS.

In the section on gross measurements the conclusion was arrived at that the frontal expansion in metopic skulls was not merely compensatory. The cranial capacity being but slightly diminished, while the length and height are reduced and the breadth remains stationary, the correlations worked out suggested that the factors of growth were modified so as to attain a given capacity by a method different from the normal, viz. a greater expansion in the forward and a smaller development in the hinder part of the vault. There is some evidence, although it is not very decisive, that with the persistence of the sutures in the frontal region there is a tendency to an earlier fusion of those in the region of the lambda. The detailed analysis confirms and amplifies these points, and tends to show that metopism is one feature only in a general change in the morphological characters of the vault.

For some reason unknown the stress of expansion exerts itself in the transverse rather than in the longitudinal and vertical directions, and this stress is at its maximum in the frontal region. In a brachycephalic series the result is an exaggeration of the typical brachycephalic characters, while in a dolichocephalic series brachycephalic characters are assumed. In short, metopism is not to be explained merely by a supposed expansion of the frontal regions of the hemispheres, but rather as an adjustment of the brain-case as a whole to its contents. To put it very crudely, for the case of the long oval type of skull metopism provides for the adaptation of a dolichocephalic brain-case to a more brachycephalic type of brain. As stated above, one of the motives underlying the detailed observations recorded was the hope that possibly some facts of more general interest might emerge. The data obtained, however, though not without a bearing on the larger issue of skull-form in general, do not carry us far, and we must be content with having demonstrated, in fuller detail than has hitherto been attempted, how the skull-form is modified when there is persistence of the metopic suture.

NOTES ON SOME MEASUREMENTS MADE ON SUBJECTS IN THE DISSECTING-ROOM. By W. L. H. DUCKWORTH, M.A., M.D., Sc.D., *University Lecturer in Physical Anthropology, Cambridge University.*

CONTENTS.

I. INTRODUCTION.

SINCE the spring of 1909 I have collected measurements of the length and breadth of the head and skull made on 160 dissecting-room subjects. Most of the work was done by myself, but I acknowledge my indebtedness to the attendant at the Anatomy School (Mr John Lane) for his assistance in increasing the number of records. The heads were measured (when the subject was brought into the dissecting-room), and, the exact spots touched by the calipers having been marked, the soft tissues were here incised down to the bone, and the measurements repeated upon the skull.

In this way I hoped to obtain a reliable series of data comparable to those recorded by Czekanowski[1] from the Anatomy School at Zürich. Czekanowski's Inaugural Dissertation is the most complete piece of work on this subject known to me, though I hasten to mention that of Gladstone.[2] But the latter investigated fewer points, and with a different object in view.

Czekanowski dealt with "material" representative of the Alpine race of Central Europe. He obtained some interesting results illustrative of the difference between the breadth index of the head and the corresponding

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[1] Czekanowski, *Das Verhältnis der Kopfmasse zu den Schädelmassen:* Inaugural Dissertation, Zürich, 1907 (published by Vieweg, Braunschweig).

[2] Gladstone, Dr R. J., *Biometrika*, vol. iv., article iii., pp. 105 *seq.*

index of the skull. He published a sliding scale to show how the differences are modified according to the absolute value of the index. For instance, where the index of the head is about 75, the sum of 1·3 units is to be subtracted if it be desired to obtain the index for the skull; whereas when the head provides an index of about 89, the difference in the "cranial" index is nil, and above 89 it may even be necessary to add to the "cephalic" index in order to arrive at the proper value for the "cranial" index.

This result is so different from the rough-and-ready mode of subtracting two units from the index provided by the head (and thus to arrive at the index for the skull), that it demands criticism, and above all confirmation from data supplied by dolichocephalic types. For, as noted above, Czekanowski worked upon the brachycephalic type common in Central Europe.

To my regret, I soon found myself unable to provide evidence of a reliable nature bearing upon this matter. Czekanowski measured cadavera to all intents equivalent to what we should call "post-mortem room" bodies. At Cambridge, on the other hand, the bodies must remain intact for six months at least before the scalp is shaved and final preparations render them suitable to the uses of the dissecting-room. The lapse of time brings with it pressure effects which distort the soft parts. The breadth measurement is chiefly affected, and if several bodies have been packed closely for storage the distortion is usually considerable.

But while I recognise failure in this respect, I think the data derived from these cadavera at Cambridge are worthy of publication. At least the skull-measurements are reliable, and we do not possess too much material definitely "sexed" and comparable with such, for instance, as is represented by the Whitechapel or the Moorfields series, or again the Glasgow collections.

II. SUMMARY.

With this introduction I proceed to give some account of my results, prefacing the latter simply with two remarks. First, that data derived from dissecting-rooms need critical consideration, and those who collect such data should be careful to explain the conditions under which the data were obtained. Secondly, and by way of summary, I will state here that the analysis of my measurements seems to show conclusively that the dissecting-room subjects fairly represent the less well-nourished sections of the general British population. And herein is confirmation of what is believed (though on quite different evidence) to be the case.

III. THE MATERIAL.

One hundred and twenty male heads were measured, and in all, save two, the corresponding cranial dimensions were obtained.

Forty female heads were measured, and in all, save four, the corresponding cranial dimensions were obtained.

IV. MEASUREMENTS AND AGE OF SUBJECTS.

The measurements made are those of maximum (glabello-occipital) length, and maximum (biparietal) breadth. From these two dimensions the breadth index has been calculated.

In regard to age: the average for the males was about 62, and for the females about 67. Both groups are therefore comparable with the oldest individuals observed by Gladstone (*Biometrika*, vol. iv. p. 110).

The measurements and the indices resulting from these are given in Table I. For the sake of convenience only, groups of ten were made, and the several totals can be used as a measure of the homogeneity in the whole series.

TABLE I.—MALE SUBJECTS.

H.L. indicates head length (max.) glabello-occipital; H.B., head breadth; Sk.L., skull length; Sk.B., skull breadth; B.I., breadth index of head or skull.

No.	H.L.	H.B.	B.I.	Sk.L.	Sk.B.	B.I.	No.	H.L.	H.B.	B.I.	Sk.L.	Sk.B.	B.I.
1	180	144	80·0	174	134	77·0	21	185	144	77·8	183	137	74·9
2	212	160	75·0	202	151	74·8	22	196	151	77·0	187	143	76·5
3	197	148	75·0	191	143	74·8	23	195	149	76·4	187	132	70·6
4	197	164	83·3	184	141	78·7	24	184	154	83·6	176	137	77·9
5	199	151	75·8	193	142	78·5	25	202	152	75·3	195	143	73·3
6	190	154	81·0	182	136	74·7	26	201	144	71·6	192	132	68·7
7	192	148	77·0	183	142	77·5	27	200	159	79·5	193	151	78·2
8	202	156	77·2	190	146	76·9	28	202	135	66·8	195	129	66·2
9	190	154	81·0	...	...	?	29	194	155	80·0	185	147	79·4
10	197	156	79·2	188	143	76·0	30	191	149	78·0	186	144	77·4
	1956	1535	784·5	1687	1278	683·9		1950	1492	766·0	1879	1395	743·1
11	201	158	78·7	183	142	77·6							
				1870	1420	761·5							
							31	192	153	79·7	187	148	79·2
12	198	162	81·7	...	...	?	32	191	152	79·6	186	148	79·6
13	197	162	82·3	190	148	77·9	33	190	157	82·6	188	151	80·3
14	198	155	78·3	188	146	77·6	34	199	154	77·4	196	149	76·0
15	202	158	78·3	193	150	77·7	35	175	142	81·1	169	138	81·7
16	190	152	79·9	188	140	74·5	36	203	148	72·9	198	143	72·2
17	199	160	80·3	190	143	75·3	37	200	154	77·0	190	144	75·7
18	199	145	72·9	189	137	72·5	38	190	149	78·4	185	142	76·7
19	193	164	85·0	180	151	83·9	39	197	158	80·2	188	145	77·2
20	195	152	78·0	186	135	72·6	40	197	150	76·2	192	145	75·6
	1972	1568	795·4	1504	1150	612·0		1934	1517	785·1	1879	1453	774·2

TABLE I.—MALE SUBJECTS (*continued*).

No.	H.L.	H.B.	B.I.	Sk.L.	Sk.B.	B.I.	No.	H.L.	H.B.	B.I	Sk.L.	Sk.B.	B.I.
41	204	159	77·9	196	149	76·0	81	198	163	82·3	188	145	77·1
42	196	147	75·0	189	140	74·0	82	196	147	75·4	186	133	71·5
43	191	143	74·9	181	136·5	75·4	83	200	163	81·5	190	145	76·3
44	185	144	77·9	180	134	74·5	84	195	143	73·3	188	134	71·3
45	197	155	78·7	190	144·5	76·0	85	198	158	79·7	188	145	77·1
46	190	151	79·5	182	139	76·4	86	193	156	80·8	185	142	76·7
47	199	157	78·9	189	147	77·8	87	204	162	79·3	193	148	76·7
48	198	155	78·3	188	137	72·9	88	198	156	78·7	191	138	72·2
49	199	158	79·4	192	147	76·6	89	185	140	75·7	179	133	74·3
50	185	154	83·7	179	146	81·6	90	198	150	75·7	190	143	75·2
	1944	1523	784·2	1866	1420	761·2		1965	1538	782·4	1878	1406	748·4
51	196	152	77·5	190	144	75·8	91	194	156	80·4	188	146	77·7
52	190	146	76·8	183	138	75·4	92	190	142	74·7	185	137	74·0
53	188	147	78·2	180	140	77·8	93	192	158	82·2	184	143	77·7
54	194	152	78·4	188	144	76·7	94	195	154	79·0	189	140	74·1
55	181	143	79·0	176	137	77·8	95	185	143	77·3	177	133	75·1
56	196	156	79·6	191	148	77·5	96	195	153	78·5	189	147	77·8
57	186	150	80·7	180	144	80·0	97	194	140	72·2	186	132	71·0
58	196	155	79·0	191	147	77·0	98	185	148	80·0	177	141	79·6
59	199	153	76·9	190	143	75·2	99	199	151	75·9	193	140	72·6
60	199	144	72·4	192	137	71·4	100	196	147	75·5	189	137	72·5
	1925	1498	778·5	1861	1422	764·6		1925	1492	775·7	1857	1396	752·1
61	194	153	78·8	185	144	77·8	101	199	157	79·0	193	149	77·2
62	184	142	77·2	174	130	74·8	102	197	138	70·1	188	131	69·7
63	204	154	75·4	194	144	74·1	103	191	143	74·9	187	138	73·8
64	200	155	77·5	194	141	72·6	104	187	152	81·3	181	142	78·5
65	188	157	83·4	179	140	78·2	105	196	152	77·6	189	142	75·2
66	205	146	71·2	200	141	70·4	106	212	164	77·4	199	151	75·9
67	190	146	76·8	184	140	76·1	107	207	153	74·0	198	142	71·7
68	200	153	76·5	192	142	73·8	108	184	140	76·2	175	130	76·5
69	186	141	75·8	180	129	71·6	109	182	140	77·0	174	134	77·0
70	194	169	87·0	182	150	82·3	110	186	150	80·6	183	142	77·5
	1945	1516	779·6	1864	1401	751·7		1941	1489	768·1	1867	1401	753·0
71	199	156	78·4	192	139	72·6	111	179	139	77·6	171	135	79·0
72	187	145	77·5	177	134	75·7	112	180	140	77·8	174	132	75·9
73	198	153	77·3	191	145	75·9	113	194	155	79·9	184	142	77·2
74	193	151	78·2	183	141	77·0	114	195	159	81·6	184	145	78·8
75	198	149	75·2	186	137	73·6	115	198	149	75·2	195	144	73·9
76	198	149	75·2	193	139	72·0	116	200	152	76·0	193	143	74·0
77	197	149	75·6	189	140	74·0	117	198	158	79·8	190	147	77·3
78	194	155	79·7	185	145	78·3	118	198	155	78·3	189	141	74·6
79	199	149	74·8	190	139	73·1	119	192	154	80·2	182	145	79·7
80	182	155	83·8	177	149	84·0	120	188	148	78·7	180	131	72·8
	1945	1511	775·7	1863	1408	756·2		1922	1509	785·1	1842	1405	763·2

TABLE I. (*continued*).
FEMALE SUBJECTS.

No.	H.L.	H.B.	B.I.	Sk.L.	Sk.B.	B.I.	No.	H.L.	H.B.	B.I.	Sk.L.	Sk.B.	B.I.
1	184	147	79·9	177	141	79·6	21	198	156	78·8	189	146	77·2
2	194	153	78·9	...	...	...	22	182	148	81·3	173	137	79·1
3	186	148	79·7	180	141	78·3	23	184	149	81·0	178	142	79·8
4	171	152	88·9	...	...	...	24	199	155	77·9	190	149	78·4
5	183	150	82·0	...	...	...	25	190	154	81·0	181	143	79·0
6	196	153	78·0	...	...	...	26	189	147	77·8	180	135	75·0
7	189	140	74·0	179	129	72·0	27	184	142	77·2	177	135	76·2
8	182	148	81·3	171	138	80·7	28	187	147	78·6	180	134	74·4
9	194	152	78·3	183	142	77·6	29	183	137	74·9	176	131	74·4
10	191	148	77·5	182	143	78·5	30	187	154	82·3	179	140	78·2
	1870	1491	798·5	1072	834	466·7		1883	1489	790·8	1803	1392	771·7
11	180	146	81·0	173	141	81·5	31	195	156	80·0	185	141	76·2
12	190	154	81·0	181	143	79·0	32	198	168	84·8	186	149	80·0
13	191	150	78·5	182·5	138	75·5	33	178	143	80·4	173	137	79·1
14	178	144	81·0	172	135	78·5	34	183	141	77·0	171	135	78·9
15	176	137	77·9	171	132	77·2	35	176	149	84·6	171	139	81·2
16	188	154	81·9	180	143	79·5	36	185	144	77·8	181	140	77·4
17	184	143	77·7	175	136	77·7	37	180	144	80·0	172	139	80·8
18	178	140	78·7	172	135	78·5	38	183	147	80·3	179	139	77·6
19	186	144	77·5	176	137	77·8	39	184	145	78·8	179	139	77·6
20	193	150	77·7	183	135	83·8	40	180	142	78·9	174	136	78·2
	1844	1462	792·9	1765·5	1375	789·0		1842	1479	802·6	1771	1394	787·0

CAMBRIDGE DISSECTING-ROOM BODIES.
Males, No. 118 *or* 120.

Heads.—Means.					*Skulls.—Means.*				
Group.	No. of Examples.	L.	B.	B.I.	Group.	No. of Examples.	L.	B.	B.I.
1	10	195·6	153·5	78·45	1	10	187·0	142·00	76·15
2	10	197·2	156·8	79·54	2	8	188·0	143·75	76·50
3	10	195·0	149·2	76·60	3	10	187·9	139·50	74·31
4	10	193·4	151·7	78·51	4	10	187·9	145·3	77·42
5	10	194·4	152·3	78·42	5	10	186·6	142·0	76·12
6	10	192·5	149·8	77·85	6	10	186·1	142·2	76·46
7	10	194·5	151·6	77·96	7	10	186·4	140·1	75·17
8	10	194·5	151·1	77·57	8	10	186·3	140·8	75·62
9	10	196·5	153·8	78·24	9	10	187·8	140·6	74·84
10	10	192·5	149·2	77·57	10	10	185·7	139·6	75·21
11	10	194·1	148·9	77·87	11	10	186·7	140·1	75·30
12	10	192·2	150·7	78·51	12	10	184·2	140·5	76·32
Nos. 1–60	60	...	...	78·23 (60)	Nos. 1–60	58	...	...	76·1 (58)
Nos. 61–120	60	...	...	77·95 (60)	Nos. 61–120	60	...	...	75·4 (60)
Nos. 1–120	120	194·3	151·5	78·01 (120)	Nos. 1–120	118	186·7	141·3	75·8 (118)

TABLE I.—CAMBRIDGE DISSECTING-ROOM BODIES (*continued*).

Females.

Heads.—Means.					*Skulls.—Means.*				
Group.	No.	L.	B.	B.I.	Group.	No.	L.	B.	B.I.
1	10	187·0	149·1	79·85	1	6	178·8	139	77·7
2	10	184·4	146·2	79 29	2	10	176·6	137·5	78·9
3	10	188·3	148·9	79·08	3	10	180·3	139·2	77·2
4	10	184·2	147·9	80·26	4	10	177·1	139·4	78·7
Nos. 1 to 40	40	186	148·0	79·6 (40)	Nos. 1 to 40	36	178·1	138·7	78·2 (36)

V. AVERAGES AND VARIABILITY.

The various means, standard deviations, and coefficients of variability are set out in Table II., and in Table III. I have arranged some of these means in series with comparable figures derived from other sources. The comparison leads to the conclusion mentioned already, viz. that the dissecting-room "material" represents the less well-nourished part of the general British population. Contrasts become marked when such a selected group as that of university students is brought into line.

TABLE II.

Dimension.	Mean.	P.E. of Mean.	S.D.	P.E. of S.D.	C.V.	P.E. of C.V.
Heads of Males [N = 120].						
Length	194·3	± ·410	6·646	± ·284	3·42	± ·146
Breadth	151·5	± ·400	6·510	± ·118	4·30	± ·184
Breadth index . .	78·01[1]	± ·191	3·260	± ·135	4·185	± ·179
Heads of Females [N = 40].						
Length	186	± ·701	6·610	± ·496	3·505	± ·265
Breadth	148	± ·639	5·990	± ·451	4·047	± ·305
Breadth index . .	79·6	± ·282	2·646	± ·199	3·320	± ·250
Skulls of Males [N = 118].						
Length	186·7	± ·392	6·325	± ·277	3·39	± ·146
Breadth	141·3	± ·341	5·360	± ·241	3·79	± ·163
Breadth index . .	75·8	± ·180	2·910	± ·127	3·84	± ·165
Skulls of Females [N = 38].						
Length	178·1	± ·573	5·080	± ·404	2·85	± ·227
Breadth	138·7	± ·500	4·470	± ·354	3·22	± ·256
Breadth index . .	78·2	± ·247	2·202	± ·175	2·81	± ·223

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[1] This is the mean of all the indices. The "index of the means" is 77·97.

I have not instituted any comparisons in respect of the female heads and skulls, as the number is so small. But I may mention here that these heads and skulls are shorter and broader than those of the males. The female heads and skulls are more brachycephalic than those of the males; and the contrast between the two sexes is in this respect more distinct in the dissecting-room series than (for instance) in the general British population.

TABLE III.

Dimension.	"Material."	Mean value in mm.
Head length (males).	General British population[1]	194·00
	118 men of Royal Engineers company[2]	194·90
	120 dissecting-room bodies at Cambridge.	194·30
Head breadth (males).	General British population	154·21
	118 men of Royal Engineers company	151·10
	120 dissecting-room bodies at Cambridge.	151·50
Skull length (males).	44 skulls from Moorfields[3]	189·10
	137 skulls from Whitechapel[3]	189·00
	405 Scottish skulls (M. Young)[4]	187·52
	184 Scottish skulls (Turner)[4]	186·60
	118 dissecting-room bodies (Cambridge).	186·70
Skull breadth (males).	44 skulls from Moorfields	143·00
	137 skulls from Whitechapel	140·70
	405 Scottish skulls (M. Young).	139·56
	184 Scottish skulls (Turner)	144·30
	118 dissecting-room bodies (Cambridge).	141·30
Breadth index of head (males).	General British population[1]	79·71
	118 men of Royal Engineers company[2]	77·50 (*i.e.* index from mean values of length and breadth.)
	120 dissecting-room bodies (Cambridge).	77·97 ,, ,, ,,
	120 dissecting-room bodies (Cambridge).	78·01 (mean of indices).
Breadth index of skull (males).	42 skulls from Moorfields	75·50
	131 skulls from Whitechapel	74·30
	405 Scottish skulls (M. Young).	74·36
	184 Scottish skulls (Turner)	77·40
	118 dissecting-room bodies (Cambridge).	75·80

Some comparisons of the standard deviation derived from the dissecting-room data, with other records for measurements of the head as distinguished from those of the skull, are given in Table IV. The dissecting-room series is the more variable, and this is due to the errors in measurement arising from

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[1] Pearson, *Biometrika*, vol. v.

[2] *Ibid.*

[3] Macdonell, *Biometrika*, vol. v. p. 104.

[4] Young, *Trans. Roy. Soc. Edin.*, vol. li. part ii. No. 9, p. 350.

the distortion of the soft parts. It will be noticed that the breadth of the head is more affected hereby than is the length. But for this, the dissecting-room heads would probably resemble more closely in homogeneity those of the general British population.

TABLE IV.—DISSECTING-ROOM SUBJECTS (CAMBRIDGE).
Head Measurements (Males). Values of Standard Deviation.

Dimension.	"Material."	Value of S.D.
Head length.	General British population[1]	6·100
	120 dissecting-room bodies (Cambridge)	6·646
Head breadth.	General British population	4·890
	120 dissecting-room bodies (Cambridge)	6·510
Breadth index.	General British population	2·954
	120 dissecting-room bodies (Cambridge)	3·260

Cranial variability now falls for notice :—

TABLE V.
Skull Measurements. Values of Standard Deviation.

Dimension.	"Material."	Mean value of S.D.
Skull length (males).	44 Moorfields English[1]	5·58
	405 Scottish (M. Young)	5·94
	137 Whitechapel English	6·27
	118 dissecting-room bodies (Cambridge)	6·32
	English in general (M. Young)	6·44
	Scottish (Turner, quoted by Young)	7·41
Skull breadth (males).	405 Scottish (M. Young)	4·76
	English (M. Young)	4·97
	135 Whitechapel English	5·28
	46 Moorfields English	5·31
	118 dissecting-room bodies (Cambridge)	5·36
	Scottish (Turner, quoted by Young)	5·94
Breadth index (males).	405 Scottish (M. Young)	2·53
	118 dissecting-room bodies (Cambridge)	2·91
	42 Moorfields English	3·00
	131 Whitechapel English	3·26

With the exception of the figure for cranial breadth, the values thus provided by the Cambridge dissecting-room material are quite in line with the other data cited. The degree of homogeneity may be termed moderate, situated as the index (standard deviation) is seen to be—midway, that is, between extremes provided by other series. Also, I may remark

[1] References as in Table III.

that the sources of the dissecting-room material are of the most diverse. The female data show greater homogeneity, but, owing to the small number of the individuals observed, no further remarks will be made here on this part of the work.

VI. Correlation of Length and Breadth.

The values of the coefficient of correlation are exhibited below in Table VI.

Table VI.

(r = coefficient of correlation.)

	Dimensions compared.	Sex.	Material.	Value of "r".
1	Head length and skull length.	Male.	Dissecting-room bodies (Cambridge)	·920 ± ·007
		,,	,, ,, ,, (Zürich)[1] .	·969
		Female.	,, ,, ,, (Cambridge)	·943 ± ·008
		,,	,, ,, ,, (Zürich) .	·972
2	Head breadth and skull breadth.	Male.	,, ,, ,, (Cambridge)	·824 ± ·017
		,,	,, ,, ,, (Zürich)[1] .	·940
		Female.	,, ,, ,, (Cambridge)	·831 ± ·027
		,,	,, ,, ,, (Zürich) .	·960
3	Head length and head breadth.	Male.	,, ,, ,, (Cambridge)	·557 ± ·037
		,,	"English" (recorded by Dr Macdonell)	·345 ± ·019
		,,	,, ,, ,,	·402
		Female.	Dissecting-room bodies (Cambridge)	·654 ± ·050[2]
4	Skull length and skull breadth.	Male.	,, ,, ,, ,,	·448 ± ·045
		,,	Scottish series (Dr Young) . .	·454 ± ·026
		,,	Whitechapel English (Dr Macdonell)	·240 ± ·055
		Female.	Dissecting-room bodies (Cambridge)	·616 ± ·059
		,,	Moorfields English (Dr Macdonell)	·619 ± ·055
		,,	Scottish series (Dr Young) . .	·187 ± ·064

A notable feature of this table is the high correlation indicated by the coefficients between the head length and breadth, and again between the cranial length and breadth in the females. In regard to the cranial relation I note that Dr Macdonell has obtained similar results from the female crania at Moorfields. And that author mentions (as one possible explanation) the large proportion of small crania in that collection. I tested the dissecting-room (female) crania by a rigorous method, and find that 13·9 per cent. are certainly to be described as extremely small. This is not a very large proportion, so that Dr Macdonell's alternative explanation (in which the shortness of the series in point of numbers is held accountable) is more probable than that first mentioned.

But the coefficient of correlation of cranial length and breadth in the

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[1] The "material" at Zürich was really "post-mortem room" material, and consequently the observations represent natural conditions more closely.

[2] Attention is directed to the high numerical value of this coefficient.

male cadavera demands consideration for a reason entirely different from the preceding one.

The value of the coefficient (·448) is not extraordinary. It is "positive," and it resembles closely the coefficient (·454) obtained by Dr Young from a very long series of Scottish skulls.

The point is that it is of the "positive" order in these and in the great majority of instances.

For there are certain facts which suggest that the relation of cranial length and breadth is really of the "negative" order. I wish to explain as briefly as possible what those facts are, and to show that they are misleading if so interpreted.

In examining collections of skulls I have taken the trouble (in several instances) of ascertaining how the skulls *absolutely* longest differed in respect of their breadth index from those in the same series and of *absolutely* shortest dimensions. The result has been quite striking in most cases (as may be gathered from Table VII. which follows), for the longest skulls provide invariably the lowest values of the breadth index, and *vice versa*.

TABLE VII.

No.	"Material."	Skulls absolutely longest.		Skulls absolutely shortest.	
		No.	Average breadth index.	No.	Average breadth index.
70	Modern Sardinians	21	67·8	21	73·8
50	Aboriginal Australians	24	68·4	26	70·5
100	Scottish (Dr Young's series K)	20	72·9	18	75·6
118	Dissecting-room bodies (Cambridge)	12	73·3	12	77·6
?	Middlesex Hospital (Gladstone)	...	76·2	...	80·9
65	Dissecting-room (Zürich)	4	78·4	5	87·4

Even more striking is the result obtained by taking definite values of the breadth index in a regular sequence, and appending to each index the mean values of length and breadth provided by the corresponding crania. Upon this basis I have constructed Table VIII., where the cranial length increases just as regularly as the cranial breadth falls in numerical value. A tendency to compensation seems to exist, as though the sum of length and breadth approached a constant quantity. And if we lose sight of the breadth indexes in Table VIII., the remaining figures suggest strongly that in each of these four instances the length varies inversely as the breadth, or in other words that the correlation of length and breadth is not positive but negative.

A biometrician would smile at the deplorable mental fog permitting such an illusion to persist for more than a moment. Yet I venture to say that the difficulty may easily present itself to, and may need a certain amount of consideration by, those not highly trained in dealing with such data. And this is my excuse for bringing it forward here.

TABLE VIII.

Breadth index not exceeding	Mean corresponding	
	Length.	Breadth.
Dissecting-room bodies (Cambridge) [N=118].		
84	179·7	150·0
82	178·7	145·0
80	182·6	144·0
78	185·7	143·4
76	187·0	140·97
74	190·2	139·2
72	192·0	136·8
70	186·5	131·0
68	195·0	129·0
"Large" Scottish skulls, series "K" (Dr Young) [N=100].		
82	178·0	144·0
80	185·3	146·7
78	185·7	142·7
76	188·8	141·5
74	190·4	139·5
72	191·1	137·2
70	193·7	135·0
68	200·0	136·0
Modern Sardinian skulls [N=70].		
82	170	138·0
78	177·8	138·0
76	182·75	137·1
74	183·6	133·6
72	186·2	132·5
70	188·8	130·2
68	187·0	124·7
Aboriginal Australian skulls [N=50].		
76	185·0	139·0
74	183·5	134·6
72	188·2	133·7
70	189·8	131·5
68	188·6	128·2

Note.—In each group (as the breadth index falls) the length increases, while the breadth diminishes.

But there is no doubt that really the correlation between cranial length and breadth is of the positive, not of the negative order. And the columns representing lengths and breadths in Table VIII. mislead, because the table is based upon a seriation of indexes, not of the dimensions themselves.

That this is the case might be shown in several ways. I have selected the most decisive, though perhaps not the shortest, method. Commencing with cranial lengths, I took these in successive groups (175 to 180, etc.) and calculated the mean value of the breadth for the skulls in each group. The result is seen in Table IX.

TABLE IX.—DISSECTING-ROOM BODIES (CAMBRIDGE). [N=118. Sex=male.]

Grouping by length.	No.	Mean length.	Mean breadth.	Mean breadth index.
Crania of length not exceeding 175 mm.	7	173·0	133·3	77·4
,, ,, from 175 to 180 mm.	15	178·0	138·6	77·6
,, ,, ,, 180 ,, 185 ,,	23	183·0	141·7	77·3
,, ,, ,, 185 ,, 190 ,,	42	187·8	141·8	75·3
,, ,, ,, 190 ,, 195 ,,	24	192·7	142·8	74·1
,, ,, ,, 195 ,, 200 ,,	6	197·8	145·6	73·8
,, ,, exceeding 200 mm.	1	202·0	151·0	74·8
Total number	118			

Other considerations arise from this result, but they are not appropriate here, my object being to point out that, where such apparently conflicting results arise as are shown in Table VIII. (the part referring to the dissecting-room bodies) and Table IX., the latter is to be taken as the guide in preference to the former.

VII. RELATION OF THE BREADTH INDEX OF THE HEAD TO THAT OF THE SKULL.

In the introductory section of this paper, I mentioned the circumstances leading to distrust of the results so far obtained in the dissecting-room at Cambridge. In this place I may add that so far as they go those results do not confirm, indeed they tend to contradict, Czekanowski's conclusions. The comparison of the results obtained by various observers fails equally to confirm the sliding scale devised by Czekanowski, so that this scale, although admittedly it holds the field, requires careful scrutiny and testing.

VIII. THICKNESS OF SOFT TISSUES ON SKULL.

Czekanowski and Gladstone have provided data for the estimation of the mean value of the thickness of the soft tissues overlying the cranium.

In the series of bodies measured at Cambridge some comparable data were obtained, and are most easily set out in a table (Table X.). The great discrepancy occurs in respect of the transverse measurements of the dissecting-room bodies. The divergence is so great as rightly to cause the rejection of the aberrant data. Yet I may mention that results as discordant as these have been reported already, the "material" being similar to that used at Cambridge, viz. dissecting-room bodies at Dorpat (Stieda and Wilt[1]). Hagen[1] has recorded equally aberrant results, but from observations on five natives of the Netherlands East Indies.

TABLE X.—THICKNESS OF SOFT TISSUES OF HEAD.

Observer.	Amount of difference.	Sex and age.	Amount of difference.	Sex and age.
A. Difference between head length and skull length.				
Czekanowski . .	7·25 mm.	♂ ?age	6·92 mm.	♀ ?age
Gladstone . . .	7·25 ,,	♂ (aged)	7·12 ,,	♀ (aged)
Duckworth . .	7·6 ,,	♂ (aged)	7·9 ,,	♀ (aged)
B. Difference between head breadth and skull breadth.				
Czekanowski . .	6·91 mm.	♂ (?age)	6·35 mm.	♀ (?age)
Gladstone . . .	7·40 ,,	♂ (aged)	6·98 ,,	♀ (aged)
Duckworth . .	10·2 ,, [2]	♂ (aged)	9·3 ,, [2]	♀ (aged)

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[1] Quoted by Czekanowski, *op. cit.*, p. 48.

[2] Unreliable for reasons stated in text.

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THE DEVELOPMENT OF THE HYPOPHYSIS CEREBRI, PRE-ORAL GUT, AND RELATED STRUCTURES IN THE MARSUPIALIA.

By KATHARINE M. PARKER, B.Sc. (Lond.), *Assistant in the Department of Zoology, University of London, University College.*[1]

INTRODUCTION.

THE following investigation of the development of the hypophysis cerebri in Marsupials was undertaken at the suggestion of Professor J. P. Hill, and I wish to express my gratitude to him for help and advice without which the work would have been impossible.

The literature of the pituitary is already vast, and for close on a century its origin has been the subject of much scientific discussion, but relatively little work has been done on the later stages of its development. The rich supply of embryological material in Professor Hill's collection makes it possible to add some facts to those already recorded by other authors, whilst the interesting conditions revealed in some of the Marsupials afford a further reason for adding this contribution to the existing literature.

The pre-oral gut (Seessel's pocket) in some Marsupials actually becomes part of the so-called anterior lobe of the pituitary, hence it becomes necessary to include as full an account as possible of that structure. Furthermore, the relations of the anterior end of the notochord to Seessel's pocket are, in some species, so close as to merit description in the same connection; whilst in intimate relation to the anterior end of the chorda there is, in some Marsupials, a mass of cells giving rise to a pair of head cavities. In fact, study of the region of the head shows that the notochord, head cavities, pre-oral gut, and the hypophysis are so closely related that to omit any one of these structures is to render the description inadequate. It is doubtless impossible at present to arrive at a correct estimation of the phylogenetic importance of the facts, and further study on the subject, more especially in the

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[1] Thesis approved for the Degree of Doctor of Science in the University of London.

lower Vertebrates, is very desirable. The difficulty of the problem is evident from the number of different structures of unknown significance which are said to be derived from either the roof of the fore-gut or the head of the notochord—*e.g.* the "præchordal Platte" described by Oppel (40) in *Anguis fragilis*; the "Gaumentasche" of Selenka (55) in Didelphys; the pharyngeal bursa, first described by Mayer (31) in 1840, whose possible identity with Seessel's pocket has since been discussed. From an investigation based on one sub-class of the Vertebrates it is obviously impossible to deduce theories of general applicability, but, at the least, some facts may be added which will in the future help in the solution of the interesting problem of the phylogeny of the Vertebrate head.

The descriptive portion of the paper is divided into two sections: the first dealing with early stages in which the relations of the notochord, fore-gut, oral plate, and hypophysis can be studied; the second, with the process of conversion of the simple evagination of the oral ectoderm into the glandular portion of the adult hypophysis. I have referred only briefly to some phases through which the infundibular process passes, and have deliberately omitted any description of the development of the portion of the diencephalic floor lying in proximity to the pituitary body. During preservation the brain is very apt to become abnormally folded, and the infundibular process is undoubtedly distorted in several of the embryos which have come under my observation. On the other hand, it is difficult to give a satisfactory description of this region of the brain from study of transverse series without making reconstructions. As I hope in the future to work out the development of the fore-brain in Marsupials, which will involve making models of several stages, I propose to deal with the diencephalic floor in a later paper, and it is probable that some further facts may then be added to the present description of the development of the infundibular process itself.

I wish to thank Mr F. C. Pittock, of University College, for much help, both in the making of a model and in various other ways.

Description of Stages.

Section I.—*Early Development of the Chorda, Fore-gut, Premandibular Somites, and Hypophysis.*

Before passing on to stages immediately prior to the formation of the hypophysis, it will be well to briefly review the relations of chorda and fore-gut which are brought about on formation of the head-fold.

From the very complete series of early stages of Perameles in Professor Hill's collection, it is possible to work out the early history of the fore-gut and chorda in considerable detail. It is not within the scope of the present paper to deal with this subject except in so far as it sheds light on the early relations of the oral plate, gut, and notochord. Perameles possesses a very well-marked protochordal plate (*cf.* figs. 69 and 71 in Wilson and Hill's "Observations on the Development of Ornithorhynchus" (63)), which, like the chorda itself in early stages, is continuous laterally with the entoderm of the gut. When the head-fold forms, this protochordal plate is involved therein and forms the wall of the anterior extremity of the fore-gut. During this period the entoderm closes in below the notochord, which accordingly becomes detached as a solid rod of cells. The protochordal plate, on the other hand, retains its original relations to the entoderm on either side of it, and continues to form the actual wall of the anterior angle of the fore-gut. Its originally anterior portion, which on formation of the head-fold becomes ventral, constitutes the entodermal layer of the oral plate.

STAGE I. *Perameles nasuta* (2 P.).—Fig. 1 represents a median longitudinal section through an embryo of *Perameles nasuta* (2 P.), the drawing being made by reconstruction from several sections near the middle line. The brain, which is as yet open except in the region posterior to the auditory neuromere, is flexed at two points, representing the dien-mesen (D.-M.) and the mesen-metencephalic (M.-Mt.) limits. Posterior to the projecting anterior border of the medullary plate is a rounded depression, the primitive infundibular recess (I.).

The gut has attained a considerable size in the dorsi-ventral direction. Its anterior wall is in intimate contact with the brain, while the anterior portion of its ventral wall forms, with the ectoderm, the oral plate (O.P.). These two portions of the gut wall, which are derived from the protochordal plate, consist of cells which are rich in protoplasm and contain a number of darkly staining granules (Pt.P.). This appearance is characteristic of the protochordal plate of earlier stages. The dorsal wall of the fore-gut consists of cubical or columnar cells with little protoplasm. Posterior to the region shown in the figure, the gut wall consists of much-flattened entoderm cells.

The notochord in the trunk region is small and typical, but becomes slightly thickened in the region of the myelencephalon (Ch.), whilst immediately posterior to the second point of flexure of the brain it passes into a dense mass of cells (P.P.) extending forwards and tapering in front of the anterior flexure to a fine point. This tapering extremity is so intimately connected with the wall of the fore-gut that the two structures are here indistinguishable, and their point of fusion represents in this stage the posterior limit of the protochordal plate.

In transverse section (fig. 2) it is seen that this mass of cells (P.P.) is narrow from side to side, while from its anterior extremity there arise a small pair of solid outgrowths (Pm.S.). (*N.B.*—Only one of these is shown completely in the figure, as the sectional plane is slightly oblique.)

In a prior stage of Perameles, represented by a flat embryo, the slender notochord is directly continuous at its anterior end with the protochordal plate, and no such mass of cells is present. From its position and relations it is clear that it represents that mass of tissue connecting the gut and notochord which has been described by Oppel (40), Platt (43), and others, in lower Vertebrates; and this lends support to the view that the small outgrowths represent the first trace of the premandibular somites. As we shall see, these structures are clearly present in embryos of *Bettongia gaimardi* and *Macropus ruficollis* of a slightly later stage. Moreover, though it is impossible to trace their history continuously, we find undoubted premandibular head-cavities in the next stage of Perameles, the

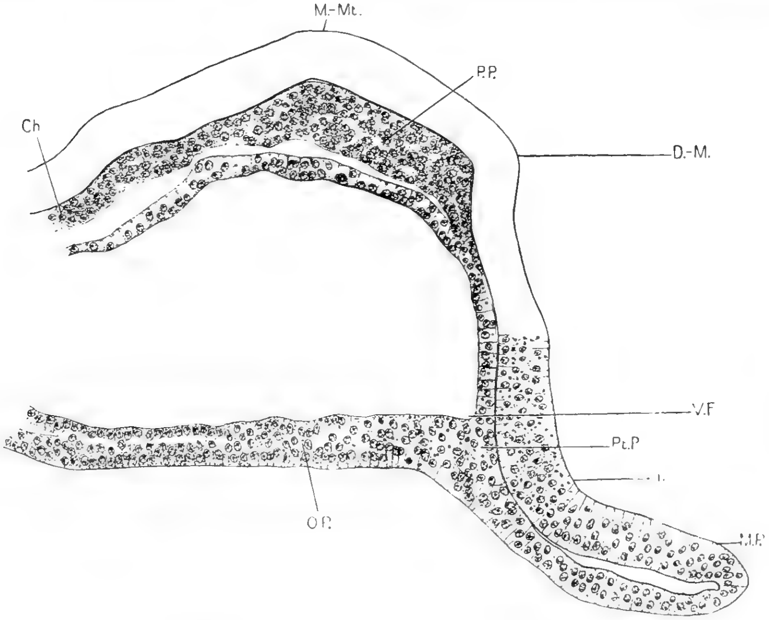

FIG. 1.—Stage I. *Perameles nasuta* (2 P.). Median longitudinal section (reconstructed).

Ch., chorda ; D.-M., dien-mesencephalic limit ; I., primitive infundibular recess ; M.-Mt., mesen-metencephalic limit ; M.P., medullary plate ; O.P., oral plate ; P.P., prechordal plate ; Pt.P., protochordal plate ; V.F., ventral angle of fore-gut.

subsequent history of which has already been described by Elizabeth A. Fraser (12) in Professor Hill's material.

We may therefore conclude that the mass of cells at the anterior end of the chorda represents the "præchordal Platte" of Oppel, and that its lateral outgrowths are the rudiments of premandibular head cavities. I shall accordingly refer to the cell mass in question as the prechordal plate.

There is no differentiation of hypophysial epithelium at this stage.

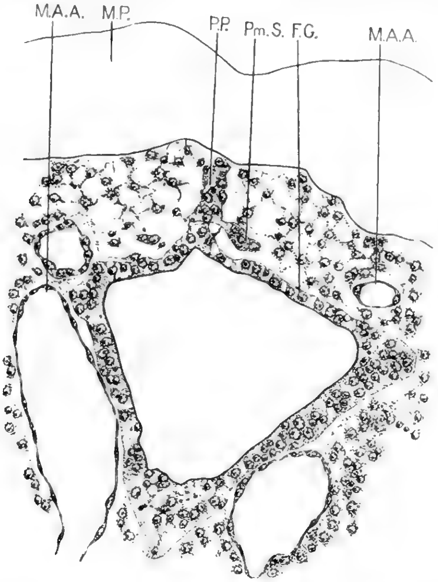

FIG. 2.—Stage I. *Perameles nasuta* (2 P.). Transverse section through prechordal plate and rudimentary premandibular somites. Sl. 1-3-4.

F.G., fore-gut; M.A.A., 1st (mandibular) aortic arch; M.P., medullary plate; P.P., prechordal plate; Pm.S., premandibular somite.

STAGE II. *Bettongia gaimardi.*—This embryo is at a slightly later stage than that of *Perameles nasuta* (2 P.), Stage I., described above, but in the relations of the brain, gut and notochord there is very close agreement between the two embryos.

The brain is flexed at two points, the hind-brain is closed, while the mid- and fore-brains are still widely open.

The anterior wall of the fore-gut lies against the floor of the fore-brain and forms a well-marked angle with the roof. It is somewhat thickened, and is presumably derived from a protochordal plate as in Perameles.

At the anterior end of the notochord is a thickened mass of cells which is bent over so that its anterior extremity lies between the floor of the fore-brain and the anterior wall of the fore-gut, while the apex of the bend lies above the antero-dorsal angle of the gut. This mass of cells represents the prechordal plate of Perameles, but is less well-marked, and, although its anterior extremity is in close contact with the wall of the fore-gut, there does not appear to be actual continuity between the two structures at this stage.

On each side of the embryo, lying posterior to the well-developed optic groove (fig. 3, O.G.), there is a mesodermal mass which can readily be distinguished by its relative density from the loose mesenchyme of the head (fig. 3, Pm.S.). Furthermore, each of these mesodermal masses contains several small but perfectly distinct cavities, two of which are shown in fig. 3, round which the cells are arranged in a radiating manner, forming an irregular epithelial wall. These cavities are not symmetrical on the two sides of the embryo. Owing to the fact that the head of the embryo is cut longitudinally, it is very difficult to determine the exact lateral and median limits of these structures, but after careful study of the series, I

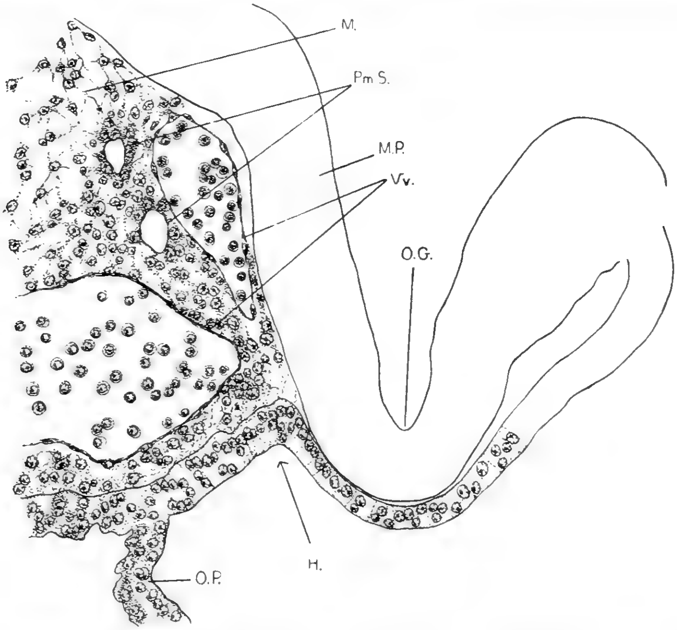

FIG. 3.—Stage II. *Bettongia gaimardi.* Longitudinal section passing through the optic groove and premandibular somites. Sl. 2-2-2.

H., hypophysial angle; M., mesenchyme; M.P., medullary plate; O.G., optic groove; O.P., oral plate; Pm.S., premandibular somite; Vv., blood-vessels.

have been able to make out that a fine strand of cells connects each mass with the anterior end of the prechordal plate. From the position and relations of these structures it is evident that they represent premandibular somites. The fact that more than one cavity is present in each mesodermal mass does not appear to indicate the presence of more than one pair of somites, for the cavities are irregularly arranged and are not symmetrical on the two sides of the embryo.

The hypophysial angle (H.) is recognisable, but there is no differentiation of the ectoderm in this region.

STAGE III. *Macropus ruficollis.*—This embryo shows a distinct advance on the Bettongia embryo described above. The brain is sharply flexed at the mesen-metencephalic junction, the hind-brain is closed, the mid-brain widely open, whilst in the fore-brain the medullary folds are closely opposed but not yet fused.

The fore-gut, in correlation with the flexure of the brain, has a well-marked antero-dorsal angle. Its anterior wall is not thickened as is the case in Perameles and Bettongia. The notochord is discontinuous in the region of the hind-brain. At its anterior end, which still persists, there is a slight enlargement, bent at an acute angle and lying between the antero-dorsal angle of the fore-gut and the floor of the mesencephalon at the point of flexure. This structure, the reduced remnant of a prechordal plate, is not in actual continuity with the wall of the fore-gut.

On each side of the fore-brain, postero-lateral to the optic vesicles, there is a group of mesoderm cells,[1] similar to those described in the same situation in *Bettongia gaimardi* (fig. 4, Pm.S.).

Each cell group is distinguishable from the surrounding mesenchyme by its relative density, and contains several small cavities around which the cells are arranged in the form of a fairly definite epithelium (Ep.H.C.). The two masses are connected across in the middle line by a transverse "bridge" (B.) consisting of a fine, solid strand of cells which runs across immediately anterior to the tip of the notochord.

The sectional plane of this series is transverse to the notochord, and the existence of the bridge is accordingly perfectly clear. On the other hand, it is very difficult to determine whether or no the tip of the prechordal plate is in contact with the bridge connecting the somitic masses. As, however, the section showing the connecting piece is next to that in which the tip of the notochord is seen, it is clear that they are at least in very close proximity to each other.

The mesodermal masses of this embryo bear to the notochord and gut

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[1] My attention was first drawn to the presence of these structures in this embryo by Professor Hill.

the relations which characterise premandibular head cavities, which we may accordingly assume them to be.

The ectoderm of the head is unmodified at the base of the oral plate, *i.e.* there is as yet no differentiation of the hypophysial epithelium.

Trichosurus vulpecula.—This stage is represented in the Trichosurus series by two embryos, one cut longitudinally, the other transversely. These embryos show a very close resemblance to that of *Perameles nasuta* (2 P.), Stage I., in the relations of gut, brain, and notochord, but in several respects they belong more properly to the same stage as the Macropus embryo described above. As they show nothing new, it is not necessary to give a separate description of them, but it may be noted that structures similar to the undoubted head cavities of *Macropus ruficollis* are present in one of the embryos of Trichosurus at this stage of development.

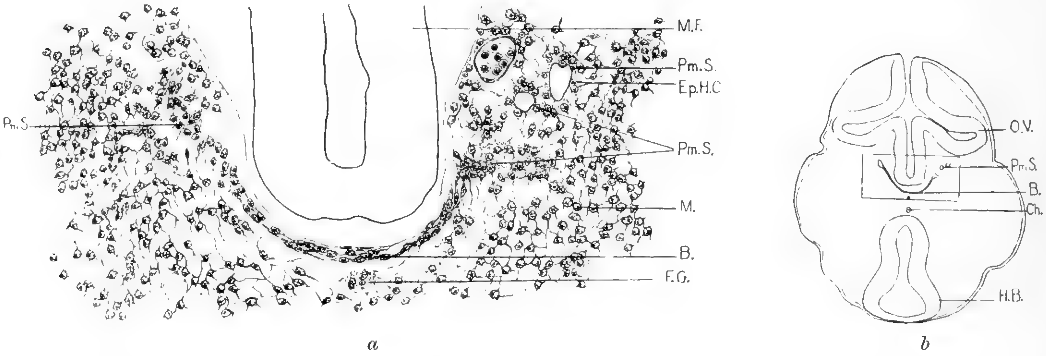

Fig. 4.—Stage III. *Macropus ruficollis.* (*a*) Transverse section through premandibular somites; (*b*) outline diagram of whole section of which (*a*) is a part. Sl. 1–4–5.

B., bridge connecting premandibular somites; Ch., chorda; Ep.H.C., epithelium of head cavity; F.G., wall of fore-gut; H.B., hind-brain; M., mesenchyme; M.F., medullary fold; Pm.S., premandibular somite; O.V., optic vesicle.

Stage IV. *Perameles nasuta* (13, VII. 05).—This embryo shows a distinct advance on the preceding, the brain being completely closed and Rathke's pouch already differentiated. It is cut in horizontal sections, and, as the relations of the parts are particularly interesting, a wax plate-reconstruction was made of the fore-brain, hypophysis, chorda, etc. (see fig. 5). Detailed observations are, moreover, made possible by the remarkably perfect preservation of the embryo.

The floor of the diencephalon shows a rounded depression, the primitive infundibular recess (I.), anterior to which is a slight ridge, indicating the future position of the optic chiasma. The hypophysial primordium—Rathke's pouch (R.P.)—is now present as a thickened stretch of ectoderm, closely applied to the infundibular depression. The pouch is very shallow anteriorly and deepens somewhat behind, where its lateral angles are fairly well marked. Its posterior wall forms the anterior wall of the fore-gut, and constitutes the ectoderm of the dorsal portion of the oral plate (O.P.), which is still complete. In its dorsal portion, the oral plate is bent at a fairly sharp angle, the apex of this angle forming in section a "plug" (P.) which projects into Rathke's pouch, and will be seen in similar stages in other species (*cf*. fig. 31, O.P.), whilst the rest of the oral plate is thin.

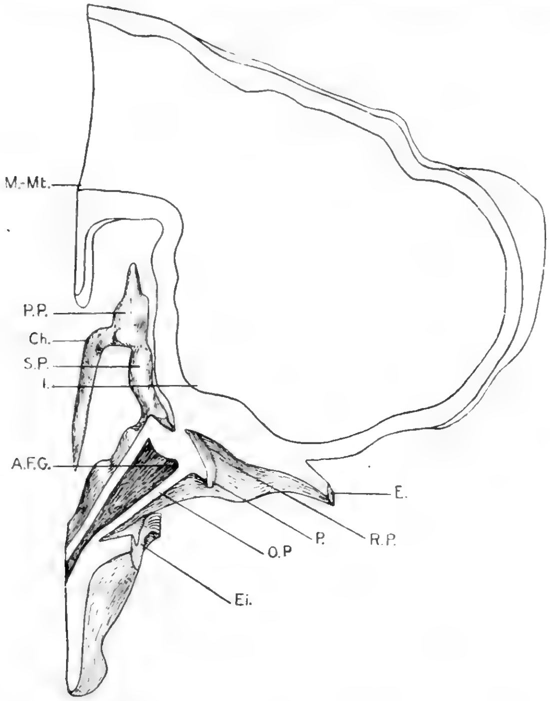

Fig. 5.—Stage IV. *Perameles nasuta* (13, VII. 05). Longitudinal section through model of fore-brain, hypophysis, Seessel's pocket, and notochord, slightly to the right side of the middle line.

A.F.G., anterior angle of fore-gut; **Ch.**, chorda; **E.**, ectoderm of head; **E.i.**, ectoderm of mandibular arch; **I.**, infundibular recess; **M.-Mt.**, Mesen-metencephalic limit; **O.P.**, oral plate; **P.**, "plug" formed by projection of oral plate into Rathke's pouch; **P.P.**, prechordal plate; **R.P.**, Rathke's pouch; **S.P.**, Seessel's pocket.

The dorsal wall of the fore-gut is thickened immediately behind Rathke's pouch, and from it there arises a small median outgrowth (S.P.), slightly dilated at its extremity and running backwards parallel with the diencephalic floor to meet the somewhat irregular prechordal plate (P.P.). This latter preserves its original form, being narrow from side to side and of relatively considerable dorso-ventral extent. The prechordal plate is continuous at its caudal extremity with the notochord (Ch.), which is here small and typical, and, following the flexure of the brain, is bent at approximately a right angle at the mesen-metencephalic junction (M.-Mt.).

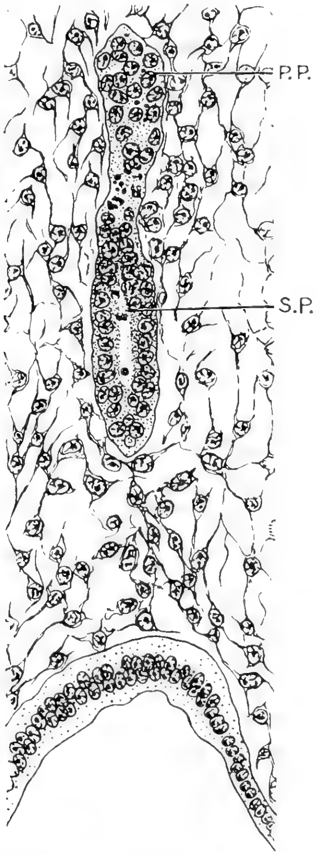

FIG. 6.—Stage IV. *Perameles nasuta* (13, VII. 05). Section through prechordal plate and Seessel's pocket. Sl. 3-3-11.

P.P., prechordal plate ; S.P., Seessel's pocket.

The small outgrowth (S.P.), arising as it does immediately behind the oral plate, represents the remnant of the pre-oral gut usually known as Seessel's pocket. It will be noticed that its distal extremity is continuous with the prechordal plate, and we may therefore conclude that it has arisen from that part of the fore-gut of the early stage of Perameles which is situated at the junction of the prechordal plate with the entoderm of the gut wall.

The minute structure of the organs in this region is also worthy of note. The thickened wall of the fore-gut immediately behind Rathke's pouch shows all the features characteristic of the protochordal plate of earlier stages, the granulation of the cells being recognisable here, and to a less extent in the portion of oral plate adjacent to it. We may therefore conclude that here, as in the previous stage, the antero-ventral wall of the fore-gut is formed by the protochordal plate. Seessel's pocket, arising from the dorsal side of this portion of the gut (fig. 6, S.P.), has no actual lumen but is obviously tubular in structure, its walls consisting of a very regular epithelium. It is impossible to define exactly the limit between the wall of Seessel's pocket and the prechordal plate (P.P.), which consists of a rather irregular mass of cells, containing darkly staining granules. From its margin, cells here and there project, giving it an irregular outline, in which respect it contrasts with the notochord proper, whose outline is perfectly definite. Some of these cells appear to represent traces of the former connection between the prechordal plate and the premandibular somites, which have now acquired a considerable size and possess a distinct cavity. In this stage they have already been described and figured by Fraser (12).

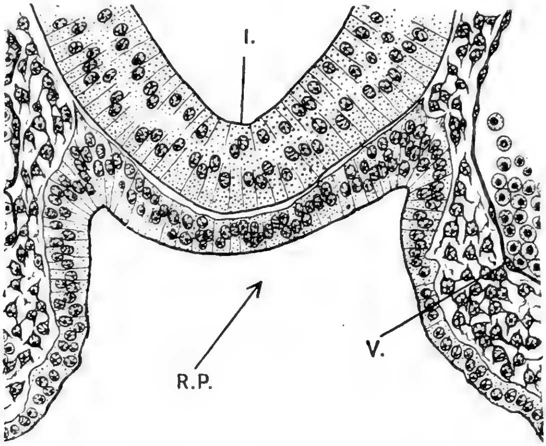

Fig. 7.—Stage IV. *Perameles nasuta* (13, VII. 05). Transverse section through primitive infundibular recess and Rathke's pouch.

I., primitive infundibular recess; R.P., Rathke's pouch; V., blood-vessel.

The walls of Rathke's pouch (fig. 7, R.P.) consist of a regular columnar epithelium which is thin in the middle line and thickens somewhat at the lateral angles, where the cells are closely packed and show evidence of rapid growth. Thus there is a tendency for the cells in these two regions to project on the outer side of the wall, giving almost an appearance of proliferation (fig. 7), a condition which is doubtless due to the rapid multiplication of the cells.

Dasyurus viverrinus.—As Dasyurus differs in some important respects from the types described above, and as, moreover, a complete series of stages showing the early development of Rathke's pouch is available, it will be best to describe the stages of Dasyurus consecutively as a series, distinct from Perameles, Bettongia, and Macropus.

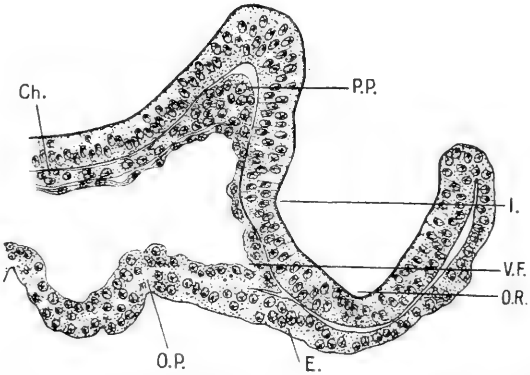

FIG. 8.—Stage I. *Dasyurus viverrinus* (I., A. 02). Median longitudinal section through the anterior end of the brain, chorda, and fore-gut (reconstructed). Sl. IV. 1–14 to 2–1.

Ch., chorda ; E., ectoderm ; I., primitive infundibular recess ; O.P., oral plate ; O.R., optic recess ; P.P., prechordal plate ; V.F., ventral angle of fore-gut.

STAGE I. (I., A. 02).—This stage corresponds approximately with Stage I. of Perameles.

The relations of brain, gut, chorda, and oral plate are best seen in median longitudinal section (fig. 8). The brain is flexed at one point, while the hind-brain only is closed. The anterior end of the medullary plate curves upwards, and two depressions in the floor of the fore-brain can be identified. Of these, the anterior is the optic (O.R.), the posterior the infundibular recess (I.). The chorda (Ch.) extends to shortly behind the point of flexure of the brain. Throughout the greater part of its length it consists of a thin strand of cells, but at its anterior end, which lies in the angle formed by the cranial flexure, there is a marked thickening, the prechordal plate (P.P.) bent at an acute angle and reaching its greatest thickness opposite the flexure of the brain floor. The tapering extremity of the prechordal plate, as in Perameles, is directly continuous with the gut-wall. The antero-dorsal angle of the gut is thin-walled while its antero-ventral angle has relatively thick walls, consisting of somewhat irregular, elongated cells. Here again the whole of the anterior wall of the fore-gut as well as the anterior part of the entoderm of the oral plate is to be regarded as derived, as in Perameles, from a protochordal plate. The latter, however, is not nearly so clearly differentiated in Dasyurus as it is in Perameles.

No traces of premandibular somites are recognisable.

The ectoderm of the hypophysial angle (E.) consists of columnar epithelium, and as yet shows no sign of differentiation.

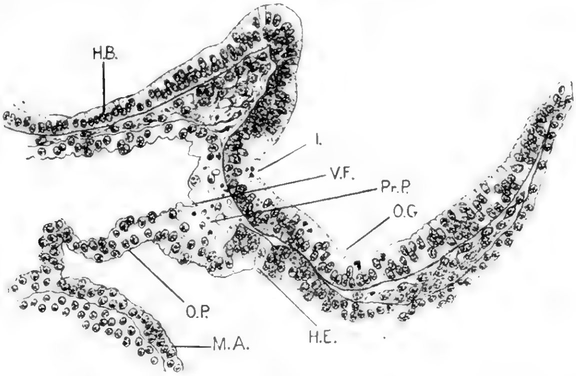

FIG. 9.—Stage II. *Dasyurus viverrinus* (1, 01). Median longitudinal section through anterior end of brain and fore-gut. Sl. 3–3–2.

H.B., hind-brain; **H.E.**, hypophysial epithelium; **I.**, primitive infundibular recess; **M.A.**, mandibular arch; **O.G.**, optic groove; **O.P.**, oral plate; **Pr.P.**, protochordal plate; **V.F.**, ventral angle of fore-gut.

STAGE II. *Dasyurus viverrinus* (1, 01).—In general features this stage resembles the preceding so closely that no detailed description will be necessary.

The brain in median longitudinal section (fig. 9) presents much the same features as in Stage I., but the infundibular depression (I.) and the optic recess (O.G.) are both more clearly defined. The prechordal plate is no longer recognisable as a distinct structure. The wall of the antero-ventral angle of the fore-gut (protochordal plate, fig. 9, Pr.P.) is now distinctly thickened and has a very characteristic appearance. The cells are regularly arranged, contain a number of darkly staining granules, and are vacuolated.

The first trace of the primordium of the hypophysis is now recognisable. Immediately anterior to the oral plate, the ectoderm consists of distinctly elongated epithelial cells (H.E.) The thickening extends forwards as far as the optic recess, and is most marked at the point of contact of the ectoderm with the entoderm of the pre-oral gut. Posterior to this point the modified ectoderm of the hypophysis thins out slightly and is directly continuous with the oral plate (O.P.), in which the ectoderm and entoderm are now indistinguishable.

In transverse section we can see the primordium of the hypophysis as a thickened and slightly invaginated stretch of ectoderm, in intimate contact with the floor of the brain.

STAGE III. *Dasyurus viverrinus* (II., *a*, 01): *Embryos a, b, and c.*—The embryos of this stage are only slightly more advanced than those of the preceding. The optic groove (fig. 10, O.G.) and the infundibular recess (I.) are slightly more clearly marked. The hypophysis has distinctly deepened and the oral plate has ruptured. The relations to the pre-oral gut in individual embryos of the stage vary slightly (*cf.* figs. 10 and 11).

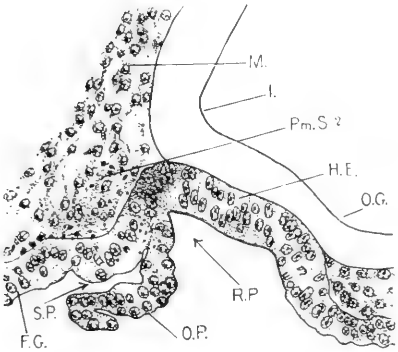

FIG. 10.—Stage III. *Dasyurus viverrinus* (II., *a*, 01). Embryo *a*. Median longitudinal section through the hypophysis and Seessel's pocket. Sl. 2–3–7.

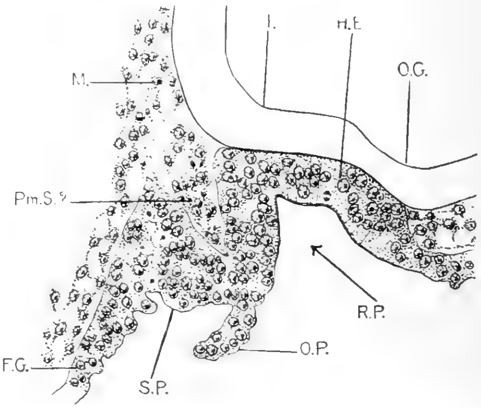

FIG. 11.—Stage III. *Dasyurus viverrinus* (II., *a*, 01). Embryo *c*. Median longitudinal section through the hypophysis and Seessel's pocket. Sl. 2–1–11.

F.G., fore-gut; H.E., hypophysial epithelium; I., primitive infundibular recess; M., mesenchyme; O.G., optic groove; O.P., oral plate; Pm.S.(?), possible trace of premandibular somite; R.P., Rathke's pouch; S.P., Seessel's pocket.

In two embryos (*a* and *b*, fig. 10), which are cut longitudinally, the hypophysis is separated from the anterior angle of the gut simply by the thickness of the oral plate, which is ruptured ventrally (O.P.). The wall of the hypophysis consists of columnar epithelial cells, very regularly arranged. The pouch (R.P.) shows an obtuse anterior angle and an acute posterior angle, and the latter has progressed back so as to lie beneath the deepest part of the infundibular recess. The regular columnar epithelium extends over the apex of the posterior angle of the pouch and passes into continuity with the thickened wall of the anterior angle of the fore-gut, as well as with the persisting upper part of the oral plate. Seessel's pocket is represented simply by the thick-walled anterior angle of the fore-gut, and is separated from Rathke's pouch merely by the persisting upper part of the oral plate.

In a third embryo (*c*, fig. 11), cut longitudinally, Rathke's pouch is somewhat larger. Moreover, instead of the posterior wall of the hypophysis being in direct contact with the anterior wall of the fore-gut, a certain amount of mesenchyme is present immediately behind Rathke's pouch. Seessel's pocket accordingly forms a small conical diverticulum whose wall is separated from that of Rathke's pouch by mesoderm. The remnant of oral plate (O.P.) is attached to the ventral border of the fold between Seessel's pocket and the hypophysis.

This condition resembles the typical arrangement in many Eutheria and birds, in both of which groups the pre-oral gut forms a short diverticulum separated from the hypophysis by a solid fold containing a mesodermal core.

In all the embryos of this stage there is on either side of the middle line, immediately posterior to the hypophysis, a group of cells lying dorsal to the gut-wall. In the first of the types described above, these cells lie posterior to the apex of the anterior angle of the fore-gut (fig. 10, Pm.S. ?); in the second, they lie between the hypophysis and Seessel's pocket (fig. 11, Pm.S. ?). This cell mass can be distinguished from the surrounding mesoderm by its density and by the presence of a number of darkly staining granules. It seems possible that it represents a pair of somites, presumably premandibular, but apart from it no trace of head cavities has been found in Dasyurus.

STAGE IV. *Dasyurus viverrinus* (β).—In this stage the floor of the infundibulum is marked by a distinct angle, but no definite infundibular process has appeared.

The hypophysis now forms a distinct pouch, with a small remnant of the oral plate attached to its posterior wall in some embryos. In one embryo only of this stage is there still a considerable remnant of Seessel's pocket; in the others, a very slight diverticulum (fig. 12, S.P.) marks the position of the pre-oral gut; but in every case the posterior wall of the hypophysis, though continuous with, is perfectly distinct from, the anterior wall of Seessel's pocket.

It is evident from the foregoing that in Dasyurus, Seessel's pocket is a variable and transient structure, for it is hardly recognisable in some embryos, and in no case does it play any part in later development.

It has not been possible to recognise in this stage the group of cells described in the preceding stage and interpreted as possibly somitic.

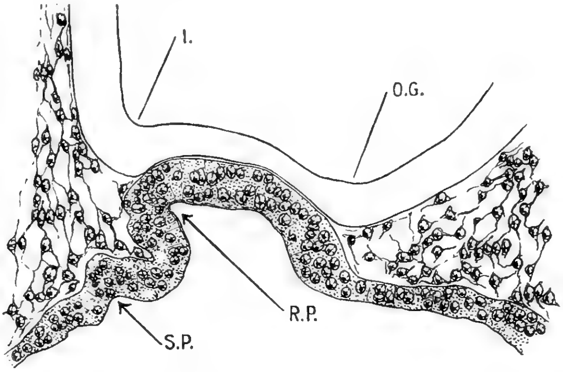

Fig. 12.—Stage IV. *Dasyurus viverrinus* (β). Median longitudinal section through hypophysis. Sl. 2-6-11.

I., primitive infundibular recess; O.G., optic groove; R.P., Rathke's pouch; S.P., Seessel's pocket.

Section II.—*The Later Development of the Hypophysis cerebri and the Pre-oral Gut.*

This section deals with the development of the hypophysis subsequent to the establishment of Rathke's pouch, *i.e.* with the origin and development of the infundibular process and the conversion of the simple buccal invagination into the so-called anterior lobe and pars intermedia of the adult.

With regard to the nomenclature of the parts of the adult hypophysis, it has already been pointed out by Tilney (58) and others that the terms "anterior" and "posterior lobes" and "pars intermedia" are open to serious criticism. They are applicable to the human subject, but not to all Vertebrates, inasmuch as the infundibular process is frequently dorsal to the rest of the pituitary and in some species is actually anterior thereto. Moreover, these terms are based exclusively on topography, and indicate neither the function nor the origin of the parts, for the "pars intermedia" is only intermediate in position and not in any other sense. Furthermore, there is good reason to suppose that the tissue of the non-nervous portion of the hypophysis which is in contact with the nervous portion consists of two parts. As these two regions have been clearly recognised, as far as I am aware, only by Tilney (59), the simplest method is to adopt the

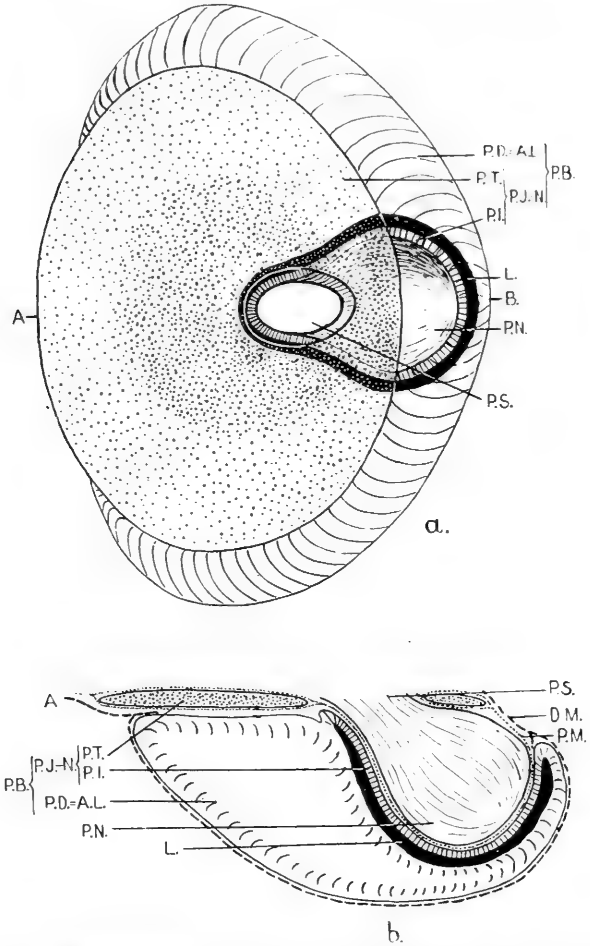

FIG. 13.—(*a*) Diagrammatic ground plan of hypophysis to show the relations of the various parts. The hypophysis is represented as removed from the brain and viewed from the dorsal surface in optical section. (*b*) Diagrammatic median longitudinal section through adult hypophysis. (Sectional plane indicated by line A B in fig. *a.*) (*N.B.*—The relations and approximate proportions of the parts in these figures were obtained by measurement with an ocular micrometer of the hypophysis in *Trichosurus vulpecula*, Stage XI. (see p. 212), H.L. 20 mm., G.L. 4 cm.)

D.M., dura mater; L., lumen; P.M., pia mater; P.S., pituitary stalk;
P.B., pars buccalis; { P.J.-N., pars juxta-neuralis; { P.T., pars tuberalis; P.I., pars infundibularis;
P.D., pars distalis = A.L., anterior lobe;
P.N., pars neuralis.

nomenclature used by him, some of the terms being originally suggested by Gentes (15).

We can accordingly recognise in the hypophysis a *pars neuralis* (fig. 13, P.N.) (=posterior lobe, infundibular process, "Hirnteil," neurohypophysis) and a *pars buccalis* (P.B.) (=anterior lobe, epithelial or glandular portion, "Hauptlappen," together with the pars intermedia). The pars buccalis is subdivided into a *pars juxta-neuralis* (P.J.-N.), in contact with the brain, and a *pars distalis* (P.D.) (=anterior lobe proper). The pars juxta-neuralis consists of a *pars tuberalis* (P.T.) (Tilney (59)), lying in contact with the tuber cinereum, and a *pars infundibularis* (P.I.) (=pars intermedia), *i.e.* the epithelial layer between the residual lumen and the infundibular process. The difference in origin and appearance of these two portions of the pars juxta-neuralis which Tilney (59) describes in the fowl, cat, rabbit, rat, and sheep, is also recognisable in Marsupials.

In early stages the use of topographical terms is necessary, and I accordingly describe the parts of Rathke's pouch as dorsal, *i.e.* on the side next the diencephalic floor; ventral, *i.e.* on the side next the pharyngeal roof; cranial, towards the telencephalon; and caudal, towards the mesencephalon.

Trichosurus vulpecula.

STAGE I. *Embryos* γ' 99, 1.01, *and* δ' 97.—The hypophysis of these embryos shows only a slight advance on that of Stage IV., *Perameles nasuta* (13, VII. 05).

The oral plate is ruptured (fig. 14, O.P.), but its ventral point of attachment is still visible, whilst dorsally a considerable remnant of it persists. Behind the oral plate is a small conical diverticulum with thickened walls. This is the only trace of pre-oral gut which occurs in Trichosurus (fig. 14, S.P.).

On the cephalic side of the oral plate the ectoderm of the head is thickened for a short distance, forming with the ectoderm of the upper margin of the oral plate the primordium of Rathke's pouch (R.P.). Transverse sections show that in its cephalic portion the pouch is widely open on its ventral side, while its dorsal wall is closely applied to the diencephalic floor. The pouch is, however, closed in its posterior portion and is bifid at its caudal extremity. The small pre-oral gut fits into the bifurcation of the pouch so that in the middle line its entoderm is in contact with the floor of the diencephalon, whilst on either side it is separated therefrom by the lateral branches of Rathke's pouch. The wall of the pouch consists of several layers of columnar cells.

The floor of the diencephalon is depressed to form the primitive infundibular recess, whose dorsal limit is indicated by a slight horizontal ridge on the inside of the diencephalon. No infundibular process is yet indicated.

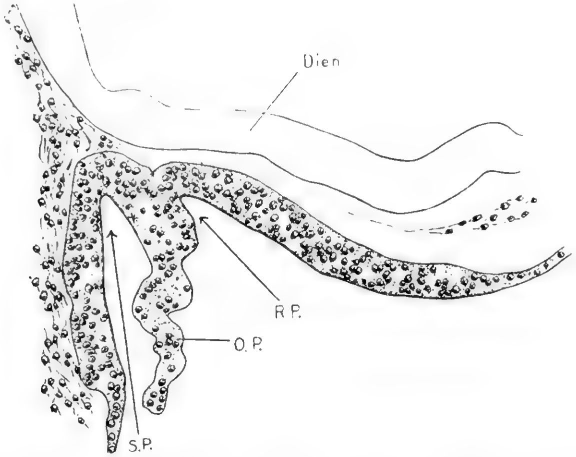

Fig. 14.—Stage I. *Trichosurus vulpecula* (1, *a*, 01). Median longitudinal section through the hypophysis and Seessel's pocket. Sl. 2–4–4.

Dien., diencephalic floor; O.P., oral plate; R.P., Rathke's pouch; S.P., Seessel's pocket.

Stage II. *G.L.* 7 *mm.* (*Embryo a′* 97).—In this stage the limits of Rathke's pouch are clearly indicated by lateral grooves. The pouch is still widely open anteriorly, but its opening has narrowed considerably. Its roof is thick, its posterior closed portion is quadrilateral in transverse section, and its caudal extremity is slightly bifid.

The infundibular depression is relatively wide anteriorly, but becomes narrower posteriorly, indicating the form and position of the infundibular process.

A small rounded diverticulum situated caudal to the opening of Rathke's pouch represents the degenerating remnant of Seessel's pocket.

Stage III. *G.L.* 7·5 *mm.* (*Embryo* XIX. 04).—The opening of Rathke's pouch has narrowed so as to form a short, wide duct, while the pouch itself is subdivided, in the portion behind the duct, by a pair of horizontal constrictions. The two lobes thus formed may be distinguished as proximal (*i.e.* nearest to the opening of the pouch, fig. 15, P.L.) and distal (*i.e.* nearest to the diencephalic floor, D.L.). The constriction disappears at the point where the hypophysial duct opens, so that the anterior, open section of the pouch is undivided. We shall see that the proximal lobe is destined to form the pars tuberalis of the adult hypophysis, the remainder of the pouch forming the pars distalis and the pars infundibularis.

Both proximal and distal lobes in this stage are slightly bifid at their caudal extremity, the distal more markedly so than the proximal.

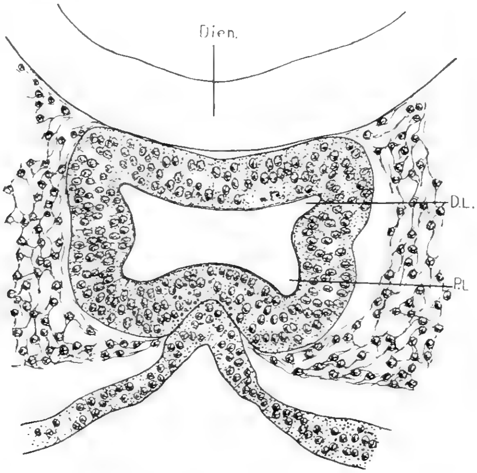

Fig. 15.—Stage III. *Trichosurus vulpecula* (XIX. 04). Transverse section through Rathke's pouch. Sl. 2–4–7.

D.L., distal lobe; Dien., diencephalic floor; P.L., proximal lobe.

STAGE IV. *G.L.* 7·25 *mm.* (XII. 02 *and* XII. A. 02).—The duct is here still further reduced, and anterior to it the pouch is relatively small and simple. The distal lobe is now considerably larger than the proximal, and extends further in the caudal direction (figs. 16 and 17). It is relatively extensive in the dorsi-ventral direction immediately caudal to the duct, and its walls are thick, consisting of a many-layered epithelium. Posterior to this it widens from side to side and becomes shallower, its dorsal wall becomes thin, while its lateral walls are thick and rather irregular. It is bifid posteriorly, the walls of the two halves being thin and forming a regular epithelium.

The proximal lobe (P.L.) is compressed dorso-ventrally, is wide from side to side, and is undivided posteriorly. The ventral wall is thin (fig. 16), its dorsal wall thicker.

A short conical infundibular process is present, fitting in between the two halves of the bifid caudal extremity of the distal lobe. Its walls, like those of the brain generally, consist simply of undifferentiated cells, uniformly distributed through its thickness. (*N.B.*—The infundibular process is not shown in the longitudinal section figured, owing to the obliquity of the sectional plane.)

A small remnant of oral plate (fig. 17, O.P.) is present, arising from the postero-ventral wall of the proximal lobe. The narrowing of Rathke's pouch has occurred in such a way as to carry this remnant of oral plate within the opening of the pouch so that a remnant of Seessel's pocket (S.P.) is carried inwards and forms a small diverticulum on the posterior wall of the short duct. Thus it happens that portions of oral plate and of the entodermal wall of Seessel's pocket come to be included in the hypophysis at this stage.

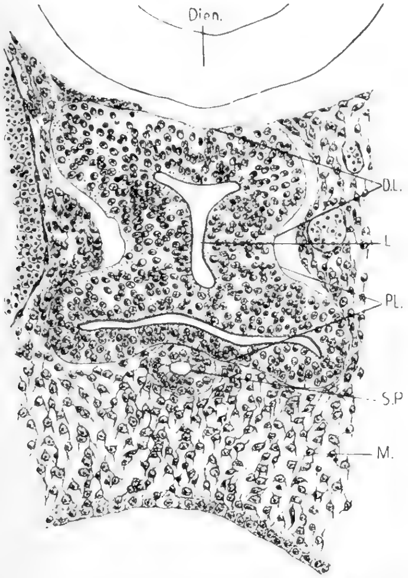

FIG. 16.—Stage IV. *Trichosurus vulpecula* (XII. 02). Transverse section through hypophysis. Sl. 5–2–8.

D.L., distal lobe; Dien., diencephalic floor; L., lumen; M., mesenchyme; P.L., proximal lobe; S.P., Seessel's pocket.

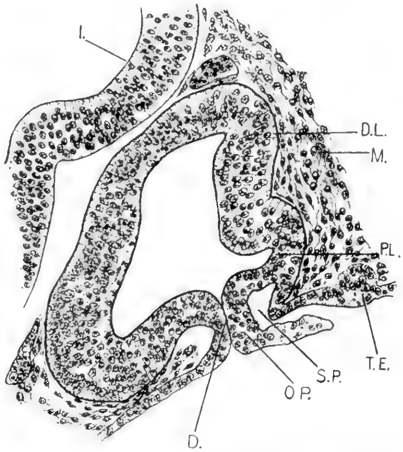

FIG. 17.—Stage IV. *Trichosurus vulpecula* (XII. A. 02). Longitudinal section through hypophysis. Sl. 8–3–2.

D., duct of Rathke's pouch; D.L., distal lobe; I., infundibular recess; M., mesenchyme; O.P., oral plate; T.E., transitory entodermal thickening; P.L., proximal lobe; S.P., Seessel's pocket.

STAGE V. *G.L.* 8·5 *mm.* (*Embryos* IV. 01 *and* 5′ 97).—The distal lobe (fig. 18, D.L.) has enlarged considerably, while the proximal lobe (P.L.) is much smaller relative to the whole buccal pouch. The duct is now reduced to a fine strand of cells. Seessel's pocket and the remnant of the oral plate have disappeared completely.

The proximal lobe, which lies entirely posterior to the remnant of the duct, is wide from side to side, but very shallow dorsi-ventrally, with a small, cleft-like cavity. Its walls are thin and its lateral margins are slightly enlarged (L.P.L.). The lumen communicates with that of the main, distal lobe by a wide opening.

The distal lobe now constitutes the main bulk of the pouch, and its walls are distinctly thickened, except the portions which lie in actual contact with the infundibular process, these being thin (fig. 18, *c* and *d*). The lobe is rounded anteriorly, then becomes enlarged in the dorso-ventral direction (fig. 18, *a*). Posterior to the remnant of the duct, it has two large dorso-lateral hollow appendages (fig. 18 *c*, L.D.L.), whose cavities open into the main lumen. The distal lobe is still bifid caudally, and the infundibular process, which is a short, conical structure, fits in between the two halves. Its walls show no change since the preceding stage.

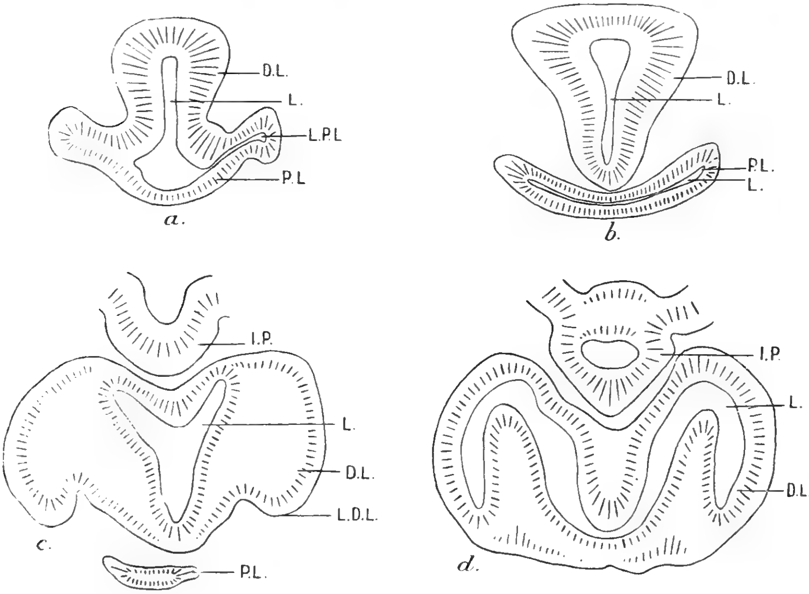

Fig. 18.—Stage V. *Trichosurus vulpecula* (IV. 01). Series of transverse sections through hypophysis, *a* being the most anterior, *d* the most posterior.

D.L., distal lobe ; I.P., infundibular process ; L., lumen ; L.D.L., lateral expansion of distal lobe ; L.P.L., lateral expansion of proximal lobe ; P.L., proximal lobe.

Up to this stage the most intimate relations between the diencephalic floor and the buccal pouch have been maintained, but in the longitudinal series of this stage there is a certain amount of mesenchymal tissue between the hypophysis and the brain floor in the region anterior to the infundibular process. This latter is, however, in direct contact with the epithelial wall of the buccal pouch.

STAGE VI. *G.L.* 11 *mm.* (*Embryos* XXII. 01 *and* XXI. 04); *G.L.* 11·5 *mm.* (*Embryo* VII. 01).—The walls of the main distal lobe (D.L.) have now thickened considerably, so that in the region anterior to the duct only a small remnant of the lumen is present (figs. 19 and 20, L.).

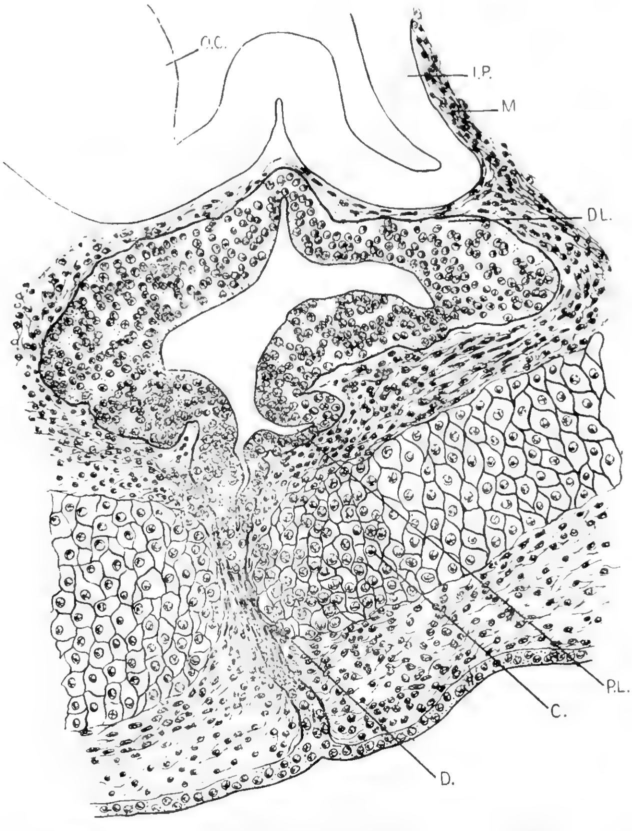

FIG. 19.—Stage VI. *Trichosurus vulpecula* (XXII. 01). Median longitudinal section through hypophysis. Sl. 11–2–1.

C., cartilage of skull; D., duct of Rathke's pouch; D.L., distal lobe; I.P., infundibular process; M., mesenchyme; O.C., optic chiasma; P.L., proximal lobe.

The lumen enlarges in dorso-ventral extent in the middle portion of the hypophysis, and narrows again posteriorly. The dorso-lateral, wing-like expansions of the previous stage are still present, but their cavity is reduced to a small cleft, in open communication with the main lumen.

The walls consist of closely packed cells, showing no trace of differentiation or grouping.

The proximal lobe (fig. 20, P.L.) is crescentic in transverse section, with thin walls consisting of a regular epithelium. Its median portion contains a small, cleft-like cavity (L.), while its lateral wings (L.P.L.) are markedly enlarged and are produced backwards along the sides of the distal lobe.

In the posterior portion of the pouch, the dorsal wall is somewhat thin, and the bluntly conical infundibular process (fig. 19, I.P.), whose walls are still undifferentiated, fits into a depression in this wall. A thin layer of connective tissue has penetrated between the neural and buccal portions of the hypophysis in this stage.

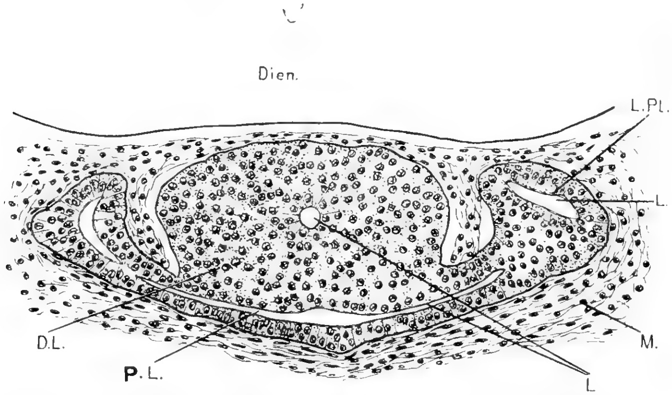

Fig. 20.—Stage VI. *Trichosurus vulpecula* (VII. 01). Transverse section through hypophysis. Sl. 4-1-9.

D.L., distal lobe; Dien., diencephalic floor; L., lumen; L.P.L., lateral expansion of proximal lobe; M., mesenchyme; P.L., proximal lobe.

No trace of Seessel's pocket is present.

Stage VII. *G.L.* 13 *mm.* (*Embryos* IX. 01 *and* VIII. 01).—In general shape the hypophysis closely resembles that of the preceding stage, but it has increased considerably in size.

The walls of the anterior half of the distal lobe have increased in thickness, so that the lumen is reduced to a small, circular cavity (fig. 21, L.), while the extreme anterior end is solid. In the mid-portion of the hypophysis the lumen of the distal lobe increases in vertical extent, and still opens into the cavity of the proximal lobe. Posterior to this it expands into a triangular cavity (fig. 22, L.) with a thin roof (P.I.) and very thick sides; whilst in the hindermost portion the lateral walls also become thinner, the cavity spacious (fig. 23, L.), and the roof indented by the infundibular process (fig. 23, I.P.).

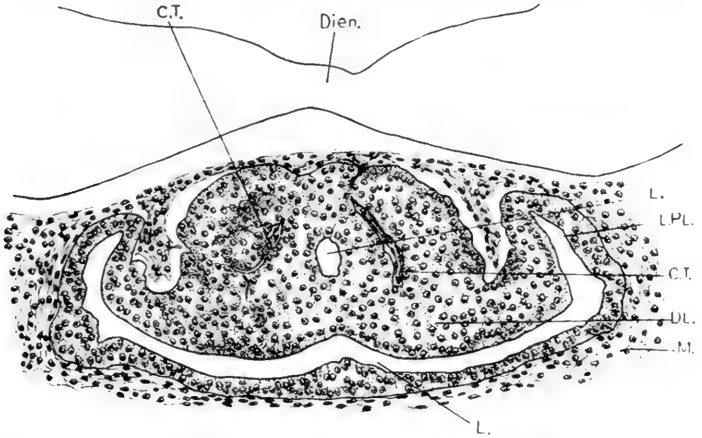

Fig. 21.—Stage VII. *Trichosurus vulpecula* (IX. 01). Transverse section through proximal and distal lobes of hypophysis. Sl. 4–5–10.

C.T., connective tissue; D.L., distal lobe; Dien., diencephalic floor; L., lumen; L.P.L., lateral expansion of proximal lobe; M., mesenchyme.

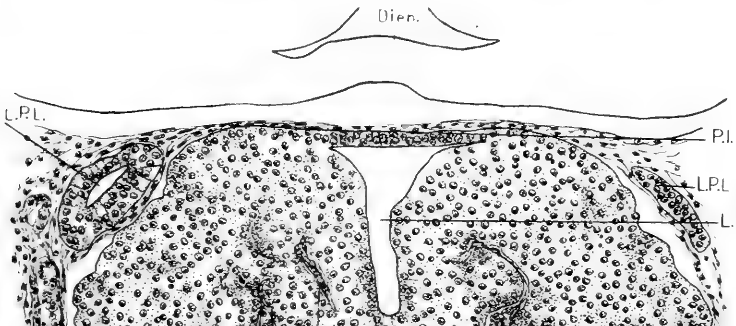

Fig. 22.—Stage VII. *Trichosurus vulpecula* (IX. 01). Transverse section through distal lobe in region of its lateral expansion. Sl. 5–1–6.

C.T., connective tissue; Dien., diencephalic floor; L., lumen; L.D.L., lateral expansion of distal lobe; L.P.L., lateral expansion of proximal lobe; P.I., portion of wall of pouch destined to form the pars infundibularis.

The proximal lobe is relatively and actually larger than in the preceding stage (fig. 21, P.L.). It is crescentic in transverse section, and has a well-marked lumen. Its walls consist of a thin and regular epithelium, its dorsal wall has fused to a large extent with the distal lobe, while its lateral margins (L.P.L.) have grown upwards towards the brain and are prolonged for some way posterior to its median portion (fig. 22, L.P.L.).

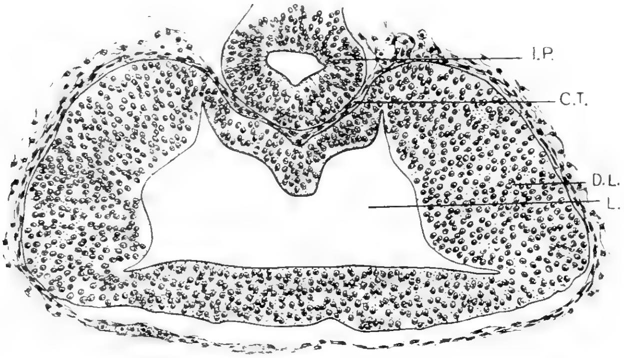

Fig. 23.—Stage VII. *Trichosurus vulpecula* (IX. 01). Transverse section through hypophysis in region of the infundibular process. Sl. 5–2–2.

C.T., connective tissue ; D.L., distal lobe ; I.P., infundibular process ; L., lumen.

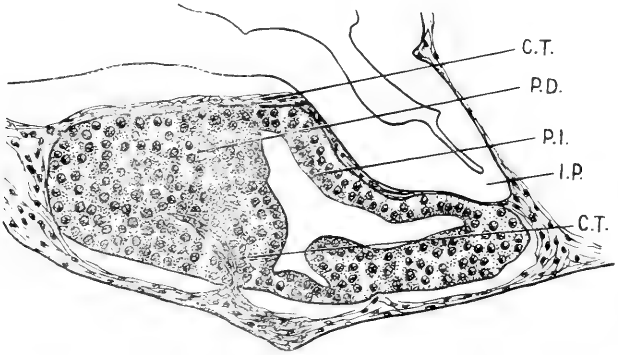

Fig. 24.—Stage VII. *Trichosurus vulpecula* (XXIV.). Median longitudinal section (reconstructed) through hypophysis. Sl. 7–1–2–4.

C.T., connective tissue ; I.P., infundibular process ; P.D., pars distalis ; P.I., pars infundibularis.

In this stage we can see the commencement of processes which convert the uniform walls of Rathke's pouch into the glandular "anterior lobe" of the typical adult hypophysis. In the more solid anterior portion of the main lobe, thin strands of connective tissue (C.T.) are penetrating into the substance of the walls, sometimes carrying small blood-vessels with them. These strands grow in more or less symmetrically on either side of the middle line, so as to split the solid walls into lobules (figs. 21 and 22); and the cells also show a tendency to group themselves into cords or lobules, but with no indication of lumina. This lobulation only affects the anterior portion of the main lobe, the posterior portion thereof and the whole of the proximal lobe having thin uniform epithelial walls.

The infundibular process is fairly long, with a bluntly pointed apex (figs. 23 and 24, I.P.), and is separated from the buccal portion of the hypophysis by connective tissue (C.T.).

The duct is still present in one embryo of this stage, but is lost in the others, its site being marked by the perforation of the cartilage of the basis cranii.

In this stage the several portions of the adult hypophysis can now be identified. The pars neuralis (fig. 24, I.P.) is pressed against the dorsal wall of the pars buccalis, which itself consists of a juxta-neural portion (P.I.), represented by the thin wall in contact with the pars neuralis and the solid pars distalis (P.D.), already in process of conversion into a gland. The primordium of the pars tuberalis is represented by the lateral enlargements (fig. 21, L.P.L.) of the proximal lobe, the median portion of which subsequently becomes incorporated in the pars distalis. Thus the pars tuberalis is the only part which has not attained approximately its adult situation.

STAGE VIII. *G.L.* 15 *mm., new-born* (*pouch fœtus* 5′ 97). — This stage shows a further advance in the process of breaking up of the solid walls of the hypophysis into lobules. In its main features the hypophysis closely resembles that of the preceding stage. The proximal lobe is much less distinct, its median portion being only represented by horizontal clefts (L., fig. 26) with a thin epithelial floor. Its lateral extensions (fig. 25, L.P.L.) are, however, considerably enlarged, and extend both anteriorly and posteriorly beyond their point of attachment, as hollow structures lying dorso-laterally to the main lobe (fig. 25, L.P.L.).

Ingrowths of connective tissue have broken up the walls of the anterior half of the distal lobe into rounded lobules (fig. 25), making the whole of the pars distalis appear less compact and less uniform than in preceding stages.

The infundibular process is rounded or slightly triangular in transverse section. It narrows to a definite stalk, connecting it with the diencephalic floor. There is a small amount of connective tissue between the infundibular process and the pars buccalis.

A remnant of the duct persists, and a thinning of the cartilage below the hypophysis marks the site of its perforation by the duct.

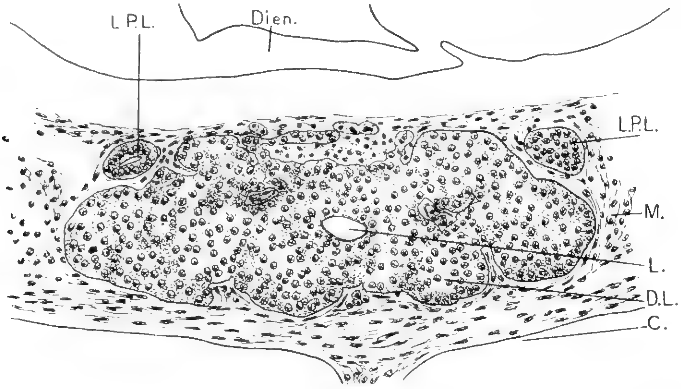

FIG. 25.—Stage VIII. *Trichosurus vulpecula* (5′ 97). Transverse section through anterior portion of distal lobe. Sl. 3–5–2.

C., cartilage ; D.L., distal lobe ; Dien., diencephalic floor ; L., lumen ; L.P.L., later expansions of proximal lobe ; M., mesenchyme.

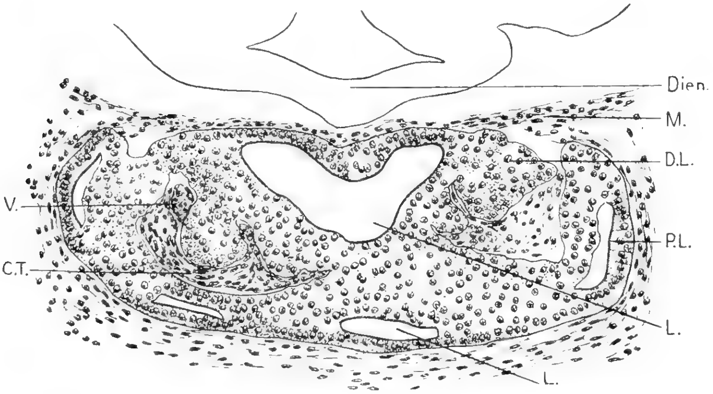

FIG. 26.—Stage VIII. *Trichosurus vulpecula* (5′ 97). Transverse section through proximal and distal lobes. Sl. 3–5–7.

C.T., connective tissue ; D.L., distal lobe ; Dien., diencephalic floor ; L., lumen ; M., mesenchyme ; P.L., proximal lobe ; V., blood-vessel.

STAGE IX. *Pouch fœtus G.L.* 17 *mm., and pouch fœtus G.L.* 17·5 *mm.*—The pars buccalis is now converted into a relatively compact structure, *i.e.* there is little indication externally of subdivision into lobes. The proximal lobe is, however, still represented in the middle line by a small, horizontal cleft, while the lateral wings are still further enlarged.

There is a considerable main lumen, which is restricted to the posterior half of the pars buccalis. The walls of the pars distalis consist of masses of cells more or less completely split up into lobules, separated by connective tissue carrying blood-vessels. The pars juxta-neuralis (infundibularis) consists of a thin epithelial layer, lying close to the infundibular process, but separated therefrom by connective tissue.

The infundibular process closely resembles that of the preceding stage, and still contains a well-marked lumen.

Remnants of the duct are present, and the point of perforation of the cartilage is still clear in one embryo.

STAGE X. *Pouch fœtus, H.L.* 11 *mm., and pouch fœtus H.L.* 12·5 *mm.*—The hypophysis has now attained its adult condition in regard to the general arrangement of the parts. Its subsequent development consists chiefly in histological differentiation in the various regions.

The pars buccalis (fig. 27) is clearly differentiated into pars distalis and pars juxta-neuralis, including infundibular (P.I.) and tuberal (P.T.) portions. The latter has now assumed its definitive position lying between the pars distalis and the diencephalic floor (T.C.), but is as yet restricted to the region anterior and lateral to the hypophysial stalk (figs. 27 and 28, P.T.).

The bulk of the organ is constituted by a compact pars distalis derived from the ventral, antero-, and postero-ventral walls of the pars buccalis of earlier stages. This is continuous on its dorsal side with the thin layer of epithelium constituting the infundibular portion of the pars juxta-neuralis (P.I.) and forming the roof of the residual lumen (L.) which forms a cup-shaped cleft surrounding the infundibular process. (Compare figs. 27 and 28, L.) There is a relatively small portion of the pars tuberalis (P.T.) in the median line, but on either side of the hypophysial stalk it has attained considerable dimensions (fig. 28, P.T.).

The pars distalis consists of a compact mass of solid cords of cells, many of which are outlined and separated from each other by strands of connective tissue which can be traced inwards from the sheath surrounding the pars buccalis. The nuclei of the cells of the pars distalis are spherical and deeply stained. The cytoplasm of the majority of the cells is stained faintly blue, but there are also a number of cells whose cytoplasm is stained a distinct reddish colour. These red cells appear to correspond with the chromophilic cells described in the hypophysis by histologists. They appear in this stage for the first time in Trichosurus, and, as will be seen from fig. 27, are most numerous in the posterior portion of the pars distalis. They appear in greater numbers and show their peculiar staining capacity in a more marked degree in the later stages of Dasyurus and Phascolarctos.

The infundibular portion of the pars juxta-neuralis (P.I.) consists of a thin layer of epithelium closely investing the pars neuralis on its anterior, ventral, and lateral surfaces, but leaving its postero-dorsal face exposed. In transverse sections this layer forms about three-fourths of a circle, surrounding the infundibular process, and also forms both walls of the dorsolateral horns of the crescentic residual lumen (fig. 28). It is slightly thickened in the region where it joins the lateral masses of the pars distalis.

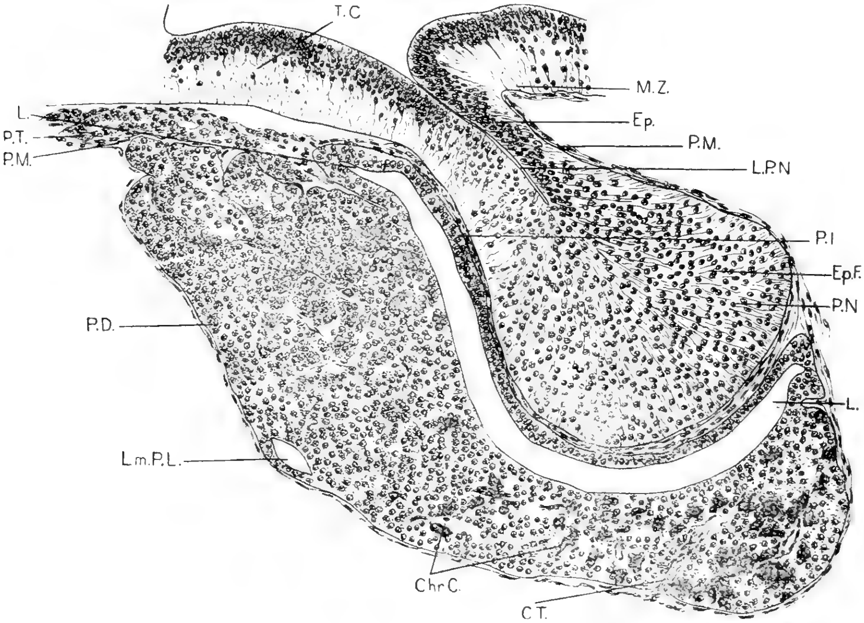

Fig. 27.—Stage X. *Trichosurus vulpecula* (H.L. 12·5 mm.). Median longitudinal section through hypophysis. Sl. 11-1-5.

C.T., connective tissue; Chr.C., chromophilic cells; Ep., ependyma; Ep.F., ependymal fibres; L., lumen; L.P.N., lumen of pars neuralis; Lm.P.L., remnant of lumen of proximal lobe; M.Z., marginal zone; P.D., pars distalis; P.I., pars infundibularis; P.M., pia mater; P.N., pars neuralis; P.T., pars tuberalis; T.C., tuber cinereum.

At its anterior extremity, the pars infundibularis is prolonged into a pocket-like diverticulum, projecting towards the pars tuberalis and lying between the tuber cinereum and the pars distalis (fig. 27, L.). The epithelium of the pars juxta-neuralis consists of two or three layers of cells with very darkly staining nuclei.

The pars tuberalis is the direct derivative of the enlarged lateral portions of the proximal lobe of earlier stages. The proximal lobe is no longer complete, but portions of it remain. A small cleft on the ventral side of the pars distalis (fig. 27, Lm.P.L.) represents the remnant of its median cavity, whilst the tubules of the pars tuberalis are connected on one side at least with the pars distalis by a solid cord of cells which runs round the side of the pars distalis and joins it ventro-laterally. This is clearly the remnant of the hollow, crescent-shaped portion of the proximal lobe. Its dorso-lateral wings have enlarged markedly, grown up towards the brain and branched, so that they now form a series of thin-walled tubules which have penetrated between the pars distalis and the tuber cinereum. Anterior to the pocket-like diverticulum of the pars infundibularis, they actually reach the middle line; in the region of the diverticulum, they lie on either side of it; posterior to it, they lie lateral to the stalk of the pars neuralis (see fig. 28, P.T., etc.). The walls of the tubules consist of two or three layers of epithelial cells whose nuclei are deeply stained, while their cytoplasm in its staining capacity resembles the lightly stained cells of the pars distalis.

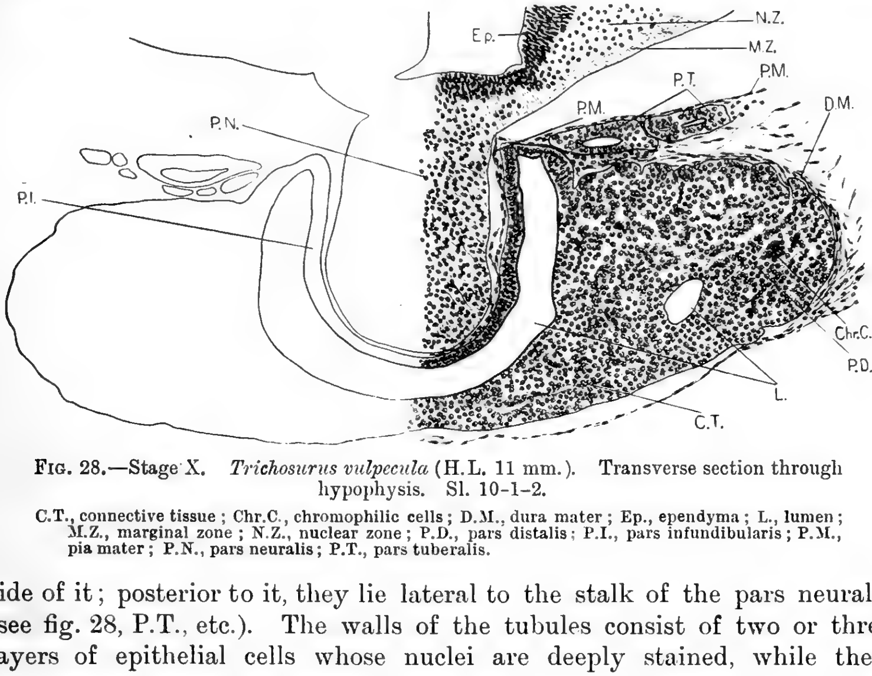

Fig. 28.—Stage X. *Trichosurus vulpecula* (H.L. 11 mm.). Transverse section through hypophysis. Sl. 10-1-2.

C.T., connective tissue; Chr.C., chromophilic cells; D.M., dura mater; Ep., ependyma; L., lumen; M.Z., marginal zone; N.Z., nuclear zone; P.D., pars distalis; P.I., pars infundibularis; P.M., pia mater; P.N., pars neuralis; P.T., pars tuberalis.

The infundibular process is connected with the floor of the diencephalon by a relatively stout stalk. It is enlarged distally (fig. 27, P.N.), and contains a small lumen in the 12·5 mm. (H.L.) embryo (fig. 27, L.P.N.), but is solid in the 11 mm. (H.L.) embryo. The ependymal layer of the diencephalic floor is continuous with that of the infundibular stalk, and extends a short way into the substance of the pars neuralis, the bulk of which is made up of fibres and scattered cells closely resembling those of the nuclear (mantle) zone of the diencephalic wall (fig. 28, N.Z.).

The connective tissue separating the nervous and non-nervous portions of the hypophysis exhibits a tendency to penetrate into the tissues of the pars neuralis, but has not as yet done so to any marked extent, nor is there any sign of blood-vessels entering the nervous lobe at this stage.

STAGE XI. *Pouch fœtus G.L. 4 cm., H.L. 20 mm.*—The hypophysis in this fœtus closely resembles that of the preceding stage in form and general relations of the parts. It has increased considerably in size, both pars buccalis and pars neuralis being much larger than in the preceding stage, whilst the process of histological differentiation has made considerable progress.

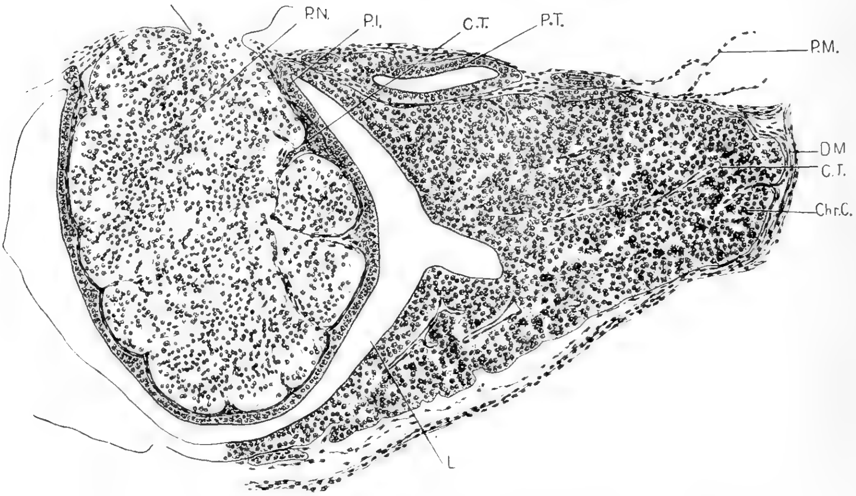

FIG. 29.—Stage XI. *Trichosurus vulpecula* (H.L. 20 mm.). Transverse section through hypophysis. Sl. 23-3-5.

C.T., connective tissue; Chr.C., chromophilic cells; D.M., dura mater; L., lumen; P.I., pars infundibularis; P.M., pia mater; P.N., pars neuralis; P.T., pars tuberalis.

The number of chromophilic cells (fig. 29, Chr.C.) in the pars distalis has increased considerably, especially in the posterior portion of that part. Moreover, these cells are now more clearly differentiated from the chromophobic cells, their cytoplasm staining a bright red, while that of the chromophobic cells is stained faint blue.

The pars tuberalis (P.T.) has increased to such an extent that it has spread into the narrow space between the pars buccalis and the diencephalic floor so as to completely encircle the hypophysial stalk (*cf.* fig. 13). Thus it comes to have the form described by Tilney (59), viz. that of a diaphragm lying between the pars distalis and the diencephalon, with the stalk of the pars neuralis passing through its aperture.

It is in the pars neuralis (fig. 29, P.N.) and the pars infundibularis (P.I.) that we find the most marked advance on the preceding stage. The distal portion of the pars neuralis has expanded considerably, while its attachment to the diencephalic floor is relatively slender. The connective tissue between these two portions has grown actively and penetrated into the tissues of the pars neuralis, breaking it up more or less completely into lobules (fig. 29, P.N.). Furthermore, it tends to carry in with it some of the cells of the pars infundibularis, so that whilst the outer side of that layer, *i.e.* that bordering the residual lumen, is still perfectly regular, the inner margin is irregular, the cells here and there penetrating a short way into the tissues of the pars neuralis. Over the greater part of its extent, however, the pars infundibularis simply consists of a single layer of epithelium.

The pars neuralis still contains a large number of cells, but its fibrous constituents have become much more conspicuous.

Capillaries do not appear as yet to have penetrated into the pars neuralis; indeed, the pars buccalis is not yet richly vascularised.

The relations of the meninges are as follows (figs. 13 and 29, D.M., P.M.):—The dura mater (D.M.) forms a connective tissue capsule for the whole of the pituitary body. The main portion passes straight round on the ventral surface of the whole structure, thus enclosing it within the same membrane with the brain. At the anterior and posterior ends of the pituitary a considerable thickness of the dura mater is reflected over the dorsal surface of the pars buccalis, but this layer extends in towards the hypophysial stalk through only a few sections. In the remainder of the pars distalis a few fibres pass round on to the dorsal surface of the lobe, and even penetrate inwards to the middle line, except in the region of the hypophysial stalk. The pia mater (P.M.) constitutes a very thin layer covering the brain and passing continuously over the surface of the pars neuralis, lying between it and the pars juxta-neuralis and penetrating into the substance of the nervous lobe in the manner already described. The pia mater also completely invests the tubules of the pars tuberalis and penetrates between them.

Phascolarctos cinereus.—In many respects the development of the hypophysis of Phascolarctos closely resembles that of Trichosurus. It shows, however, one or two points of interest, notably the persistence of Seessel's pocket. I have accordingly described such stages in development as serve to illustrate these points.

Stage I. *G.L. 4 mm.*—The hypophysis is already developed as a wide pouch, fairly deep posteriorly where it is closed, but shallow and widely open in its anterior portion. It is very noticeably bilobed (*cf.* fig. 30), the lateral angles being thick-walled, while in the middle line the epithelium is much thinner.

There is a small remnant of the oral plate, posterior to which lies Seessel's pocket, in the form of a short, rounded diverticulum of the fore-gut, whose tip lies between the floor of the hypophysis and the wall of the gut.

No infundibular process is present, and from the fact that the diencephalon is still unclosed it is evident that the hypophysis appears at an earlier stage in Phascolarctos than it does in Trichosurus.

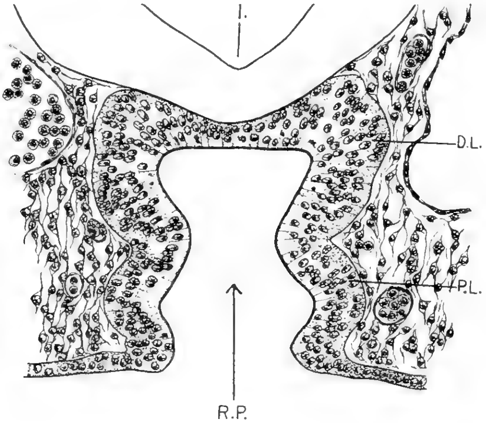

FIG. 30.—Stage II. *Phascolarctos cinereus.* Transverse section through Rathke's pouch. Sl. 5–11–2. Note the markedly thickened lateral angles of Rathke's pouch.

D.L., distal lobe ; I., infundibular recess ; P.L., proximal lobe ; R.P., Rathke's pouch.

STAGE II. *G.L.* 7·5 *mm.*—In this stage we find a remarkable development of the pre-oral gut.

The hypophysis forms a deep pouch, which is differentiated anteriorly into proximal and distal lobes by a well-marked equatorial constriction.

The oral plate is ruptured ventrally, but a considerable portion of it persists dorsally, being inserted at the apex of Rathke's pouch and separating this from the pre-oral gut. The oral plate is slightly convex on its posterior face, so that in the sections immediately behind that which passes through its full expanse, the convex projection of the oral plate is cut and appears in section as a sort of plug (cf. *Perameles nasuta,* (13 VII. 05), fig. 5). The section represented in fig. 31 passes through almost the complete expanse of oral plate dorsally, and shows the ventral portion of the oral plate projecting into Seessel's pocket.

Seessel's pocket forms a vesicle of considerable dimensions (figs. 31 and 32, S.P.) opening by a small duct immediately posterior to the oral plate. It is of the same depth as the hypophysis, and its distal wall is in actual contact with the diencephalic floor (fig. 32, Dien.), whilst it also, like Rathke's pouch, shows an indication of an equatorial constriction.

Its walls are thick, and are composed of a regular, columnar epithelium. Histologically it is, in fact, indistinguishable from the hypophysis. The anterior extremity is pressed against the posterior wall of Rathke's pouch, which is thereby indented slightly in the middle line.

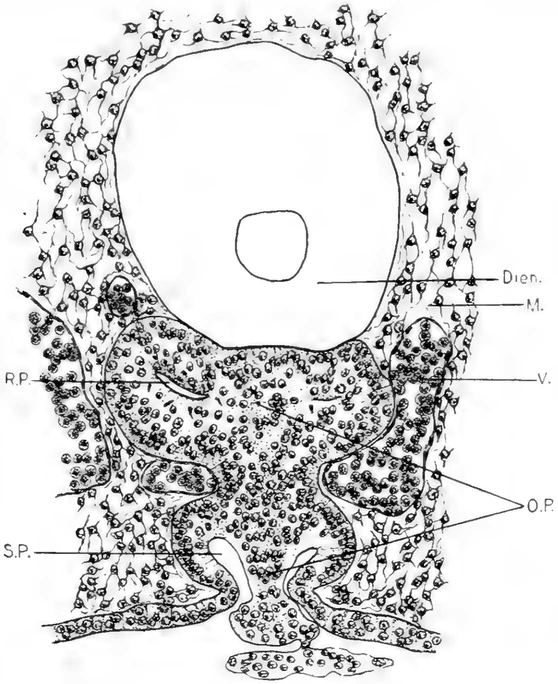

Fig. 31.—Stage II. *Phascolarctos cinereus.* Transverse section through hypophysis, Seessel's pocket, and the oral plate. Sl. 5–1–5.

Dien., diencephalic floor; M., mesenchyme; O.P., oral plate; R.P., Rathke's pouch; S.P., Seessel's pocket; V., blood-vessel.

A rounded depression in the diencephalic floor represents the primitive infundibular recess, but no infundibular process is yet differentiated.

The notochord in this embryo reaches actually to the level of the posterior wall of Seessel's pocket, but is not in actual contact therewith.

Stage III. *G.L.* 9 *mm.*—The hypophysis has increased considerably in size, but is still widely open anteriorly and consists of proximal and distal lobes.

A definite infundibular process is present in the form of a short conical outgrowth of the diencephalic floor (fig. 34, I.P.). This is in intimate contact with both Rathke's pouch and the pre-oral gut (*vide infra*).

Remnants of the oral plate are present in the form of a solid, knob-like mass of tissue lying outside the pouch and a small portion lying free in the lumen of Rathke's pouch.

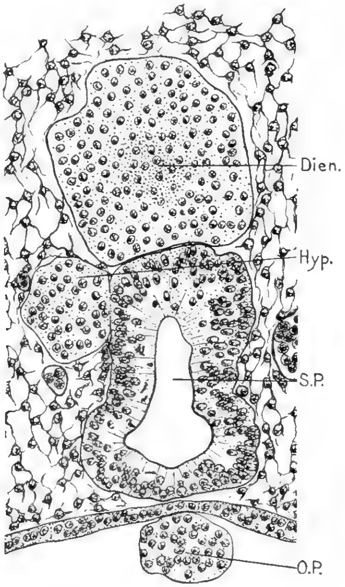

FIG. 32.—Stage II. *Phascolarctos cinereus.* Transverse section through Seessel's pocket. Sl. 5–1–2.

Dien., diencephalic floor; Hyp., posterior wall of one of lateral caudal lobes of the hypophysis; O.P., oral plate; S.P., Seessel's pocket.

Seessel's pouch has lost its opening into the gut and simply forms a closed, hollow vesicle, in intimate contact with Rathke's pouch, but having no communication with it. It is elongated in the antero-posterior direction, and is divided as before into two lobes, whose cavities are now completely separate from each other. Its walls consist, as before, of regular columnar epithelial cells, and resemble those of the hypophysis so closely that in the posterior region, where Rathke's pouch is bifid and Seessel's pocket lies between the two halves, there appear to be three precisely similar lobes of the hypophysis (fig. 34).

Anterior to the point of bifurcation of Rathke's pouch, the pre-oral gut is excluded from contact with the brain floor. It is constricted in this region and has no lumen, but widens again anteriorly and has a small, cleft-like cavity (fig. 33, S.P.). At one point (fig. 33) it is partially separated from Rathke's pouch by a small blood-vessel, but elsewhere the walls of the two structures are in close contact.

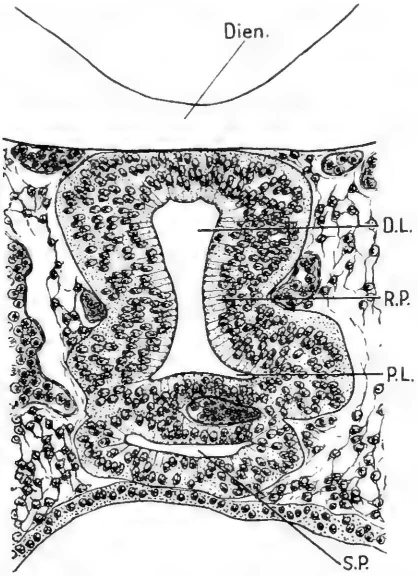

Fig. 33.—Stage III. *Phascolarctos cinereus.* Transverse section through Rathke's pouch and Seessel's pocket. Sl. 4–4–3.

D.L., distal lobe; Dien., diencephalic floor; P.L., proximal lobe; R.P., Rathke's pouch; S.P., Seessel's pocket.

Stage IV. *G.L.* 11 *mm.*—This stage shows the beginning of the process of formation of tubules. Unfortunately, the series is broken in the region of the hypophysis, so that it is impossible to give a full description.

The walls of the distal lobe in Phascolarctos, instead of undergoing subdivision by ingrowths of connective tissue, as occurs in Trichosurus, proliferate actively and give off numerous outgrowths which penetrate into the connective tissue surrounding the hypophysis (fig. 35). The proximal lobe is much curved (fig. 35, P.L.), so that its lateral margins, which are enlarged and prolonged both anteriorly and posteriorly, lie dorso-lateral to the main lobe (L.P.L.).

Seessel's pocket is still present, and forms a closed vesicle with a small, cleft-like lumen. It is much flattened, and is applied to the ventral surface of the hypophysis (S.P.).

STAGE V. *G.L.* 12·25 *mm.*—In this stage the process of conversion of the simple buccal pouch into the compact glandular lobe of the adult is proceeding.

The posterior portion of the pars buccalis has fairly uniform thick walls and a large lumen. Its dorsal wall is indented by the infundibular process. The walls of the anterior portion of the main lobe are produced into numerous outgrowths, some of which now possess a small lumen. The spaces between these processes are filled with connective tissue in which as yet there are few blood-vessels. The proximal lobe shows the same relations as in the preceding stage. Its walls are produced into a few short solid processes.

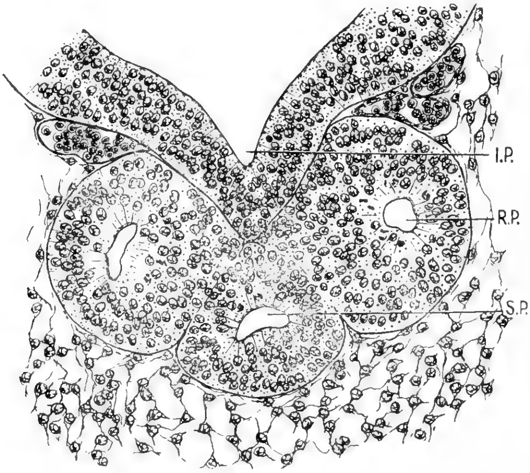

FIG. 34.—Stage III. *Phascolarctos cinereus* (9 mm.). Transverse section through posterior portion of Rathke's pouch and Seessel's pocket. Sl. 4–2–7.

I.P., infundibular process ; R.P., Rathke's pouch ; S.P., Seessel's pocket.

The infundibular process is short and conical, and a certain amount of connective tissue has penetrated between it and the pars buccalis, but has not yet reached the middle line.

Seessel's pocket forms a closed vesicle in the same position as in the preceding stage. At its posterior end it increases in dorso-ventral extent, forming a rounded vesicle with thick walls and a small lumen. Anteriorly it becomes flattened and widens out so as to form a thin plate with a cleft-like lumen, while its dorsal wall is confluent with the substance of the rest of the pars distalis. Its lumen, however, does not communicate with that of the hypophysis.

The pre-oral gut therefore now forms an apparent part of the hypophysis, from which it can only be distinguished by a slight difference in staining capacity and by the fact that its lumen, unlike any portion of the main lumen of the pars buccalis, is completely isolated.

A small remnant of the hypophysial duct is present in this stage, lying outside the cartilage of the skull, but there is no trace of it within the skull, nor any indication of perforation of the cartilage.

Fig. 35.—Stage IV. *Phascolarctos cinereus* (11 mm.). Transverse section through proximal and distal lobes of hypophysis. Sl. 6-1-10.

C.T., connective tissue; D.L., distal lobe; Dien., diencephalic floor; L., lumen; L.P.L., lateral enlargement of proximal lobe; P.L., proximal lobe; S.P., Seessel's pocket.

Stage VI. *GL.* 13·5 *mm.: longitudinal and transverse series.*—In general form the hypophysis in this stage closely resembles that of the preceding, but the process of tubule-formation has increased so far as to convert the distal portion of the pars buccalis into a compact mass of tubules separated from each other by connective tissue (fig. 36).

The minute structure of the pars buccalis differs considerably in this stage from that of any stage of Trichosurus. Fig. 36, which represents a longitudinal section about 6–8 sections (15μ) from the middle line, shows this structure. In place of the solid, irregular, and ill-defined lobules of Trichosurus, the cells are arranged in a series of relatively definite tubules (T.), some of which possess a lumen (L.i.), while the outline of these tubules, instead of being indicated simply by a cleft, is marked by a definite though fine line, representing a basement membrane of the cells constituting the walls of the tubules.

The infundibular process is narrow and pointed, and is separated from the pars buccalis by connective tissue, which has penetrated to the middle line in some places.

Seessel's pocket can be readily identified, and has undergone no change since the preceding stage.

STAGE VII. *G.L.* 16·5 *mm.: new-born.*—This stage shows little advance on the preceding. The pars distalis has become more compact, its tubules having increased in size and number and become pressed more closely together.

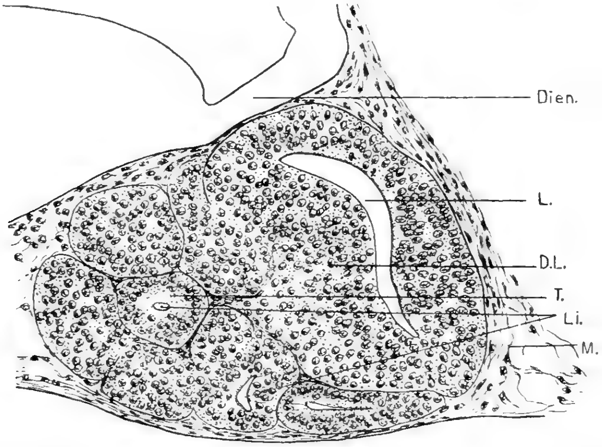

FIG. 36.—Stage VI. *Phascolarctus cinereus* (13·5 mm.). Longitudinal section through hypophysis. Sl. 12–2–7.

D.L., distal lobe; Dien., diencephalic floor; L., lumen of pars distalis; L.i., lumina of tubules; M., mesenchyne; T., tubule of pars distalis.

The lateral portions of the proximal lobe have grown round the main body of the pars buccalis, and now lie almost entirely dorsal thereto.

Seessel's pocket is clearly recognisable. As before, it is dorso-ventrally compressed and wide anteriorly, while posteriorly it forms a vesicle triangular in section and having a small lumen.

STAGE VIII. *Pouch fœtus G.L.* 17 *mm.*—A noticeable feature of this stage is the very rich supply of capillaries to the pars distalis. They occupy the spaces between the tubules, and have also penetrated between the infundibular process and the pars buccalis. A pair of small vessels, symmetrically disposed, enter the pars distalis on its ventral surface. The distal lobe in this, as in other similar stages of Phascolarctos and in Trichosurus (*cf.* fig. 22), is produced into two large wing-like processes, and the blood-vessels enter on the under side of these and penetrate deeply into the tissue of the lobe. Another vessel enters in the middle of the posterior wall of the pars buccalis.

The lateral prolongations of the proximal lobe are now branched (fig. 37), and form a collection of tubules lying dorsal and dorso-lateral to the rest of the pars buccalis. These constitute the primordium of the pars tuberalis (P.T.).

It is not possible in this embryo to identify Seessel's pocket with certainty.

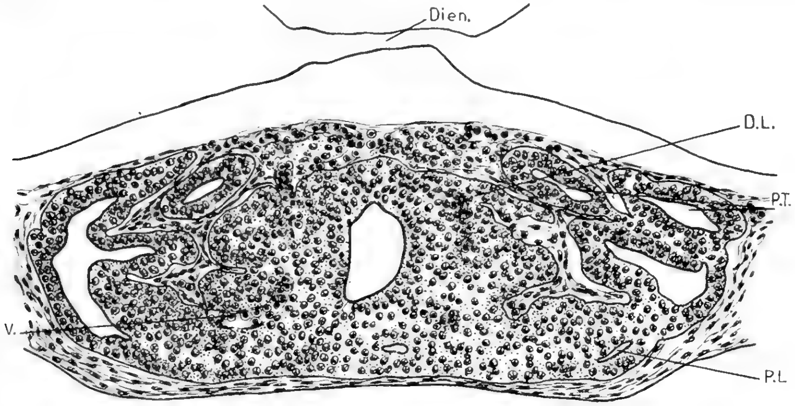

FIG. 37.—Stage VIII. *Phascolarctos cinereus* (17 mm. G.L.). Transverse section through proximal and distal lobes of hypophysis, to show the branched lateral expansions of the former (primordium of pars tuberalis). Sl. 3-2-8.

D.L., distal lobe ; Dien., diencephalic floor ; P.L., proximal lobe ; P.T., primordium of pars tuberalis ; V., blood-vessel.

STAGE IX. *Pouch fœtus G.L.* 18 *mm.*—The series is broken in the region of the hypophysis, but it is worth noting that Seessel's pocket is clearly recognisable and has exactly the same form and relations as in Stage VII.

STAGE X. *Pouch fœtus G.L.* 18·5 *mm.*, *H.L.* 9·5 *mm.*—This stage shows in general little advance on the preceding. The pars buccalis is somewhat more compact, its tubules being closely pressed together. In this stage for the first time chromophilic cells can be identified in the pars distalis. They are very brightly stained, and are most numerous in the posterior region.

The lateral wings of the proximal lobe are slightly less branched than in the preceding stage.

The infundibular process is small relatively to the size and advanced condition of the pars buccalis. It forms a simple, thin-walled diverticulum with a somewhat constricted neck.

It is not possible to identify Seessel's pocket with absolute certainty in this stage. A small, flattened structure, closely resembling Seessel's pocket in other embryos, is present, but is in such close relation to the proximal lobe that it is impossible to draw an absolute distinction between the two structures.

Stage XI. *Pouch fœtus G.L.* 24 *mm., H.L.* 11·5 *mm.*—The hypophysis has increased markedly in size. The tissue of the pars distalis has unfortunately shrunk away somewhat from the connective tissue, which now forms an interlacing network penetrating throughout the substance of the pars distalis. The appearance of compactness is accordingly destroyed.

Fig. 38.—Stage X. *Phascolarctos cinereus* (H.L. 11·5 mm.). Transverse section through pars distalis. Sl. 10–1–3.

C.T., connective tissue ; Chr.C., chromophilic cells ; L., lumen ; P.I., pars infundibularis ; S.P., Seessel's pocket.

The pars distalis consists of numerous rounded lobules, all of which have now lost their lumina. The cells are very clearly differentiated into chromophilic (Chr.C.) and chromophobic types, the former showing up as clear bright-red patches in the tissue (represented black in figures).

The pars tuberalis forms a collection of branched tubules lying between the body of the pars distalis and the diencephalic floor anterior to the infundibular process. It is still connected by a cell cord with the ventral side of the pars buccalis.

The infundibular process has increased somewhat in size, but is still relatively small, and is hollow. Its walls have increased in thickness to a slight extent.

Seessel's pocket can be clearly identified in the posterior portion of the hypophysis. Its caudal portion is free, and is separated from the substance of the pars buccalis by a definite connective tissue sheath. Its caudal extremity retains its original form and relations, lying partly ventral to and between the two halves of the posterior extremity of the pars buccalis. The anterior portion of Seessel's pocket fuses with the ventral side of the pars distalis and becomes absolutely indistinguishable from it (fig. 38, S.P.).

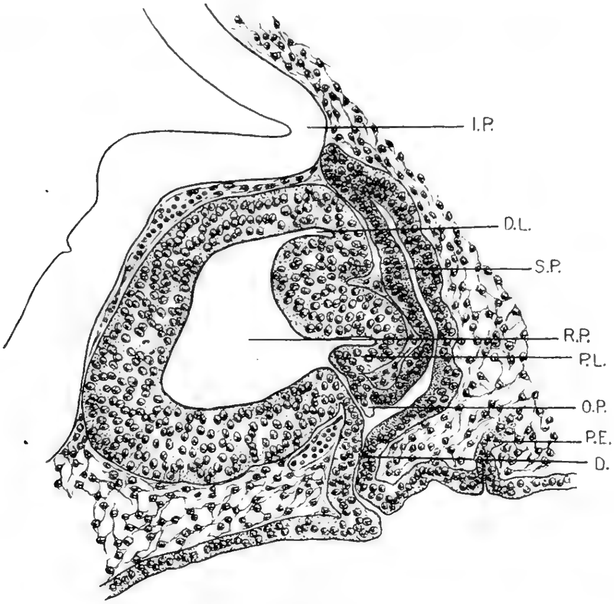

Fig. 39.—Stage I. *Phascolomys mitchelli* (G.L. 8·5 mm.). Longitudinal section through hypophysis and Seessel's pocket. Sl. 8–2–8.

D., duct; D.L., distal lobe; I.P., infundibular process; O.P., remnant of oral plate; P.E., proliferation of entoderm; P.L., proximal lobe; R.P., Rathke's pouch; S.P., Seessel's pocket.

Phascolomys mitchelli.—In Phascolomys also Seessel's pocket persists and forms part of the hypophysis, but certain points of difference may be noted between the development in this form and in Phascolarctos.

Stage I. (*a*) *G.L.* 9 *mm.*—Rathke's pouch is already established, and closely resembles that of Phascolarctos, Stage II., having well-marked proximal and distal lobes. It is widely open in its mid-region, but is closed at both anterior and posterior ends.

No definite infundibular process is present.

The distal lobe of Rathke's pouch is bifid at its caudal extremity, and lying between the two halves is a well-developed Seessel's pocket, which in this instance differs considerably from Rathke's pouch in its staining capacity. It is a hollow, conical structure, its walls being composed of a regular epithelium, the cells staining more darkly than those of the hypophysis. It runs forwards, ventral to the hypophysis and in the middle line, for a short distance, and then twists to one side. In correlation with this asymmetry, the remnant of oral plate is displaced from its normal plane and lies obliquely, forming, as usual, the partition wall between Seessel's pocket and the hypophysis.

(*b*) *G.L.* 8·5 *mm.*—The hypophysis of this embryo differs from that described above mainly in the fact that the opening of Rathke's pouch is reduced to a narrow duct (fig. 39, D.).

Seessel's pocket (S.P.) has retained its original relations, but the elongation of the duct has taken place ventral to the opening of the pre-oral gut, *i.e.* between the base of that structure and the pharyngeal roof, so that there is a relatively long and narrow duct (D.) which is common to both Seessel's pocket and the hypophysis. A small remnant of oral plate (O.P.) can still be recognised attached to the posterior wall of Rathke's pouch, at its point of junction with Seessel's pocket.

It may be noted that in both the 8·5 mm. and the 9 mm. embryos there is a small entodermal outgrowth (fig. 39, P.E.) posterior to Seessel's pocket.

This structure is a thin tubular diverticulum, and closely resembles the hypophysial duct. It has a minute lumen opening into the pharynx, is very short, and tapers to a blind extremity. I have not observed the occurrence of this structure in other species, unless it corresponds with the entodermal proliferation shown in fig. 17 of Trichosurus, Stage IV.

In a later stage of Phascolomys (15·5 mm. G.L.) there is possibly a trace of it still indicated by the fact that the cartilage is perforated at two points. Through the anterior of these perforations the hypophysial duct passes, whilst on the pharyngeal side of the second there is a small diverticulum, possibly representing a remnant of the structure described above.

In its subsequent stages the hypophysis of Phascolomys very closely resembles that of Phascolarctos. The walls of the pouch grow out as solid processes which become pressed together to form the compact pars distalis. The origin of the pars tuberalis is exactly the same as in Phascolarctos.

Seessel's pocket is still recognisable in an embryo of 17·5 mm. G.L., but no later stages are available.

In Phascolomys the extremely rich vascular supply to the pars distalis in stages of 15·5 mm. G.L. and 17·5 mm. G.L. is noteworthy, and is even more marked than in Phascolarctos at similar stages.

Dasyurus viverrinus.—A series of Dasyurus stages, from the establishment of Rathke's pouch to a stage in which the infundibular process has become solid, is available, and from study thereof it is evident that the development of the hypophysis in Dasyurus closely resembles that process in Trichosurus. With regard to the process of conversion of the simple pouch into the glandular lobe of the adult, Dasyurus seems to be in some respects intermediate between Trichosurus and Phascolarctos, for both outgrowth of solid processes and ingrowth of connective tissue play a part in the elaboration of the gland. After the establishment of Rathke's pouch and its subdivision into proximal and distal lobes, its walls become considerably thickened and produced into short rounded processes. At the same time the walls are subdivided by ingrowths of connective tissue so that the two processes occur contemporaneously.

A definite infundibular process appears relatively early in Dasyurus, viz. in a stage corresponding approximately to Trichosurus, Stage IV., where it forms a relatively long, conical diverticulum.

There is no trace of Seessel's pocket in Dasyurus subsequent to the last stage described in Section I. of this paper.

From the more complete series of late stages in Dasyurus it is possible to make out some points, more particularly with regard to the infundibular process, which are not shown in the Trichosurus series. I propose, therefore, to give a brief description of the three oldest stages of *Dasyurus viverrinus.*

STAGE H. *Pouch fœtus, G.L.* 13·5 *mm., H.L.* 8 *mm.*—In the general arrangement of the parts, this stage closely resembles Trichosurus, Stage X.

From the longitudinal section (fig. 40) it will be seen that the pars buccalis extends further round on to the posterior side of the infundibular process than it does in Trichosurus, so that only a small portion of the neck of the latter is exposed. The residual lumen is narrow and cup-shaped, following the outline of the pars neuralis, from which it is separated by a thin epithelial layer, the pars infundibularis (P.I.), which in most places is only one cell thick. A thin layer of connective tissue lies between the pars infundibularis and the pars neuralis.

In the transverse section of this stage the differentiation of two types of cells in the pars distalis is very well marked, the cytoplasm of the chromophilic cells, which are still few in number, staining a bright, clear red. In the longitudinal section figured, however, there are few chromophilic cells, and these are not markedly differentiated.

The pars tuberalis forms a thin sheet of much-flattened tubules (P.T.), lying between the diencephalic floor and the pars distalis (P.D.), and invested by a thin layer of connective tissue. A small amount of this section of the pars buccalis has penetrated to the middle line anterior to the hypophysial stalk, but the greater part of it lies laterally thereto. The cellular connection of the pars tuberalis with the ventral side of the pars distalis is lost, but its origin from the proximal lobe is clear from earlier stages of Dasyurus.

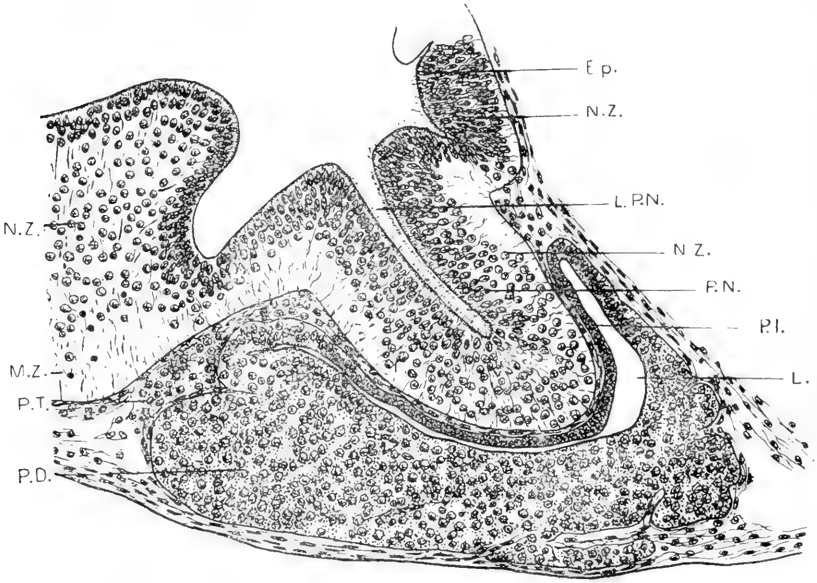

Fig. 40.—Stage H. *Dasyurus viverrinus.* Median longitudinal section through hypophysis. Sl. 3-1-12.

Ep., ependyma; L., lumen; L.P.N., lumen of pars neuralis; M.Z., marginal zone; N.Z., nuclear zone; P.D., pars distalis; P.I., pars infundibularis; P.N., pars neuralis; P.T., pars tuberalis.

The infundibular process is thick and bluntly pointed, and contains a well-defined, narrow cavity (L.P.N.). The walls of the process contain a large number of cells. In the region of the neck these are restricted to the inner half of the wall, *i.e.* that bordering the lumen, whilst the outer part is exclusively composed of fibres. The cells of the innermost layer constituting the ependyma are apparently ciliated, and are continuous with the ependymal cells lining the brain vesicles. They are not histologically different from the remaining cells which constitute the nuclear or mantle zone (N.Z.). In the distal half of the infundibular process the nuclei of the mantle zone extend out to the periphery, leaving no distinct marginal zone, though they are less closely packed in this region.

STAGE I. *Pouch fœtus, G.L.* 17 *mm., H.L.* 10 *mm.*—The only change which has occurred in the pars buccalis consists in the increase in the number of the chromophilic cells, which are particularly numerous in the posterior portion of the pars distalis.

The infundibular process has thickened, but its cavity still persists. The ependyma cells can be more readily distinguished from the cells of the nuclear zone, and form a layer, several cells in thickness, lining the lumen.

Fibres can be traced from the internal limiting membrane, passing outwards amongst numerous nuclei scattered through the thickness of the wall. In this stage, as in the last, it is only in the neck of the pars neuralis that a definite marginal zone, consisting of fibres only, can be recognised. In this stage, however, the number of cells is less in comparison with the thickness of the wall than in the preceding, and the fibres are correspondingly more conspicuous.

In the transverse series of this stage the lumen of the infundibular process is already obliterated, but in other respects it shows no difference from the longitudinal series.

STAGE J. *Pouch fœtus, G.L.* 20 *mm., H.L.* 12·5 *mm.*—The pars buccalis shows no advance on the preceding stage.

The infundibular process (fig. 41), on the other hand, has undergone considerable changes. The whole structure is considerably enlarged, and now has a round, expanded distal portion and a slightly constricted neck. The cavity is obliterated, but its site is indicated by an axial mass of ependymal cells (Ep.). The number of cells in the infundibular process as a whole is relatively, at least, much smaller, so that the pars neuralis now appears to consist of an interlacing mass of fibres with nuclei scattered amongst them. These cells are not restricted to any one portion of the structure, but, apart from the concentration of ependymal cells at the line of closure of the lumen, they are uniformly distributed, so that even in the region of the neck a marginal zone is no longer recognisable. On the other hand, in the region of the tuber cinereum, immediately anterior to the neck of the infundibular process, typical mantle and marginal layers are differentiated.

It thus appears that the infundibular process arises as a diverticulum of the diencephalic floor, whose walls undergo differentiation into ependymal, mantle (nuclear), and marginal zones similar to those of the brain wall.

Subsequently, however, the walls of the pars neuralis undergo modification, becoming more fibrous than those of the brain. As already seen in Trichosurus (Stage XI.), it later undergoes further changes due to the ingrowth of connective tissue and cells of the pars infundibularis.

Perameles nasuta.—Apart from details of no apparent importance, such as the differences in the shape of the hypophysis in some stages, the development of the pituitary body in Perameles closely resembles that of Trichosurus. The differentiation of proximal and distal lobes and the process of formation of glandular tissue follows the same course as in Trichosurus.

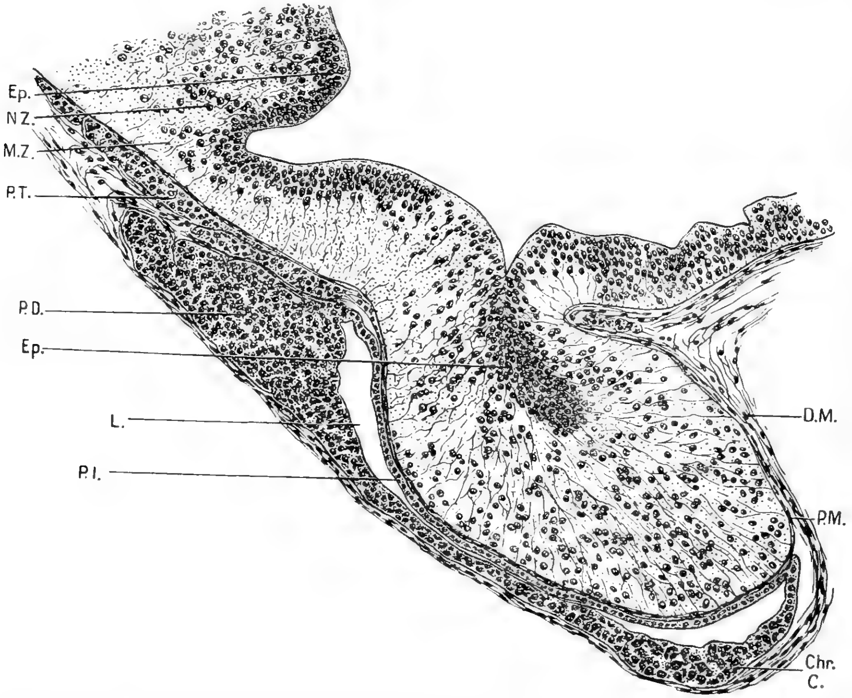

FIG. 41.—Stage J. *Dasyurus viverrinus.* Median longitudinal section through hypophysis. Sl. 1–2–7.

Chr.C., chromophilic cells; D.M., dura mater; Ep., ependyma; L., lumen; M.Z., marginal zone; N.Z., nuclear zone; P.D., pars distalis; P.I., pars infundibularis; P.M., pia mater; P.T., pars tuberalis.

It is interesting to note that, in spite of the marked development of Seessel's pocket in *Perameles nasuta* (13, VII. 05), Stage IV., described in Section I. of this paper, there is no trace of this structure in any subsequent stage.

The relations of the meninges to the various parts of the hypophysis in a Perameles pouch young of 35 mm. G.L., 18·5 mm. H.L., are precisely the same as in Trichosurus, Stage XI. (p. 212).

SUMMARY AND DISCUSSION.

I. *The Premandibular Somites, Prechordal Plate, and the Anterior End of the Notochord.*

It is not within the scope of the present paper to deal in any detail with the literature relating to the premandibular head cavities, which is discussed at greater length in relation to the development of the eye muscles in Marsupials by Elizabeth A. Fraser (12).

That the relatively small and irregular structures described in Section I. of this paper are in reality the precursors of the definitive premandibular head cavities described in later stages by E. A. Fraser (12) is evident from comparison with lower Vertebrates, more especially Selachians and Reptiles. In Selachians (Platt, 42, 43), the premandibular head cavities are structures of considerable size, and are connected with each other by a transverse canal (see fig. 42, Pm.B.). Both the premandibular head cavities and the connecting bridge are derived, according to Platt (42, 43), from an entodermal outgrowth from the fore-gut.

Oppel (40) describes the occurrence of premandibular head cavities and a connecting bridge in *Anguis fragilis.* These originate from a mass of entoderm cells to which he has given the name "præchordal Platte," situated between the wall of the fore-gut and the head of the chorda.

C. E. Johnson (25) describes the premandibular somites in an early stage of Chelydra (3·5 mm.) as consisting of a small group of cells arranged in a radiating manner around a central lumen (*cf.* figs. 3 and 4). These are connected by a bridge, the median portion of which forms part of a mass of cells arising from the anterior wall of the fore-gut. A similar mass of cells has been described as the point of origin of head cavities by Hoffmann (23).

Filatoff (10), Corning (7), Salvi (48), and Dorello (9), on the other hand, describe the origin of the premandibular cavities from the wall of the fore-gut itself.

The embryos of Perameles (Stage I., Section I.), Bettongia (Stage II., Section I.), and Macropus (Stage III., Section I.), described above, form a series of stages in which we can trace the origin of a pair of outgrowths clearly corresponding with the premandibular somites of Selachians and Reptiles, arising, as in lower Vertebrates, from a prechordal plate, and connected in Macropus by a transverse bridge.

This prechordal plate is not yet developed in a stage of Perameles preceding the first described in the present paper, but there is present in early stages of Perameles the massive protochordal plate described by Wilson and Hill (63). The protochordal plate from the first shows evidence of active growth power, and gives rise to the pre-oral gut (Seessel's pocket), and to the upper portion of the oral plate. It seems evident that it also gives rise to the prechordal plate in Perameles, for continuity is retained between that structure and the wall of the fore-gut derived from protochordal plate in Stage I. (fig. 1), and again between the prechordal plate and Seessel's pocket in Stage IV. (fig. 6).

The history of the protochordal plate has been fully described in the dog by Bonnet (6), who points out that here it gives rise not only to a portion of oral plate, but also to the "pre-oral entodermal pouch" and to mesoderm. He homologises the "interepithelial cell-mass" of Rex (47) with the protochordal plate, and points out that the difference in the various accounts of the development of the premandibular head cavities refer only to their mode of origin from the "interepithelial cell-mass."

The above account of Perameles agrees closely with that given by Bonnet (6). The pre-oral entodermal pouch of Bonnet (6) and Dorello (9), the interepithelial mass of Rex (47), the præchordal Platte of Oppel (40), the Zwischenplatte of Filatoff (10), as well as the unnamed mass of cells described by Platt (42, 43) and others as the point of origin of premandibular somites, all alike represent derivatives of the protochordal plate. Moreover, as the wall of the anterior angle of the fore-gut is also a derivative of the protochordal plate, the origin of premandibular somites directly from the fore-gut, as described by Corning (7) and Salvi (48), may readily be interpreted on the same lines, for in either case the ultimate source of the premandibular somites and their connecting bridge is the protochordal plate.

Attention may here be drawn to a possible interpretation of the structure described and figured by Selenka in Didelphys (55) under the name of "Gaumentasche." This structure he regards as the branched and hollow anterior end of the chorda. In a later paper (56) he states that he has observed a similar structure in the chick and the duck, as well as other Vertebrates. I have found no trace of such a branched gland as he describes in an embryo of *Didelphys virginiana* (8·5 mm. G.L.) in Prof. Hill's collection which I have examined. Selenka's fig. 16, plate xxx. (55), shows so close a resemblance to the condition described and figured in *Perameles nasuta* (Stages I. and IV., Section I., figs. 1 and 5) as to suggest that the "Gaumentasche" which he observed is nothing more than a prechordal plate in continuity with a well-developed Seessel's pocket.

With regard to the relations of the anterior end of the chorda to the fore-gut and Rathke's pouch, a number of observers have described the apex of the notochord as being in continuity with the hypophysis in birds (Mihalkovics, 33), and in Eutheria (Bonnet, 6; Woerderman, 64; and Miller, 35). This condition is purely secondary, and my own observations lend not the slightest support to the view of Miller that the notochord makes a considerable contribution to the developing hypophysis.

The primitive relation of the anterior end of the chorda is one of continuity with the protochordal plate. The subsequent history can be clearly followed in stages of Perameles, for, as the various derivatives of the protochordal plate become established, the chorda retains its continuity therewith until we get the condition shown in figs. 5 and 6 in which the notochord is continuous with the prechordal plate and this again with Seessel's pocket. In forms in which a transverse premandibular canal is developed, the continuity between chorda and pre-oral gut is of necessity interrupted, so that the primitive condition is transient. Moreover, the hypophysis at this period grows rapidly backwards, while Seessel's pocket, at the same time, in most Vertebrates degenerates. It will be readily seen that this would produce, in a stage immediately succeeding Perameles, Stage IV. (fig. 5), a condition of contact of Rathke's pouch with the prechordal plate or with a "bridge" connecting the premandibular somites.

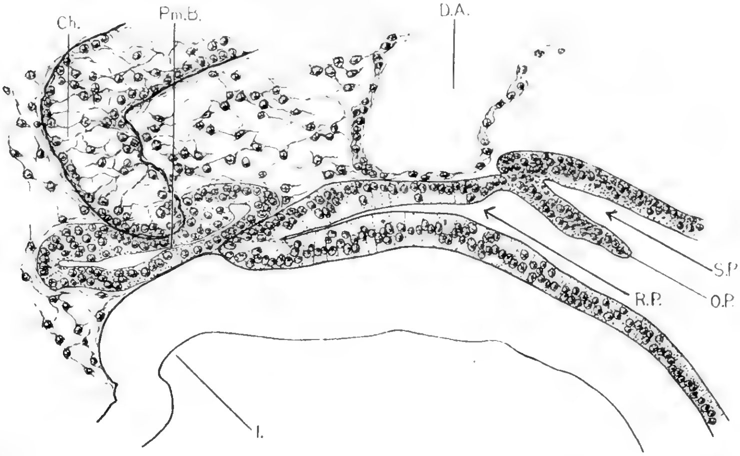

FIG. 42.—*Squalus acanthias* (14 mm. embryo). Median longitudinal section (reconstructed) through the hypophysis and chorda. Sl. 1-4-2-9.

Ch., chorda; D.A., dorsal aorta; I., primitive infundibular recess; O.P., oral plate; Pm.B., bridge connecting premandibular head cavities; R.P., Rathke's pouch; S.P., Seessel's pocket.

This latter condition occurs in Selachians (fig. 42), and is described by van Wijhe (62). In Eutheria, in which neither a definite prechordal plate nor a bridge connecting premandibular somites has been described, the notochord naturally comes into contact with Rathke's pouch, and in some cases—pig, Miller (35), Woerderman (64); dog, Bonnet (6)—there is temporarily established a continuity between the two structures.

II. *Seessel's Pocket* (*Pre-oral Gut*).

In 1877, Seessel (54) first described in the chick a small diverticulum of the gut wall, lying posterior to the hypophysis and in such close contact therewith that its lower concave surface lies exactly on the upper convex surface of the hypophysis. He states that it has a narrow funnel-shaped cavity and a wall of radially placed cylindrical cells, of the same thickness as the hypophysis wall. The reduced remnant of this structure he observed at a later stage as a short diverticulum attached to the duct of the hypophysis.

Seessel's pocket has been described by Nusbaum (39) in the dog as occurring immediately behind a fold which separates it from the hypophysis. In 80 per cent. of the dog embryos examined by Nusbaum, Seessel's pocket comes into close relation with the hypophysis. The lower portion is connected with the pharyngeal epithelium, and contains a small lumen. The distal half breaks up into several cell-groups, one of which passes, in part at least, into the wall of the hypophysis, while the rest of Seessel's pocket disappears completely. Nusbaum regards these facts as evidence that Seessel's pocket and the hypophysis are both parts of one and the same structure, viz. an ancestral communication between the pharynx and the exterior, similar to the unpaired naso-hypophysial duct of Myxinoids.

A portion of pre-oral gut has also been recognised by Bonnet (6) in the dog, and by numbers of other workers in various Vertebrates. Salvi (50), in a detailed study of the pre-oral gut of birds, describes the formation of a succession of "intestinal vertices" of which the tertiary one represents Seessel's pocket. The obliteration of this gives rise to the final "quaternary intestinal vertex." He also describes (48) intimate relations between the pre-oral gut, premandibular somites, and the hypophysis, but does not find any contribution from the entoderm of Seessel's pocket to the hypophysis.

This participation of the entoderm of Seessel's pocket in the formation of Rathke's pouch has also been described by von Kupffer (30) and Saint-Remy (52).

In the Marsupials which I have examined, Seessel's pocket is of common occurrence. In Dasyurus it is very small and variable in its relations, (*cf.* Stage III. of *Dasyurus viverrinus*, Section I. of this paper), but in this species, as the hypophysis deepens and closes, Seessel's pocket disappears, leaving no trace.

In Trichosurus, Seessel's pocket bears relations to the hypophysis similar to those described by Seessel for the chick. It forms a small conical diverticulum, separated from Rathke's pouch by a remnant of oral plate; and, as the posterior end of the hypophysis is slightly bilobed, Seessel's pocket lies between the lobes. (Trichosurus, Stage I.) In the process of narrowing of the mouth of Rathke's pouch, the posterior point of constriction is situated behind the opening of Seessel's pocket (fig. 17), so that that structure becomes included in the hypophysial duct and forms for a time a small pocket-like diverticulum on the posterior side of the duct. This subsequently disappears, and it cannot definitely be said that it contributes actively to the formation of the hypophysis, for it is merely continuous with the duct, which is itself destined to disappear. It is perfectly clear, however, that the insertion of the oral plate, which marks the point of junction of ectoderm and entoderm, comes to be situated within the tissues of the hypophysis, which accordingly cannot be regarded as of exclusively ectodermal origin.

In Perameles a well-developed Seessel's pocket is present in one stage (*P. nasuta*, Stage IV. of Section I.). It arises undoubtedly from the region of the fore-gut derived from the protochordal plate, and is directly continuous with the remnant of the prechordal plate. In subsequent stages, however, all trace of Seessel's pocket has disappeared.

In Phascolarctos and Phascolomys we find the most remarkable development of Seessel's pocket. In Phascolarctos, Stage III., it appears at first sight to form a third median lobe of the bilobed caudal portion of the hypophysis, and its identity is only clear from the fact that it arises posterior to the oral plate. The constriction of Rathke's pouch then occurs in such a manner that Seessel's pocket is included in the hypophysis, and, instead of degenerating as it does in other cases, it persists as a portion of the pars buccalis. Up to a relatively late stage it is recognisable as a flattened vesicle lying on the ventral surface of the hypophysis, and in several embryos its original relations to the caudal bifid extremity of Rathke's pouch are retained, so that sections through the hinder end of the hypophysis in the last stage of Phascolarctos described above bear a very close resemblance to those of the third stage (fig. 34). In some cases Seessel's pocket has the appearance of being an integral part of the hypophysis (fig. 38), whereas in other cases its walls are completely separated by connective tissue from the rest of the pars buccalis and it retains to some extent its own identity. In later stages, however, it appears simply as a slightly differentiated tubule or lobe of the hypophysis.

In Phascolomys, again, we find a well-developed Seessel's pocket which, like that of Phascolarctos, becomes included in the buccal portion of the hypophysis. In early stages of Phascolomys (fig. 39) Seessel's pocket forms a long, conical diverticulum, opening on to the posterior face of the hypophysial duct. The walls are slightly less regular than those of Rathke's pouch, and its cells are distinguishable from those of the hypophysis by reason of their greater staining capacity.

We have thus undoubted evidence that Seessel's pocket in at least two Marsupials (*Phascolarctos cinereus* and *Phascolomys mitchelli*) actually enters into the composition of the pars buccalis of the pituitary body, whilst in Trichosurus a doubtful amount of entoderm is included in the hypophysis.

Professor Hill has drawn my attention to the fact that in an Echidna embryo in his collection there is a well-developed Seessel's pocket. From Professor Hill's graphic reconstruction of this embryo it is clear that Rathke's pouch has just formed; the oral plate is ruptured, and behind it is a conical diverticulum, slightly longer than the hypophysis. Whether this structure subsequently degenerates in Echidna or forms part of the hypophysis is unknown. The condition in the above-mentioned embryo closely resembles that in Phascolarctos, Stage II., 7·5 mm., in which, however, the hypophysis is further advanced and is accordingly slightly longer than Seessel's pocket.

The occurrence of such a well-developed Seessel's pocket in Monotremes and Marsupials and its inclusion in the hypophysis in Phascolarctos and Phascolomys is remarkable, and its significance is uncertain. It must be admitted as a possibility that the inclusion of the pre-oral gut in the pars buccalis indicates nothing more than a slight variation from the normal Vertebrate method of closure of the hypophysial pouch. Further observations are necessary to prove how frequently the phenomenon occurs in other groups of Vertebrates.

In connection with the discussion as to the fate of Seessel's pocket, it may be well to make a brief reference to the pharygneal bursa, a structure of doubtful significance, which has been identified with Seessel's pocket by some workers (Meyer). This structure was first described by A. J. C. Mayer (31) in 1840, and has since been discussed by Killian (28), Grünwald (17), Meyer (32), Huber (24), and others. Huber, in a full discussion on the subject, decides against Meyer's theory that the pharyngeal bursa is merely a persistent Seessel's pocket, on the ground that the two structures are separated by almost the whole length of the future pharyngeal vault;

and the same objection applies to the suggestion that the pharyngeal bursa is a persistent hypophysial duct.

I have not been able to find any trace of a pharyngeal bursa in any Marsupial embryo which I have studied; but if such a bursa is present at any stage in Marsupials, it cannot be derived from Seessel's pocket, as that structure either degenerates completely or becomes part of the hypophysis; neither can it represent a persistent hypophysial duct, as that retains for some time its relations to the hypophysis and then disappears completely.

III. *The Formation of Rathke's Pouch.*

An excellent historical note on the pituitary body is given by Herring (22) in a recent paper, and it is unnecessary to recapitulate here the many different views that have been held as to the ontogenetic and phylogenetic origin of the hypophysis. Rathke (46), in 1838, was the first to describe the origin of the anterior lobe of the pituitary from a pouch-like ingrowth. Subsequent work has established the ectodermal origin of this structure beyond question.

In early stages of Dasyurus described above, we see the exact relations of Rathke's pouch to the fore-gut and oral plate. In Stages I. and II. the oral plate (figs. 8 and 9, O.P.) is still complete, and in the former there is as yet no indication of the formation of the hypophysis. In Stage II. no definite invagination has taken place, but the hypophysial epithelium is differentiated, and this differentiation affects a small portion of the ectoderm of the oral plate. In the next stage the oral plate is ruptured (fig. 10), but a considerable remnant of it persists. Instead of lying, as it does in the preceding stage (fig. 9), in approximately the same line with the ectoderm of the head, it has become bent forwards so as to form an acute angle therewith. The wall of the fore-gut, which in Stage II. lies in contact with the brain floor, has ceased to do so in Stage III., and a mass of cells, possibly representing a head somite, lies above it (figs. 10 and 11). The modified stretch of epithelium now forms a shallow pouch with its dorsal wall pressed closely against the brain floor. It is evident that the apex of the pouch has grown actively backwards, for in Stage II. (fig. 9) it lies anterior to the infundibular depression, whilst in Stage III. it lies immediately below it. The posterior limitation of the pouch is brought about partly by the backward growth of this apex, and partly, as stated by Mihalkovics (33) and Kraushaar (29), by the forward bending of the oral plate. This movement of the oral plate does not, however, appear to be a purely mechanical result of its rupture, for in *Perameles nasuta* (Stage IV.), in which the oral plate is still complete, there is a distinct forward projection thereof, close to its dorsal insertion (fig. 5, P.), and this projection forms the posterior wall of Rathke's pouch. The anterior and lateral folds limiting the pouch are simply the result of the active growth of the epithelium of the pouch. Lying as it does with one wall in close contact with the brain, the natural result of active growth and division of the cells is firstly to increase the area in contact with the brain, and secondly to produce round this area folds, or lips, thus converting the structure into a shallow pouch. Stage III. of Dasyurus (fig. 12) shows a further result of this growth in the deepening of the pouch posteriorly.

That the chorda does not in Marsupials play a mechanical role in drawing Rathke's pouch inwards is self-evident from the fact that it stops some way behind the hypophysis in most cases, and is never in actual contact therewith.

As Herring (22) remarks, the close contact between the hypophysial epithelium and the infundibular depression in these early stages is doubtless of importance in bringing about the development of a definite pouch. In most of the early stages there is evidence of very active growth at the lateral angles of the pouch (fig. 7), and it is clear that rapid growth at these points will tend of itself to bring about a deepening of the pouch.

The narrowing of the mouth of the pouch requires a different explanation. Müller (36) put forward the theory that this was due to the pressure of the internal carotid arteries. Mihalkovics (33) and Kraushaar (29) both regard it as due to the development of the primordium of the skull. In Marsupials there are no blood-vessels in a position to cause the narrowing of the mouth of the pouch, and, as far as it seems possible to give any explanation of this phase of development, that given by Mihalkovics and Kraushaar is probably correct, for the narrowing of the opening of the pouch and its final reduction to a slender duct occur contemporaneously with the condensation of the mesenchyme which ushers in the formation of the cartilage of the skull.

The appearances of transverse sections through Rathke's pouch in early stages, such as are shown in figs. 7 and 30, are exceedingly suggestive of a bilobed origin of the hypophysis; whilst in Stage I. of Phascolarctos the condition is even more marked, the epithelium in the middle line being remarkably thin. The activity of the cells of the lateral angles of the pouch is indicated, in most of the early stages which I have examined, by such appearances as are shown in fig. 7. Moreover, these lateral angles tend to be prolonged backwards beyond the median portion of the pouch, thus giving rise to a distinctly bilobed caudal extremity. In Trichosurus, and more especially in Phascolarctos, this branching of the pouch may be due to the presence of a median Seessel's pocket, indenting the posterior wall of Rathke's pouch. In Trichosurus the caudal bifurcation persists and even becomes more marked after Seessel's pocket has become a mere remnant attached to the duct, and the conical infundibular process, which is just appearing, lies between the two halves.

It is impossible to say at present whether this bilobed condition indicates the origin of Rathke's pouch from a structure consisting of two symmetrical portions. On the whole, it seems more probable that it is merely due to three independent factors, viz. active growth and multiplication of the cells at the angles of the pouch, the pressure of Seessel's pocket on the middle line of the posterior wall of the pouch, and the subsequent protrusion of the infundibular process into the same position.

It may be noted that Gaupp (13) and Salvi (48) have described a threefold origin of the hypophysis in Reptiles, but the lateral lobes in this case probably represent nothing more than an early establishment of the primordia of the pars tuberalis.

IV. *The Later Development of the Hypophysis cerebri.*

The development of the hypophysis subsequent to the establishment of Rathke's pouch consists in the outgrowth and differentiation of the infundibular process, and in the conversion of the simple thin-walled buccal pouch into the various regions characteristic of the pars buccalis of the adult, viz. the solid glandular pars distalis, the pars infundibularis, and the pars tuberalis.

(*a*) *The Development of the Pars buccalis.*

1. *Development of the Pars juxta-neuralis.*—The separation of the primordium of the pars tuberalis occurs in Marsupials at a very early stage, and this fact gives confirmation to the view of Tilney (59) that the pars tuberalis and pars infundibularis constitute two distinct morphological elements in the pars juxta-neuralis.

According to Tilney (59), the pars tuberalis in the adult cat, dog, rabbit, rat, sheep, and fowl "is moulded to the base of the brain in such a manner that the saccular eminence of the tuber cinereum rests in it as one saucer in another" (Tilney, 59, p. 263), whilst a median aperture in the pars tuberalis admits of the passage of the infundibular process. With regard to its ontogeny, he describes in a 14-mm. cat embryo the appearance of a pair of processes from the lateral borders of the dorsal surface of the buccal pouch in the region where the neck of the pouch joins the body. These are destined to form the pars tuberalis, and he accordingly calls them tuberal processes. They grow up towards the brain, and also extend both posteriorly and anteriorly, to fuse eventually and form a continuous structure lying between the tuber cinereum and the pars distalis. In the chick of 5 days, 20 hours he describes the origin of tuberal processes "near the cephalic pole of the body of the pituitary anlage."

Although Tilney alone has clearly recognised both the origin and fate of this portion of the hypophysis, it seems probable that certain structures described by other authors may prove to be identical with it. Thus Mihalkovics (33) and Kraushaar (29) have described the development of a solid process arising from the lower end of the hypophysial sac and growing forwards towards the optic chiasma. Salzer (51) has given special attention to the subject, and finds that in the pig there is an epithelial thickening which corresponds to the process described by Mihalkovics (33) in the rabbit, and by Kraushaar (29) in the mouse. This sends forwards "towards the chiasma" a process consisting of glandular substance. Salzer states also that he finds a similar anterior process in the guinea-pig.

Herring (21 and 22) describes "a tongue-like process of the pars intermedia" in the cat and monkey, and from his figures it seems probable that this structure is the anterior portion of the pars tuberalis. (Compare figs. 2 and 5 of Herring (21) with Tilney's (59) longitudinal sections, figs. 1, 2, 5, 7, 9, etc.) With regard to the development of this portion, Herring (22) states that the neck of the hypophysial sac retains a tubular character for some time and becomes somewhat convoluted. "One of these convolutions applies itself to the under surface of the brain and gives rise to the tongue-like process which extends forwards from the anterior lobe towards the optic chiasma": Herring (22, p. 171).

Baumgartner (4), in a description of the development of the hypophysis in turtles, describes the presence in an early stage (5-mm. embryo) of a main pouch and two lateral buds. The free ends of these lateral buds grow forwards and dorsalwards, and later their distal portions become wing-like and extend forwards beneath the brain floor, whilst their proximal parts lateral to the anterior lobe are crescentic in transverse section. In the newborn animals the lateral lobes have fused across the median line, whilst their crescentic, proximal portions are united by outgrowths of their free edges both dorsally and ventrally around the "anterior lobe," so that this latter is enveloped by the layer so formed. This description probably refers to a pars tuberalis such as is described by Tilney (59), and having an origin similar to that described for Marsupials.

It may further be noted that Baumgartner's description affords an explanation of the threefold origin of the hypophysis decribed by Gaupp

(13) and Salvi (48) in Reptiles. Baumgartner finds a median pouch developed first, followed by two lateral buds. Gaupp (13) similarly describes three invaginations, the two lateral ones forming elongated slit-like depressions separated from the median one by fairly considerable folds in which lie a pair of veins (*cf.* fig. 33). In later development, the three invaginations deepen and become simultaneously nipped off from the mucous membrane. The lateral lobes separate from the median and may degenerate, but Gaupp finds in almost adult lizards two groups of cells, apparently derived therefrom, actually embedded in the walls of the diencephalon. These groups of cells may represent a displaced pars tuberalis.

Salvi (48) describes similar lateral primordia in Reptiles, but does not trace their subsequent history. On the ground of a connexion between these structures and the premandibular somites, he regards the lateral pits as equivalent to the ectodermal invaginations of a pair of gill slits. The development of the premandibular somites in Marsupials lends no support to the theory that they represent gill pouches, nor is there any evidence in this group in support of Salvi's interpretation of the significance of the lateral pits of Gaupp.

Comparing Gaupp's (13) and Salvi's (48) accounts with that of Baumgartner (4), and with the mode of development of the pars tuberalis in Marsupials, it seems probable that the threefold origin described by Gaupp and Salvi may prove to represent an early differentiation of the primordium of the pars tuberalis.

The development of the pars tuberalis in Marsupials is perfectly clear. In quite early stages the portion of Rathke's pouch lying posterior to the duct becomes subdivided into two lobes, which are respectively distal and proximal in relation to the hypophysial duct, and are separated from each other by a horizontal constriction. While the distal lobe thickens and forms the glandular tissue of the pars buccalis as well as the pars infundibularis, the proximal lobe remains thin-walled. It becomes drawn out laterally, and early becomes crescentic in transverse sections. (Compare figs. 18, 20, 21, and 26.) Its lateral borders enlarge and curve up towards the dorsal side of the pars buccalis (figs. 26, 37). These wing-like structures are prolonged anteriorly considerably beyond the main body of the proximal lobe. In subsequent stages the median portion of this lobe becomes greatly reduced, loses its lumen, and fuses with the ventral surface of the distal lobe, whilst the enlarged lateral portions grow up towards the brain floor. Finally they branch and form a collection of flattened tubules which, increasing greatly in number, extend first anteriorly and meet and fuse in the middle line in front of the infundibular process, whilst later they penetrate to the caudal side of that structure and thus come to form a complete ring around it.

Up to the latest stage which I have studied (Trichosurus, Stage XI., fig. 29), the pars tuberalis consists of hollow, flattened tubules with thin walls for the most part only one cell in thickness, and consisting of cubical epithelial cells. No variation in staining capacity is evident in these cells.

From the above summary it becomes clear that the pars tuberalis takes its origin at a very early stage from Rathke's pouch. In Reptiles, if my interpretation of Baumgartner's and Gaupp's descriptions is correct, it arises from a pair of hollow outgrowths which are at first separate from the main median hypophysial invagination. The three primordia become simultaneously nipped off from the buccal ectoderm, thus acquiring a common duct In the Marsupials, the narrowing of the mouth of the pouch takes place before the differentiation of the tuberal primordium, but this is still a hollow outgrowth whose subsequent history clearly shows its homology with the lateral invaginations described by Baumgartner (4). In the Eutheria, according to Tilney (59), the pars tuberalis is derived from a pair of solid processes arising from the point of junction of the neck and body of the hypophysis, this being also the position of the proximal (tuberal) lobe in Marsupials.

The development of the pars infundibularis shows no point of special interest. The postero-dorsal wall of Rathke's pouch represents the primordium of this portion. Unlike the rest of the distal lobe, it never thickens markedly, but on the contrary, as development proceeds, becomes reduced to a thin and very regular layer of epithelium. The infundibular process as it grows downwards indents it from above, and during the growth of the hypophysis as a whole the pars infundibularis spreads round in all directions, so that it eventually comes to cover the infundibular process on its anterior and lateral sides, and to a certain and variable extent on its posterior face. It is noticeable that in the Marsupials the thin epithelium of the pars infundibularis forms not only the layer in contact with the pars neuralis, but also extends beyond this, forming the ventral wall of the anterior and posterior angles of the residual lumen (*cf.* fig. 27), and the dorsal wall of its lateral horns (fig. 28).

With regard to the time of penetration of connective tissue between the buccal and neural portions of the hypophysis, various statements have been made. As noted by Herring (22) and Salzer (51), in the initial stages these two parts are in intimate contact. In a Trichosurus embryo of 8·5 mm. G.L. (Stage V.), connective tissue has penetrated between the primordia of the pars neuralis and the pars buccalis. This connective tissue is derived from the pia mater, and not, as would be supposed from Stendell's (57) description and figure (fig. 17), from the dura mater.

In the final stages of development (Trichosurus, Stage XI.) some of the cells of the pars infundibularis become carried by growth and penetration of the connective tissue into the substance of the pars neuralis, while the remainder form a thin epithelial layer surrounding that structure.

2. *Development of the Pars distalis.*—In the Marsupials which I have studied, two methods of conversion of the walls of Rathke's pouch into the glandular pars distalis may be observed. Of these methods, that observed in Phascolarctos is probably the more primitive, and will accordingly be dealt with first, that of Trichosurus being more specialised. In both cases the cells of the walls of the distal lobe of Rathke's pouch multiply freely except in the region of contact with the developing infundibular process. In both cases also there is produced from the posterior half of the pars buccalis a pair of large, dorso-lateral outgrowths into which a narrow cleft-like lumen extends. (*Cf.* fig. 22, in which, however, the actual section figured passes not through the lumen but through the solid wall.) In Phascolarctos capillaries supplying the pars distalis enter by the ventral cleft between this lateral wing-like process and the median lobe. I have not been able to ascertain with certainty whether this is the case in Trichosurus or not, though a large amount of connective tissue undoubtedly penetrates at these points. It therefore seems possible that the separation of these lobes by a pair of ventral clefts merely serves to afford a point of entry for connective tissue and blood-vessels.

In Phascolarctos, the rapid multiplication of the cells of the walls of Rathke's pouch results in the outgrowth of numerous processes from the outer surfaces of the walls. These are at first short and rounded, but soon become longer; their extremities enlarge and in some cases acquire a lumen (*cf.* fig. 36). They increase rapidly in number, so that the pars distalis comes to consist of a mass of tubules and cell cords, separated from one another by connective tissue which, from the nature of the process of development, inevitably becomes included in the walls.

Although in Phascolarctos, Stage VIII. and in the following stages, as well as in Phascolomys, the very rich vascularity of the pars buccalis is noticeable, there is no indication of sinusoidal development such as Herring (22) describes in the pig. In earlier stages there are blood-vessels lying in close proximity to Rathke's pouch, but these do not penetrate until Stage V., and at no stage is there any indication of the processes from the walls of Rathke's pouch growing into the blood-vessels and pushing the endothelial walls before them as described by Herring (22). On the contrary, several definite points of penetration of the capillaries into the substance of the pars distalis can be recognised, viz. the ventro-lateral clefts as already mentioned and the posterior wall of the pars distalis.

It seems, therefore, that in Phascolarctos there occurs, contemporaneously with the outgrowth of processes from the walls, a certain amount of ingrowth of connective tissue, and more especially of blood-vessels.

Salzer (51) describes a similar condition in the pig, and draws attention to the fact, which is true also of Phascolarctos, that the lumina of the tubules arise entirely independently of the main lumen. Mihalkovics (33) in the chick, and Kraushaar (29) in the mouse, both describe the formation of tubules simply by outgrowth from the wall of the buccal pouch.

In Trichosurus, on the other hand, the walls of Rathke's pouch thicken considerably, so that the lumen is much reduced; but up to Stage VII. the walls retain their original compact form, with a regular, unbroken outline. The process of "tubule" formation then begins, and is ushered in by the ingrowth of connective tissue strands at a number of points. The cells of the wall then gradually become grouped so as to form lobules and cell-cords, but in no stage in Trichosurus do these acquire a lumen. By further ingrowth of connective tissue, and by a process of grouping and rearranging of the cells, the pars distalis of Trichosurus acquires a glandular structure. As might be expected from the difference in the mode of development, the pars distalis in Trichosurus is throughout its history a very much more compact structure than that of Phascolarctos.

A similar process of gland formation by ingrowth of connective tissue was described by J. Müller (36) for the pig; but, according to Salzer's (51) very full and careful description, outgrowths of processes from the wall also play a large part in the development of the hypophysis of this Mammal.

It would be natural to assume that the primitive mode of elaboration of a glandular structure such as the pars distalis is that of the formation of outgrowths, probably hollow, from the walls of a simple pouch. The tubules thus formed would, as they increase in number, become pressed together until they constitute a relatively compact gland. In the adult hypophysis in Mammals the tubular structure is almost entirely lost (*cf.* Herring, 22), and there seems to be a tendency to omit in development the stage of formation of hollow outgrowths.

In the Mammalia both the process of outgrowth and that of penetration of connective tissue occur contemporaneously, and the Marsupials which I have studied form a well-graduated series in this respect. In Phascolarctos and Phascolomys the process of formation of outgrowths from the walls of Rathke's pouch undoubtedly plays a markedly preponderating part in development, while ingrowth of connective tissue occurs to a relatively slight extent. In early stages in Dasyurus, outgrowths form on the walls, but they are neither so numerous nor so long as those in Phascolarctos and Phascolomys. In Trichosurus and Perameles outgrowths of the walls play but a very small part, the adult condition of compactness being attained by a far less circuitous method by direct increase in thickness and by contemporaneous rearrangement of the constituent cells of the walls as cell-cords or lobules.

In this connection it may be noted that whilst in Stage V. of Phascolarctos the bulk of the pars distalis consists of definite tubules, the lumina of these is lost for the most part, if not entirely, in later stages.

Embryological evidence thus agrees with the facts of comparative anatomy, for the anterior lobe in lower Vertebrates consists simply of a greater or less number of branching tubules (Stendell, 57, figs. 63, 65, 66), and we may conclude that the pars buccalis of the Mammals also arose as a branched tubular gland which in the course of evolution became more and more compact until it has in some cases lost, even in ontogeny, all trace of the process by which it has developed.

3. *Histological Differentiation of the Pars distalis.*—The final stage in the development of the pars distalis is the process of histological differentiation. In embryological material not stained for special histology, it is naturally impossible to follow this process in great detail, and it was not my original attention to deal with this subject at all. It may, however, be noted that in later stages in all the types examined the cells of the pars distalis exhibit a very conspicuous differential staining capacity (see figs. 27, 28, 29, 40, and 41). The bulk of the pars distalis in these stages consists of cells with oval or spherical nuclei and cytoplasm which stains a typical hæmatoxylin blue. Amongst these occur a few cells with spherical nuclei and cytoplasm which stains bright red. These two types of cells appear to represent respectively the "chromophobic" and "chromophilic" cells described by Flesch (11) and referred to by Herring (21). Herring (*loc. cit.*) himself describes three types of cells: one small and non-granular, the second larger, with granulated cytoplasm, and thirdly, the deeply staining type. I have not observed any cells which correspond with this second granular type, and merely record the occurrence of the chromophilic cells for the purpose of indicating the stage at which they first appear, viz. in Trichosurus, Stage X. (11 mm. H.L.); Phascolarctos, Stage IX. (9·5 mm. H.L.); Dasyurus, Stage H. (13·5 mm. G.L.). It may also be noted that in all the cases in which these chromophilic cells can be observed they are most numerous in the posterior portion of the pars distalis.

Neither the time of appearance of these cells nor their mode of origin, scattered as they are in the substance of the hypophysis, nor any other facts in development in Marsupials, lend any support to the view of Miller

(35) that the existence of two histologically distinct types of cells in the "anterior lobe" is due to the origin of the one group from ectoderm and the other from entoderm (head of the notochord).

The Fate of the Lumen.—With increase of thickness of the walls of the buccal pouch, the lumen naturally becomes reduced, and in the course of reduction it passes through a variety of forms which do not seem of sufficient importance to justify a detailed description. Two distinct portions of the lumen persist up to Stage X. of Trichosurus: one forming the cup-shaped residual lumen surrounding the pars neuralis; the second, a small isolated cleft on the ventral side of the pars distalis (fig. 27, Lm.P.L.), representing the last trace of the median lumen of the proximal (tuberal) lobe of earlier stages. This small cleft subsequently disappears, whilst the main cavity persists in a pouch fœtus of 4 cm. G.L. (Stage XI.) as a cup-shaped residual lumen.

(*b*) *Development of the Pars neuralis.*

In early stages of development of the brain, prior to closure, a rounded depression of the floor of the diencephalon occurs. This represents the primitive infundibular depression, and it is from the posterior angle of this that the infundibular process grows out. As already stated, I am unable at present to describe the process of development of the diencephalic floor or to identify with certainty the post-chiasmatic and post-infundibular recesses and eminences described by Tilney (60), and the development of the infundibular process is so closely related to that of the diencephalic floor that it is impossible to discuss the former satisfactorily in the absence of definite knowledge of the latter. A few points may, however, be noted.

The infundibular process itself arises as a short, conical or rounded hollow outgrowth from the diencephalic floor, and its walls for a considerable time retain the primitive character of the brain-wall in early stages of its development. Subsequently its cavity becomes reduced and the walls show some indication of differentiation into the three zones, ependymal, mantle (or nuclear), and marginal, characteristic of the developing brain-wall. Complete differentiation is, however, restricted to the neck of the pars neuralis, while in the distal portion cells are scattered throughout the substance of the wall, leaving no specialised marginal zone. The substance of the wall in this stage is traversed by fine fibres, probably both ependymal and neuroglial. In later stages the infundibular process enlarges considerably and its lumen becomes obliterated. The walls undergo several changes, the cells become fewer, the fibres much more conspicuous; and in the last stage which I have observed, the connective tissue has penetrated to a considerable extent into the substance of the pars neuralis, carrying with it a few of the cells of the pars infundibularis.

V. *Note on the Relation of the Meninges to the Parts of the Hypophysis cerebri.*

In both Trichosurus and Perameles it is possible in late stages to observe the relations of the meninges to the parts of the hypophysis, and in both these types the pia mater completely invests the pars neuralis and also the pars tuberalis (fig. 13, P.M.). This statement differs from the account and diagram (fig. 17) of Stendell (57), according to which the pia mater is perforated by the pars neuralis, while the dura mater passes between the pars neuralis and the pars infundibularis. In the forms which I have examined, the dura mater constitutes a connective tissue capsule, the greater part of it passing ventral to the whole of the pituitary, while a thinner layer passes over the dorsal surface of the pars buccalis but thins out considerably as it approaches the hypophysial stalk, and is not continued between the pars neuralis and the pars infundibularis (see fig. 13). In Marsupials the pia mater does not end, as described by Stendell (57) for Vertebrates generally, at the point of origin of the infundibular process, but penetrates between this latter and the pars infundibularis.

FINAL SUMMARY.

1. In Bettongia, Macropus, Perameles, and Trichosurus there is present a pair of head cavities whose early relations and subsequent history (see Elizabeth A. Fraser (12)) show them to be premandibular somites. The origin of these structures has been traced only in Perameles, in which they arise from a prechordal plate which represents a derivative of the antero-dorsal wall of the fore-gut, which is formed from the protochordal plate.

2. A well-developed Seessel's pocket (pre-oral gut) occurs in some Marsupials, and in *Phascolarctos cinereus* and *Phascolomys mitchelli* forms a constituent part of the hypophysis.

3. The primitive relation of the tip of the notochord is one of continuity with the protochordal plate, and in Perameles continuity is retained between the chorda and the derivatives of the protochordal plate (prechordal plate and Seessel's pocket). As a secondary condition, continuity may be established between the chorda and the hypophysis.

4. The development of Rathke's pouch is due to rapid growth of the

differentiated epithelium of the hypophysial angle, and not to any mechanical power exercised by the chorda or any other structures.

5. From Rathke's pouch in Marsupials there arises a proximal lobe, at the point of junction of the duct with the body of the pouch. This forms the pars tuberalis of the adult pituitary body.

6. The glandular structure of the pars distalis (anterior lobe) of the adult is produced either by outgrowth of processes from the walls of Rathke's pouch or by ingrowth of connective tissue into the thickened walls of that structure.

7. Two types of cells, "chromophilic" and "chromophobic," are differentiated *in situ* in the pars buccalis before the adult condition is fully reached.

8. The pars neuralis arises as a hollow conical outgrowth of the diencephalic floor. It is gradually transformed into a solid, swollen lobe, and is then penetrated by connective tissue.

ADDENDUM.

Since the completion of the above, a paper has appeared on the development of the hypophysis in Reptiles by Baumgartner (*Journal of Morphology*, vol. xxviii., No. 1, Dec. 1916), who describes the origin of the pars tuberalis in a considerable number of Reptiles from lateral buds such as are described by Gaupp (13), and by Baumgartner (4) in an earlier paper. This is in agreement with the interpretation given above, according to which the lateral buds described in Reptiles are homologous with the proximal lobe found in early stages in Marsupials.

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THE ARTERIES OF THE PONS AND MEDULLA OBLONGATA: PART III.[1]

By J. S. B. STOPFORD, M.D., *Lecturer in Anatomy, University of Manchester.*

PART III.

THE CLINICAL APPLICATION OF PARTS I. AND II.

IT is not within the scope of this thesis to consider fully the theoretical "vascular" etiology which has been proposed for so many cerebral and spinal diseases of obscure origin. The striking correspondence in size and position between the distribution of certain arteries and the areas of sclerosis in several diseases is extremely significant and has been remarked upon by many writers. The localisation of acute anterior poliomyelitis to the distribution of the anterior spinal, which has been observed by Marie (95), Goldscheider (63), Dauber (42), and Seimerlung (122), and cases of posterior sclerosis which have marked out the area supplied by the posterior spinal, as in Buzzard's (31) case, are particularly interesting examples, which at least suggest the possibility of the vascular origin of many nervous diseases whose etiology is difficult to determine. The close relationship between the patches of sclerosis in disseminated sclerosis (or myelitis) and the distribution of spinal blood-vessels has been repeatedly referred to: a typical illustration was reported by Dreschfeld (51).

Williamson (154) and more recently Starr (132) have reviewed fully the relation of nervous diseases to the distribution and lesions of the cerebral and spinal blood-vessels, and reference to their papers shows that greater anatomical knowledge of the nutrient vessels and more extended pathological examinations of the diseased tissues are necessary, if the vexed question of etiology is to be decided. Attention will be briefly directed to this subject again on a later page.

The applied anatomy dependent upon the investigations described in the preceding pages may be most concisely divided into the following parts:—

I. Occlusion of { (A) the main arterial trunks.
  (B) the small bulbar or pontine branches.
II. The significance of the neuro-vascular relationships.

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[1] Continued from *Journ. of Anat. and Phys.*, 1916, vol. l., p. 255.

I. General.

(A) *Occlusion of the Main Arterial Trunks.*

The two exciting causes of occlusion of the large vessels are thrombosis and embolism, and certain of the anatomical arrangements predispose to one or the other. The lesions produced by occlusion only form one section of the elaborate classification of bulbar palsies suggested by Batten (12), but a more perfect anatomical knowledge assists in eliminating many of the recognised difficulties experienced in an endeavour to make a differential diagnosis between the various sections.

Trousseau (143) and Duménil (53) were the first to describe and recognise labio-glosso-laryngeal paralysis as a definite clinical entity, and since their time our knowledge has steadily increased, although it is still very incomplete. Emboli are liable to be arrested:—

1. Most frequently in branches which arise, more or less, in the direct line of the parent vessel. Hughlings Jackson (76) was the first to show that the middle cerebral, being "more directly in the way of strain from the heart," was "plugged" more constantly than any other cerebral artery.

Huret (78) indicated that the *left* vertebral exhibited a greater disposition to embolism than the right, on account of its more direct position in the axis of the flow from the left ventricle. Many anatomists have stated that the left common carotid is more in the line of the ascending aorta than the innominate.

As an embolus usually consists of a detached vegetation from the mitral or aortic valves (Savelieu (119) found embolism associated with heart disease in 89 per cent.), the gross anatomical arrangement of the vessels suggests that embolism should be found most frequently on the left side in both the carotid and vertebral systems. Furthermore, the size and anatomical position of the left common carotid would predispose to its occlusion by an embolus more frequently than the left vertebral.

Clinical statistics support these anatomical conclusions. Jeanin (80) only succeeded in finding 19 cases of embolism of the right side in the literature, but more recently Jones (81) traced 639 cases of embolism, all verified by autopsies, of which 332 were on the left and 307 on the right.

In 372 cases of thrombosis the latter discovered 196 on the left and 176 on the right.

2. In the region of the bifurcation of a vessel, as there is usually a

reduction in calibre at the site of division. This is well illustrated by the basilar artery, which is most frequently obstructed by an embolus at the point where it bifurcates to form the two posterior cerebral arteries, although it is necessary to point out that embolism of this vessel is rare.

3. At any point where there is a sudden diminution in the diameter of an artery. This will be clearly demonstrated subsequently by the vertebral artery.
4. Naturally more frequently in the smaller arteries. Embolism of the basilar is rare, because fragments which have passed uninterruptedly through the vertebral would scarcely be likely to become lodged in the former artery, which is larger than the latter.

Another anatomical factor which influences the clinical result of arterial obstruction is the possibility of the maintenance of the circulation in cases of obstruction by the normal anastomoses.

The circle of Willis is undoubtedly the most important of these. It has been seen that the posterior communicating arteries connect the carotid and vertebral systems, and furthermore that the anterior communicating forms a junction between the cerebral arteries of the two sides, although under normal circumstances the circulation of the two hemispheres may be described as practically distinct. From this it is not difficult to realise that this arterial circle, when complete, may compensate for complete occlusion of the internal carotid. This explains the very frequent absence of symptoms, or transient hemiplegia, which follows ligature of the internal carotid, and the clinical significance of absence (4 per cent. on right side and 3 per cent. on the left) or diminutive size of the posterior communicating artery, which may cause permanent hemiplegia when the internal carotid is obstructed. Alexander (4) introduced ligature of the vertebral (even both) as a treatment for certain diseases of the spinal cord, and stated there was an improvement in the majority of the cases; but what is more interesting in connection with the present consideration is the absence of clinical manifestation of such a marked reduction in the intracranial blood supply.

Leidy (88) described a most illustrative case of thrombosis of the circle of Willis, in which there was an amelioration of symptoms until a further thrombosis caused a fatal termination; the improvement was thought to be due to the presence of an unusually large posterior communicating artery, which was found at the autopsy, and which had to some extent compensated for the obstruction. In addition to the communications at the base, the cortical branches of the cerebral and cerebellar arteries also anastomose, which tends to reduce the area of cortical degeneration produced by obstruction; although it is probable that the freedom of these communications is variable.

The circle of Willis has other physiological functions. It equalises the cerebral blood pressure on the two sides, and also reduces it, as seen from the investigations of Corin, who found the blood pressure in the internal carotid of the cat to equal 120 to 180 mm. of mercury, whilst in the circle of Willis it was only equal to 80 or 90 mm. As Deaver has demonstrated, the tortuosity of the vessels at the base diminishes the risk of apoplexy.

It now becomes necessary to briefly consider the individual arteries separately, stating the symptoms which would ensue from their occlusion according to the distribution described.

Vertebral Artery.

Embolism is found to be rare, but, when it occurs, is seen more frequently on the left side.

Part I. shows that an embolus would tend to be arrested at three points where there may be considerable diminution in diameter.

1. *Immediately beyond the point where it perforates the dura in fully* 50 *per cent.*—Provided the lumen remained patent distal to the site of obstruction, occlusion here would only cause interruption of the blood supply through the inferior set of bulbar branches. This would result chiefly in degeneration of a few pyramidal fibres and the caudal part of the spinal nucleus of the trigeminal nerve, both on the same side as the lesion. The clinical manifestation of the latter is difficult to decide, as many writers maintain that this part of the fifth nucleus receives pain and thermal impulses conducted by the fibres in the ophthalmic division, whilst Woods (158) is of the opinion that it receives similar impulses from a narrow strip of skin extending from the vault of the skull to the chin, just in front of the ear.

The caudal limit of the nucleus and tractus solitarius might be affected also, which would cause probably some impairment of the sense of taste in the posterior part of the tongue on the same side, and disturbance of the fibres in Gower's tract.

Campbell's (32) case of thrombosis of the inferior cerebellar artery is an ideal example of the result of occlusion of the vertebral at this level. Undoubtedly it was primarily a case of thrombosis of the former artery, but it is clear from the history and microscopic examination that the cerebellar artery had a low origin from the vertebral and failed to provide any branches for the retro-olivary region, and that the symptoms were due to extension of the clot to the caudal part of the vertebral.

The observations in Parts I. and II. elucidate all the difficulties experienced by the reporter, and make the interpretation of the case much simpler. The careful histological examination illustrates most beautifully (although not realised by the reporter owing to deficient anatomical details) the distribution described of the inferior set of bulbar branches; paresis of the arm and leg on the side of the lesion supports the conclusion that the vertebral supplies a portion of the lateral cerebro-spinal tract at its formation.

Menzies' (97) case, in which the symptoms were also thought to be due to occlusion of the inferior cerebellar artery, is similar; only, in this instance a note is made in the report of the extension of the clot to the caudal part of the vertebral.

2. *At the normal origin of the posterior inferior cerebellar artery.*—A narrowing at this level was found four times on each side. Occlusion here would almost inevitably also result in suspension of the bulbar supply of the posterior inferior cerebellar artery, and, as it would appear impossible to make a differential diagnosis from simple occlusion of the latter vessel, its consideration will be partially deferred until that vessel is discussed.

This investigation has introduced two facts which may assist both in localising an embolus at this level and differentiating direct occlusion of the posterior inferior cerebellar from that which is secondary to obstruction of the vertebral at its origin. *If there is any paresis of limb or trunk muscles the vertebral must be affected, alone or in addition to the posterior inferior cerebellar artery. Furthermore, if there is any paresis of limb or trunk muscles without any tactile anæsthesia, with or without symptoms of a retro-olivary lesion* (i.e. *the so-called posterior inferior cerebellar syndrome*), *the vertebral is occluded probably about the mid-olivary level and not at its cephalic extremity.* The paresis in these cases would be "crossed," as the lesion must be situated above the pyramidal decussation. These important anatomical conclusions are supported by the clinical histories and also pathological examinations of cases described as occlusion of the posterior inferior cerebellar. In Spiller's (129) first case there was some weakness of the limbs on the side opposite to the lesion, and at the autopsy the clot was found to occlude both the posterior inferior cerebellar and vertebral arteries. In Wilson's (156) case, which survived, of supposed occlusion of the posterior inferior cerebellar artery, there was some weakness of the leg on the side of the body opposite to the lesion. The cases reported by Stewart (133) and Hun (77), which have been proved at the autopsy to be uncomplicated examples of posterior inferior cerebellar occlusion, failed to show any motor paresis.

3. *At the cephalic extremity.*—Obstruction at this level would probably cause hemiplegia and hemianæsthesia on the opposite side of the body, but, what is in contradiction to the teaching of most medical treatises, need not invariably produce such symptoms. The paralysis and anæsthesia need not be necessarily so widespread, owing to the supply in this region from the anterior spinal and basilar, as the injections clearly and emphatically show that total suspension of the bulbar distribution of one vertebral need not cause inevitably complete hemiplegia. There would also be some paresis of the tongue muscles on the same side. And, owing to the fact that at this level the vertebral has, as a rule, very considerably replaced the posterior inferior cerebellar artery, the above manifestations would be associated probably with the symptom-complex described as a result of occlusion of the latter vessel.

Spiller (130) devised a symptom-complex for occlusion of the uppermost part of the anterior spinal and adjoining portion of the vertebrals, and described the symptoms of an alleged example. His case reads like a case of obstruction of the lower end of the basilar from embolus, as the onset was sudden and the symptoms were spastic paresis of all the limbs with some disturbance of the sense of position and movements of the tongue—precisely the symptoms expected after occlusion of the most caudal limit of the basilar; furthermore, simultaneous occlusion of both vertebrals appears a most unlikely occurrence.

Handford's (68) incomplete report of the symptomatology and autopsy of a case of thrombosis, in which there was gradual increasing weakness of the arm and leg on one side, dysphagia (nucleus ambiguus), and death from extension of the clot to the other vertebral and basilar, is more instructive. Duffin (52) records a very similar case. Taylor (138) describes another excellent example of embolism of the vertebral at this level, in which there was numbness of the opposite arm and leg and the loss of the power of deglutition, which resulted in death from starvation. Wilks (153) reported five cases of what Duménil designated labio-glosso-laryngeal paralysis, and four of these appear to be probably examples of vertebral occlusion. Ormerod's (105) first case of obscure bulbar and pontine disease, together with several cases of supposed posterior inferior cerebellar occlusion, read like cases of obstruction of the vertebral at this level, with possible extension of the clot to the basilar. In 8 per cent. abducent paralysis on the same side is to be expected.

Thrombosis would cause more extensive obliteration of the lumen than embolism, and some or all of the above symptoms might be produced, but, as elsewhere, the differential diagnosis would be facilitated by the more gradual onset, with possibly remissions. Thrombosis of the vertebral is certainly more frequent than embolism.

Pope (109), in 1889, described a case of thrombosis of the vertebral associated with unilateral loss of taste at the back of the tongue, palatal paralysis, dysphagia, and paresis of the arm and leg. From the gross findings at the autopsy, he attributed the former to pressure of the plugged artery on the vagus and glosso-pharyngeal nerves, but it appears likely that our present neurological knowledge and improved histological methods would have shown that obliteration of the bulbar supply of the vessel was the true cause. The account of even such an old case illustrates the application of many of the anatomical features observed in the preceding pages.

I have searched the carefully kept records of the medical post-mortem examinations for the last twelve years at the Manchester Royal Infirmary, and have only succeeded in finding one case of occlusion of the vertebral artery in 1887 autopsies. This was on the left side and due to thrombosis, but unfortunately no clinical notes were available, as the patient was moribund on admission.

Anterior Spinal Artery.

The size and other anatomical features of this vessel suggest its immunity from embolism, and it is obvious that the very numerous reinforcements received throughout its course and the free anastomosis with the posterior spinal system tend to prevent any widespread occlusion. The rarity of its obstruction is further emphasised by the fact that I have been able to find only one authentic case reported in the literature. This was described by Coupland (35) in 1889. The symptoms were sudden right hemiplegia without loss of consciousness, followed by paralysis of the left arm and leg, and some dysphagia; the level of the thrombosis is not described, but the softening was only seen at the pyramidal decussation. Two points are of extreme interest, and were not discussed by the reporter: first, the absence of anæsthesia, which is explained by the fact that the anterior spinal at the level of the motor decussation does not supply the fibres conveying tactile impulses; and secondly, the dysphagia, which suggests implication of the vertebral, although in one case the anterior spinal was seen to supply a branch to the postero-lateral sulcus.

The clinical importance of the investigation of origin of the anterior spinal, and the question of fusion of its two parts, may now be considered. In those cases in which the artery arises by a single stem (9 per cent. on the left, 3 per cent. on the right, and in 3 per cent. from the angle formed by the junction of the two vertebrals), the cephalic portion is much more predisposed to complete occlusion, since the anterior spinal is known to fill from above, and is more likely to be affected by occlusion of the vertebral from which it gains origin, since the possible collateral channel of the opposite side is absent. If the two branches of origin fail to fuse or communicate (6 per cent.) until they reach the cord, it is clear that the obstruction of one need not cause bilateral symptoms, although it has never been realised that anterior spinal thrombosis may cause hemiplegia and hemianæsthesia. In cases of normal distribution the clinical manifestation of symptoms will vary according to the site of the occlusion. If the obstruction was in the region of the upper part of the medulla, the symptoms would probably be paralysis of the muscles of the trunk, arms, and legs and the extrinsic and intrinsic muscles of the tongue, associated with anæsthesia of the skin except in the trigeminal region. Respiratory failure or other pulmonary or cardiac disturbances would cause, almost inevitably, a fatal termination either immediately or in a very short time. In the lower part of the medulla the clinical manifestations are perfectly illustrated by Coupland's case, with the exception of dysphagia, which would not be expected frequently. If the occlusion occurred in the spinal course it would probably be very limited, owing to the numerous reinforcements, and only cause paresis of a few muscles as a result of anæmia of the grey matter of the anterior cornua of one or more segments. Degeneration in the white matter, unless an extensive thrombosis occurred, would be largely prevented by the anastomoses with branches of the posterior spinal system.

An interesting case, the symptoms of which Ross (116) thought to be due to obstruction of several of the lumbar spinal arteries, is reported by Hamilton (67), in which paraplegia occurred after the development of an aneurysm of the abdominal aorta, in the region of the origin of the renal arteries, although there was no possible compression of the cord. The significance of the spinal reinforcing vessels has been further illustrated by the experiments of Schiffer (120) and Weil (152), in which the aortæ of animals were ligatured, and paralyses demonstrated as a result of anæmia of the lumbar cord.

Posterior Spinal Artery.

The cause of the rarity of occlusion of this artery is similar to that described for the anterior spinal; in fact, its involvement must be usually secondary to obstruction of either the vertebral or posterior inferior cerebellar arteries. For clearness it has been considered separately, although clinically it is not recognisable, except under the conditions described in the section on occlusion of the minute nutrient branches. Its occlusion would cause impairment or absence of tactile sensibility on the same side, with probably some ataxia and giddiness owing to degeneration of some of the fibres in the dorsal and caudal part of the inferior cerebellar peduncle.

Posterior Inferior Cerebellar Artery.

As this artery is the largest branch of the vertebral and usually arises almost in the direct line of the parent trunk, it is predisposed anatomically to occlusion by emboli. For reasons previously stated, the left will have a greater tendency than the right. In 17 reported cases, the lesion was on the left side in 14, although it is necessary to state that in several of these the vertebral was found also to be plugged by clot at the autopsy. The frequency on the left is therefore marked clinically and anatomically. The described retro-olivary syndrome resulting from obliteration of the posterior inferior cerebellar artery is familiar to all neurologists, and it seems to have received attention at the expense of the other vessels, especially the vertebral.

An attempt has been made previously to show that Campbell's and Menzies's atypical cases were really clinical manifestations of occlusion of the vertebral.

Ormerod's (105) case was obviously also an example of vertebral obstruction.

The cases reported by Spiller (two), Thomas (140), and Senator (121) were found to show vertebral thrombosis at the autopsy. Wilson's (156) and Courtney's (36) cases both survived, but clinically showed indications of some slight affection of the region supplied by the vertebral.

FIG. 23.—Photomicrographs from Dr R. M. Stewart's case of occlusion of posterior inferior cerebellar artery.

Stewart's (133) and Hun's (77) cases were proved to be true uncomplicated cases of posterior inferior cerebellar thrombosis. The clinical histories of the cases reported by Abrahamson (1), Gillis (case 2), Judson Bury and the writer (30), Head and Gordon Holmes (71), Harris (69), and Robinson (113) suggest no involvement of the vertebral, but without an autopsy it is impossible to exclude this possibility. This rapid survey of 17 cases reported as occlusion of the posterior inferior cerebellar artery shows the confusion with the vertebral, and the difficulty of excluding extension of the clot to the latter vessel. The anatomical study of the distribution of these two arteries unfortunately has failed to assist directly—in fact, it has shown that occlusion of either vessel may cause precisely the same symptoms; but the following conclusions may indirectly help in some instances, and prevent all cases exhibiting the retro-olivary syndrome being unreservedly reported as examples of thrombosis of the posterior inferior cerebellar artery.

1. Any paresis of trunk or limb muscles definitely denotes vertebral or anterior spinal involvement.
2. The vertebral may nevertheless be occluded without any manifestation of paresis of the trunk or limb muscles.
3. The vertebral may absolutely replace the bulbar supply of the posterior inferior cerebellar. In a few of these cases its complete occlusion would cause symptoms which are identical with the syndrome described for the latter vessel, without any additional clinical manifestations which would indicate the artery affected.
4. Crossed hemianæsthesia to pain and thermal stimuli unassociated with dysphagia and laryngeal paralysis is most probably due to vertebral occlusion, as the spino-thalamic tract is never supplied by the posterior inferior cerebellar artery below the lowest limit of the nucleus ambiguus.

Gillis's (62) first case has not been included in the previous 17, and merits special reference.

Briefly, the symptoms were analgesia and thermal-anæsthesia over the area of skin supplied by the ophthalmic and superior maxillary divisions of the trigeminal nerve on the right side and the whole of the left side of the body below the nipple. There was no paresis of the pharyngeal or laryngeal muscles, but the usual sympathetic disturbances were present, as well as a more marked patellar reflex on the right side. The history suggests obstruction of the lowermost bulbar branches of the vertebral, as in Campbell's and Menzies's cases, but in the latter there was the extra assistance in diagnosis obtained from the post-mortem examination. The unusual distribution of the analgesia is very significant, although neglected by the reporter of this case. Its absence in the region supplied by the second, third, and fourth cervical nerves suggests that their fibres conveying "pain" and "temperature" impulses had not crossed at the level of the lesion, which was therefore probably lower than the region supplied by the posterior inferior cerebellar artery. This supposition, together with the absence of any signs of involvement of the nucleus ambiguus, coincides with the opinion that the case is really an example of vertebral occlusion about the level of the pyramidal decussation. This suggestion with regard to the level of crossing of pain and thermal fibres of the upper cervical nerves requires further investigation, but I offer it provisionally as a new and most useful guide to localisation.

Most of the recorders of cases maintain that the symptoms of posterior inferior cerebellar occlusion are extremely constant. Neither careful study of the reported examples nor the anatomical distribution supports this, and greater care ought to be adopted in the selection of examples of this interesting type of bulbar palsy. I do not intend to enumerate the symptoms, as they have been described repeatedly, and my intention is more to indicate the difficulty in excluding other vessels whose occlusion may cause identical symptoms.

Dr R. M. Stewart, medical officer at Prestwich County Asylum, has very generously supplied me with the carefully prepared sections of the medulla from his proved case of posterior inferior cerebellar occlusion. Photo-micrographs, at the most instructive levels, are seen in fig. 23, and they will be seen to strikingly resemble the area of distribution ascertained by injection.

Basilar Artery.

For the anatomical reasons stated, embolism of this artery is very rare, and practically only seen at its bifurcation to form the two posterior cerebral arteries. Chadwick (33) and Maudsley (96) each report one case of embolism of the basilar at this point.

Occlusion of this vessel, from embolism or thrombosis, must almost inevitably result in death, as it will cause degeneration of all the descending fibres on both sides, including those which pass to the vital centres in the bulb and caudal part of the pons. The rapid death in these cases from asphyxia was recorded in 1868 by Hayem (70), and extension of the thrombus to the basilar has been seen to herald a fatal issue in several cases of vertebral occlusion.

Bastian's (11) case may be cited as a typical illustration of basilar obstruction, in which there was an apoplectic seizure followed by profound coma, irregular stertorous breathing, absence of reflexes, and death in five and a half hours. In some cases there is conjugate deviation of the eyes and rotation of the head, as described by Eichhorst (57). Many have recorded hyperpyrexia.

Weber (150) gave an account of a case of thrombosis of the basilar of unusual etiology, the clot being secondary to a gumma which arose from the lining of the cephalic extremity of the right vertebral.

Thomson (141) described a valuable case of supposed pontine thrombosis. There was anæsthesia to all forms of stimuli over the left side of the face, partial thermal anæsthesia of the left leg and left side of the trunk, but in the latter situation there was also some analgesia and impairment of the tactile sensibility. Sensory disturbances of the skin of the left arm were "barely noticeable."

In addition, there was loss of taste on the left side, and the left leg was ataxic. The onset was sudden, and undoubtedly indicated vascular origin, but I suggest that it cannot be due to any pontine obstruction, chiefly because the fibres from the gustatory epithelium pass to the nucleus solitarius, which is not found in the pons. The associated affection of the nucleus (or tractus) solitarius, spino-thalamic tract, and some of the medial lemniscus fibres (as obviously the tactile fibres must have crossed, since they are impaired on the same side as the "pain" and "temperature" fibres which cross in the cord) without any involvement of somatic or splanchnic efferent fibres suggests a lesion between the lowest limit of nucleus ambiguus (about the level of the sensory decussation) and the formation of the lateral cerebro-spinal tract. Reference to the discussion of posterior inferior cerebellar and vertebral occlusion will make this clearer. A lesion at this point, if of vascular origin and not due to hæmorrhage, could only be caused by obliteration of the inferior bulbar branches of the vertebral. In fact, very slight variation in the normal distribution of this vessel might cause it; the fifth nucleus might easily escape and a few fibres of the medial lemniscus be included. The sole objection to this theory is the very complete anæsthesia in the trigeminal area, but lack of accurate information prevents this being definitely dealt with, and it is not so insurmountable as the contra-indications to the localisation in the pons.

As complete occlusion of the basilar is almost invariably fatal and must cause most extensive symptoms, no advantage can be gained by enumerating the results of such a calamity. Ross (116) has referred to the possibility of attachment of a thrombus to the wall of the vessel causing merely obliteration of a few branches. If this occurred in the upper part of the pons the result would be paralysis of the fourth and possibly also the third cranial nerves on the same side, with complete paralysis of the muscles of limbs, trunk, mastication, face, palate, tongue, and pharynx, and hemianæsthesia (to all types of sensation) on the side opposite to the lesion. In the lower part the sixth nerve and muscles of the face and mastication would be paralysed on the same side, and the muscles of the limbs, trunk, palate, tongue, and pharynx on the opposite side. Owing to our imperfect knowledge of the arrangement of the trigeminal fibres it is impossible to state accurately the distribution of anæsthesia of the face, but the limbs and trunk would be anæsthetic (to all types of sensation) on the side opposite to the obstruction. It is necessary to repeat that in 19 per cent., owing to the more caudal origin, the basilar supplied the upper part of both hypoglossal nuclei, and in 9 per cent. the vertebral, as a result of the more cephalic origin of the basilar, supplied the abducent nucleus.

The Anterior Inferior and Superior Cerebellar Arteries.

Owing to their origin being almost at right angles to the basilar, these vessels are rarely obstructed by embolism. Their distribution to the pons is too indefinite to justify the description of any symptomatology in connection with their occlusion, except to say that affection of the anterior inferior cerebellar artery would probably result in some disturbance of the auditory and vestibular fibres.

(B) *Occlusion of the small Bulbar or Pontine Branches.*

These small end arteries may be occluded by a thrombus, minute embolus, or even by an obliterative arteritis. Nervous diseases of syphilitic origin probably provide the most interesting examples of the latter cause.

The much-discussed vascular etiology of innumerable diseases of the central nervous system has been previously mentioned, but its final decision must be left to the clinician and the pathologist, and the necessity to them of accurate anatomical data is obvious.

Recently several obscure cases of bulbar and pontine degeneration have been described, and, in the absence of more definite explanations, sclerotic changes in the nutrient blood-vessels have been alleged as the cause. The varying range of nervous symptoms and pathological discoveries in cases of arterio-sclerosis, combined with inadequate accounts of the distribution of the bulbar arteries, are the probable reasons for this supposition.

Space only permits reference to two cases which may be cited as examples.

Spiller (128) reported a case suffering from complete bilateral oculomotor paralysis, rigidity of the limbs, and stertorous breathing. The onset was sudden, and the suggested cause was thrombosis of the small blood-vessels supplying the nuclei of the third nerve on each side, which at autopsy exhibited softening. Unfortunately, the notes are far from complete, but a more acceptable diagnosis of this case appears to be embolism of the basilar at the point where it bifurcates to form the posterior cerebrals. This would be a simpler and equally efficient explanation of the condition, and would be in absolute agreement with the anatomical researches described in this thesis and by other observers. It is difficult, from the symptoms described, to imagine why this diagnosis was ignored.

The other selected example of obscure paralysis alleged to be possibly due to sclerotic changes in the nutrient blood-vessels has just been described by Taylor (137). The disease is hereditary, occurs after the fiftieth year, and terminates fatally. The only symptoms are bilateral ptosis and dysphagia. The ocular movements and phonation are normal. Precisely the same clinical manifestations have been noticed in two generations of the same family. The constancy of the symptoms and the association of such anomalous palsies point against a vascular etiology, and the study of the distribution of individual groups of the minute bulbar and pontine branches makes such a supposition untenable.

It is quite beyond the range of possibility to imagine such a coincidence as the bilateral occlusion of the small vessels supplying the cells giving origin to the fibres innervating the levator palpebræ superioris muscle in members of two generations, even if the curious association of dysphagia was eliminated. The suggestion that the symptoms are due to obstruction of the larger vessels is no more justifiable, and it would appear wiser not to hazard any explanation rather than cloak our ignorance with such an impossible and unscientific one. Most of the suggested examples of occlusion of minute bulbar or pontine branches appear equally unjustifiable, when studied in conjunction with the anatomical distribution of the arteries.

Conclusions to Sections A and B.

The conclusions conveyed by the review of the more important reported examples of vascular lesions of the bulb and pons coincide with the opinions and observations expressed in the purely anatomical parts, and intensify the immense difficulties to contend with in attempting to diagnose and localise cases of arterial occlusion. The demand for still further research in the arrangement and function of the nuclei and tracts enumerated in the preceding pages is very apparent. The danger and inevitable failure resulting from a too stringent regard for the various syndromes is manifest.

Practically all the vessels are subject to such wide variation in distribution that it is quite inadvisable to associate emphatically a single group of symptoms with any one artery. A good illustration of the result of placing too much reliance on a syndrome is seen in the case of the posterior inferior cerebellar artery, where it seems to have caused many inaccurate diagnoses, and probably sometimes prevented efficient examinations being made, owing to the ease with which this freely published group of symptoms may be applied to occlusion of other arteries.

The most important conclusion, then, appears to be that every case must be most diligently examined and judged on its own merits, regardless of any syndrome, if the affected vessel and the position of the obstruction are to be accurately defined. Vague unsupported diagnoses are to be deplored, as they must tend to depreciate rather than advance our knowledge.

It seems possible that more careful clinical records, extensive pathological examinations, and further anatomical research may overcome many of the difficulties described.

II. THE SIGNIFICANCE OF THE NEURO-VASCULAR RELATIONSHIPS.

All the cranial nerves, with the exception of the olfactory, have a longer or shorter intracranial course before they emerge from the skull. During the greater part of that course they lie in intimate relation with the bones of the cranium, and in consequence are very susceptible to compression. The exciting causes of compression are numerous, but it is only intended to refer here to those of vascular origin. The conditions of an artery, under which it is possible for a nerve to be compressed against a resistant structure like bone, may be grouped into three classes:—

1. Arterio-sclerosis, or any degenerative or inflammatory condition by which the arterial wall is thickened and rendered harder and less elastic.
2. Aneurysm. Usually only the slow-growing, thick-walled type or those exhibiting calcification manifest compression symptoms. Beadles (14) found a history indicating compression of one or more cranial nerves in 14 per cent. of the cases of aneurysm of the larger cerebral arteries.
3. Possibly vascular spasm may result in serious pressure upon cranial nerves. This cause is naturally obscure and its existence difficult to prove, but it is nevertheless necessary to mention it.

Illustrative cases of the first two, and possibly the latter, causes of palsy of the cranial nerves are to be seen in the literature, and a few will be mentioned subsequently. Whilst reading the reports of these cases it is evident that the writers have experienced great anatomical difficulties owing to the omission of neuro-vascular relationships, a clear knowledge of which is required by many of the writers.

The possible compression of cerebral nerves by arteries has been realised for some considerable time, but more recently writers have directed our attention to the possible "constriction" of nerves by vessels. Cushing (40) has very clearly marshalled the facts of this important subject before us and brought strong evidence to support the view that, in conditions which cause enlargement of the brain stem, the arteries which extend laterally tend to be stretched, and consequently constrict the nerves if the former are situated ventral to the latter. He examined very carefully 39 cases of intracranial tumour and found "grooving" of the pons by normal (not sclerosed) transverse arterial rami in 21, and in 10 of these the growth was subtentorial. This grooving was seen only once in a control series of 20. He further showed evidence of a similar constriction of certain cranial nerves, especially the third and the sixth. In 11 cases out of 14 which displayed symptoms of ocular disturbance during life, he found evidence of arterial constriction at autopsy. In this paper Cushing regrets the lack of anatomical information about the normal relations between these nerves and arteries within the cranium; and, even if his conclusions will not account for the nerve palsies in so many varying lesions as he suggests, it is necessary to extend our present knowledge of the normal state in order to better understand and interpret morbid conditions.

Each nerve will be briefly considered separately, as this appears more practicable than a separate study of the vessels:—

1. *Olfactory nerve and tract.*—No artery of any size is related to the minute branches of this nerve as they pass through the cribriform plate, but the tract may be affected by large aneurysms of the basal trunks. Beadles (14) mentions an instance of aneurysm of the intracranial portion of the internal carotid which seriously damaged the left olfactory tract.

2. *Optic nerve, chiasma, and tract.*—The intimate relation between the terminal part of the internal carotid and the optic nerve, chiasma, and tract is well known. In any of these three parts of their course the optic fibres may be compressed by pathological conditions of the internal carotid.

Many cases have been reported of damage being done to these fibres by aneurysm, but it is not realised that simple atheroma of the internal carotid may mechanically produce optic atrophy, as the nerve is not placed in such a favourable position for compression as many of the others. Elliot Smith (123) has reported one case and seen five others where this has occurred. This factor in the production of optic atrophy is persistently disregarded by ophthalmologists, although, since there is repeated evidence in the dissecting-room of pressure on the optic nerve being exerted by a diseased internal carotid artery, it appears evident that the clinical and pathological aspects of this subject require investigation.

On the other hand, the compression of the optic nerve by the ophthalmic artery against the optic foramen has received attention, and cases have been reported by Bernheimer (23).

It is quite clear that the optic chiasma may be compressed against the cranial base by an aneurysm of the anterior communicating artery. Mitchell's (98) case, in which bitemporal hemianopsia was produced by the pressure of an aneurysm of an anomalous communication between the two internal carotid arteries, has previously been noted. The only other example of bitemporal hemianopsia due to aneurysm was reported by Bramwell (27), and on this occasion the internal carotid was the affected vessel.

3. *Oculo-motor nerve.*—Aneurysm of the internal carotid has frequently caused paralysis of the third nerve; the position of the two in the cavernous sinus fully explains this, and the associated involvement of the fourth, sixth, and ophthalmic division of the trigeminal makes the localisation of the lesion usually a simple task.

Delpech (46) recorded a case of compression by an aneurysm of the cephalic part of the basilar.

Beadles (14), in his collection of 555 cases of aneurysm of the larger cerebral arteries, found that the oculo-motor was the nerve most frequently compressed by aneurysms of the posterior communicating artery, and that dilatation of this vessel clinically produced mechanical symptoms more frequently than any other (47 per cent.).

Aneurysm of the posterior cerebral or superior cerebellar arteries, near their origin from the basilar, must also easily cause oculo-motor palsy. This nerve lies in the angle formed by these two vessels at their origin, but the intimacy of this neuro-vascular relation is subject to some variation. In the majority, the two arteries arise practically by a common trunk, and consequently atheroma of either may easily produce ocular disturbance. Owing to the constant anatomical disposition of the posterior cerebral, which extends transversely cephalic to the nerve, it is possible, as Cushing has shown, for the artery to indent the third nerve in cases of cerebral tumour accompanied by any considerable alteration in the position of the brain stem.

Therefore oculo-motor palsy may result from aneursym of the internal carotid, basilar, posterior cerebral, and superior cerebellar arteries, or atheroma of the two latter, or even constriction by a normal posterior cerebral under certain pathological conditions.

The third and more disputed type of palsy due to vascular compression may be illustrated by this nerve. Many writers have published accounts of recurrent oculo-motor paralysis. The affection may be limited to one division of the nerve or even a single muscle, and no decisive pathology is known. It has been repeatedly suggested that the attacks are due to vascular spasm or paralysis of the vaso-motor nerves causing distension of the vessels and consequent compression of the nerve.

Fleming (60) has recently described an example of this condition in a girl of twelve, in which there were three attacks in three years. The disease is often associated with migraine, which is rather significant, as two theories for its etiology lend support to the suggested cause of transient and periodic oculo-motor paralysis. Some maintain that migraine is of vascular origin, whilst Spicer, Holmes, and Ormerod (127) consider it as secondary to cerebral œdema, a condition which could disturb the position of the brain stem, and consequently produce constriction of the third nerve, and similarly the sixth, paralysis of which is sometimes associated in these cases.

4. *Trochlear nerve.*—Special consideration of this nerve is unnecessary, as its position obviously renders it liable to compression by aneurysm of the same vessels as the third.

5. *Trigeminal nerve.*—The ophthalmic division may clearly be affected by aneurysm of the internal carotid in the cavernous sinus, but it is not so apparent that the other divisions may be affected through compression of the gasserian ganglion by the same vessel. Hutchinson (75) has recorded an excellent example associated with paralysis of the external rectus.

Romberg (114) described a case of intermittent neuralgia due to irritation of the gasserian ganglion by a rigid dilated internal carotid artery. Basilar aneurysm, especially the saccular type, may exert pressure on this nerve proximal to the ganglion.

6. *Abducent nerve.*—Reference has previously been made to affection of this nerve during its passage through the cavernous sinus, and many examples are to be found in the literature. But its possible compression against the basi-sphenoid appears to have been completely neglected. My examinations (see fig. 24) have shown that the nerve is in relation to this bone for fully half an inch, as it passes from its superficial origin to the cavernous sinus, and that the anterior inferior cerebellar artery is dorsal to the nerve (*i.e.* may compress the nerve against the bone under certain conditions) in 14 per cent. on the right side and 19 per cent. on the left. It is easy to see that an atheromatous vessel in this percentage might easily produce convergent strabismus, and very deep "grooving" of the nerve from that cause has been seen once in this investigation; and it is important to note that in this case the artery was in the ventral position, and had no resistant structure to compress the artery against. Space does not permit further discussion of this point, but it offers a feasible explanation of uncomplicated sixth-nerve paralysis, which has been unscientifically attributed to "its long course and exposed position."

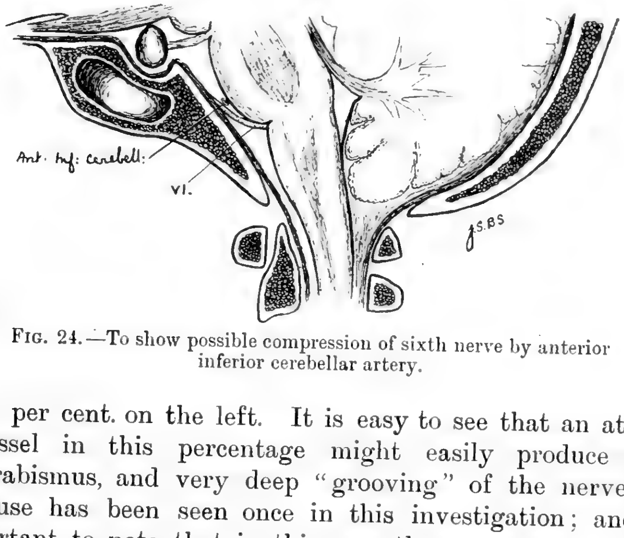

FIG. 24.—To show possible compression of sixth nerve by anterior inferior cerebellar artery.

Some years ago I saw a case which now appears to be probably an illustration, as the patient suffered from chronic nephritis and arterio-sclerosis in addition to the transient paralysis of the external rectus of one side, which at the time of examination defied explanation. There was no suspicion of syphilis, and the man recovered from the paralysis in a few weeks and is alive to-day, but unfortunately I have been unable to hear whether the paralysis has ever recurred.

Strangulation or constriction of the abducent can only occur when the artery occupies the ventral position; and from Cushing's results, this certainly appears to account for the frequent occurrence of affection of this nerve in cases of cerebral tumour, and possibly in several more obscure nervous diseases owing to the associated cerebral œdema.

7. *Facial and auditory nerves.*—These two nerves pursue the same course from their superficial origin to the internal auditory meatus, and for the greater part of this course are in contact with the petrous portion of the temporal bone. Consequently any compression paralysis of one is likely to be accompanied by paralysis of the other, and associated with loss of taste on that side owing to affection of the pars intermedia.

Loomis (91) has given an account of a case of saccular aneurysm of the basilar, which suffered from deafness, facial paresis, and loss of taste on the affected side, as well as symptoms resulting from compression of the trigeminal and hypoglossal nerves and the pyramidal fibres.

Hale White (66) has described a case of aneurysm of the vertebral which resulted in facial paralysis.

From the examination of a number of examples of advanced arteriosclerosis of the vertebral it seemed likely that this condition might easily cause compression of the seventh and eighth nerves, as the elongated sclerosed vessel was very frequently displaced laterally and found in contact with these nerves in the cerebello-pontine angle.

In Part I. it has been stated that the anterior inferior cerebellar artery usually crossed these nerves dorsally, and therefore it is easy to see how diseased conditions of this vessel might compress them against the bone. In the few where the artery crossed ventrally, the nerves would be in danger of constriction under the conditions mentioned by Cushing with regard to the third and sixth nerves. Ogle (104) reported an example of "stretching" of the facial nerve by aneurysm of the anterior inferior cerebellar artery.

8. *Glossopharyngeal, vagus, accessory, and hypoglossal nerves.*—All these nerves lie in contact with the occipital bone before they emerge from the cranium.

Compression by aneurysm of the vertebral is obviously possible, and several instances have been recorded. The hypoglossal has been most frequently affected, as is to be expected from the intimate relation which normally exists between the artery and this nerve. Aneurysm of the lower part of the basilar will also endanger the same nerves, and Klippel and Boetean (84) described such a case in which the patient suffered from persistent dysphagia, pharyngeal anæsthesia, palatal paresis, and defective speech.

Lebert (87) and Kingston (83) have each recorded instances of paralysis of the vagus and hypoglossal nerves associated with symptoms indicating compression of the pyramidal fibres as a result of aneurysm of the caudal part of the basilar.

From the position of the vertebral artery discovered in cases of advanced arterio-sclerosis it appeared reasonable to suppose that this condition might produce paralysis of one or more of the above nerves by compression, although no standard medical work is prepared to admit it. It appears infinitely more probable than compression of the optic nerve by an atheromatous internal carotid, proved illustrations of which have previously been quoted.

9. "*Grooving*" *of the brain.*—In conclusion, it is necessary to refer to the possible mechanical effect of the foregoing pathological conditions of the vessels upon the brain itself.

On several occasions aneurysm of the basilar or vertebral have compressed either the pons or medulla sufficiently to produce a depression, and this has resulted in clinical symptoms in several of the cases quoted. From their anatomical position the pyramidal fibres, either in the pons or medulla, are most exposed to such compression, and I have been unable to find reports of the clinical manifestation of compression of any other part of the brain tissue. Similarly, arterio-sclerosis may cause compression symptoms, and deep transverse grooving of the medulla has frequently been seen in the dissecting-room when marked sclerosis of the vertebral artery has existed.

Cushing found grooving of the pons, produced by *normal* transverse branches of the basilar, 25 times in 39 cases of cerebral tumour; therefore it is only likely that a sclerosed artery may cause considerable disturbance.

The compression of the brain or cranial nerves by aneurysm is generally realised by all, but the *conclusion* to be drawn from the examination of a series of diseased vessels is that it appears probable that simple arterio-sclerosis may mechanically produce symptoms more frequently than text-books suggest, and that many obscure palsies of the cranial nerves (especially the sixth) may in the future be proved to be a result of this condition.

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FURTHER STUDIES ON THE PERITONEUM AND INTESTINAL TRACT IN MONOTREMES AND MARSUPIALS. By W. COLIN MACKENZIE, M.D. (*From the Laboratories of the Royal College of Surgeons of England.*)

IN a previous communication[1] I drew attention to the presence of three primary peritoneal folds in Monotremes and Marsupials, which are traced in varying degrees throughout the Mammalia and play an important part in the fixation of the gut coadjusted to the erect posture of man:—

(*a*) Mesial fold approximating the colon to the pyloric region (see fig. 1).
(*b*) Duodenal or right lateral, passing from the ascending duodenum to the right aspect of the mesocolon (dorsal mesentery) of the distal colon (see fig. 1).
(*c*) Left lateral or lieno-mesocolic from the left, dorsal, or posterior process of the spleen to the left aspect of the mesocolon of the distal colon (see fig. 2).

In connection with studies on the spleen the importance was shown of the last fold as a factor in fixation of the colon in the left hypochondrium, to which dorsal fixation of the "descending" colon is subsequent. In this paper I propose to deal with the mesial and duodenal folds in the same two orders, viz. Monotremata and Marsupialia.

1. MESIAL FOLD.—My attention was first directed to this band in a study of the peritoneum of the koala (*Phascolarctos cinereus*). The intestinal tract of this Marsupial is characterised by the great development of the colon, which is suspended to the pyloric and commencing duodenal region by a tough fibrous band—mesial fold—measuring 1·5 cm. long and 1 cm. broad (see fig. 1). By means of this band we distinguish a left, narrow, looped distal colon and a shorter, but wider, right or proximal colon.[2]

(*a*) *Left or Distal Colon.*—This may measure 210 cm. in length. It is swung freely on its own mesocolon, the width of which may measure

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[1] *Journal of Anatomy*, vol. li. part i.

[2] "Factors concerned in causing Rotation of the Intestine in Man," J. E. Frazer and R. H. Robbins (*Jour. Anat. and Phys.*, 1915, L. 75–110). In this important paper the first reference is made to a retention band in the human embryo at the "colic angle," *i.e.* junction of mid and hind gut.

20 cm., and is attached along the dorsal abdominal wall mesial to the kidneys and psoas minor muscles.

(*b*) *Right or Proximal Colon.*—This measures in an adult 150 cm., and is swung, together with the small intestine and cæcum, on the common mesentery. Thus the intestine from the duodeno-intestinal flexure to the mesial fold may be lifted in one piece; and although three divisions of the common mesentery are recognised, yet these have a single root of origin. The greatest circumference of the right colon in the usual post-mortem state may equal that of the cæcum, viz. 15 cm.; but as we approach the pylorus it narrows, the gut becoming more contracted and the circumference 5–7 cm. The right colon is continuous with a large cæcum which represents the greatest instance of cæcal development in the Mammalia. It may reach 240 cm. in length. It tapers gradually to the blind termination, or terminates somewhat abruptly so as to give a vermiform character to the extremity, as first pointed out by Huntington.[1]

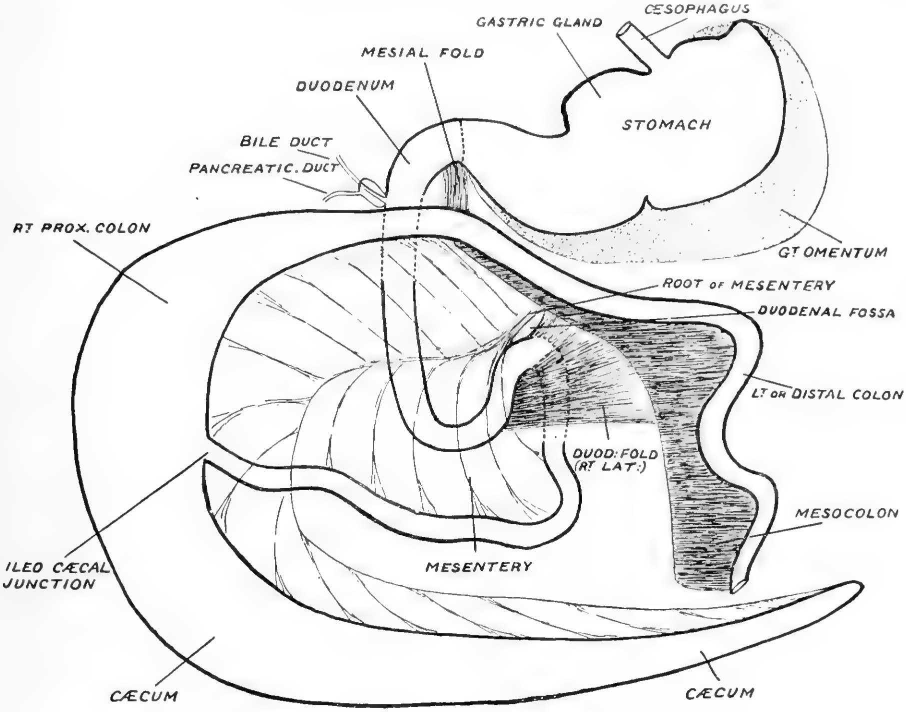

Fig. 1.—The gastro-intestinal tract of Koala (*Phascolarctos cinereus*).

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[1] *Anat. of Human Peritoneum and Abdominal Cavity*, Philadelphia, 1903.

2. RIGHT LATERAL OR DUODENAL FOLD.—This fold I also found to be well developed in koala. The duodenum forms a somewhat V-shaped loop, and we can distinguish a descending or proximal limb 7–14 cm. long, and an ascending or distal limb 4–8 cm. The duodenal loop is swung on a somewhat narrow mesoduodenum which is free, and, together with the duodenum, can be raised off liver, kidney, and dorsal wall. The descending limb is crossed below by the root of the mesentery and above by the right colon (fig. 1). Passing from the dorsum of the ascending duodenum to the right aspect of the mesocolon of the distal or left colon, close to its dorsal attachment, is a well-defined fold which is free below. Between the upper part of the fold, the root of the mesentery on the right, and the duodeno-intestinal flexure below is a fossa—the primary duodenal fossa—which in an adult measures ·5 cm. across and 1·25 cm. long, with a depth of ·75 cm.[1]

THE FOLDS IN THE MONOTREMES.

(*a*) *Platypus* (*Ornithorhynchus anatinus*).—From the pyloric knob the duodenum passes nearly vertically down, with a slight inclination to the right, for a distance of about 2·5 cm. to where the common duct enters (fig. 2). It then curves out for 6 cm., passing nearly horizontally to the right. After descending for about 5 cm., it finally passes in and upwards to the left, ventral to the lower pole of the right kidney, for about 5 cm., reaching the mesial line at the duodeno-intestinal flexure. In this last portion a transverse and ascending portions may be distinguished, although the latter may or may not be well developed. Thus we have a well-defined duodenal loop which is swung on a mesoduodenum or duodenal mesentery with a greatest width of 5 cm. The duodenal loop and mesoduodenum can be raised off the right kidney and dorsal wall. The distal 3 cm. of duodenum (asc. duodenum) is connected to the mesocolon of the left or distal colon by a fold—the right lateral or duodenal. This is free below; and between its upper extremity, which is usually well defined, the root of the mesentery on the right, and the duodeno-intestinal flexure below, a pocket is found. This is the primary duodenal fossa. It measures 1–2 cm. long and ·75 cm. in width.

From the duodeno-intestinal flexure we have swung on the common mesentery a portion of intestine together with the tubular cæcum (fig. 2). The part proximal to the cæcum is small gut, that distal is proximal or right colon. This right colon is 17 cm. long, and crosses the transverse

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[1] "The Intestinal Tract of Mammals," P. Chalmers Mitchell, *P.Z.S.* (Lond.), **1916**, i. 183–251. In this paper Dr Mitchell's more recent researches in connexion with the differentiation of gut patterns throughout Mammalia are dealt with.

duodenum, being traced upwards and to the left, ventral to the mesoduodenum, for about 6 cm. For the first 2·5 cm. of this portion, both colon and mesentery are free from mesoduodenum, though in one case I have seen bands of adhesion between colon and duodenum. We then find for the next 1·5 cm. that the mesentery is bound down to the mesoduodenum. Then on to its termination the right colon and mesentery are adherent to the mesoduodenum, constituting a definite "fixed" part of the colon tract. The termination corresponds to the junction of common mesentery and mesocolon of the left colon, and a distinct "tucking-in" effect is noted. The distance between the "fixed" colon and duodenum is 2 cm., and traces of a band—mesial band—may be present between the two, ventral to the mesoduodenum. From the "fixed" point the left or distal colon is continued on to the vestibule. It measures 22 cm., and

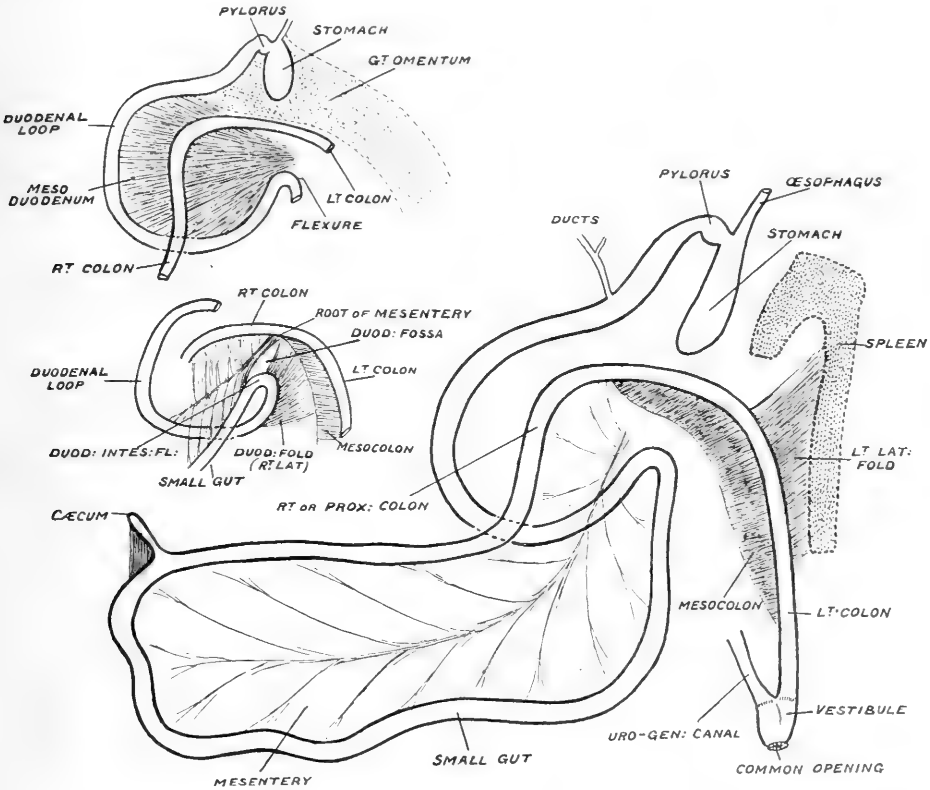


Fig. 2.—The gastro-intestinal tract of Platypus.

is swung freely on its own dorsal mesentery or mesocolon, which is traced back to the dorsal wall between the psoas muscles and has a greatest width of 5 cm. Related to its dextral aspect is the right lateral or duodenal fold, and on its left the left lateral or lieno-mesocolic fold (fig. 2).

(*b*) *Echidna* (*Echidna aculeata*).—There is a well-defined duodenal loop, not so constant in character as in Platypus. Owing to the dorsal fixation of the pancreas there is less mobility of the loop, though it can be raised off the liver and right kidney. The first or ascending portion, 2·5–5 cm. long, passes from the pylorus to the visceral surfaces of the right cystic and right lateral lobes of the liver. The duodenum then descends for 3 cm., and finally inclines inwards and to the left for 1 to 1·5 cm.—terminal or transverse portion—dorsal to the commencement of the mesentery and proximal colon, terminating at the duodeno-intestinal flexure, which is fixed dorsally about the root of the mesentery and pancreas. Compared with Platypus there is little more than a "tucking in" of the termination of the descending duodenum—reminding one of the condition in the American opossum. A membranous band may be traced from the flexure to the mesocolon of the distal colon, and a small duodenal fossa noted; but the particular point to be noted is, that associated with the dorsal fixation of pancreas and duodeno-intestinal flexure there is no duodenal fold nor fossa in the Echidna. As in Platypus, from the flexure we have swung on the common mesentery a portion of intestine together with the appendix. The portion proximal to the appendicular region is small gut, and that distal is right or proximal colon. This measures 30–35 cm. long, and passes with the mesentery ventral to the lower part of the descending duodenum, off which it can be lifted. It then becomes fixed dorsally about the root of the mesentery, pancreas, and duodeno-intestinal flexure for about 1·5 to 3 cm. No mesial fold is present, but fixation begins opposite the pylorus. This "fixed" colon marks the distinction between the proximal and distal colon, and corresponds to the junction of common mesentery and mesocolon of distal colon. The left or distal colon is mobile, being swung on its own dorsal mesentery or mesocolon. The degree of mobility is extremely variable, however. In one specimen in which this colon was bound dorsally the total length from "fixed" point to vestibule was only 13 cm., while in another with the left colon freely mobile on a defined mesocolon the length was 28 cm.

THE FOLDS IN MARSUPIALS.

(*a*) *Wombat* (*Phascolomys*).—There is a well-defined duodenal loop, and, as in the human, four portions may be recognised (fig. 3). It first passes down and out for 2–3 cm., then descends for 9–12 cm., then inwards for 1·5 cm., and finally passes up and to the left of the mid line to the duodeno-intestinal flexure for 3 cm. Owing to the dorsal fixation of the pancreas, which fills the loop, the duodenum presents little independent mobility, being less mobile than in other Marsupials—*i.e.* it has a shorter mesoduodenum, although I have not met any case of actual adhesion of the descending duodenum to liver or kidney as in

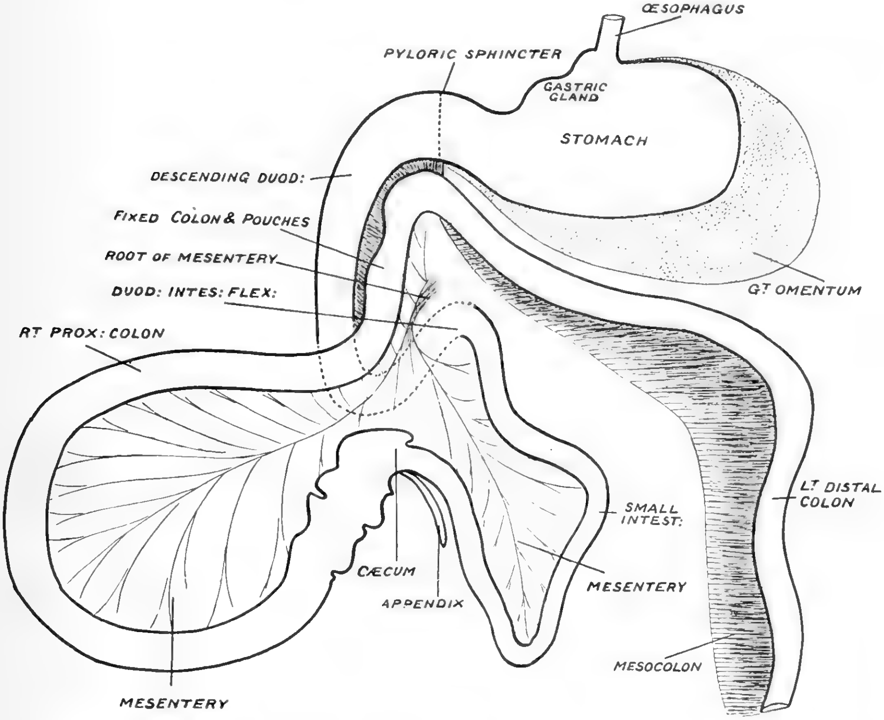


FIG. 3.—The gastro-intestinal tract of Wombat (Phascolomys).

Echidna In relation with the distal portion there is a right lateral or duodenal fold connecting it to the dorsal wall ventral to the left psoas minor and proximal to the attachment of the mesocolon of the left colon. The fold is transverse above, being ·5–1 cm. in width, while below the lower free margin is 2–2·5 cm. in width and more oblique. Between the upper part of fold—the root of mesentery—and duodeno-intestinal flexure a small pocket is noted—primary duodenal fossa. In one specimen with the duodenum more fixed dorsally no duodenal fold nor fossa could be demonstrated, thus resembling Echidna.

The ileo-cæcal region lies close to the root of the mesentery, and may be regarded as a fixed part of intestine. The distance between this region and the attached colon at pylorus is 6 cm. The proximal or right colon extends from the ileo-cæcal junction to the pyloric region, where it is firmly attached (mesial fold). It measures 175–220 cm., and is freely mobile, being suspended like the small gut on the common mesentery. Towards its termination the right colon ascends ventral to the loop of the duodenum, pancreas, and mesoduodenum, and becomes closely applied by adhesion to the descending and first part of the duodenum as well as to the pyloric region. It is interesting to note the presence of a dilatation, or often two large pouches on the colon at the duodenal attachment. The left or distal colon extends from the pylorus to the pelvis. It measures 230–280 cm., and is swung freely on its own mesentery or mesocolon, the greatest width of which may equal 25 cm. Dorsally the mesocolon extends mesial to the two kidneys, and its length is about 15 cm.

(*b*) *Kangaroos and Wallabies* (*Macropodidæ*).—The duodenum forms a V-shaped loop ventral to the right psoas, kidney, and the liver, so that a descending and an ascending portion may be recognised (fig. 4). Either the ascending or descending limbs may be the longer, though occasionally in the wallaby the two stems may be of equal length. In the kangaroo the descending limb varies from 5–8 cm. and the ascending from 7–9 cm. The duodenum does not cross the mid line. The loop is free, and being provided with a mesoduodenum it can be raised from the psoas and kidney. Ventral to the lower part of the loop is the proximal colon and the root of the mesentery. There is a well-defined duodenal or right lateral fold connecting the ascending duodenum and the mesocolon (dorsal mesentery) of the left or distal colon. It is narrow above but wider and more oblique below, where its width may reach 3 cm., and it may be traced caudally almost to the pelvis. The finger can be passed behind the caudal margin of the fold. Between the duodeno-intestinal flexure, root of the mesentery, and the upper margin of the fold is a small but well-defined duodenal fossa. The macropod has a well-defined cæcum much larger in the kangaroo (25–35 cm.) than in the wallaby (7–12 cm.). Variability is a characteristic of the wallaby's cæcum. The important feature of the colon is its relative fixidity to the pyloric sphincter and adjacent great curvature of the stomach. The position of the pyloric sphincter indicates the separation of the colon into two portions, viz. right, short, wide, proximal colon, and left distal colon. It is interesting to note the presence of a band 2–2·5 cm. broad which passes across the thickened pyloric sphincter from the right of the lesser to the right of the greater omentum. This band, though adherent slightly to the pylorus, forms a continuity between the colon in this region and the lesser omentum. In chameleon (as a type of Reptilia) the commencement of the colon is almost brought into contact with the pylorus by a ventral fold, which, crossing the latter, becomes continuous with the ventral mesogaster at the abdominal wall. In a bat from the middle of the fine mesial fold and from the gastro-hepatic omentum two slender membranes are given off, traceable to the ventral wall, where they meet. In a male adult kangaroo, ascending from the ileo-cæcal junction, which was close to the lower part of the duodenal loop, was 4·5 cm. of right colon. This was mobile, being swung on the common mesentery with the small gut—the distance between the two intestines being 10 cm. It lay with the mesentery ventral to the duodenal loop, off which it could be raised. It

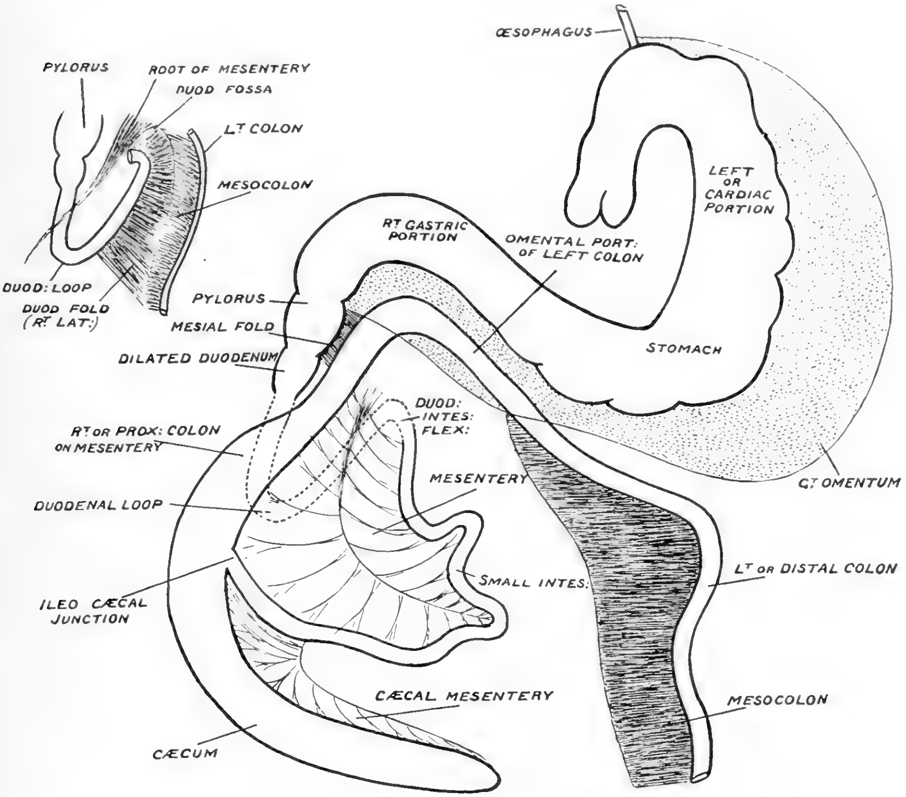


Fig. 4.—The gastro-intestinal tract of Macropus.

was closely applied at the pylorus by a mesial fold—the distance between colon and sphincter being only 1·5 cm. This was followed by a comparatively fixed portion of colon (proximal portion of distal or left colon), 14 cm., really attached to the mesocolon but closely related to the great curve of the stomach, owing to the fact that it and its mesocolon have been included in the great omentum. This is in contrast to the koala, and obviously is associated with the erect attitude of the macropod. The relationship is to the great curvature of the right division of the stomach—*i.e.* non-sacculated and sacculated parts,—and never extends to the apex of the stomach bend. The colon is nearer the greater curvature of the stomach in wallaby than in the kangaroo, and there is a closer attachment of the colon on the right than on the left in both. In other words, the fixation of colon and mesocolon to the great omentum begins from right to left.

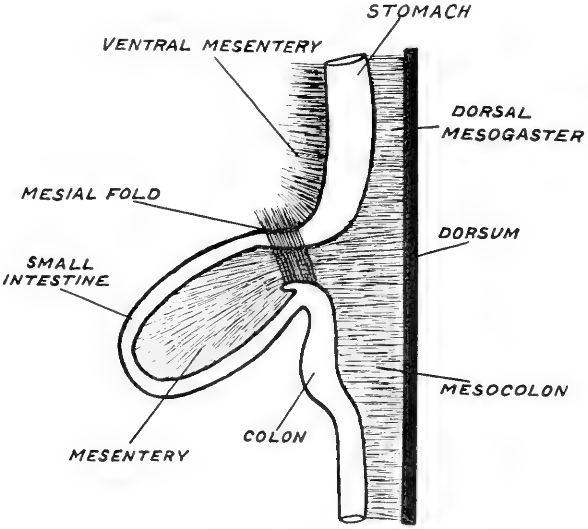


Fig. 5.—Mesial attachment in Chameleon (Reptilia).

In the above specimen the distance between the colon and the greater curvature near the pyloric sphincter was 2 cm., on the left 7 cm., and between these points 3 cm., *i.e.* the separation of mesocolon from great omentum was gradual; but in another the distance between the two on the right was 3·5 cm. and on the left 4·5 cm., and so the separation of mesocolon from great omentum was more sudden. In a kangaroo whose cæcum was 35 cm. long and right free proximal or mesenteric colon 10 cm.

the attachment at the pylorus and the great curvature was 17 cm.; and in a wallaby whose right free colon was 10 cm. the attachment was 14 cm. We frequently see peritoneal adhesions or bands from the dextral margin of the right free colon to the descending duodenum even as far as its lower third, and in a fœtus I have seen a band connecting the right colon to the whole of the descending duodenum. Here nature gives us an indication of her method of dorsal fixation of the colon. The common mesentery, though shortened here, is not dorsally fixed, *i.e.* its base or dorsal attachment is not lengthened; and, further, the mesoduodenum is present and the duodenal loop is mobile. The left colon begins opposite the pyloric sphincter, and, as above stated, is at first attached to the great omentum (lesser sac). Leaving the great omentum on the left, it is seen to be swung freely on its mesocolon (dorsal mesentery), the greatest width of which may equal 7–12 cm. This latter is attached dorsally between the two psoas muscles and the kidneys for about 10 cm., and gradually disappears into the pelvis. The left colon measures in the kangaroo 80–100 cm., and in wallaby about 46 cm. As showing the method of inclusion of the distal colon by the great omentum, a peritoneal band may be noted passing from the left of this structure to the distal colon, where it is commencing to be swung freely on the mesocolon. The large intestine may be thus summed up:—There is a well-defined, freely mobile cæcum. This is followed by a mobile, wide, but short right or proximal colon swung on the common mesentery with the small gut. This extends as far as the pylorus, where it is closely applied; and, furthermore, it is frequently connected by a band or bands to the descending duodenum. The left or distal colon begins opposite the pyloric sphincter. At first it is related to the great curve of the stomach, being with its mesocolon included in the great omentum (lesser sac). Leaving the omentum, it is traced into the pelvis, being looped and swung freely on its mesocolon or dorsal mesentery.

(*c*) *Tasmanian Devil* (*Dasyurus sarcophilus*).—On displacing the intestinal tract and dorsal mesentery to the left, the termination of the right lateral or duodenal fold is noted at a point 10 cm. from the pylorus. This corresponds to the termination of the duodenum, and here also a well-defined independent branch of the right vagus is noted, as shown in the diagram of my previous communication. So fine may be the fold here, that it may be necessary to stretch the last 2 cm. to detect it. The base of the fold, which is well defined, runs along the mesocolon near its dorsal attachment, from the root of the mesentery above, disappearing into the pelvis below. If the duodenum were looped this fold would form part of the boundary of a primary duodenal fossa. There is no mesial fold bringing the colon into relation with the pyloric region—the minimum interval in an adult being about 18 cm.

(*d*) *Australian Opossum* (*Trichosurus and Pseudochirus*).—1. *Trichosurus.*—A reference to my previous diagram (*Journal of Anatomy*, 1916, vol. li. p. 8) of Trichosurus shows, as in koala, a well-defined duodenal loop formed by a descending limb (10 cm.) and an ascending shorter one (4 cm.). The loop is mobile, there being a free mesoduodenum present. From the ascending limb is a well-defined right lateral or duodenal fold, transverse above and traceable to the mesocolon of the distal colon, and oblique below, being prolonged dorsally by the side of the attachment of the mesocolon into the pelvis, where in the female it may become continuous with the right broad ligament. The greatest width of the fold is 2·5 cm. Between the upper part of the fold—the root of the mesentery—and duodeno-intestinal flexure lies the primary duodenal fossa. As in koala, we have relatively a large cæcum (45–55 cm.) and right or proximal colon (25 cm.) swung with the small intestine on the common mesentery; and a left or distal colon (90 cm.) swung freely on its own dorsal mesentery (mesocolon), which is traced along the dorsal wall between the two psoas muscles for 7 cm. The colon is not, however, as in koala, closely attached to the pyloric region As the right colon, after crossing with the common mesentery the lower third of the descending limb of the duodenum, approaches the root of the mesentery, it narrows and becomes closely bound down for a limited extent of about 1 cm. to the mesoduodenum and pancreas; but in addition, for 3 cm. before the "fixed" area is reached the right colon may, as in the Platypus, be related by peritoneal adhesions to the descending duodenum and the mesoduodenum. Occasionally a fine process (mesial) may be traced from the "fixed" colon (corresponding to the separation of right from left colon) to the pyloric region across the pancreas—the distance between the two being about 3 cm. in an adult.

2. *Pseudochirus.*—Here the duodenal loop is not so mobile as in Trichosurus, nor is the right lateral fold so well developed. There is a relatively large cæcum (33 cm.) in contrast to the narrow large intestine. The right proximal colon for the first 6 cm. is swung freely with the cæcum and small intestine on the common mesentery. It crosses the lower part of the descending pole of the duodenum, and ascends more or less parallel to it—there being only an interval of about 1·25 cm.—till the commencement of the duodenum is reached. Peritoneal adhesions are noted connecting this portion of the colon and its mesentery to the duodenum and mesoduodenum. The left or distal colon measures 54 cm., and at first (8–10 cm.) comes into relation with the lesser sac, being included by the great omentum.

This portion forms an arch from right to left, following practically the great curve of stomach as far as the extremity of the right process of spleen. It is then continued into the pelvis, being swung freely on mesocolon off which the great omentum gradually recedes. As regards the fixation of colon, it is important to note that Pseudochirus approaches more closely the human type than Trichosurus.

(*e*) *American Opossum* (*Didelphys marsupialis*).—In this Marsupial the peritoneal arrangement is less specialised than in Platypus, although the stomach is more mammalian than that in Monotreme (see fig. 6). There is no approximation of the colon to the pyloric region—3 cm. intervening,—but a mesial fold is seen extending from the former to the mesoduodenum about the termination of the duodenum level. There is a descending duodenum with a "tucking in" at its termination. In some specimens this latter may be so developed as to produce a duodenal loop, but we never have the duodenal development seen in Monotremes or Australian Phalangers. From the dorsal aspect of the "tucked-in" part is a small band, 1 cm. long and ·5 cm. wide—right lateral or duodenal,—passing to the right aspect of the dorsal mesentery of the colon; and the earliest trace of a duodenal fossa is seen between it, the intestine, and the

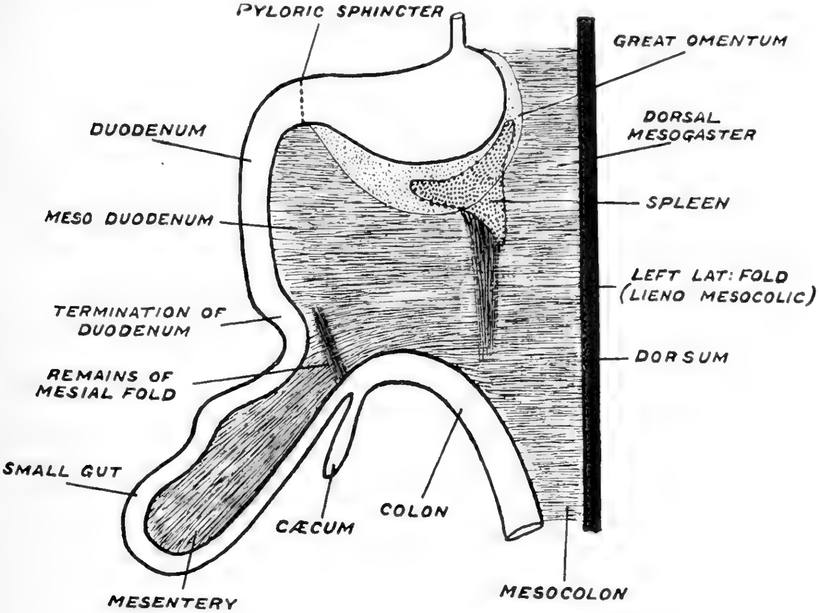


FIG. 6.—Intestinal plan of American Opossum (*Didelphys marsupialis*).

mesentery. If we divide or stretch the mesial and duodenal folds we can produce what corresponds to a simple reptilian condition (*e.g.* Agama) of an intestinal loop swung on a dorsal mesentery. There is a great omentum supporting the body and right process of spleen, while the left process is suspended on the lieno-mesocolic (left lateral) fold. This is free from the kidney. The tubular cæcum may be only 3 cm. long, and usually there is not more than 1 cm. of colon proximal to the mesial fold, *i.e.* swung on the mesentery of the small intestine. As in the Tasmanian Devil, we have a short primitive colon swung on its dorsal mesentery (mesocolon).

In a Virginian opossum (32 cm. snout to vent) the short wide cæcum was 5 cm. long, but there was no development of colon on the mesentery of the small gut, *i.e.* to right of mesial fold, which terminated on the mesoduodenum. The commencement of the colon was not approximated to the pyloric region, about 3 cm. intervening. There was marked inequality of growth between the mesoduodenum (3 cm. wide) and mesentery of small gut (8 cm.). The duodenum was better defined than in the preceding, and the "tucked-in" termination formed a small though decided loop. There was a duodenal band (·75 cm. long and ·3 cm. wide) from the duodenal loop to the mesocolon of the colon, and a duodenal fossa was present.

(*f*) *Bandicoot* (*Peramelidæ*).—In this Marsupial the intestine is less specialised than in either of the Monotremes (fig. 7). There is no defined duodenal loop, and the arrangement of the small gut resembles that of the carnivorous dasyures. In a specimen kindly given to me by Professor J. P. Hill the duodenum was defined as a portion extending 2·5 cm. from the pylorus, whose dorsal mesentery or mesoduodenum was narrowed—inequality of growth—compared with that beyond it. The greatest width of this mesoduodenum was 1·75 cm., while that of dorsal mesentery of small gut reached 7 cm. Apart, however, from this shortened mesentery we have, defining the termination of duodenal portion, a band—right lateral or duodenal—about 5 cm. long and passing dorsal to the mesentery of the small gut. This was narrow above at its attachment to the mesenteric edge of the duodenal termination, but broadening below at its attachment to the right aspect of the mesocolon, and finally became continuous, ventral to the colon before it enters the pelvis, with the left lateral or lieno-mesocolic fold. The result is that a pouch is formed between the ventral aspect of the gut and the junction of the two folds, which is traceable into the pelvis. The large intestine was swung on the mesocolon, *i.e.* was all primitive distal or left colon, there being no development on the common mesentery of the right, proximal, or mesenteric colon. At the commencement of the colon a curved cæcum was noted (5 cm.) connected to the termination of the small intestine. The distance between the pylorus and the ileo-colic junction, which were practically in the same mesial plane, was about 5 cm. At the latter a mesial band was seen, traceable only as far as the root of the mesentery and not to the pyloric region. The body (3 cm.) and large right process (5 cm.) of spleen are suspended on the great omentum, while connected to the small left process (1·25 cm.) and great omentum is the left lateral fold (lieno-mesocolic). Below, this is related at first to the left aspect of mesocolon, but more caudally to the dorsal wall between the dorsal attachment of the mesocolon and the left kidney. Its left margin is free, and measures 4 cm. The fold, with the pancreas it supports, is free from the dorsal wall and left kidney. Just above the level of the fundus of the bladder it is continuous, as stated, with the duodenal fold ventral to the colon.

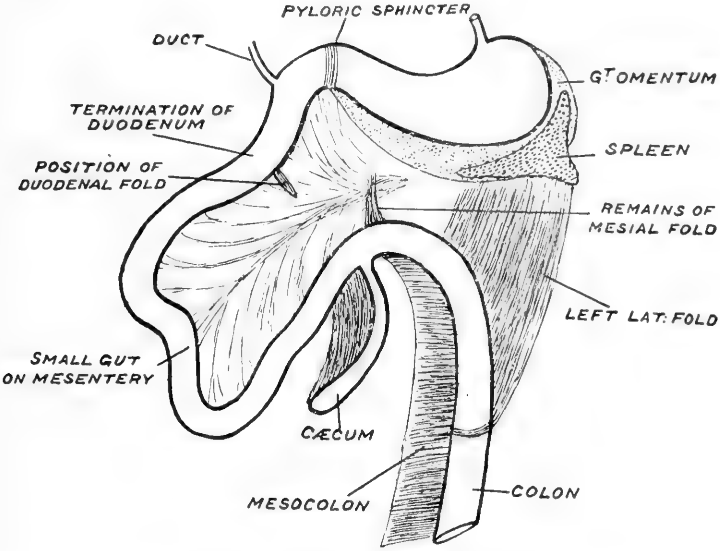


Fig. 7.—Gastro-intestine of Bandicoot (Peramelidæ).

Generalisations.

Owing to the diversity of intestinal types met with in the two orders Monotremata and Marsupialia, light is thrown on the method of fixation of the mammalian gut and the significance of bands in connection with the human intestine.

1. *Duodenal (Right Lateral) Fold.*—The definition of the mesoduodenum is a result of inequality of growth between it and the common mesentery,

dependent primarily, however, on the functional activity of the duodenum. The duodeno-intestinal junction corresponds to the termination of a direct branch of the right vagus, as is well seen in the Tasmanian Devil. The duodenal fold can only be regarded as a secondary or adhesion fold (zygosis) —a view held by Moynihan. An early stage of its development is seen in Didelphys, while its maximum development is seen in Trichosurus and the kangaroo. The disappearance of both the fold and fossa is associated with dorsal fixation of duodenal loop and pancreas, as is shown in Echidna and occasionally in the wombat. The duodenal fossa described in the above orders is the primary duodenal fossa, and is met with as such throughout the Mammalia up to Anthropoids.

2. The *left lateral* (*lieno-mesocolic*) *fold* as a factor in approximating spleen, colon, pancreas, and left kidney has been previously dealt with in detail.

3. *Mesial Fold.*—From the above studies the proximity of colon to pyloric region is seen to have "selection" value, being associated with development of the proximal colon—the part situated on the common mesentery. Absence of this proximity, with non-development of the mesial support, is associated with non-development of the right or proximal colon. The two extremes in Marsupialia are met with in the koala and carnivorous dasyures. Intermediate grades are met with in Peramelidæ and Didelphydiæ. The right colon—like the mesial hepatic lobe—might be regarded as a new or "experimental" colon. Here we find large and small cæca, appendices, coils and loops. The somewhat complicated right colon of rodents is simplified in Lemuroidea, and the human type appears in the Platyrrhines. In the Tasmanian Devil a well-defined direct branch of the right vagus is traced to the commencement of the colon (left, primitive, or mesocolic), so that development of the proximal or mesenteric colon is dextral not only to the mesial attachment but to the "vagal" area. It is interesting to note, as seen in Lemuroidea, Platyrrhines, Catarrhines, and great Anthropoids, that fixation of the right colon, *i.e.* shortening and dorsal fixation of its common mesentery, takes place from above downwards, *i.e.* begins at the mesial attachment. In the wombat the dorsal fixation of ileo-cæcal region is associated with a free right colon. From the mesial fold also begins the attachment of distal colon and mesocolon to great omentum, as evidenced in Macropus, and which extends in higher mammals to the spleen. Fixation of the "descending" colon follows fixation of the "splenic" flexure, proceeding from above downwards.

SOME NEW POINTS IN THE ANATOMY OF THE NASAL SEPTUM, AND THEIR SURGICAL SIGNIFICANCE. By J. L. Aymard, Captain R.A.M.C. (Temp.), Cambridge Hospital, Aldershot.

In recent years more particularly, the progress of the anatomy of a part appears to advance concurrently with its surgical or medical importance, and the anatomy of the nasal cavities is no exception.

The existence of two distinct movable joints in the septum does not appear to have been recognised as such, and the distribution of the perichondrium cannot be said to have been either described by the anatomist or understood by the surgeon.

The presence of a permanent vascular arrangement within the septal cartilage has apparently also been overlooked.

The septal cartilage is usually represented as being a perpendicular plate attached behind, below, and above, and is illustrated as presenting a free border covered only by the soft parts extending from the anterior border of the nasal bones forwards and downwards, and embedded between the median borders of the lateral cartilages. In the first place, exception must be taken to the designation of the upper lateral cartilages. They never exist as separate cartilages, neither are they separable except by force from the rest of the septal cartilage. Would it not be far more correct to describe each so-called lateral cartilage as the lamina triangularis, and the vertical cartilage as the lamina perpendicularis of one large cartilage, say the cartilago nasalis major? Professor Macalister has already described them as the "lateral expansions of the septal cartilage."

Cartilago nasalis major.

For practical purposes it would be much better to designate landmarks indicating the general position and extent of these cartilages, rather than give dimensions which vary so considerably in each individual case.

The lamina perpendicularis (L.P., fig. 1) of this cartilage presents four distinct borders.

The posterior border is firmly attached to the anterior edge of the lamina perpendicularis ethmoidalis (L.P.E.), the perichondrium of the former being directly continuous with the periosteum covering the latter, thus forming a strong ligamentous band.

The superior border between i. and ii., fig. 1, and A, fig. 2, is flattened and grooved to receive the prominence caused by the median junction at the under surface of the nasal bones; the groove is continued forwards, where it widens out to form the lamina triangularis (L.T., figs. 1 and 2) or so-called lateral cartilages. This plate L.T. is triangular in shape, its base being attached to the anterior edges of the nasal bones and its apex (fig. 1, iii.) extending to the superior angle of the anterior free border. In flat noses the lamina triangularis takes a gentle curve, and in sharp narrow ones a shape corresponding.

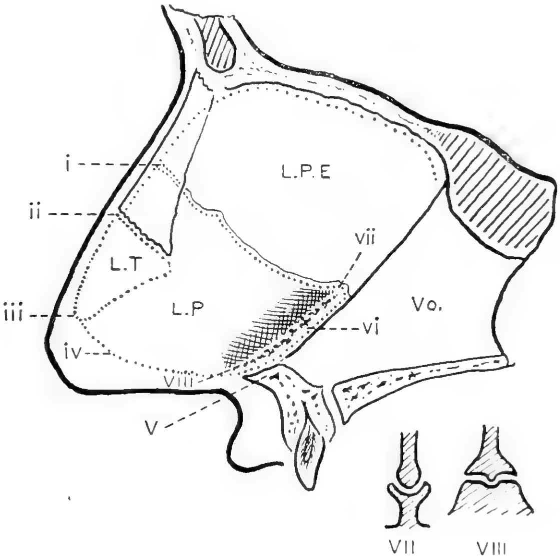


Fig. 1.—Septum of the nose showing the relationships of the septal cartilage.

VII., section across chondro-vomeral joint; VIII., section across chondro-maxillary joint.

The anterior border (fig. 1, iv.) is free and rounded, and can be readily seen through its coverings when the columna is held aside.

The inferior border is pear-shaped in section (fig. 1, vi.; also fig. 2, C) and more oval (fig. 1, vii., and fig. 2, B). Where it forms the chondro-maxillary joint with the crista incisiva (fig. 1, v., and fig. 2, D) it is flattened and terminates in an obtuse angle.

Surface markings for localising the posterior border of the lamina perpendicularis.—The posterior border of this lamina lies a third of an inch behind the anterior edge of the nasal bones, from which it slopes irregularly downwards and backwards.

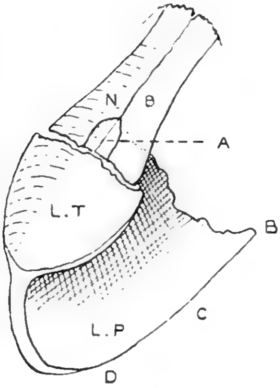


Fig. 2.—The parts of the septal cartilage. (For explanation see text.)

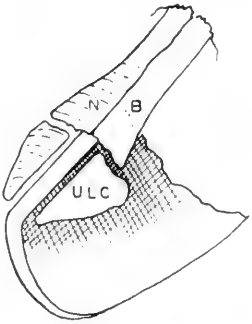
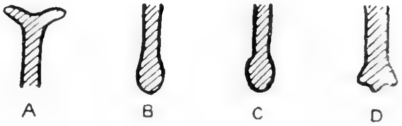


Fig. 3.—The parts of the septal cartilage as described in accepted works.



A, B, C, D, sections across the margin of the septal cartilage at the points indicated in fig. 2 by corresponding letters.

The Chondro-Vomeral and Chondro-Maxillary Joints.

The descriptions given in the leading works of anatomy merely state that the rounded end of the septal cartilage is received into the groove upon the anterior superior edge of the vomer and maxilla. This is correct as far as it goes, but at the same time they offer no proofs that this is not a mere osteo-cartilaginous junction.

The movement permissible at the lower septal joints forms a complete semicircle limited to a right angle each side of the perpendicular.

This, I think, is the only joint in the body permitting such extensive movements, and it appears to be constructed for the purpose. Further, it is, I believe, the only freely movable joint entirely composed of cartilage on the one hand, and a non-cartilage-covered bone on the other. A study of the joint demonstrates the fact that pressure upon the anterior superior surface of the septal cartilage causes it to bend in the direction of its long axis. Pressure upon the anterior inferior border causes the cartilage to bend obliquely upon itself, with a certain amount of transverse movement across the chondro-maxillary joint, combined with the lateral movement described.

Were it not for this joint, fractures and dislocations of the cartilage would obviously be far more frequent than they are. There would be no object in a joint of a similar description with the ethmoid plate, therefore it does not exist.

The chondro-vomeral joint (figs. 4 and 5), as I prefer to term it, is in every sense of the word a very perfect joint constructed for a definite object. The perichondrium and periosteum are in a sense continuous, but there is much more than this to be noted.

In the first place, whatever the condition of the vomeral groove may be —that is to say, though the edges may be irregular or even absent here and there,—the pear-shaped lower portion of the cartilage remains fairly constant and the capsular attachments likewise. The definite object of this joint is without doubt to allow of free lateral movement when from any cause pressure is applied from above.


Fig. 4.

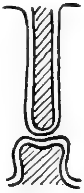


Fig. 5.

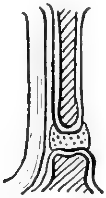


Fig. 6.

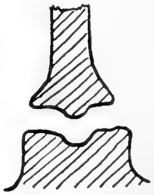


Fig. 7.

Fig. 4.—Transverse section of chondro-vomeral joint, with covering membranes removed.
Fig. 5.—Showing the disposition of perichondrium and periosteum at chondro-vomeral joint.
Fig. 6.—The same joint showing included fat and the covering of mucous membrane on one side.
Fig. 7.—The articulating surfaces of the chondro-maxillary joint.

A concussion plate is also provided in the shape of a layer of fat (fig. 7) between the periosteal perichondrial layers. The amount of movement possible, owing to the loose attachment of the perichondrium and periosteum, accounts for the fact that in a deviated septum the articular portion of the cartilage may easily occupy a transverse position across the groove (fig. 10), forming a projection not infrequently mistaken for a crest.

The chondro-maxillary joint.—The portion of the inferior border of the septal cartilage entering into the formation of this joint is usually represented by the anterior third. The cartilage is flattened and pointed (fig. 7) to rest upon the corresponding junction of the maxillary bones known as the crista incisiva. If this crest is rounded or otherwise shaped the cartilage takes a corresponding form. The corresponding coverings are similar to those of the chondro-vomeral joint, but much tougher, thicker and looser.

The apparent object here is to allow lateral rotation as well as a diagonal lock-gate motion.

The surgical importance of the above is that a blow directed upon the anterior edge of the cartilage bends it vertically upon itself, allowing a position to be taken diagonal to the crista incisiva and thus avoiding fracture. Another point is that, unless the membranous disposition and its nature in this area of the septum is thoroughly understood, the surgeon will find himself in difficulties.

The structures referred to should always be divided carefully with a blunt-pointed bistoury.

THE IMMEDIATE JOINT COVERINGS.

It is generally taught that the perichondrium covering the cartilage and the periosteum covering the vomer are continuous and attached along the crest. Only to a certain extent is this correct. The perichondrial arrangement is somewhat complex.

In the first place, careful investigation shows that the perichondrium does not, as the usual description implies, merely merge into the periosteum. Below the orifices of the chondro-vascular system (fig. 1, vi.) the perichondrium is continued loosely around the cartilage, and is continuous with the perichondrium of the opposite surface (fig. 5).

The periosteum (fig. 9), on the other hand, instead of being continuous with the perichondrium, as generally described, merely sends a process upwards to be attached to the perichondrium below the vascular openings, thus loosely covering the vomeral trough (sulcus vomeralis). The perichondrium in a similar manner sends a process downwards to join the periosteum, thus forming a joint ligament.

THE SURGICAL SIGNIFICANCE OF THE POINTS REFERRED TO.

The anatomy of the septal cartilage is principally interesting from the point of view of its partial removal, and here I must protest against the teachings in our leading text-books. Most nasal surgeons will agree with me that at least 75 per cent. of the cases presenting themselves for obstruction require the removal of only a moderate amount of cartilage and bone. The illustrations referred to advise an eighth of an inch of the anterior pillar of the septum to be left, whereas no experienced surgeon would think of leaving less than a quarter of an inch as a general rule. Further, the removal of the foundation of even this support by chiselling the maxillary crest is recommended freely without reserve and without any warning as to possible ultimate cosmetic effects. In the above case, we should teach the student not to remove a given area, but only just so much cartilage or bone as will give the necessary space for free passage of air or any other purpose.

Most surgeons use Ballenger's knife to remove cartilage, an ingenious but by no means ideal instrument. The usual procedure is to pass the knife along the upper edge of the area to be removed, down the back, and along the lower border. A reference to figs. 10 and 11 shows the difficulty (with the cartilage lying over, and particularly with three sides cut through) of cutting the cartilage close to the bone—since any downward pressure of the knife only further depresses the free cartilage. The point to remember is, that the piece of cartilage is left possibly lying across the vomer. It being mechanically impossible to remove this portion of the cartilage with Ballenger's knife unless the sides of sulcus vomeralis are absent, I prefer to cut flat the front, top, and back, and then remove the lower margin with a small trough-shaped gouge, having, if necessary, first divided the perichondrium with a blunt bistoury.

I would draw attention to the fact that the vascular system extends to the inferior angle of the antero-inferior margin of the cartilage, and that this blood-supply is not likely to be re-established if once cut off, which is of importance with reference to the pillar of support proposed to be left.

The Septal Coverings.

The perichondrium is very firmly attached to both surfaces of the cartilage, whereas the periosteum is only loosely attached to the bone and readily removed.

This attachment is marked everywhere except within the joint, and is due to the perichondrial processes which extend deep into the cartilage, so that when the membrane is removed these processes are for the most part torn and remain behind.

The periosteum and perichondrium are about equally adherent to the mucous membrane. Over the chondro-ethmoidal junction there is no special attachment, the one membrane merging into the other. Although the perichondrium is described as being divisible into many layers by mechanical means, I have been able to separate two layers.

The mucous membrane covering the septum has been fully described in standard works. I recognise three layers—a superficial, a middle, and an inner layer; between the two latter run the large vessels and nerves. The mucous membrane is closely attached to the perichondrium and periosteum except over the anterior third of the cartilage. In this position the membrane is very loosely attached. This fact should be noted, because it is entirely due to this loose condition in this region that failure so often takes place.

The usual incision for resection is made the full length required at the start, and cuts down to the cartilage, severing the perichondrium. The difficulty of endeavouring to separate the (in this region) tough mucous membrane from the closely attached perichondrium is the cause of operative trouble.

It is far better not to incise the perichondrium at first and only to make a sufficient cut to allow the introduction of the elevator used on Watkins Williams' principle. The incision can be enlarged to the full length when the membrane around is free for a good start.

Experts teach that the cartilage be now cut through and the elevator passed in between the same and the perichondrium and raised to the full extent. As a matter of fact, I think this procedure is more apt to take place by accident than design.

I would draw the attention of students to some other special points of importance. In the first place, all serious hæmorrhage can be avoided when operating if the positions of the larger trunks of vessels are remembered.

Just inside the anterior choana, behind its lower internal border, the palatine arteries must be carefully noted, especially when preparing to remove a portion of the crest.

The next group of vessels likely to be injured are those coursing along the vomer in the mucous membrane and in the region of its crest.

Should the mucous membrane be separated into layers (a not uncommon occurrence), it follows that in using the punch forceps these vessels are very likely to be divided between the bone and the punch. The palatine nerve may also be destroyed in a similar manner, thus leading to subsequent trophic changes in the mucous membrane.

The Significance of the Perichondrial Attachment in relation to the Operation of Sub-Mucous Resection.

In all the leading works upon this subject, this operation is *primarily* described as a muco-perichondrial detachment. I say primarily, because in one illustration the sub-mucous resection is referred to, and upon the same page it is described as muco-perichondrial, thus greatly confusing the student. It is clearly wrong to describe the operation as a sub-mucous perichondrial one. The illustrations upon this subject show quite correctly the mucous membrane loosely separated outside the speculum, whereas a sub-muco-perichondrium could not be so illustrated.

It is better to imagine the cartilage of the septum to be suspended in a covering (fig. 5), completely enclosed in front and only opening behind at the ethmoid margin, where it is anatomically continuous with its periosteum.

If this fact be grasped, it will be at once seen that any elevator once entering beneath this covering has no chance of exit except by force.

An elevator passed between the perichondrium and the cartilage and pressed downwards will find its way into the joint round the cartilage and up the opposite side. This fact can be readily proved by experiments.

The perichondrium itself is capable of being split into at least two different layers. Upon the lateral surface of the cartilage it is very firmly attached, and less so to the mucous membrane; but, once it reaches around the articular surface below the edge of the osseous groove, it is only loosely attached. The real periosteum rolls loosely over this bony edge, where it lines the bony trough (the sulcus vomeralis) and joins the opposite layer. If the cartilage is pushed well over to either side, the condition of the attachment, at one time loose and another time tight, is readily seen. A layer of fat is met with between the perichondrium and periosteum, and also between the periosteum and floor of the vomeral groove.

If the cartilage removed from a recent septum be examined it will appear to be destitute of covering, but an incision into it and firm pressure with an elevator will reveal the perichondrium intact. In some instances the perichondrium may be found to have been removed for a short distance on the proximal side of the cartilage, but seldom, if ever, on the distal one.

I am not advocating any attempt to remove the perichondrium intact. I think it is very questionable whether two intact surfaces of perichondrium left behind would serve any useful purpose, much less if they were in a bruised and torn condition.

THE MEMBRANOUS FOLDS OF THE CHONDRO-VOMERAL JOINT.

When passing the elevator downwards, it is a golden rule, upon approaching the joint, to stretch the parts well outwards, or, where considerable deformity exists, to cut the membrane *from behind forwards and towards the cartilage* with a curved blunt-ended bistoury. In most cases, if the elevator is pressed firmly outwards at this point and force used, the attachments will give way and the elevator pass downwards between the bone and the periosteum.

It must be remembered that, if the cartilage is (for example) leaning over to the left, the attachments on this side will be loose, and it is quite easy to force the elevator, membrane and all, into the joint. It is a good plan, therefore, when dividing the same with a bistoury, to press the cartilage well over to the opposite side to that on which the incision will be made, for by so doing the membranes attached are put upon the stretch.

The membranous folds of the chondro-maxillary joint are for all practical purposes similar, but (as before described) thicker, looser, and tougher.

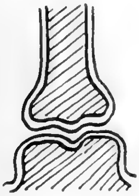


Fig. 8.

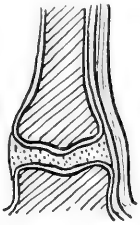


Fig. 9.

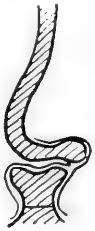


Fig. 10.

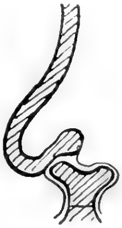


Fig. 11.

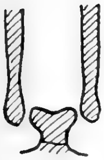


Fig. 12.


Fig. 13.


Fig. 14.


Fig. 15.

Fig. 8.—Section of chondro-maxillary joint showing the arrangement of the perichondrium and periosteum.

Fig. 9.—Another diagrammatic section showing the included layer of fat, the capsule and mucous membrane (on one side).

Fig. 10.—Dislocation of septal cartilage presenting a condition frequently mistaken for a spur of bone.

Figs. 11, 12, 13, 14.—Types of dislocation at the chondro-vomeral joint.

Fig. 15.—Type of chondro-maxillary displacements.

Fractures and Dislocations of the Septal Cartilage.

Although acute conditions of the above are frequently referred to in the text-books, their nature is seldom defined, for very obvious reasons, whereas the chronic conditions of luxation and dislocation are extensively dealt with. Fig. 10 is by no means an uncommon condition: fig. 11 is rare; while fig. 12 shows a direct dislocation either side of the sulcus vomeralis. I have never seen such a dislocation. The loose condition of the joint coverings allows for extensive displacement, but long before this direct lateral dislocation could take place the cartilage would probably double up. Further, unless the nose be crushed in or the cartilage be torn from the under surface of the nasal bones and the whole margin of the ethmoidal, any sudden dislocation is a mechanical improbability. In figs. 13 and 14 we notice quite common forms due to the absence of the rim of the sulcus. Fig. 15 is not an uncommon form. The main portion of the cartilage is retained in the vomeral joint, but that over the crista incisiva is dislocated diagonally.

With regard to fractures, I am far more inclined to look to the upper and posterior borders for possible trouble, because they are not provided with movable joints. Sufficient force applied to the anterior portion of the nose must do one of two things—either fracture and dislocate the nasal bones, or depress, dislocate, and tear the upper grooved edge of the cartilage from the under surface of the nasal bones, and in this case it will probably break it off from the lamina ethmoidalis perpendicularis, and thereby deflect the anterior aspect of the nose. In this way only can I account for the fact of a crooked nose without displacement of the nasal bones after an accident.

THE CHONDRO-VASCULAR SYSTEM.

Situated in an irregular line (fig. 1, vii.) will be seen the orifices and branching of the canals forming this complete system. These canals occupy the whole area described as the pear-shaped lower border, and also the portion anterior to this. They contain blood-vessels which arise from the mucous membrane and penetrate the perichondrium. These canals do not in any case communicate with each other, the vessels entering and returning by the same orifice. This vascular system is best studied and demonstrated in the septal cartilage of the sheep, when the septum, devoid of perichondrium, has become nearly dry. It may be beautifully seen by holding the cartilage before a strong light against a bright white background. In well-developed fresh human subjects the same arrangement can easily be recognised. These vascular canals are very characteristic and distinctive; they never anastomose, they present rounded ends, and seldom, when branched, project beyond the centre of the cartilage. Upon the other hand, single straight canals can frequently be seen passing across the upper portions of the cartilage.

Since writing this article my work as a plastic surgeon at the Cambridge Hospital, Aldershot, has given me an unique opportunity of examining a large number of costal cartilages, and I have no hesitation in saying that they possess a vascular system precisely similar to that described above in the septal cartilage. The system is very plain to the naked eye, and can be easily traced by the presence of blood. I therefore venture to disagree with those anatomists who describe such a condition as mere prolongations of persistent perichondral processes. The only difference I have so far been able to find between the vascular canals in fœtal cartilage and the vascular canals in the permanent cartilages referred to, is that in the former the ends of the canals are more pointed and branched, whilst in the latter they are rounded. Injections of these canals produce very interesting conditions, but their description I must leave to another occasion.

SURGICAL IMPORTANCE.

If the coverings of the cartilage are removed upon both sides at the chrondo-maxillary joint, the complete internal blood-supply of this thickened piece of cartilage will be found destroyed, a fact which leads to the question as to what eventually becomes of this pillar base which is left by the surgeon for cosmetic purposes.

I have very great pleasure in acknowledging valuable assistance from Professor Wood Jones, who very kindly prepared illustrations from my rough drawing, and from Dr Watkins Pitchford of the South African Institute for Medical Research, Johannesburg.

A SUBJECT WITH COMPLETE TRANSPOSITION OF VISCERA.

By M. Amin Abdel Rahman, *Assistant Professor of Anatomy, Cairo.*

The body was that of a typical old Egyptian male, between 85 and 90 years of age, very well developed, and without any external signs of disease. On opening the body on its ventral aspect we found the following conditions:—

1. *Thorax.*

(*a*) Right subclavian vein and right jugular united to form the right innominate, which was found passing downwards and to the left to meet the left innominate on the left side of the ascending aorta, to form the superior vena cava. As the right innominate vein passed to the left it crossed the arch of the aorta with the commencement of the subclavian, carotid, and innominate arteries, in that order from right to left.

(*b*) *Heart.*—On opening the pericardium, the heart was found lying in position with its apex pointing downwards, forwards, and to the right, instead of to the left. From the base of the heart the vessels were found arising in the following order:—

Pulmonary artery.—Arising from the left ventricular chamber, then going upwards and to the right, where it was found bifurcating under the arch of the aorta.

Aorta.—Arising from the right ventricular chamber and going upwards and slightly to the left, this was then directed upwards, backwards, and to the right in an arched manner, becoming continuous with the descending thoracic aorta that was found lying on the right side of the vertebral column. The vessels arising from the convexity of the arch were found, as already mentioned, to be, from right to left, the right subclavian, right carotid, and innominate; this last bifurcated at the left side of the root of the neck into left carotid and subclavian. The right vagus was found crossing the arch superficially, and giving in its concavity its recurrent branch, which looped below the arch and then went upwards to the right side of the larynx.

The auricle situated on the left side of the heart received from above the superior vena cava and from below the inferior vena cava. Its appendix was seen to a great extent from the front, overlapping the origins of the two great arteries.

The vena azygos major arched over the root of the left lung and opened into the superior vena cava.

The ventricle of the left side was found to have a very much thinner wall than the corresponding right chamber; it gave origin to the pulmonary artery, and communicated with its auricle by the tricuspid opening. This chamber occupied more than half of the anterior surface of the heart.

The ventricle on the right side had much thicker walls, about 23 mm. thick. It gave origin to the aorta, and communicated with its auricle by the mitral opening. This chamber occupied less than half of the anterior surface of the heart.

The auricle on the right side received the four pulmonary veins, coming from both lungs. Its appendix was hardly seen from the front of the heart.

(*c*) *Lungs.*—It was difficult to find the three fissures in either the right or left lung, but the left one was shorter and broader than the right.

(*d*) The *descending aorta* passed down on the right of the vertebral column and œsophagus, behind the root of the right lung and pericardium.

2. *Abdomen.*

The *liver* was found lying with its larger lobe and gall-bladder on the left side of the body, while the smaller lobe was on the right. The notch on the posterior surface for the œsophagus was to the right side of the middle line of the body, while that for the inferior vena cava was on the left. The round ligament passed towards the left from the navel, and disappeared in the fissure between the two lobes (fig. 1: 5).

Stomach.—The cardiac opening, fundus, and body were found lying in the right side of the abdomen; the pylorus, directed to the left, lay under the large lobe of the liver. The lesser curvature was directed from right to left and downwards, as was also the great curvature.

The *spleen* was found lying behind and to the right side of the fundus of the stomach, in the right hypochondriac region (fig. 1: 8).

Duodenum.—Began at the pylorus on the left side of the abdomen, and had the convexity of the second portion directed to the left. Its third part passed from left to right, crossing first the inferior vena cava and then the aorta, and ended on the right at the level of the 2nd lumbar vertebra, where it became continuous with the jejunum.

The *pancreas* had its head directed to the left, lying in the concavity of the duodenum, whilst its tail lay on the right side, abutting against the hilum of the spleen.

The *cæcum and appendix* were found in the left iliac fossa, with the appendix hanging into the cavity of the true pelvis (fig. 1: 13, 14).

Fig. 1.—From a photograph of the case here described.

1, aorta ; 2, superior vena cava; 3, "left" lobe of liver; 4, "right" lobe; 5, round ligament; 6, cardiac part of stomach; 7, pyloric part; 8, spleen; 9, tail of pancreas; 10, inferior mesenteric vein; 11, superior mesenteric vessels; 12, inferior vena cava; 13, cæcum; 14, appendix; 15, pelvic colon.

Colon.—The ascending part lay in the left side of the abdomen. The transverse colon began on the left, under the larger lobe of the liver, and ended on the right, under the spleen; from this the descending colon passed down on the right side of the abdomen to be continuous with the pelvic colon (fig. 1: 15).

The *kidneys* were both on the same level.

The *aorta* descended slightly to the right of the middle line and bifurcated into the common iliac arteries at the level of the 4th lumbar vertebra. Its branches:—

The gastric artery passed to the right and, after reaching the cardiac end of the stomach, followed the small curvature.

The splenic artery was directed to the right, ending in the hilum of the spleen.

The superior mesenteric artery passed downwards, forming a curve with its concavity to the left. The inferior mesenteric artery, taking origin from the right side of the aorta, crossed the right common iliac to become continuous with the superior hæmorrhoidal artery.

Inferior vena cava.—Formed on the left side of the body of the 5th lumbar vertebra by union of the two common iliac veins, the right vein crossing to the left. It then ascended on the left of the aorta, passing behind the third and second portions of duodenum and liver, to end in the left auricle after piercing the left side of the central tendon of the diaphragm.

The left spermatic vein ended in the left side of the vena cava itself, while the right vein ended in the right renal vein.

The right renal vein crossed superficial to the aorta to reach the vena cava, so was longer than the left.

The *inferior mesenteric vein* was found ascending on the right side of the abdomen and then crossing to the left at the level of the hilum of the right kidney, then crossing behind duodeno-jejunal flexure, passing superficial to the superior mesenteric artery, and then terminating in the superior mesenteric vein near its junction with the splenic.

The *superior mesenteric vein* was found on the left side of the corresponding artery, ascending to join the splenic vein, thus forming the portal vein on the left side of the middle line.

Mesentery proper.—The attached border of this was found fixed above to the right side of the body of the 2nd lumbar vertebra; it then passed downwards and to the left, ending in the region of the cæcum in the left iliac fossa.

The specimen was kept and preserved in gelatin jelly, after being injected in the usual manner with formalin solution.

NOTE ON LENGTH OF VERMIFORM PROCESS IN 220 CONSECUTIVE POST-MORTEM EXAMINATIONS. By S. RUTHERFORD MACPHAIL, M.D., *Derby Mental Hospital.*

THE following summary is based on the result of the examination of the vermiform process in 220 consecutive "sections," viz. 115 males and 105 females, in a period of four years. All the cases were adults—the youngest being 20, and the oldest 92 years; they are classified into those under 50 and those over 50 in each sex. The shortest appendix examined was 25 mm. (1 inch), the longest 187·5 mm. (7½ inches).

220 examinations gave an average length of 99·2 mm. (3·97 inches).

115 males, average length 102·2 mm. (4·09 inches).
105 females, average length 96·2 mm. (3·85 inches).

62 males under 50, average length 104·2 mm. (4·17 inches).
53 males over 50, average length 100·5 mm. (4·02 inches).

45 females under 50, average length 95·2 mm. (3·81 inches).
60 females over 50, average length 97 mm. (3·88 inches).

The average length was therefore slightly greater in males than in females. While there was not much difference in cases over 50 and cases under 50, the average for males under 50 was slightly greater than for those over 50, while the opposite was the case among females.

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THE PRIMORDIAL CRANIUM OF MICROTUS AMPHIBIUS (WATER-RAT), AS DETERMINED BY SECTIONS AND A MODEL OF THE 25-MM. STAGE. WITH COMPARATIVE REMARKS.

By Edward Fawcett, M.D., *Professor of Anatomy, University of Bristol.*

The specimen about to be described was kindly afforded me by Prof. J. P. Hill, of University College, London; it was cut by me into serial sections of 20 μ thick and stained with Mallory's triple connective-tissue stain, a stain which stains cartilage very well and (if properly manipulated) bone magnificently even in its very earliest condition. As a corrective another specimen was sectioned of 17·5 mm. total length, for which I am indebted to my colleague Dr W. D. Henderson; but of this specimen no model was made, nor was it necessary, for the conditions in the two were practically identical, the latter no doubt having shrunk somewhat in the various processes of hardening. In both ossification had proceeded to a degree which I had not anticipated, but the outlines of the ossifying cartilage were sufficiently clear to easily determine.

A model of the 25-mm. specimen was made at a magnification of fifty diameters by the wax-plate method. Both neural and visceral skeleton were modelled, and, as far as possible, the various bones were modelled too. Where accessory cartilages appear in connection with the covering bones, these are represented. Nerves and blood-vessels were, in cases of interest, modelled *in situ*, but for the most part were removed later. A separate model of the auditory capsule with membranous labyrinth was made.

General Description of the Complete Model.

In this description I have to a certain extent been guided by the very exhaustive description of the primordial cranium as given by Voit in the *Anatomische Hefte*, which will stand as a model of what a description ought to be; but, in the light of what seems to me to result from a prolonged series of researches into the primordial cranium of various mammals, some modifications seem desirable.

I have therefore determined on the following mode of description, viz.: firstly, to describe that part more especially connected with the central nervous system; secondly, to give an account of that part derived more particularly from the visceral appendages; thirdly, to describe the bones.

THE PRIMORDIAL NEURAL CRANIUM.

In describing this part in the light of what seems to result from my general researches I have adopted a different plan from that usually done, and therefore will consider the primordial neural cranium as consisting of the following parts:—

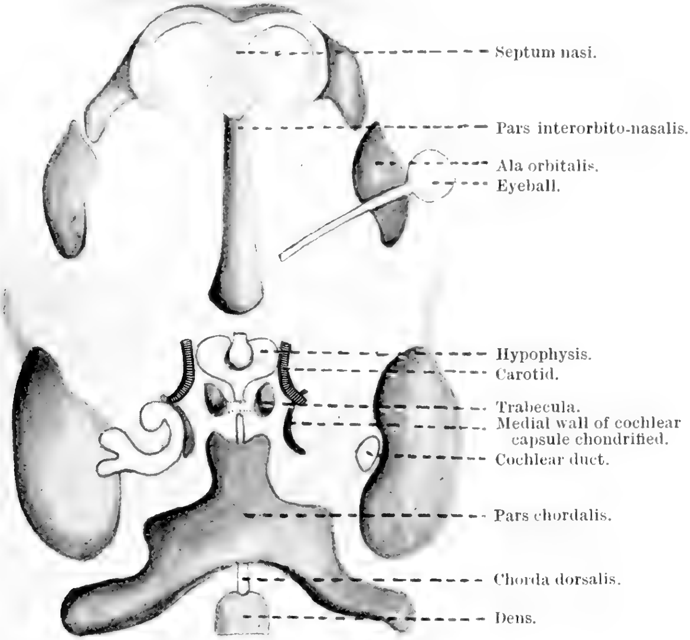
1. A central stem, to which are appended, at more or less constant positions,
2. Appendages to the central stem;
3. Lateral structures;
4. Commissures binding these lateral structures together;
5. Dorsal structures, viz. those which lie dorsal to the encephalon and form a cartilaginous roof to the cavum cranii.

1. THE CENTRAL STEM.

The central stem (Pls. 1, 2) stretches from the anterior margin of the foramen magnum to the tip of the nose, and as far forwards as the back of the nasal capsule consists of a long flattened plate, wide behind but narrowing as it is traced forwards to the hinder part of the nasal capsule. As far forwards as the region just named the central stem is wider than deep; but once it has been included in the nasal capsule (of which it forms the septum) it suddenly increases in depth (Pl. 9), so that its vertical height is very much greater than its transverse width.

Constituent Parts of the Central Stem.—So far as my experience goes, the central stem appears to be made up, in the various mammals examined, of the following parts, ontogenetically: (1) a hinder broad part closely associated with the chorda-dorsalis, differing in various genera in its relation to that structure. This part may be termed the *chordal part* (pars chordalis) (Pls. 1, 2). Anterior to the chordal part comes (2), a part of variable breadth, but still of considerable breadth, which is formed from trabeculæ, and may be therefore designated the *trabecular part* (pars trabecularis) (Pls. 1, 2). This is followed anteriorly by a part which posteriorly lies between the optic foramina, more anteriorly between the orbital cavities, and more anteriorly as the septum nasi. All these parts taken together form (3) the *interorbito-nasal septum* (Pls. 1, 2, 9). Ontogenetically these parts all chondrify independently of one another in Talpa, Cavia, Tatusia novemcincta, and ? Homo. In the latter the trabeculæ are formed quite independently of the pars chordalis and of one another, but I do not know if they arise independently of the interorbito-nasal septum.

Although I have no specimen of Microtus young enough to state definitely that this is the mode of development in Microtus, yet it seems justifiable to describe the central stem at the stage modelled on the same lines; and although no distinct traces of such subdivision are evident at this stage, all being now fused, it is not difficult to indicate with some precision their limits.



TEXT-FIG. 1.—Talpa. Chondrocranium of 11-mm. embryo, viewed from below.

Detailed Description of the Central Stem.—The chordal part of the central stem is roughly triangular in form as seen either from above or below (Pls. 1, 2). The basal region of this triangular plate forms the anterior concave margin of the foramen magnum. The apical region is marked by a small median foramen (Pl. 1), the remains of the basi-cranial fenestra through which the chorda-dorsalis dips down from the dorsal aspect of the chordal plate towards the pharyngeal root. The sides of the triangular plate are in relation with the auditory capsules (Pls. 1, 2) antero-laterally, whilst postero-laterally they are directly continuous with those outrunners of this region which I shall allude to as the exoccipital cartilages (pila occipitalia) (Pls. 1, 2), an imaginary antero-posterior line drawn through the hypoglossal canals only separating this part of the central stem from the exoccipitals which lie lateral to its basal angles. The pars chordalis is only directly connected with the auditory capsule through a cartilaginous commissure which, starting about the middle of the lateral border, fuses with the intero-medial aspect of the "vestibular" segment of the pars cochlearis, thus breaking up into two parts an otherwise large fissure between the pars chordalis and the auditory capsule. That part of the fissure which lies in front of this cartilaginous commissure—and which from its mode of development may perhaps be termed the *chordo-cochlear commissure* (Pls. 1, 2)—is the basi-cochlear fissure, whilst that part of the common fissure which lies behind the commissure in question is the foramen jugulare (Pls. 1, 2). To the under aspect of this chordal segment of the central stem are attached the prevertebral muscles which reach the head, and on the under aspect of the basal border at its most lateral part on each side is that part of the condyle which belongs to the pars chordalis.

Ossification has commenced in the pars chordalis, both of the entochondral and perichondrial type, and the chorda dorsalis can be traced along the whole length of the dorsal aspect of the ossifying cartilage, but deep to the perichondrial bone. This pars chordalis is therefore hypochordal in position. The chorda-dorsalis (Pl. 1) dips down through a small foramen at the anterior limit of the pars chordalis to reach the dorsal aspect of the pharyngeal mucous membrane, but it cannot be traced further onward at this stage. The foramen through which the chorda-dorsalis passes is the remnant of a much larger one in the younger stages, and represents the gap between the pars chordalis and the pars trabecularis—in other words, the basi-cranial fenestra of reptilia. In the stage modelled it lies opposite the anterior limit of the basi-cochlear fissure (Pl. 1), and exactly in the mid-line. In front of a line drawn transversely through this foramen we reach the pars trabecularis.

The Pars trabecularis (Pls. 1, 2).—That part formed by the fused trabeculæ, and in intimate relation with the hypophysis, is of about the same width as the anterior part of the pars chordalis. From behind forwards, as seen from above, it shows first a slight transverse ridge, the crista sellaris (Pl. 1); in front of this is a shallow hollow, the fossa hypophyseos

(Pl. 1), in which rests the hypophysis, and whose floor was no doubt at an earlier state perforated by its stomodæal duct. In front of the hypophyseal fossa the pars trabecularis narrows somewhat, and passes without line of demarcation histologically into the interorbito-nasal septum; but from this septum at its hindmost part laterally two triangular processes are given off, one on each side—alæ hypochiasmatæ (Pls. 1, 2); a line drawn transversely through their hinder edges will separate the pars trabecularis from the septum interorbito-nasalis. The prehypophyseal segment of the pars trabecularis is unusually long in Microtus.

From each side of the pars trabecularis two processes or commissures project, viz.: one, a more posterior, connecting the pars trabecularis with the cochlea behind the carotid artery: the other running also laterally and then posteriorly from the side of the pars trabecularis and in front of the carotid artery to the upper aspect of the apex cochleæ. These commissures may be termed respectively the *posterior* and *anterior trabeculo-cochlear commissures* (Pls. 1, 2, 5). Between the two lies the *foramen caroticum* (Pls. 1, 2, 5). From the front of the middle of the anterior trabeculo-cochlear commissure the *ala temporalis* projects in a general outward direction, and for this reason, perhaps, the term alicochlear commissure is the one usually given to what I have termed the anterior trabeculo-cochlear commissure. The posterior trabeculo-cochlear commissure seems to have escaped attention, save in the mole, in which it persists as a narrow bar, and as such is figured by Fischer, but not described. This commissure is narrow in the mole, but tends in many other animals to so increase in antero-posterior width as to ultimately fuse with the chordo-cochlear commissure and so obliterate the basi-cochlear fissure, of which it forms the anterior limit normally. This is evidently the case in the calf, ferret, hedgehog, and man. In the cat the basi-cochlear fenestra is persistent, and so it is in the rabbit (Voit) and in Tatusia. Only a few emissary veins pass through it when persistent.

The pars trabecularis in the mole arises as two cylindrical cartilaginous rods placed on each side of the hypophyseal duct at the 10–12-mm. stage; in Tatusia novemcincta as a perforated isolated plate interposed between, but independent of, both interorbito-nasal septum and pars chordalis of the central stem, at 12 mm.; in man as two precartilaginous rods on each side of the hypophyseal duct, independent of one another and of the pars chordalis, but as the interorbital septum is not chondrified at the stage in question, viz. 13·5 mm., it could not be determined whether it was independent of this.

The Pars interorbito-nasalis (Pls. 1, 2, 9).—This, to be alluded to subsequently as the interorbito-nasal septum, is recognised at its hindmost part by its giving off two triangular processes—the alæ hypochiasmatæ. These processes, triangular in form—since they always serve at some time or other for the attachment of one or other of the rectus system of muscles of the eyeball, they might as well be termed *processus musculosi*,—may be taken as indicating at their hindmost points the posterior limit of the interorbito-nasal septum. Laterally, in front of the alæ hypochiasmatæ, the interorbital part of the interorbito-nasal septum is bounded by the two optic foramina (Pls. 1, 2), which in Microtus are incomplete behind, recalling the condition observed in Metatheria. Anterior to these foramina the interorbito-nasal septum is fused with the anterior narrow limb or root of the ala orbitalis of each side, in front of which the septum is now narrowed and forms the median or septal boundary of the two orbito-nasal fissures and the two orbital cavities. It is customary to limit the term interorbital septum to that part which lies septal to the two orbital cavities, but from its mode of development I have here preferred to carry the septum further back, *i.e.* to the level of the hindmost part of the alæ hypochiasmatæ.

Beyond the orbito-nasal fissures the interorbito-nasal septum enters on its intra-narial stage, and may now be called the *septum nasi* (Pls. 1, 2, 9). As such its height greatly exceeds its width, and this more especially as it is traced forwards. The upper edge is partly subcerebral, say for one-third of its extent; the remainder is præcerebral.

The subcerebral part of the upper border of the septum nasi rises rapidly as it is traced forwards, until at its anterior end it culminates in a small backwardly curved *crista galli* (Pls. 1, 9).

From the hindmost part of each lateral border of this part of the septum the posterior wall of the lateral nasal capsule projects as the *planum antorbitale* (Pls. 1, 9, 10), and from the remainder of the lateral margin the *lamina cribrosa* (Pls 1, 9,) runs outwards. From the crista galli forwards the upper border of the septum nasi is præcerebral; and, at first flush with the rest of the tectum nasi, of which it forms the median part, it gradually sinks to a lower level so as to lie at the bottom of a median shallow longitudinal furrow, the *sulcus dorsalis nasi* (Pls. 1, 9). The subcerebral and præcerebral parts of the septum nasi are inclined to one another at an angle convex upwards.

The inferior border of the septum nasi (Pls. 2, 3, 9) lies almost horizontally and forms only a very obtuse angle with that part of the central stem behind it; in fact, so obtuse is this angle that the two are almost in the same horizontal line—a feature which seems to characterise the chondrocrania of all mammals which I have examined up to Carnivora at some stage or other of their development, *e.g.* Dasyurus viverrinus, Tatusia, Talpa, Erinaceus, Bos, Ovis, Lepus. In the 12-mm. stage of Tatusia the angle is more acute, and has straightened out at the 17-mm. stage.

The lower border of the septum is thicker than the upper one, and it is convex from side to side; for the most part it is free, but posteriorly it is directly continuous with the hinder wall of the nasal capsule, and anteriorly, shortly behind the tip of the nose, it is directly continuous with the floor of the nose at the *lamina transversalis anterior* (Pl. 2, fig. 1). Between the latter and the hinder end of the nasal capsule, the lower part of the septum nasi is in close relation on each side with the *paraseptal cartilage* and the *lamina transversalis posterior* (Pls. 2, 9, fig. 1), a very narrow septo-paraseptal fissure only intervening. The septum ends anteriorly by bifurcating into two laminæ which, recurving, form on each side the *cupula nasi anterior* (Pls. 1, 2, 9).

A small perforation is met with in the septum some distance above the anterior margin of the lamina transversalis anterior, and is termed the *foramen internasale* (Pl. 9). This foramen in the actual specimen is closed by fibrous tissue covered by the mucous membrane of the two narial passages. A slight swelling is met with not far from the anterior end of the septum, which, when covered by mucous membrane, simulates a septo-turbinal.

The total length of the interorbito-nasal septum amounts to almost the equal of the remainder of the central stem behind it.

2. STRUCTURES APPENDED TO EACH SIDE OF THE CENTRAL STEM.

These structures are from behind forwards.

(*a*) The exoccipital cartilage or pila occipitalis.
(*b*) The auditory capsule.
(*c*) The ala temporalis.
(*d*) The ala orbitalis.
(*e*) The lateral nasal capsule.

The two last may also be regarded as lateral structures, and may perhaps be considered later in that category.

(*a*) *The Exoccipital Cartilage.*

Each exoccipital cartilage (Pls. 1, 2, 3) springs from the corresponding basal angle of the triangular chordal part of the central stem, and it is in direct histological continuity with it. As before said, an imaginary line drawn antero-posteriorly through the hypoglossal canals—of which there are two in Microtus, viz. a smaller anterior and a larger posterior—will indicate its commencement. The subsequent ossification more precisely distinguishes the exoccipital cartilage from the pars chordalis. The under aspect of this region lateral to the hypoglossal canals forms the greater part of the occipital condyle. The anterior margin of the exoccipital cartilage projects freely under the cochlear part of the auditory capsule, from which it is separated by the foramen jugulare; and more laterally the same anterior margin is prolonged at first forwards under the pars canalicularis of the auditory capsule as a thin horizontal plate, the lamina alaris (Pl. 2), which is overlain by the 9th, 10th, and 11th cranial nerves, as well as by the processus perilymphaticus from the interior of the auditory capsule, and by the lateral sinus. Only a small fissure, itself hidden to a large extent by the terminal part of the lateral sinus, and visible only from the cavum cranii, separates the lamina alaris from the pars canalicularis of the auditory capsule. The fissure is the *recessus jugularis* (Pl. 5). As one follows outwards the anterior margin of the exoccipital cartilage, one finds that it projects laterally underneath the pars canalicularis of the auditory capsule, and here a certain amount of superficial fusion takes place between the two. The lateral projection is quite small in amount, being very different from that figured by Voit as the paracondyloid process of the rabbit; but it may be regarded as equivalent to the root of the *paracondyloid process* (Pl. 3) of the rabbit, and will be named as such here. The lamina alaris in this specimen is in process of ossification, both entochondral and perichondrial, the latter greatly predominating, but there is as yet no sign of ossification in the paracondyloid process. The anterior border of the exoccipital cartilage above the level of the paracondyloid process may be now traced upwards, arching over the hinder margin of the pars canalicularis as far as the cupula of the latter In this part of its course this border is separated from the auditory capsule by a well-marked fissure, which may be named the *fissura occipito-capsularis inferior* (Pls. 3, 4). On looking through this fissure from the exterior the lateral venous sinus may be seen.

The posterior margin of the exoccipital cartilage, a margin which is also median, forms a great part of the antero-lateral boundary of the foramen magnum. Opposite the cupula posterior of the auditory capsule the exoccipital cartilage may be regarded as ending; for though at this stage in Microtus no histological difference is evident, a distinct fissure exists in the calf at 19 mm., in the hedgehog at 25 mm., and in Tatusia novemcincta at 17 mm. In Microtus, as no histological boundary seems to limit the upward extent of the exoccipital cartilage at this stage, one may say that this cartilage runs directly into the supraoccipital cartilage above it (Pls. 3, 4). The supraoccipital cartilage, however, will be dealt with later.

(*b*) *The Auditory Capsule* (Pls. 1, 2, 3, 4, 5, 6, 7, 8).

This exceedingly complicated structure, which, taken as a whole, may with Voit be described as approximately ovoidal in form, whose long axis lies almost in the horizontal plane, contains the membranous labyrinth, and owes its general form especially to the structure composing this labyrinth. Thus the hinder cupola-like termination is caused by the bifurcation of the hind end of the crus commune into anterior (superior) and posterior semicircular canals, whilst the anterior cupola contains the anterior blind end of the ductus cochlearis. Two main parts are readily distinguished in the auditory capsule, viz.: a posterior—the pars posterior or pars canalicularis, which lies behind the plane of the foramen jugulare, and more particularly over the horizontal part of the exoccipital cartilage, and which forms the lateral wall in great part of the cerebellar segment of the cavum cranii; and an anterior—the pars anterior or pars cochlearis, which converges towards its fellow and the central stem, and so compresses the latter to a much smaller width anteriorly than posteriorly.

The auditory capsule is moored by various commissures to neighbouring parts of the chondro-cranium (Pls. 1, 2, 5). Thus the pars cochlearis by three distinct commissures is attached to other parts, as follow, viz.: an *anterior*, or anterior trabeculo-cochlear (so-called alicochlear), commissure stretches from the upper aspect of the cupula cochlearis forwards on the outer side of the carotid foramen to the so-called processus alaris of the corresponding trabecula; another, the posterior trabeculo-cochlear commissure, passes from the medial upper aspect of the cupula cochlearis medial to the foramen caroticum to the corresponding trabecula opposite the crista transversa, such as that is in Microtus; a third, which connects the hinder medial part of the pars cochlearis with the chordal segment of the central stem, may be called the chordo-cochlear commissure. This commissure separates the basi-cochlear fissure or fenestra in front from the foramen jugulare behind.

The pars canalicularis is very slightly and only superficially connected directly with the paracondyloid process of the exoccipital. At its hinder pole it is fused with the commencement of the supraoccipital cartilage (Pls. 3, 4), or perhaps in some cases, too, at this region with the upper end of the exoccipital where that is confluent with the supraoccipital cartilage. Between this commissure and the one between the pars canalicularis and the paracondyloid process of the exoccipital a narrow fissure—the *inferior (posterior) occipito-capsular fissure*—is found (Pls. 3, 4). Next, the anterior half of the upper margin of the pars canalicularis is connected with the orbito-parietal commissure and the anterior process of the supraoccipital cartilage by the *parietal plate* (Pls. 3, 5). Between the parietal plate and the posterior commissure of the pars canalicularis is a fissure, the *superior occipito-capsular fissure* (*v.* fissura parieto-capsularis). The anterior part of this fissure transmits the lateral jugular vein from the interior of the skull, and is sometimes called the *foramen jugulare spurium.* In front of the parietal plate the auditory capsule is separated from the orbito-parietal commissure by the large *fenestra spheno-parietalis.* As Voit says for the rabbit, "Die Form der ganzen Labyrinthkupsel wird so sehr von ihrem Inhälte, dem häutigen Labyrinth bestimmt, dass ich es für zweckmässig halte, hier die Abbildung eines Modelles eingefügen . . . von dem häutigen labyrinth. . . ." So in the description, which follows here very closely that given by Voit for the rabbit, it will be seen that the external form of the capsule is intimately dependent on that of its contents.

The Pars canalicularis (Pls. 1, 2, 3, 4, 5, 6, 7, 8) contains especially the utricle and the semicircular canals, and is influenced in its entire form chiefly by the course of the latter. It is pyramidal in form, *i.e.* a three-sided pyramid whose borders are clearly formed by the projections caused by the semicircular canals which run in the interior. These borders, which from their position may be named superior, infero-lateral, and infero-medial, all converge posteriorly on the posterior pole of the pars canalicularis. Three surfaces are to be distinguished, viz. a supero-medial, a lateral, and an infero-medial.

The Borders (Pls. 5, 6, 7).—The upper border or *prominentia semicircularis anterior* commences at the posterior pole, ascends in an arched fashion in a forward direction to end anteriorly in an ill-marked prominence, the *prominentia utriculo-ampullaris superior.* This prominence is rendered indistinct by the *parietal plate* springing from the region where it is found, and the upper border itself is only visible from within, since it is overlapped by the *opercular process* of the anterior prolongation of the supraoccipital cartilage (tectum synoticum). Along this upper border runs the *sinus sigmoideus*, from the region of the foramen jugulare spurium to the posterior pole of the pars canalicularis.

The Infero-lateral Border (Pls. 3, 4, 6)—*prominentia semicircularis posterior*—commences at the pole of the pars canalicularis and runs forwards, outwards, and downwards at an angle of about 70° with the upper border to end near the inferior basal angle of the lateral surface. Not far from the anterior end of the prominentia semicircularis posterior commences the prominentia semicircularis lateralis, but this will be described along with the lateral surface of the pars canalicularis.

The Infero-medial Border of the pars canalicularis (Pls. 5, 7) commences behind at the posterior pole, forms the upper boundary of the sulcus sigmoideus, in which the sinus sigmoideus lies, and is caused by the *prominentia cruris communis* in its hinder part and more anteriorly by the arch of the posterior semicircular canal; anteriorly it ends in a rounded swelling, the prominentia utriculo-ampullaris posterior, just below and behind the meatus auditorius internus. The prominentia cruris communis is perforated by a small canal for the ductus endolymphaticus (Pls. 5, 7); behind this canal is a groove which later sinks into a large foramen leading into the site of bifurcation of the crus commune into anterior and posterior semicircular canals. The groove is caused by the pressure of the saccus endolymphaticus.

The Surfaces (Pls. 1, 2, 3, 4, 5, 6, 7, 8).—The lateral surface of the pars canalicularis is triangular in form, with apex of triangle backwards at the cupula posterior. The upper and lower sides of the triangle are, as we have seen, formed respectively by the prominentia semicircularis superior and prominentia utriculo-ampullaris superior and the prominentia semicircularis posterior, and the upper side has projected upwards from about its anterior third the parietal plate (Pl. 5).

The base of the triangular lateral surface is of interest in that it gives forwards at its upper angle the tegmen tympani (Pls. 3, 6), which is a curved shell-like cartilage projected forwards over the incus and malleus cartilages, and medially it is fused with the lower part of the parietal plate and with the lower edge of the orbito-parietal commissure: below the tegmen tympani, the base projects as the crista parotica (Pls. 3, 6), which is separated from the tegmen tympani above by a notch, the incisura incudis. The crista parotica, itself somewhat pyramidal in form, by its apex gives attachment to and is fused with the styloid process, between which and the lower side of the crista parotica the facial nerve emerges, the site of emergence being the *primary stylomastoid foramen*. Below this a small notch interrupts the base, the *incisura stapedii* (Pl. 6), which lodges the hindmost end of the stapedius muscle. Below this again is a slight elevation which may from its position be termed *mastoid process*, but it does not give origin to any muscles, nor does it project in any way like that of the rabbit as figured by Voit.

The surface enclosed by these three sides, viz. the *lateral surface*, is directed somewhat backwards as well as outwards. This surface is marked near its middle by a curved almost horizontal ridge, a ridge which, slightly concave upwards, is caused by the out-bulging of the fossa subarcuata superior, and may be therefore termed the *prominentia subarcuata superior* (Pl. 6). From the base of the crista parotica another semicylindrical ridge runs downwards and backwards towards the anterior end of the prominentia semicircularis posterior. This ridge is the *prominentia* *semicircularis lateralis.* A triangular hollow is now mapped out between the three just-named prominences, bounded above by the prominentia subarcuata superior, below and behind by the prominentia semicircularis posterior, below and in front by the prominentia semicircularis lateralis. This area corresponds with the solid mass of cartilage intervening between the fossa subarcuata superior and the cavities of the lateral and posterior semicircular canals, and which is termed the *massa angularis.*

The lateral surface of the pars canalicularis is overlapped from above as far as the most prominent part of the prominentia subarcuata superior by the *opercular process* of the anterior prolongation of the supraoccipital cartilage.

The Medial or Supero-medial Surface (Pls. 5, 7, 8), like the lateral, is triangular in form, the upper side of the triangle being formed by the prominentia semicircularis anterior, which is better marked from this aspect than the lateral. The lower side of the triangle is formed to a large extent by the *prominentia cruris communis,* but more anteriorly by the *prominentia utriculo-ampullaris inferior.* The base of the triangular surface, which is anterior, is an imaginary line drawn vertically through the hinder part of the meatus auditorius internus, commencing above at the prominentia utriculo-ampullaris superior and ending below at the prominentia utriculo-ampullaris inferior. A large part of this surface is sunk beneath the prominentia semicircularis anterior to form the *fossa subarcuata anterior* (Pls. 5, 7), a fossa which, ovoidal in form, is very deep everywhere, but below and in front is directly continued by a foramen of considerable size into the vestibular cavity, and on one side the middle of the floor of this fossa subarcuata anterior was perforated to allow of blood-vessels passing through to the exterior. This fossa seems to vary in depth at different ages, for in the cellular and precartilaginous condition it is scarcely present, but later it gradually deepens until it is only separated from the exterior by a thin wall of cartilage, which is the upper part of the massa angularis. This fossa frequently goes by the name of floccular fossa; perhaps the term parafloccular would better meet the case. It must, however, be at a comparatively late period of fœtal life that this body occupies this fossa, for I have only once seen it so doing, and that in Miniopterus Schreibersi, at the 17-mm. stage.

The Infero-medial Surface (Pls. 5, 7) is only to a slight extent visible from within the cavum cranii. It is for the most part directed towards the exoccipital and particularly to the lamina alaris thereof, between which and the inferior medial surface in question is a narrow fissure, *the recessus supra-alaris* (Pl. 5), visible from the interior of the cavum cranii, and which in the region of the posterior (inferior) occipito-capsular fissure is visible from the exterior, but anteriorly is closed by the fusion of the lateral border of the lamina alaris with the auditory capsule, and cranialwards is continued directly into the recessus jugularis. But towards the cavum cranii this cleft enlarges to form the sulcus sigmoideus, in which the sinus sigmoideus runs forwards in order to appear in the region of the recessus jugularis as the jugular vein. The whole fissure is thus only visible from the cavum cranii on removal of the sinus sigmoideus (Pls. 5, 8). The infero-medial surface is triangular in shape, the base of the triangle being anterior. Laterally it is bounded by the prominentia semicircularis posterior, and medially by the prominentia cruris communis, and more anteriorly on the medial side by the prominentia utriculo-ampullaris inferior. Immediately medial to its lateral boundary a fossa is met with, which perhaps deepest posteriorly may with Voit be termed the *fossa subarcuata posterior.* It is formed at the expense of the under aspect of the massa angularis; medial to the fossa subarcuata posterior the inferior surface is slightly hollowed out by the sinus sigmoideus. The basal region of the inferio-medial surface is slightly convex from side to side, and corresponds with the terminal part of the posterior semicircular canal and its ampulla, and the 9th, 10th, and 11th nerves lie beneath it here, as well as the terminal part of the sinus sigmoideus.

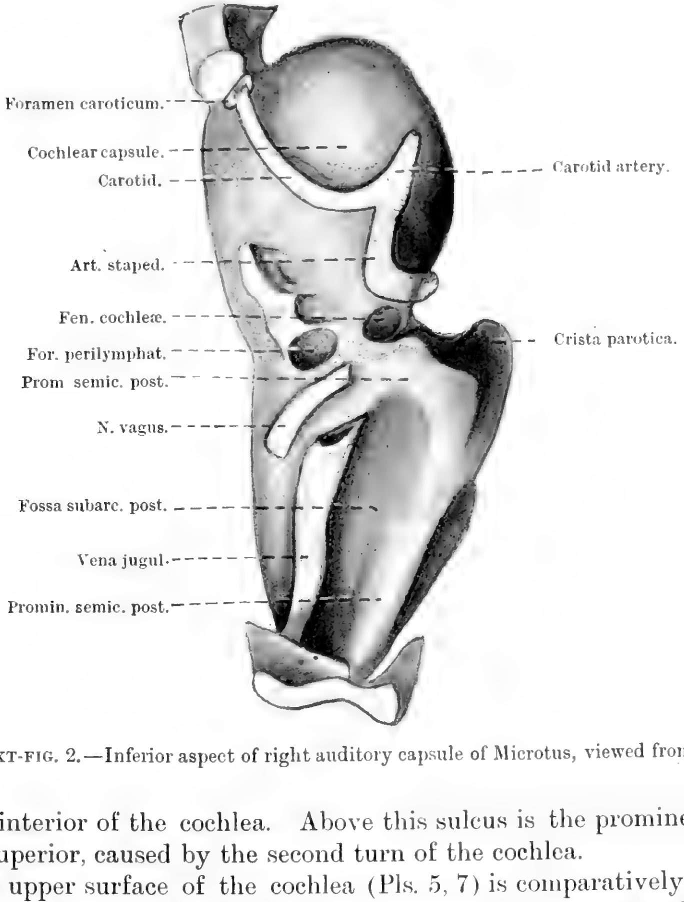
The basal region of the pars canalicularis is partly free and partly continuous with the pars cochlearis of the auditory capsule (Pls. 3, 6, 7). The free part lies medial to the basal boundary of the lateral surface of the pars canalicularis. The free part mainly looks forwards, and from above downwards shows first the forward continuation of the *tegmen tympani* (Pls. 3, 6), whose under surface and root are hollowed out to form the *epitympanic* recess, in which the body and posterior process of the incus cartilage are to a large extent lodged. This fossa deepens inferiorly on the upper aspect of the crista parotica to form the *fossa incudis,* in which lies the pointed posterior end of the short or posterior process of the incus cartilage. Immediately medial to the epitympanic recess and fossa incudis lies the *sulcus facialis* (Pl. 6), in which the facial nerve in its downward and backward course lies. This sulcus is continued downwards and backwards deep to the *crista parotica*, where it still lodges the facial nerve but also the *musculus stapedii*, and when the facial nerve turns forwards out of the primary stylomastoid foramen, the sulcus, now entirely occupied by the stapedius muscle, ends at the *incisura musculi stapedii* (Pl. 6) in the basal border of the lateral surface.

The remainder of the basal surface of the pars canalicularis is continued directly into the pars cochlearis of the auditory capsule. The pars cochlearis (Pls. 1, 2, 3, 5, 6, 7) is a dome-like structure whose general direction is forwards and medianwards, and its apex or *cupula* ends just below and lateral to the carotid foramen. It contains the cochlear duct and the saccule, and may be divided into two parts, a hinder and a fore part. The hinder part is characterised by the presence of a number of openings, viz. on the lateral aspect the *fenestra vestibuli* (Pl. 6), on the infero-lateral aspect the *fenestra cochleæ* (rotunda) (Pl. 6), and on the infero-medial aspect the *foramen perilymphaticum.* On the median wall, at the bottom of the meatus auditorius internus (Pl. 5), the openings for the divisions of the auditory nerve are met with. This hinder part into which these various openings lead may with Voit be termed the "vestibular" segment of the pars cochlearis.

The lateral wall of the vestibular segment (Pl. 6) bears the large oval fenestra vestibuli which lodges the foot of the stapes. Above the fenestra vestibuli the lateral wall of the vestibular segment is grooved by the stapedial artery and the facial nerve (Pl. 6), the former lying more anteriorly. Below the fenestra is the hinder part of the *promontorium* (Pl. 6), caused by the first turn of the cochlea; and below this, at its hinder end, the fenestra tympani (cochleæ) is met with—but that will be referred to again in connection with the inferior surface of the vestibular segment of the pars cochlearis.

The inferior or ventral surface of the vestibular segment of the pars cochlearis is convex and wide from side to side. It is perforated by two foramina, of which the more lateral is the fenestra tympani (cochleæ) and the more medial the foramen perilymphaticum (aquæductus cochleæ). The fenestra tympani (cochleæ) is closed by a thin membrane, the secondary tympanic membrane, and it is separated from the foramen perilymphaticum by a bar of cartilage, under which are placed the jugular sinus and the root ganglion of the vagus, from which starts here to run outwards and upwards the auricular branch of that nerve. The foramen perilymphaticum, which is directed somewhat medially as well as inferiorly, transmits the saccus perilymphaticus and a vein which opens into the jugular vein. This complete separation of the foramen perilymphaticum from the fenestra cochleæ (foramen rotundum) is perhaps in Microtus a precocious condition, for I have not observed it at what may be assumed to be the corresponding period in any other mammal. The ductus perilymphaticus, after leaving the interior of the auditory capsule in the manner aforesaid, runs medially and opens into the subdural lymph space. Its interior is intersected with fine connective-tissue strands.

Passing now to the cochlear segment of the pars cochlearis, we see on its lateral surface (Pl. 6), from below upwards, first the prominentia cochlearis inferior, caused by the first turn of the cochlea. This is crossed at right angles in its hinder part immediately below the foramen vestibuli (ovale) by a sulcus for the stapedial artery, which in Microtus is of very large size, larger in fact than the internal carotid. Above the promontory and running downwards and forwards from the foramen vestibuli is a sulcus, the *sulcus septalis*, which corresponds with the septum spirale of the interior of the cochlea. Above this sulcus is the prominentia cochlearis superior, caused by the second turn of the cochlea.



TEXT-FIG. 2.—Inferior aspect of right auditory capsule of Microtus, viewed from below.

The upper surface of the cochlea (Pls. 5, 7) is comparatively small. It is connected anteriorly with the processus alaris of the trabecular part of the central stem by the anterior trabeculo-cochlear commissure, lateral to which lies a longitudinal sulcus which contains the great superficial petrosal nerve, and which broadens posteriorly to form the sulcus ganglion geniculi; more laterally there is a flattened area for the tensor tympani muscle (Pl. 6). To the lateral side of this appears a well-marked band or ridge of dense fibrous tissue, which reaches outwards almost to the goniale, and most likely represents the forerunner of the processus cochleariformis.

The medial surface of the pars cochlearis (Pls. 5, 7) is posteriorly and below continuous with the inferior surface in the neighbourhood of the foramen perilymphaticum; further forwards it is continuous with the upper surface of the central stem. Along the upper aspect of the chordo-cochlear commissure more anteriorly it is again below continuous with the inferior surface of the "cochlear" segment of the pars cochlearis through the basi-cochlear fissure. In front of this fissure the medial surface is continuous through the posterior trabeculo-cochlear commissure with the trabecular region of the central stem, and in front of this it runs into the lateral wall of the carotid foramen. In the hinder vestibular segment of this surface the meatus auditorius internus is met with, which by a septum running from before backwards is divided into two main parts, viz. an upper and a lower (Pls. 5, 7). The upper segment has two foramina in it—one more anterior, the foramen faciale, and one more posterior, the foramen acusticum superius, through which the nerves to the utricle, the ampullæ of the anterior and lateral semicircular canals, as well as the upper nerve to the saccule, run. The *foramen acusticum inferius* is divisible into three parts, viz.: a small opening immediately below the crista falciformis, for the lower nerve to the saccule—the saccule being here, as described by Voit for the rabbit and for man, supplied by two nerves; a larger area for the cochlear nerve; and a small foramen in the hinder wall of the lower half of the meatus auditorius internus—the *foramen singulare*, through which the nerve to the ampulla of the posterior semicircular canal runs. The upper anterior wall of the meatus auditorius internus is formed by the *suprafacial commissure* (Pls. 5, 7), a cartilaginous bridge which runs from the cochlear part of the pars cochlearis to the vestibular part of the same region, and develops as a spur from the cochlear segment to grow backwards and outwards over the facial nerve and fuse with the vestibular segment over the foramen acusticum superius. Before concluding the description of the meatus auditorius internus it may be said that the saccule lies on the lateral side of the crista falciformis.

No foramen faciale externum vel secundarium, such as is described by Voit, exists at this stage in Microtus, but it is quite possible that it may be present at a later stage, for the appearances suggest it.

The Interior of the Auditory Capsule (Pl. 8).—This, like the exterior, is divisible into a pars anterior and a pars posterior, of which the former is subdivisible into the cavum vestibulare and the cavum cochleare; whilst the latter is divided into the cavum utriculo-ampullare and the spaces for the semicircular canals, including the crus commune.

The cavum vestibulare fills the whole of the vestibular segment of the cochlear capsule and receives the openings of the foramina acustica, fenestra vestibuli, and the foramen perilymphaticum (aquæductus cochleæ) and the foramen rotundum.

The posterior wall of the aquæductus cochleæ is bent upwards into the interior of the cavity so as to form a sort of septum, which lies anterior to the cavum utriculo-ampullaris inferius and shuts it partially off from the main cavity. The medial border, too, of the aquæductus cochleæ is bent upwards and later outwards into the main cavity, so that it forms a small roof to the saccus perilymphaticus. This roof perhaps more strictly belongs to the crista falciformis, which is bent out at its lower margin to form a well-marked ridge in the cavum, which may be traced back along the lateral side of the foramen singulare (canal for nerve to ampulla of posterior semicircular canal), and which may be traced forwards to direct continuity with the septum spirale, a small foramen, for the nerve to the lower part of the saccule, slightly interrupting that continuity. The septum spirale from this junctional point sweeps upwards along the roof, then forwards and downwards along the lateral wall, and finally inwards along the floor of the pars cochlearis, where it dies away. It separates partially the cavity of the first turn of the cochlea from that of the second turn. As has been before stated, the saccule rests against that surface of the crista falciformis directed towards the cavum vestibulare, and above and behind the saccular fossa (fovea saccularis or spherica) and in the same horizontal line with the foramen acusticum superius is the fovea utricularis or elliptica for the upper part of the utricle. On the lateral wall of the cavum vestibulare, almost opposite the outbent lower margin of the crista falciformis, a small groove is found on the upper surface of the inwardly projected upper margin of the foramen cochleæ. This groove lodges the hinder part and blind end of the cochlear duct. The subdivisions of the cochlear cartilaginous tube are not sufficiently well defined at this stage to warrant description, but the hinder part of the scala tympani (the cavum perilymphaticum tympanicum) can be followed back to the aquæductus cochleæ as the saccus perilymphaticus, and thence through the foramen to the subdural space, as already described. In all cases the parts of the membranous labyrinth are separated from the cartilaginous wall of the cavum vestibulare by soft connective tissue of very loose texture, and the membranous semicircular canals lie always near the convexity of the corresponding cartilaginous canals. As a point of accuracy one may say that the prominences designated utriculo-ampullaris are not really caused anywhere by the utricle, but actually in each case by the corresponding ampulla, together with the adjacent part of the corresponding semicircular canal.

(c) *The Ala temporalis* (Pls. 1, 2, 3, 5, 9).

This exceedingly interesting structure projects laterally from the middle of the anterior aspect of the anterior trabeculo-cochlear commissure and soon afterwards divides into three processes, of which one, a *median* process, projects downwards and inwards under the anterior trabeculo-cochlear commissure and comes into contact with the cartilaginous part of the pterygoid (Pl. 9), and at this stage this medial process is surrounded by perichondrial bone. The remainder of the ala temporalis runs outwards into the large spheno-parietal foramen and partly breaks it up into an anterior and a posterior segment (Pls. 2, 9), of which the anterior segment persists as the superior orbital fissure (sphenoidal fissure), whilst the posterior—the representative of the fenestra pro-otica of the reptile—becomes gradually obliterated by the conversion of the membranous tissue closing it into bone belonging to the hinder part of the ala temporalis. This outwardly running part of the ala temporalis is slightly concave on its upper aspect, where it lodges the under surface of the semilunar (Gasserian) ganglion. It terminates by turning somewhat sharply upwards and dividing into two branches, of which the hinder and smaller is placed behind the mandibular division of the fifth cranial nerve and is tipped with ectochondral bone; the more anterior and much larger branch, which perhaps may be looked upon as the processus ascendens of the ala temporalis of other quadrupeds, is split by a fissure into two parts, between which the forward continuation of the stapedial artery enters the cavum cranii. This processus ascendens is not continued up so far as the orbito-parietal commissure, as was shown to be the case and so figured by Broom (*Proceed. Linn. Soc. N.S.W.*, 1902) in Dasyurus viverrinus, but stops at some distance from it, and its place is taken by the bony alisphenoid, which has ossified ectochondrally for the most part.

The relations of the ala temporalis to neighbouring structures are of some interest. On its upper aspect lies the Gasserian ganglion, together with the first and second divisions of the fifth nerve; the mandibular division of that nerve passes through the notch between the two branches into which the horizontal part of the ala divides, the notch then being homologous with the foramen ovale; and in this connection it is interesting to note that of the three main branches of the fifth nerve only the mandibular in any sense perforates the ala temporalis either at a notch or a foramen.

Thus it is only, so far as my series go, in Carnivora and in man (? other Primates) that the maxillary division perforates the cartilage of the ala temporalis through a foramen rotundum for that purpose. In all others that I have had the opportunity of examining, *e.g.* Dasyurus, Tatusia, Talpa, Erinaceus, Crocidura, Lepus, Bos, Ovis, Cavia, Miniopterus, a foramen rotundum is absent,[1] and the mandibular nerve either passes through a notch behind the horizontal part of the ala temporalis or on its lateral aspect, or through a foramen ovale (as in Bos and Ovis). So far as muscles are concerned, in Microtus from the under aspect of the horizontal part as far outwards as the notch for the mandibular division of the fifth nerve the pterygoideus internus arises, whilst from the processus ascendens cartilaginous as well as ossified part the pterygoideus externus arises. It has already been stated that the forward continuation of the stapedial artery passes through the fissure in the processus ascendens.

Mode of Development of the Ala temporalis.

So far as this could be determined from the material at hand, the ala temporalis seems to chondrify independently, but in Talpa from the first a well-marked outrunner of dense connective tissue seems to project from the trabecula dorso-anterior to and independent of the anterior trabeculo-cochlear commissure, and I have been unable to make out independent chondrification here. It is quite evident, however, in Cavia and Tatusia, Bos and Felis catus, as well as in man; and in man at the 27-mm. stage all the appearances associated with early joint formation are seen—all, in fact, save the actual joint cavity. The whole appearances presented strongly suggest its homology with the palato-quadrate cartilage, as surmised by Broom and supported by Watson,[2] and very strikingly is this view supported by the conditions observed by me in 7-mm. embryos of an unknown species of lizard from India. In man, as I pointed out in this journal, the anterior trabeculo-cochlear commissure, which may or may not actually reach the cochlear capsule (I have sections of 27-mm. human embryos which clearly show this commissure reaching the cochlea, as was seen by Jacoby) chondrifies independently and afterwards ossifies independently. As cartilage it has been called the processus alaris in man, and as bone the lingula, but this independence is possibly a secondary condition. Owing to want of material I am unable to say how the ala temporalis of Microtus arises, nor do I know if a separate ossific centre appears in the anterior trabeculo-cochlear commissure.

(*d*) *The Ala orbitalis* (Pls. 1, 2, 3, 9).

This structure, which becomes attached to the central stem at the hinder part of the interorbito-nasal septum, not only belongs to the

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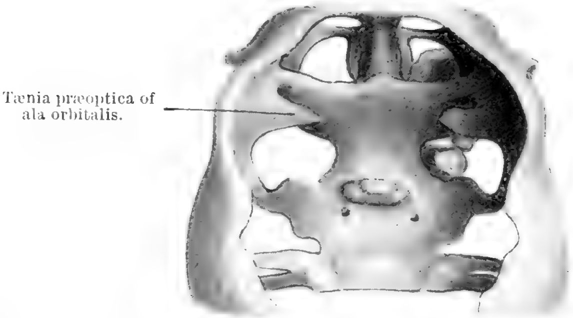
[1] Miss Esdaile pictures the ala temporalis of *Perameles nasuta* as having a foramen rotundum (*Phil. Trans.*, Series B, vol. 207).

[2] *Phil. Trans.*, Series B, vol. 207.

appendages of that stem, but may be included amongst the lateral structures composing the primordial cranium, and it will be referred to again when these structures are described. It may be described as a large, somewhat triangular plate, whose base enters into the lateral wall of the cavum cranii, whose main mass forms a part of the floor of the cavum, and whose apical region is attached to and fused with the interorbito-nasal septum anterior to the foramen opticum. In mammals belonging to the Eutheria it is usual for the apical or medial region of the ala orbitalis to bifurcate into a limb, tænia præoptica, which passes towards the interorbito-nasal septum anterior to the optic nerve and foramen and fuses with that septum, and a limb which reaches the upper aspect of the ala hypochiasmata behind the optic foramen and so indirectly is fused with the central stem at the interorbito-nasal septum. This hinder limb is the tænia metoptica, or at all events its representative; but in Microtus, in the specimen modelled and in the "control" specimen not modelled, this hinder limb does not reach the ala hypochiasmata, hence the foramen opticum is not completed posteriorly, and a condition results which recalls that of the Metatheria (Pl. 11), where no foramen opticum is present, the optic nerve passing through the superior orbital fissure (sphenoidal) accompanied by the other nerves destined to the orbit. In Microtus the tænia præoptica is very narrow, as in the mole and hedgehog, and it very closely approaches in form that of Dasyurus viverrinus, in which its mode of growth may very easily be followed, for at the 7-mm. stage its median pointed end is not fused with the interorbito-nasal septum (text-fig. 3), whereas in a stage a little older fusion has taken place. In Tatusia both tæniæ reach the interorbito-nasal septum, but the ala orbitalis lateral to the foramen opticum is perforated



TEXT-FIG. 3.—Part of chondrocranium of Dasyurus viverrinus, from above. 7-mm. stage.

by a foramen of considerable size, though smaller than the foramen opticum, which very much recalls the foramen epiopticum of Lacerta. To return again to the general description of the ala orbitalis. Its posterior border forms the anterior limit of the common spheno-parietal foramen, and at the same time the anterior border of that part of this large foramen in front of the ala temporalis; in other words, the anterior boundary of the superior orbital fissure (sphenoidal). The anterior border of the ala orbitalis is directed towards the nasal capsule, from whose posterior wall it is separated by the *orbito-nasal or ethmoidal fissure* (Pls. 1, 2, 3), through which the nasal (ethmoidal) nerve re-enters the cavum cranii. The outer end or base of the ala orbitalis has two basal angles, of which the anterior is prolonged forwards to meet and fuse with a like but backwardly growing process from the frontal prominence of the pars intermedia of the lateral wall of the nasal capsule (Pl. 3), and the result of fusion is the *commissura spheno-ethmoidalis* (Pl. 3). The mode of growth of the spheno-ethmoidal commissure may be observed in Bos, for at the 19-mm. stage both the anterior basal process of the ala orbitalis and the process from the frontal prominence of the nasal capsule are separate from one another, but at the 25-mm. stage they have fused. In Ovis, according to Dursy—and I can confirm his observation on the specimens I have,—the two do not fuse, at all events in the stages I have sectioned; but it is the general rule to have a complete spheno-ethmoidal commissure, and it may be of large size. The posterior basal angle of the ala temporalis of Microtus is prolonged backwards as the orbito-parietal commissure to fuse with the parietal plate (Pls. 1, 3, 5, 7) which is developed in connection with the pars canalicularis of the auditory capsule; but where one ends and the other begins in Microtus I know not. In Tatusia the greater part of this orbito-parietal commissure grows forwards from the parietal plate, as may be seen at the 12-mm. stage, where fusion has not taken place between the parietal and orbital elements of the commissure.

(*e*) *The Lateral Nasal Capsule.*

This, though being appended to the central stem, will be considered after in the special section dealing with the nasal capsule. We may therefore at once enter upon the consideration of the lateral structures, *i.e.* those structures which enter more especially into the constitution of the lateral wall of the cavum cranii.

3. LATERAL STRUCTURES.

Under this heading fall the ala orbitalis, the parietal plate, and the supraoccipital cartilage, and incidentally the commissures which bind them together, though these last fall under heading 5 of the original scheme.

The Ala orbitalis has already been fully described, so that no more may be said than that only the basal part enters into the lateral wall of the cavum.

The Parietal Plate (Pls. 3, 5, 7) is that plate of cartilage which extends upwards and forwards from the prominentia utriculo-ampullaris anterior of the pars canalicularis of the auditory capsule. It passes forwards, forming the upper boundary of the large spheno-parietal foramen, to join the posterior basal angle of the ala orbitalis. But where the actual developmental point of junction takes place is not ascertainable from the specimen or model at this age. The part arching forwards from the site of origin may be looked upon as the orbito-parietal commissure, or perhaps the whole structure leading back from the ala orbitalis to the auditory capsule might be given that name. In man no orbito-parietal commissure is formed at all, and the plate projecting from the auditory capsule is then easily termed parietal plate. Chondrification appears to take place somewhat later here than in the ala orbitalis. The inferior margin of the orbito-parietal commissure immediately over the tympanic region of the auditory capsule is arched upwards and outwards as the tegmen tympani (Pl. 3). The posterior margin of the orbito-parietal commissure (or parietal plate) is fused with the supraoccipital cartilage, helping to form the so-called tectum synoticum; but at its lower edge forms the anterior boundary of the superior occipito-capsular fissure, through which, at this spot, the lateral jugular vein runs out of the cavum cranii.

The Supraoccipital Cartilage (Pl. 3).—This structure, by joining its fellow in the middle line over the cavum cranii, forms the so-called tectum synoticum. If it develop along the same lines as it does in the calf, it must be regarded as being of large size in Microtus. It may be said to commence below, opposite the cupula posterior of the auditory capsule (Pl. 3), and is here, in common with the upper end of the exoccipital cartilage (with which it is directly fused), fused with that cupula. It spreads upwards, then divides into an anterior and a median or posterior limb. The anterior limb, which greatly increases in depth as it is traced forwards, arches over the dorsal border of the pars canalicularis of the auditory capsule, from which it is separated by the superior occipito-capsular fissure (Pl. 3), and fuses with the parietal plate or hind end of the orbito-parietal commissure along an imaginary line drawn vertically through the anterior border of the superior occipito-capsular fissure. Its inferior free margin is prolonged downwards as an *operculum* (Pl. 3) over the upper third of the lateral surface of the pars canalicularis, concealing from view from the outside the prominentia semicircularis anterior and the upper part of the prominentia fossæ subarcuatæ anterior as well as part of the lateral sinus. The free under margin of the operculum affords attachment to muscles reaching the shoulder girdle. The median or posterior process arches backwards and medianwards over the cavum cranii, forming a small part of the upper margin of the foramen magnum, at the incisura posterior thereof, and joins its fellow in the mid-line; the conjoined structures of the two sides forming the so-called tectum synoticum or tectum posterius (Pl. 1), perched on the upper edge of which on each side of the middle line is a small interparietal membrane bone (Pls. 1, 4). In adopting this method of description I have been guided by what happens in the calf at 19 mm. and later at 25 mm.; further, too, by the appearances in the hedgehog of 25 mm. The terminology is not quite satisfactory, since primarily the tectum synoticum has nothing whatever to do with the auditory capsule, and the term tectum posterius is not quite satisfactory, because in man at the 30-mm. and perhaps some later stages there are two tecta here—one a large one which corresponds with that usually called tectum posterius, and which, as I showed some years ago, gave off a processus ascendens in the mid-line; the other is very narrow from before backwards and of considerable width from side to side, but unconnected with any other cartilage. This second cartilage was described by Bolk and confirmed by me *loc. cit.* Gaupp, perhaps rightly, regards this region of the chondrocranium as being in a progressive condition. On the whole, from what has been said, Parker's original name "supraoccipital cartilage" seems the best name to adopt, more especially as that bone is developed from a considerable part of it.

The Lateral Commissures (Pl. 3).—These are from before backwards, the spheno-ethmoidal connecting the frontal prominence of the pars intermedia of nasal capsule with the anterior basal angle of the ala orbitalis, and it has been shown that it is formed equally from both, and is present in all examined save the sheep.

The orbito- or spheno-parietal commissure (Pl. 3), in the light of what has already been said, may be regarded as stretching from the posterior basal angle of the ala orbitalis to the anterior half of the upper margin of the pars canalicularis of the auditory capsule. It is to be regarded essentially as primarily a support for the temporal muscle. It forms the upper boundary of the spheno-parietal foramen.

The Occipito-capsular Commissure (Pl. 3).—This term, perhaps, may be introduced to imply that part of the anterior process of the supraoccipital cartilage which fuses with the hind margin of the parietal plate or spheno-parietal commissure. Its mode of origin is well seen in the calf at 25 mm.

THE NASAL CAPSULE.

This, rightly described by Voit as an extremely complicated structure, in Microtus is of great size and length: at the stage modelled its length is about one-third of the total length of the primordial cranium (Pls. 1, 2, 3, 9, 10). It forms a striking contrast to that of man, which is very short; but in man what the nasal capsule has lost in length it has gained in height. The nasal capsule consists of a central stem and of two lateral appendages. The central stem or septum is the direct forward continuation at this stage of the central stem of the primordial cranium, and at younger stages of the interorbito-nasal part of that stem (Pls. 1, 2, 9).

The septum nasi has already been described along with the central stem; it will therefore only be referred to from time to time as necessity demands, and we may proceed directly to the examination of the appendages, which form a roof, lateral wall, and floor to the right and left narial passages. Of these parts the lateral wall is the most complete, the roof next so, and the floor most incomplete. The lateral wall may be regarded as quite complete; the roof, however, at its hinder part is perforated by the numerous *foramina cribrosa* (Pls. 1, 9, 10), and in front of these by the small *foramen epiphaniale* (Pl. 1) on each side. At the junction of the roof and lateral wall near the anterior end of the nasal capsule a series of small *fenestra dorsalia* (Pl. 3) is found. The capsule opens out anteriorly on each side of the septum at the *fenestra narina* (Pl. 2), whilst the floor shows a long antero-posterior vacuity, the *fenestra basalis* (Pl. 2); further, between the septum and the paraseptal cartilage on each side is a narrow fissure which has already been alluded to as the *septo-paraseptal fissure* (Pl. 2).

The whole nasal capsule is connected in the middle line with the remainder of the chondrocranium by means of the central stem (septum nasi), and dorso-laterally by means of the spheno-ethmoidal commissures with the corresponding anterior angle of the ala orbitalis (Pls. 1, 3). The hinder third or so of the capsule lies under the brain in the recent condition, and is therefore subcerebral; the remainder is præcerebral.

We may examine the capsule in the first place from the exterior, then from the interior, after dissection of the model.

Of the exterior we have to study the roof or tectum nasi, the lateral wall or paries nasi, and the floor or solum nasi.

The Tectum nasi (Pl. 1) clearly consists of a hinder, much perforated, subcerebral part forming roughly one-third of the whole, and an anterior præcerebral part which is practically complete. The two are inclined at an angle with one another: thus the subcerebral part looks upwards and backwards, whereas the præcerebral part slopes gently downwards and forwards.

The hinder or *subcerebral part* is almost entirely formed by the two cribriform plates or *laminæ cribrosæ*, separated from one another by the *septum nasi* and its *crista galli*, but behind this the tectum is complete where it forms the root of the hindmost part of the pars posterior of the capsule, of which more will be said later. Each lamina cribrosa is triangular in shape, the base of the triangle being at the septum, the shorter side antero-lateral, and the longer one postero-lateral. The antero-lateral boundary is more prominent than the postero-lateral one, and can be traced from the root of the crista galli to the spheno-ethmoidal commissure. The postero-lateral border forms at the same time the anterior or lower border of the orbito-nasal fissure. In this border a slight notch is noticed which indicates the upper end of the postero-lateral sulcus of the paries nasi, to be later described (Pl. 3). This notch also marks the commencement of a crest, the *crista intercribrosa*, which runs obliquely from behind forwards and inwards across the lamina cribrosa, and so divides the *foramina cribrosa* into an antero-lateral and a postero-median group. Through the antero-lateral group the bundle of olfactory nerves from the pars intermedia of the nasal capsule runs to the olfactory bulb, whilst the postero-median foramina transmit the nerves from the pars posterior, the septum, and the organ of Jacobson, the latter especially passing through the most anterior of the foramina by the side of the septum nasi. At the anterior basal angle of the lamina cribrosa, and just lateral to the cribro-ethmoidal crest, a separate foramen, the foramen cribro-ethmoidale (Pl. 1), is found through which the nasal (ethmoidal) nerve leaves the cavum cranii to enter the nasal cavity.

The roof of the præcerebral part of the nasal capsule (Pl. 1) descends gradually. As it is traced forwards from the region of the lamina cribrosa it is continuously blended with the dorsal border of the septum nasi, which, save at a spot just in front of the crista galli, is slightly sunk in a dorsal median sulcus. In its hinder part the tectum passes almost insensibly into the paries nasi of the pars intermedia, but more anteriorly at the pars anterior the passage into paries nasi is much more abrupt, and between the tectum and the intermediate part of the paries nasi a small foramen, the foramen epiphaniale, for the transmission of the lateral branch of the nasal (ethmoidal) nerve, is seen (Pl. 1). From this foramen a slight furrow runs forwards to reach the upper end of the well-marked *sulcus antero-lateralis* (Pls. 1, 3), which marks the separation of the pars intermedia from the pars anterior of the paries nasi, and which forms an important landmark as coinciding with the site of attachment of the upper limb of the crista semicircularis of the interior. At its anterior end the tectum nasi bends over on each side to form the *cartilago cupularis* (Pls. 2, 3), which ends below in a small spinous projection, the *processus alaris superior* (Pl. 3), behind which the naso-lacrimal duct (Pl. 3) becomes confluent with the mucous membrane of the nasal sac.

The Lateral Wall of the Nasal Capsule.—Paries nasi (Pl. 3) may be divided into three parts, *i.e.* a pars posterior, a pars intermedia, and a pars anterior.

The Pars posterior is the smallest of all, and is separated from the pars intermedia by the *postero-lateral sulcus,* a curved sulcus which, commencing above at the notch above mentioned as seen in the postero-lateral border of the lamina cribrosa, descends, curving forwards and downwards, behind the pars intermedia to reach the lower border of the paries nasi; it coincides in the interior with the line of attachment of the first ethmo-turbinal. From this aspect the pars posterior presents a somewhat triangular outline whose base is forwards at the postero-lateral sulcus, whose apex (at the cupula nasi posterior) is jammed somewhat tightly against the antero-inferior aspect of the tænia præoptica of the ala orbitalis. Its upper side, which is directed upwards as well as backwards and is confluent at a rounded margin with the postero-lateral border of the lamina cribrosa—and marked, as before said, by a notch, the upper end of the postero-lateral sulcus,—forms the anterior boundary of the orbito-nasal fissure, through which passes the nasal nerve into the cavum cranii. Its lower border is rounded and continued partly into the floor of the cupula nasi posterior and partly into the lamina transversalis posterior, which forms the greater part of the floor of the pars posterior, but will be described later. This lateral surface of the pars posterior is flattened or even hollowed out by the pressure of the contents of the orbit, and the greater part of it frequently goes by the name *planum ant. orbitale*—an area which, however, is not confined to the pars posterior, for, as we shall see, it is continued on to the pars intermedia. But the pars posterior really has in addition a posterior surface which, when traced medialwards, runs directly to the interorbital septum; it is partly tilted forwards, and forms part of a posterior tectum nasi, which has already been mentioned. Here the lateral nasal capsule is directly fused with the nasal septum, but whether this is a primary or a secondary condition I do not know.

The Pars intermedia (Pls. 1, 2, 3) projects more than any part of the paries nasi away from the nasal septum. It is limited both in front and behind by a sulcus. The sulcus in front, known as the *sulcus antero-lateralis*, separates it from the pars anterior, whilst the sulcus lateralis posterior separates it from the pars posterior. On closer inspection this greatly prominent pars intermedia is seen to be made up of three smaller prominences, which may be named, with Voit, the *prominentia superior*, the *prominentia inferior*, and the *prominentia anterior*. Each of these prominences corresponds with a hollow in the interior of the capsule (Pl. 10); thus the prominentia superior corresponds with the *recessus frontalis*, and might be called the *prominentia frontalis* additionally, because it is covered by the frontal bone. The prominentia inferior is caused by the *recessus maxillaris*, and covered by the maxilla, and therefore might be called the *prominentia maxillaris*. Faint sulci separate these various prominences from one another. The frontal prominence always gives attachment to the spheno-ethmoidal commissure. The maxillary prominence is covered to a large extent by the frontal process of the maxilla, and is crossed at first horizontally, then vertically, by the naso-lacrimal duct, and to its hinder surface and a little below its middle the musculus obliquus inferior is always attached.

The prominentia anterior, which projects forwards at the point of meeting of the maxillary and frontal prominences, is caused by the hollow marking the junction of the recessus maxillaris and frontalis on the internal aspect of the lateral wall of the nasal capsule. It is covered in front by the upper end of the frontal process of the os incisivum. The under margin of the pars intermedia is inrolled, and more posteriorly is directly continuous with the *lamina transversalis posterior* (Pls. 2, 9, 10), whilst more anteriorly it forms a floor to the recessus maxillaris, and more anteriorly still a floor to the *recessus glandularis*, just as in the rabbit as described by Voit.

The Pars anterior (Pls. 1, 2, 3).—This is the longest division of the paries nasi. It is separated, as has been before stated, from the pars intermedia by the antero-lateral sulcus, a sulcus which, commencing just in front of the foramen epiphaniale, arches downwards and forwards in front of and somewhat medial to the prominentia anterior of the pars intermedia, below which prominence it tends to bifurcate into two secondary sulci, of which one, the more posterior, contours the front of the prominentia maxillaris and is almost vertical, whilst the other runs obliquely downwards and forwards to end at about the middle of the lower border of the pars anterior. Between these two limbs a somewhat flattened triangular area exists which is the outer surface of a lamina of cartilage projecting downwards below the level of the maxillo-turbinal (which projects into the interior), and is consequently called the *lamina infraconchalis* (Pl. 3). Across the lateral surface of the lamina supraconchalis a sulcus runs which lodges the middle part of the naso-lacrimal duct, and which may therefore be named the naso-lacrimal sulcus. Above the level of the lamina infraconchalis a horizontal projection is met with which corresponds to the hollow in the interior which lies above the maxillary concha. The above-mentioned parts belong to the hinder half of the pars anterior of the paries nasi. The anterior half of the pars anterior of the paries nasi is not so deep as the posterior half, and it is marked about midway between its upper and lower margins by several small foramina which perhaps correspond with the fenestra superior of the rabbit, but do not correspond in position with the duct of the lateral nasal gland which lies against the internal aspect of the lateral wall of the nasal capsule. Of these foramina the most anterior is only separated from the fenestra narina by a very narrow bridge of cartilage. Directly below the most anterior fenestra (Pl. 3) the lower margin of this region passes into the lamina transversalis anterior (Pls. 2, 3, and fig. 1), which connects the paries nasi directly with the septum nasi, no fissure existing between the lamina in question and the septum, as in the rabbit according to Voit; there is thus in Microtus a true *zona annularis.*

The inferior margin of the anterior half of the pars anterior may be described as consisting of three parts, viz. a hinder main part which is continuous with the anterior end of the lower margin of the lamina infraconchalis, and at the same time with the anterior end of the maxilloturbinal. It arches upwards and then downwards, and in the recent condition is hidden from external view by an outpouching of the mucous nasal sac, along whose outer edge lies the naso-lacrimal duct after leaving the sulcus on the lamina infraconchalis. When this part of the nasal sac is removed there are exposed to view from the exterior the lower part of the septum nasi and the bilaminar part of the paraseptal cartilage (Pl. 3). As the lower margin is traced forwards it is found to join at an acute angle —the *incisura post-transversalis* (Pls. 2, 3)—the hinder edge of the lamina transversalis anterior. Then, as above mentioned, the lower border is continued into the lamina transversalis anterior, a slight sulcus, in which the naso-lacrimal duct rests, marking the point of junction of the two. In front of the lamina transversalis anterior the inferior border of the pars anterior is free, and a deep notch is formed in it, the *incisura transversalis anterior* (Pl. 3), at which the terminal part of the naso-lacrimal duct is confluent with the nasal mucous membrane. In front of this notch the inferior border ends at a downwardly directed process, the *processus alaris superior* (Pl. 3), which is formed at the angle of junction of the inferior border of the lateral surface with the lateral border of the fenestra narina.

The Lamina transversalis anterior (Pls. 2, 3) is a plate of cartilage of some considerable size which directly connects the lateral wall of the nasal capsule with the septum nasi, no fissure intervening between it and the septum, such as is described and figured for the rabbit by Voit. A true zona annularis therefore exists in Microtus. The lamina transversalis passes outwards from the septum nasi and then suddenly upwards to join the under margin of the lateral wall of the nasal capsule, and at the point of junction both are turned upwards into the interior of the nose to form a well-marked projection, the atrio-turbinal (Pl. 10); and the sulcus which corresponds with this on the under aspect lodges the naso-lacrimal duct.

The Processus alaris superior (Pls. 3, 10) is of great size, resembling in form that of the mole. Starting out from the junction of the margin of the incisura prætransversalis with the margin of the fenestra narina by a somewhat narrow stalk, it soon deepens, to end above in an angular process and below in a somewhat similar one.

The Fenestra narina anterior (Pls. 2, 3) looks forwards and outwards and is bounded medially and in part anteriorly by an *anterior cupolar cartilage* (Pls. 2, 3, 9) of considerable size, which is continued back medially to the anterior part of the septum nasi, and superiorly and posteriorly is continuous with the tectum nasi.

The fenestra narina is filled at this stage in the complete condition by a solid epithelial plug.

The Floor of the Nasal Capsule (*Solum nasi*) (Pl. 2, fig. 1).—Owing to the large size of the lamina transversalis anterior, the lamina transversalis posterior, and the paraseptal cartilage, the floor of the nasal capsule is unusually complete, but there are vacuities in it; for instance, a long antero-posterior vacuity—the *fenestra basalis*—exists bounded in front by the lamina transversalis anterior, behind by the lamina transversalis posterior, medially by the paraseptal cartilage, and laterally by the lower margin of the paries nasi. The greater part of this vacuity is closed by the palatine processes of the maxilla and palate bones, only the anterior end remaining in continuity with the mouth as the primary choana, which intervenes between the os incisivum and the maxilla. Another vacuity is the *septo-paraseptal fissure*, which intervenes between the paraseptal cartilage and the lamina transversalis posterior laterally and the infero-lateral margin of the septum nasi medially. This fissure in the recent condition is closed above by the connective tissue attaching the upper border of the paraseptal cartilage to the septum, and it is also partly closed by the corresponding lamella of the vomer.

The Paraseptal Cartilage (Pls. 2, 3, 9, fig. 1).—This ontogenetically and perhaps phylogenetically in the mammal is double in origin, consisting of a large *anterior* part which is usually bilaminar, forming a sort of trough in which the organ of Jacobson rests, and which anteriorly is directly continuous with the lamina transversalis anterior, and a *posterior* which is attached to the lamina transversalis posterior.

At the stage modelled there is a common paraseptal cartilage stretching from the antero-median angle of the lamina transversalis posterior to the hinder border of the lamina transversalis anterior, and in its whole length its upper border is connected with the septum nasi by a band of connective tissue. Tracing from behind forwards the paraseptal cartilage (Pl. 2), one observes that its hinder part is very small and cylindrical in form and that this part is to a large extent surrounded by a bony tube derived from the vomer; suddenly, however, the cartilage enlarges, and becomes bilaminar, consisting of a medial or septal and an inferior lamella (Pl. 3). Of the two the septal is the larger, and between them the main part of the organ of Jacobson is lodged, towards the anterior end of the organ of Jacobson; in point of fact, where the duct of that organ is being developed, the septal and inferior lamellæ unite to form a short tube through which the duct runs in an outward direction to open into the nasal cavity, and beyond this point the inferior lamella is alone continued forwards to join with the lamina transversalis anterior. The anterior unilamellar part of the paraseptal cartilage is covered inferiorly by the body of the os incisivum, whilst the greater part of the inferior surface and part also of the medial surface of the inferior lamella are covered by the palatine process of that bone. The medial lamellæ of the anterior paraseptal cartilages are so closely swung together posteriorly that they are only separated from one another by a narrow vertical fissure, and by the anterior end of the vomer which is insinuated between them at this spot.

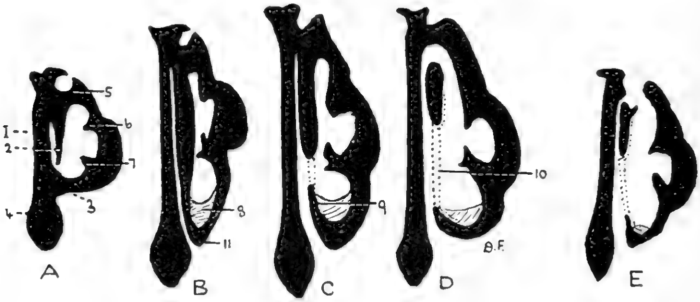
The Lamina transversalis posterior (Pls. 2, 9, 10, fig. 1).—This, a large triangular plate, forms almost the entire floor of the subcerebral segment of the nasal capsule (as it does in the rabbit—Voit). The apex of this triangular plate is directed backwards to form the floor of the cupula posterior nasi. Laterally it is continuous with the lower rounded margin of the pars posterior of the paries nasi as well as the lower margin of the hindmost part of the pars intermedia. Medially it is directed towards the septum nasi, but separated from it by a fissure in which lies the corresponding lamella of the vomer, and which is to a certain extent invading it. The medial basal angle of the lamina is directly continuous with the paraseptal cartilage. The under surface of the lamina is almost completely hidden from view from below by the palatine process of the corresponding maxilla.

The Lamina transversalis anterior.—The remaining cartilage which completes the solum nasi has already been described, so that nothing further may be said in that direction.

The whole solum nasi is of great interest phylogenetically as well as ontogenetically. Nothing can be said as to the latter in Microtus, as the necessary stages were not available, but an examination of models of other animals reveals some interesting facts.

In all save man the lamina transversalis anterior exists, and is variable in form with age and species. In Semnopithecus maurus, according to E. Fischer, a small lamina transversalis anterior also exists. In all orders which I have examined the lamina transversalis anterior is in direct continuity with the anterior paraseptal cartilage, until the Carnivora are reached, and here continuity fails in Mustela and Felis catus. In Homo no continuity exists at any time, and this is associated in man with deficiency of the lamina transversalis anterior, so that the fenestra basalis and the fenestra narina are confluent, forming a long fissura rostro-ventralis. In Dasyurus viverrinus the anterior paraseptal cartilage is a long pointed structure reaching along the whole length of the septum nasi almost as far as the posterior wall of the nasal capsule, at the 7-mm. stage. At a little later stage it has fused with this, and as a backward growth of the nasal sac has begun to burrow into the posterior block-like end of the nasal capsule. A lamina transversalis posterior is formed at a still later stage, where a large lamina transversalis posterior is formed, and its medial antero-basal angle is attenuated to form the posterior paraseptal cartilage, which is in direct continuity with the anterior one. In Tatusia novemcincta the anterior paraseptal cartilage alone exists in a procartilaginous condition at the 12-mm. stage, and as a backward projection of the lamina transversalis anterior; but by the 7-mm. stage a posterior paraseptal cartilage has appeared connected in front by fibrous tissue with the anterior one, and behind with the median basal angle of the lamina transversalis posterior, also by fibrous tissue. Whether a complete common paraseptal cartilage ever exists in Tatusia I know not; probably, however, it does not. It is complete in Halmaturus (Seydel), in Dasyurus (Broom and my own observations), in Trichosurus vulpecula (Broom), in Lepus (Voit), and in Microtus, as shown in the model described. When incomplete, the part especially awanting appears to be that formed at the original junctional region between hinder wall of nasal capsule and the anterior paraseptal cartilage.

The lamina transversalis posterior is developed mainly by the thrusting back of the centre of the hinder wall of the capsule by the nasal mucous sac. It may be followed out in all its stages in Dasyurus viverrinus. At the 7-mm. stage it is non-existent; by the 9·5-mm. stage it has just begun to form in the way mentioned; and by the 25-mm. stage, so far has the posterior wall of the nasal capsule been pushed back that a large triangular lamina transversalis posterior results, and its medial basal angle, which has previously fused with the hinder-pointed end of the anterior paraseptal cartilage, is drawn out to form the slender posterior part of the resulting common paraseptal cartilage. In all the orders and species I have personally examined and modelled, a lamina transversalis posterior exists, although not in the very young stages. It is a comparatively late formation. Its presence is generally denied in Primates and man, but in a model of the chondrocranium of a 65-mm. embryo in my possession a small lamina transversalis posterior is distinctly present, and it is formed precisely as in other animals. In the schemes illustrated by fig. 4 the various forms are shown.



Text-fig. 4.—The evolution of the paraseptal cartilages and the lamina transversalis posterior (schematic).

A. The 7-mm. stage in Dasyurus viverrinus.
B. The 9-mm. stage in Dasyurus viverrinus. and in rabbit, water-rat, Trichosurus.
C. Talpa.
D. Ferret, cat.
E. Man.

1, 4, interorbito-nasal septum ; 2, anterior paraseptal cartilage ; 3, part which, by thrusting back and hollowing out, forms posterior paraseptal cartilage, lamina transversalis posterior, and cupula posterior ; 5, lamina transversalis anterior ; 6, crista semicircularis ; 7, first primary ethmo-turbinal ; 8, lamina transversalis posterior ; 9, posterior paraseptal cartilage ; 10, fibrous internal covering of common paraseptal cartilage persisting after disappearance of cartilage itself ; 11, cupula posterior.

The Medial Aspect of the Lateral Wall of the Nasal Capsule (Pl. 10).—This, like the lateral aspect. is divisible into three parts, viz. a posterior, an intermediate, and an anterior part.

The Pars posterior or pars ethmoidalis is characterised in the first place by showing a series of parallel projections which project inwards from the lateral wall of this segment and run a course at right angles to the lamina cribrosa. These projections are the primary ethmo-turbinals, or, as sometimes termed, the endo-turbinals. In the passages between the endo-turbinals are small projections, which I term here secondary turbinals, as they develop later than the primary ones; they are the ecto-turbinals of Paulli. At this stage only one secondary turbinal is developed, and it lies at the bottom of the hollow between the first and second primary turbinals. There, however, is a hint at a second secondary turbinal between the second and third primary ethmo-turbinals. But the more precise description of these turbinals will be undertaken at a later stage, and we may now consider the boundaries of the medial aspect of the pars posterior of the nasal capsule.

Above it is roofed by the lamina cribrosa (cribriform plate) (Pls. 1, 9, 10), and especially by the postero-median division of the plate as previously described. Below it is almost completely floored by the lamina transversalis posterior (Pls. 2, 9, 10). Posteriorly it is bounded by the tectum superius and the cupula posterior nasi. Its anterior limit is formed by the anterior edge of the first primary ethmo-turbinal. This edge consists of an upper and a lower slope of about equal length, the two slopes meeting in front at a prominent spur. The upper slope commences above and behind at the crista intercribrosa; the lower slope commences at the lower border of the lateral wall of the nasal capsule immediately in front of the lateral basal angle of the lamina transversalis posterior.

The Ethmo-turbinals (Pl. 10).—These, for the reason above stated, may be divided into *primary* and *secondary*. They are sometimes called endo- and ecto-turbinalia, or major and minor respectively.

The primary ethmo-turbinals, at this stage at all events, are three in number, and are named from before backwards, first, second, and third; and of these the first is by far the largest, the third the smallest.

The first primary ethmo-turbinal is not only the largest, but is at the same time the most complicated of the turbinals. It springs from the medial aspect of the lateral wall of the nasal capsule by three roots, an upper, a lower, and an anterior, all of which are continuous with one another at a common centre. The upper and lower roots together form a curve convex in front, which corresponds with the sulcus lateralis posterior of the outer aspect of the lateral wall. The third root passes forwards from the point of greatest convexity of the combined upper and lower roots and forms the floor of that part of the pars intermedia which will afterwards be described as the *recessus frontalis*.

Beyond its roots the first primary ethmo-turbinal projects forwards and inwards, hiding from view from the medial aspect a considerable part of the pars intermedia, of which it also forms the posterior wall. It now splits into two lamellæ, viz. an anterior and a posterior, of which the anterior is by far the larger, and which further differs from the posterior in that it is a triangular plate whose apex forms the prominent spur already mentioned. The posterior lamella is straight. Between these two lamella a large hollow exists which leads upwards to a special foramen for nerves. The first ethmo-turbinal in all young stages of species I have examined is unilamellar, the splitting into two being a later condition, and, according to Peter and Seydel, it may as in man remain single throughout life.

The Second Primary Ethmo-turbinal is separated from the first by a deep recess or meatus. It reaches from the lamina cribrosa above to the point of confluence of the lower root of the first primary turbinal with the lateral basal angle of the lamina transversalis posterior. At the bottom of the meatus, between the first and second primary ethmo-turbinal, the first secondary turbinal is met with; this runs parallel with the two primary ones between which it lies. The meatus in which it lies opens above to the cavum cranii by a special foramen in the cribriform plate.

The third primary ethmo-turbinal is the smallest. It starts from the hinder part of the lamina cribrosa and runs downwards and forwards to end on the medial aspect of the lateral wall at little above and behind the lateral basal angle of the lamina transversalis posterior. Behind this ethmo-turbinal is a passage which may be called the cupolar recess. It leads upwards to a foramen in the lamina cribrosa.

All these cartilaginous processes are covered by thick olfactory mucous membrane, from which nerves may be traced through the postero-median group of foramina cribrosa to the olfactory bulb.

The Pars intermedia.—This at first sight is a large crescentic or perhaps boomerang-shaped recess in the medial aspect of the lateral wall of the nasal capsule. Its convexity is placed forwards. It is bounded posteriorly by the first primary ethmo-turbinal and also to a certain extent medially by the same plate, and it is very nearly cut into two equal parts, an upper and a lower, by the anterior root of the first ethmo-turbinal. Anteriorly it is limited by a curved projection into the interior of the nose, called the *crista semicircularis*, which corresponds on the outer wall of the lateral wall of the nasal capsule with the greater part of the sulcus antero-lateralis. This crista semicircularis forms the common boundary between the pars intermedia and the pars anterior of the median aspect of the lateral wall of the nasal capsule. It commences above confluent with the upper end of the first primary ethmo-turbinal and cribro-ethmoidal crest at the lamina cribrosa. At its commencement it is perforated by the canal for the lateral branch of the nasal nerve, which after its passage through the cribro-ethmoidal foramen runs at first medial to the crista semicircularis as in the rabbit (Voit); then it perforates the crista, reaching its lateral side, after which it leaves the interior of the nasal capsule by running through the foramen epiphaniale. For the greater part of its course the crista semicircularis runs downwards and forwards more or less parallel with the upper slope of the anterior lamella of the first primary ethmo-turbinal. It then, opposite the spur developed on that lamella, bends sharply downwards in front of the recessus antero-lateralis of the pars intermedia, to end in a faint ridge in the floor of the recessus maxillaris. In this respect it differs here from that in the rabbit, where, according to Voit, it forms a sort of bridge over the lateral wall of a part of the recessus maxillaris (Voit), and is the cartilaginous processus uncinatus. This does not exist in Microtus, though the faint ridge above mentioned may be regarded as its representative.

Turning now to the description of the pars intermedia itself within the boundaries as defined, we may say at once that it is to a large extent hidden from view from the medial aspect by the close approximation of the first primary ethmo-turbinal to the crista semicircularis. Taken as a whole, it is deeply recessed in the outward direction, which recessing causes the great outward projection of the lateral wall of the nasal capsule in this region, and this general recess is subdivisible into a series of smaller recesses. Two of these, viz. an upper or *recessus frontalis* or superior, and a lower, the *recessus maxillaris* or inferior, are almost completely separated from one another by the anterior root of the first primary ethmo-turbinal. Where the said anterior root dies away in front, these two recesses communicate with one another at what is named the *recessus anterior*, which lies under cover (as viewed from the medial aspect) of the crista semicircularis. We have already seen that these recesses produce corresponding prominences on the exterior of the pars intermedia.

The Recessus superior or frontalis (Pl. 10) lies above the anterior and superior roots of the first primary ethmo-turbinal, and under cover to a large extent of the crista semicircularis. It is placed almost at right angles to the recessus inferior or maxillaris, produces the prominentia frontalis on the exterior (Pl. 3), and is subdivided into three secondary recesses, which, however, are not marked on the exterior by two frontal turbinals which, running parallel with one another, are roughly parallel with the upper slope of the anterior lamella of the first primary ethmo-turbinal. Each commences above at the antero-lateral part of the lamina cribrosa, and the more anterior of the two is the larger and more prominent, and reaches as far down as the anterior end of the anterior root of the first primary ethmo-turbinal. The passages or recesses into which the recessus frontalis is broken up each open by a special foramen into the cavum cranii through the antero-lateral segment of the lamina cribrosa (Pls. 1, 10).

The inferior main division of the lateral recess is subdivisible into three parts, viz. the recessus maxillaris proprius, the recessus anterior, and the recessus glandularis.

The Recessus anterior (Pl. 10) is that recess which is at the junction of the upper and lower main subdivisions of the recessus lateralis. It projects deeply forwards under the most forwardly bent part of the crista semicircularis, and causes on the exterior the prominentia anterior, which there is to a large extent hidden from view by the frontal process of the os incisivum.

The Recessus maxillaris (Pl. 10) is the largest of the three subdivisions of the inferior part of the lateral recess. It is considerably overhung from behind by the inferior root of the first primary ethmo-turbinal. Into it from the front enters the lower end (processus uncinatus) of the crista semicircularis. From its lower anterior part may be separated off the *recessus glandularis* (Pl. 10), which lodges the lobules of the lateral nasal gland. This is the lowest and most anterior of the subdivisions of the inferior part of the lateral recess. It is not very distinct, and it is only definable by modelling *in situ* the lobules of the said gland.

The Pars anterior (Pl. 10) of the medial aspect of the lateral wall of the nasal capsule is roughly triangular in form, with its base backwards at the crista semicircularis, which thus forms its posterior boundary. It reaches forwards from this to the tip of the nose. Inferiorly and posteriorly the pars anterior is confluent with the inferior part of the pars intermedia, the site of confluence being the recessus glandularis.

The pars anterior is characterised more particularly by its great antero-posterior length, and by the projection into it of three turbinals, of which perhaps the most striking is the *naso-turbinal*; the others are the *maxillo-turbinal* and the *atrio-turbinal*.

The naso-turbinal extends over quite two-thirds of the whole length of the pars anterior. Commencing at the junction of the anterior and middle thirds, it runs backwards almost midway between the upper and lower limits of this region, and it ends shortly in front of the crista semicircularis by bifurcating into an upper and a lower limb. For a very large part of its extent it is not fused to the lateral wall of the nasal capsule; in fact, fusion only occurs anteriorly and posteriorly. The naso-turbinal may be looked upon as a convex sheet which practically divides the general concavity of the pars anterior into two equal channels, the upper of which is roofed by the tectum nasi, whilst the lower is floored by the maxillo-turbinal. It may be mentioned that, of the two hinder limbs of bifurcation, the upper is the shorter one, and is only bound to the lateral wall by fibrous tissue, whilst the longer lower limb is confluent in its whole length. Between the two limbs is a foramen through which blood-vessels and nerves run.

The Atrio-turbinal (Pl. 10) commences anteriorly as an inrolling of the lateral wall of the incisura narina, which takes place just medial to the foramen superius, and is continued backwards as an invection of the lamina transversalis anterior, corresponding with the sulcus naso-lacrimalis. It comes abruptly to an end near the posterior border of the lamina transversalis anterior, a notch—the *incisura maxillo-atrioturbinalis* (Voit)—separating it from the anterior end of the maxillo-turbinal (Pl. 10). As in the rabbit (Voit), this notch is filled with fibrous tissue, there being no such interruption in the soft parts.

The Maxillo-turbinal (Pl. 10) commences in front, immediately behind the incisura maxillo-atrioturbinalis, as a simple, very slight inrolling of the lower border of the pars anterior, and as such is continued backwards for almost half its extent, and under its convexity one sees the naso-lacrimal duct; further backwards the maxillo-turbinal runs along the upper edge of the lamina infraconchalis, which stands nearly vertically, and when the latter ceases to exist the maxillo-turbinal once more makes itself evident as the inrolled lower margin of the pars intermedia of the nasal capsule; but here, as Voit truly remarks of the rabbit, "da in diesem Gebiete an dem mit Schleimhaut bekleideten Präparat kein Vorsprung zu bemerken ist." But the amount of inrolling seems to be much less than in the rabbit, for the sulcus which lies above it—the sulcus supraconchalis (Pl. 10)—is very little expressed, and posteriorly that sulcus is continued into the recessus glandularis of the pars intermedia, whilst anteriorly it runs out at the incisura narina, having joined in front with the passage in the lateral wall above the naso-turbinal to form a sort of vestibule which laterally is perforated by the foramen superius.

The Naso-lacrimal Duct (Pls. 2, 3).—This, formed by the union of an upper and a lower canaliculus just above the maxillary prominence on the pars intermedia of the *paries nasi*, passes at first horizontally forwards under the prominentia anterior, then rapidly descends, lying below the primordium of the lacrimal bone, which has only to the very slightest extent ossified, and has not been represented in the model. The duct then descends along the front of the maxillary prominence immediately above the maxillary origin of the masseter muscle and, descending between the frontal process of the maxilla and the body of that bone, it comes to lie against the upper edge of the lamina infraconchalis in what I have previously termed the naso-lacrimal sulcus, opposite and above which in the interior of the nose is the lateral nasal gland; here it is surrounded by a vascular plexus, and is covered externally now by the body of the maxilla and by a somewhat dense sheet of connective tissue. Then, when the lamina infraconchalis dies out in front, the duct lies along the under margin of the paries nasi between that and the socket for the large incisor tooth uncovered in part by bone; next it lies above that outpouching of the nasal sac which projects below the lower margin of the paries nasi, and which is not covered laterally by any cartillage, and, coursing along in the relation just mentioned to the mucous membrane, it reaches the lateral margin of the lamina transversalis anterior, in a groove of which it lies, the groove corresponding with the atrio-turbinal. In this region it is accompanied by a small gland-like structure which opens independently into the interior of the nose and is not in any way connected with the naso-lacrimal duct; now the naso-lacrimal duct sinks into the incisura prætransversalis under cover of the descending process of the processus alaris superior, lying still below the atrio-turbinal, and suddenly ends by communicating with the nasal sac below the atrio-turbinal. At no part of its course was I able to observe any lumen in the duct.

The Nerves of the Olfactory Region.

The nasal (ethmoidal) nerve enters the cavum cranii extradurally through the anterior part of the orbito-nasal fissure lying lateral (dorsal) to that bunch of olfactory nerves coming from the recessus frontalis. After a short course it gives off a lateral branch which, entering a special canal which traverses the root of the crista semicircularis, emerges on the tectum nasi at the foramen epiphaniale and later descends under cover of the nasal bone. The parent trunk passes through the cribro-ethmoidal foramen in company with a few olfactory filaments, and cannot be traced very far in the mucous membrane. It therefore coincides very closely with that of the rabbit, as described by Voit.

The Olfactory Nerves require but little description. They are divisible into three groups of septal, postero-median, and antero-lateral. The septal group includes the large trunks coming from the organ of Jacobson, which run from that organ obliquely upwards and backwards along the septum to enter the cavum cranii by a large slit-like foramen lying by the side of the crista galli; they ultimately enter the median anterior aspect of the olfactory bulb. The antero-lateral group leave the recessus frontalis through the foramina in the antero-lateral region of the lamina cribrosa, and in front of the cribro-ethmoidal crest, and, joining together to form a large bundle, enter the antero-lateral aspect of the olfactory bulb. The postero-median group enter the cavum cranii through the postero-median foramina behind the cribro-ethmoidal crest, and then bend forward—at all events the hindmost of them—to enter the lower and hinder part of the olfactory bulb. The bulb is hollow, and the hollow communicates posteriorly with the interior of the corresponding lateral ventricle of the brain.

VISCERAL SKELETON.

The first visceral arch is that formed by Meckel's cartilage, which at its hinder end passes directly into the cartilaginous malleus (Pls. 3, 9). The cartilage of Meckel is of great length, passes from the malleus in a somewhat wavy course inwards and downwards at first, then downwards and outwards: after which, bending once more inwards for a short distance, it runs almost horizontally forwards, converging on its fellow ultimately, to fuse with it and form a double-pointed common anterior extremity. For the greater part of its length it is cylindrical in form, but not far from its anterior extremity, where it is undergoing ossification, it elongates in the vertical direction; and where it is becoming absorbed, which it does to a very large extent when incorporated within the mandible, it assumes a crescentic form, the concavity of the crescent being outwards.

Soon after leaving the malleus cartilage Meckel's cartilage is covered on its lateral side by the antero-superior limb of the tympanic bone (Pl. 5), and in this region too it has below it the flat goniale (prearticulare) (Pls. 5, 6); on its lateral aspect, at a greater distance than the os tympanicum, is that large mass of cartilage which forms the condyle and neck of the mandible (Pls. 3, 9). The cartilage next comes more immediately into relation with the mandible, in a large deep groove (Pl. 9) of which it lies almost buried from view from the medial side. It is overhung here by the inner alveolar wall, which at its hinder end develops an accessory mass of cartilage (Pls. 3, 9); below and to its lateral side is a large accessory cartilage (Pls. 3, 9), which forms the angle of the jaw at this stage; beyond this cartilage Meckel's cartilage sinks entirely into the mandible and remains within it as far as the foramen mentale, beyond which it again emerges on the medial side as far as its termination; on the lateral side of Meckel's cartilage, just before its termination, a small accessory cartilage (Pls. 3, 9) is in relation to it, separating it from the bony mandible, which lies more laterally. But these accessory cartilages will be described later along with the bony mandible, because they have nothing whatever to do with the primordial cartilage of the skull.

The Malleus Cartilage (Pls. 3, 4) is of large size, forming above a head whose upper aspect is practically in continuity with the plane of the upper margin of Meckel's cartilage. This head is overlapped above by the tegmen tympani; posteriorly it is in articulation with the incus; below, it runs into the neck, into whose inner and lower part is inserted the tendon of the tensor tympani muscle (Pl. 6), below and behind which the chorda tympani nerve runs. Below the insertion of the tensor tympani and on the lateral side a prominent processus brevis is met with (Pl. 3). The manubrium mallei below this passes downwards and forwards, following the line of the sulcus spiralis of the cochlear capsule (Pls. 3, 6).

The Incus Cartilage (Pl. 3) resembles very much the bony incus; it consists of a bony short posterior process which, together with the body, is overhung by the tegmen tympani and its downward continuation the crista parotica. The short process is lodged in a well-marked fossa incudis (Pls. 3, 6). The long process descends not quite parallel with the malleus, and, diverging at an acute angle from it, at the level of the processus brevis articulates with the stapes cartilage (Pls. 3, 6), no joint cavity at this stage intervening between the two.

The Second Visceral Cartilaginous Arch (Pls. 3, 6).—This is only imperfectly represented. Commencing with the stapes, which has the usual form and which is perforated by an enormous stapedial artery, and further has inserted into the posterior aspect of its neck the stapedius muscle, we pass, with a great break, to the stylo-hyal, which is confluent with the crista parotica and descends from this along the front of the pars canalicularis of the auditory capsule almost to the level of the processus paracondyloideus, when, after a slight interruption in continuity in cartilage, it again assumes a comparatively large calibre and bends sharply inwards under the cochlear capsule, then as cartilage it comes to an end opposite the point where the stapedial artery is given off from the internal carotid. It once more reappears at the junction of the thyro-hyal with the basi-hyal as the cerato-hyal. It is separated from both by connective tissue.

The thyroid or third-arch visceral skeleton is represented by an unusually small cartilage not much larger than the cerato-hyal, and it has no connection with the thyroid cartilage (Pl. 3).

The skeleton of the fourth arch, represented by the thyroid cartilage, is of large size; its ala is perforated by a blood-vessel accompanied by the internal laryngeal nerve Large superior and inferior cornua are present, and an enormous inferior marginal tubercle projects laterally and somewhat downwards from the middle of the inferior margin of the ala.

The skeleton of the fifth arch is represented by the cricoid, which is surmounted in the usual fashion by the arytenoid cartilages.

The epiglottis is represented as a stalked cartilage, whose blade is folded medianly, so that in section it has a somewhat V-shaped appearance. Joint cavities are developed between the arytenoids and the cricoid, but no joint cavity has as yet appeared between the inferior cornua of the ala and the cricoid.

The visceral skeleton as a whole will be dealt with later, in a subsequent communication. It may suffice to say here that it resembles much that of other Eutheria, and is probably derived from five arches as in Metatheria.

THE OSSEOUS SKELETON.

The Covering Bones.—These for the most part are well developed.

Interparietalia.—Commencing behind we note the two interparietalia (Pls. 1, 4), placed near the middle line above the tectum posterius (synoticum), and separated by a considerable interval from the parietalia, as in rabbit; a considerable space exists between the two interparietalia, which is occupied by the fibrous, non-cartilaginous roof of the cavum cranii.

Parietalia (Pl. 4).—Each is of considerable size, narrow behind, broader in front, covering the processus anterior of the supraoccipital cartilage. The upper part of the parietal plate and the hinder part of the orbito-parietal commissure each reaches towards its fellow, but does not meet it, and a considerable fibrous space is left between the two above the limits of the cartilage of the lateral wall of the cranium. A somewhat oblique coronal suture separates the frontal from the parietal bone, whilst the under edge of the parietal in its anterior half or so is overlapped by the upper edge of the squamosal (this is not shown in the model).

The Frontalia (Pls. 1, 4) are larger than the parietalia, with which they come into close contact behind; each covers the greater part of the orbito-parietal commissure, the upper half or so of the ala orbitalis, and anteriorly passes along the spheno-ethmoidal commissure to cover a considerable part of the prominentia frontalis of the nasal capsule, on which the frontale splits into a median and a lateral part, the former of which lies over the tunnel in which is contained the lateral branch of the nasal (ethmoidal) nerve, and which opens out under this median process of the frontal bone at the foramen epiphaniale. Over the orbital fossa a slight ridge is formed on the frontal bone, which divides this part into an upper part (pars frontalis) and a lower part which forms the very oblique bony roof of the orbit (pars orbitalis). This ridge, which is not very well marked anywhere, is the *arcus supraorbitalis* (Pl. 4), and, unlike that of the rabbit, does not develop posteriorly a processus supraorbitalis posterior. Before passing on to the recessus frontalis of the nasal capsule, the anterior part of the frontale forms a roof to the subcentral part of the nasal capsule and so completes the cavum cranii above and in front.

The pars orbitalis projects downwards over the outer side of the upper part of the orbito-ethmoidal fissure. Postero-superiorly the frontale is separated at the upper end of the coronal suture by a wide notch filled by fibrous tissue, which is the homologue of our human bregmatic fontanelle.

The Squamosum (Pl. 4) is a bone of considerable size, which consists of a large squame overlapping the lower and fore part of the parietal plate, and more anteriorly the hinder part of the orbito-parietal commissure. From its posterior end two narrow processes pass backwards, one an upper, which lies to the outer side of the parietal plate and is horizontal in position: the other, the post-auditory process (Pls. 4, 6), crosses the lateral jugular vein superficially, then the upper parts of the malleus and incus cartilages, to reach and cover the junction of tegmen tympani with the crista parotica. In its hindmost part an accessory cartilage is developed. The upper border of the main part of the squama overlaps the lower edge of the parietal, and reaches forwards beyond that bone to the under margin of the frontale. Its anterior margin articulates with the alisphenoid, whilst the lower margin is somewhat complicated. It may be best described as bifurcating into a median and a lateral lamella (Pl. 6), of which the former descends on the lateral aspect of the parietal plate and of the hinder end of the orbito-parietal commissure almost as far as the upper surface of the tegmen tympani as it lies to the medial side of the cartilaginous condyle of the mandible. This median lamella forms the medial part of the glenoid cavity (Pl. 6). The outer lamella of the lower margin of the squama develops as the processus zygomaticus, which, after overlapping on the outer side the cartilaginous condyle of the mandible (Pl. 4), turns forwards almost horizontally as far as the coronoid process of the mandible, where it ends obliquely to support the hind end of the os zygomaticum. Nowhere in the region of the glenoid fossa is any accessory cartilage discoverable, such as is found in man and some other mammals.

The Nasale (Pls. 1, 4) lies on the dorsal aspect of the pars anterior of the nasal capsule, reaching laterally almost as far as the oblique upper anterior edge of the frontal process of the incisivum. Posteriorly it is practically coincident in extent with the frontal process of the incisivum, and, as in the mole as figured by Fischer, it bifurcates into two plates, of which the medial extends further back than the lateral. Anteriorly the nasale does not reach so far as the foramen superius, nor does it cover any of its satellites.

Here and there the two nasalia seem to be united across the middle line, more especially in the anterior part; posteriorly they recede somewhat from one another and the middle line.

The Incisivum (Pls. 1, 2, 4) is a very large bone, its size, as in the rabbit, depending upon the large size of the upper incisor tooth. It lies on the lateral and under aspects of the pars anterior of the nasal capsule, and may be described as consisting of a body, a frontal process, a median and a lateral palatine process. The body contains a single alveolus for the lateral large incisor tooth, there not being any germ for the median one at this stage. It covers the lamina infraconchalis and the naso-lacrimal duct, as well as the anterior part of the fenestra basalus of the nasal capsule and a considerable part of the paraseptal cartilage, but at this stage at all events does not reach so far forwards as the lamina transversalis anterior, which can be seen freely from the side in front of the medial alveolar wall of the incisor alveolus (Pls. 2, 4). The upper border of the body of the incisivum is separated by a small interval from the nasale, so that part of the nasal capsule is seen between them; and if the anterior border of the body be traced upwards, it will be seen to lie in the same line as the anterior border of the nasale, the two forming the lateral boundary of the bony apertura pisiformis. Beyond this apertura pisiformis the apex of the pars anterior of the nasal capsule is projected for very nearly half its extent, so that, amongst other things, the whole of the lamina transversalis anterior, the anterior end of the incisura post-transversalis, and of the naso-lacrimal duct, as well as the fenestra superius and its satellites, are exposed to view (Pl. 4). The frontal process (Pl. 4) projects obliquely backwards into the gap between the nasale and the maxillare, but does not reach the frontale, a considerable part of the pars intermedia of the nasal capsule being exposed to view between the two (Pl. 4). The lateral palatine process is very massive; it forms the under aspect of the body of the bone and lies underneath the hinder part of the lamina infraconchalis (Pl. 2). Posteriorly it seems to blend with the maxilla, or at all events to be separated by a very fine suture from it. The processus palatinus medialis (Pl. 2) passes backwards along the medial and under aspect of the paraseptal cartilage, and can be traced along it for about half the length of the organ of Jacobson; and almost immediately behind it and somewhat above, the vomer follows in the gap between the two paraseptal cartilages.

The Maxillare (Pls. 1, 2, 4) consists of a body, a frontal process, an outer and an inner alveolar process, a palatine process, and a zygomatic process. The body is of comparatively small size, and is perforated by an enormous infraorbital foramen, through which are exposed to view the maxillary prominence of the pars intermedia of the nasal capsule as well as a part of the naso-lacrimal duct. From the body the large triangular frontal process is continued upwards over the pars intermedia of the nasal capsule in the gap between the frontal process of the incisivum and the frontale, but it is separated by a tolerable interval from the two.

Both the anterior part of the body of the maxillare and its frontal process are curved around the anterior aspect of the pars intermedia towards the antero-lateral sulcus of the nasal capsule.

The inferior surface of the body (Pls. 2, 9) is convex, and posteriorly divides into the two alveolar processes, outer and inner. As this rounded inferior surface is traced inwards it is found to bound laterally the foramen incisivum and at the same time to form the under bony border of the paries nasi. Opposite the middle of the infraorbital foramen the body of the maxillare divides below into two backwardly directed processes, viz. the median and lateral alveolar (Pl. 9); of the two the lateral is much the smaller, but at two spots its line backwards is continued by two isolated masses of bone, one of which is placed opposite the coronoid process of the mandible, the other intervening between the one just mentioned and the hinder end of that part of the lateral alveolar process which is in continuity with the body of the maxilla. The median alveolar process, starting at the same point as the lateral one, is much the larger, and may be traced backwards as far as the hinder third of the palatinum, where it ends in a pointed posterior process. It overlaps on the outer side the angle of the palate bone at the junction of the vertical and horizontal laminæ of that bone.

The palatine process of the maxilla is a horizontal shelf of bone projected towards its fellow of the opposite side, which more anteriorly it almost meets; but more posteriorly it recedes somewhat from its fellow, and it dies away as the palate bone is approached. It forms part of the floor of the ductus naso-pharyngeus. In no part of its length is it in contact with the vomer at this stage, nor is any cartilage developed along its medial border, as is so common in animals.

The zygomatic process of the maxilla projects backwards from the body of the bone opposite the hinder wall of the infraorbital canal, and it stretches away back as far as the zygomaticum, which it meets opposite the anterior border of the coronoid process of the mandible, under whose anterior oblique border it passes for some distance (Pl. 4).

Before leaving the description of the maxilla one may say that, except anteriorly, the premolar and molar teeth have no bony roof to the common alveolus, but they are separated from the orbit by a thin sheet of connective tissue in which afterwards bone is doubtless developed.

Opposite the upper hinder part of the infraorbital foramen, and behind and under cover somewhat of that part of the frontal process of the maxilla, a very small os lacrimale is met with; this, as has previously been mentioned, is of very small size, and lies for the most part above the naso-lacrimal duct. It has not been represented in the model.

The Os zygomaticum (Pl. 4) is a narrow bone pointed at each end; its anterior point passes fowards over the zygomatic process of the maxilla, whilst its posterior process sinks backwards under the anterior extremity of the zygomatic process of the temporal bone. From its deep side arises the zygomatico-mandibularis muscle.

The Os palatinum (Pls. 2, 9) is a comparatively large bone which commences under the cupula posterior, in close contact with which it lies; it is continued backwards under the trabecular and interorbito-nasal parts of the central stem as far as the front of the ala temporalis. It consists of two lamellæ, one the vertical lamella or plate, which is vastly greater than the other or horizontal plate: and it is this vertical plate that by its upper border comes into contact with cupula nasi, interorbito-nasal (lamina hypochiasmata), and trabecular parts of the central stem. The vertical plate joins at right angles the horizontal plate, and from the angle of junction posteriorly a well-marked tuberosity, such as is seen in man, projects backwards and outwards along the anterior edge of the ala temporalis; medial to the vertical plate and above the horizontal plate the ductus naso-pharyngeus passes backwards. Along the lateral side of the vertical plate lies the comparatively large spheno-palatine ganglion. Along the under aspect of the horizontal plate, and not far from the tuberosity, a well-marked forwardly running groove is seen which is chiefly occupied by a large palatine vein. As one traces the vertical plate further backwards one sees on its lateral side the Gasserian ganglion, and one notices how very closely the bone approaches the floor of the cavum cranii; and in this region too the Vidian nerve lies laterally to the upper end of the vertical plate. The root of the tuberosity comes to lie over the cartilage of the pterygoid bone (parasphenoid of Gaupp), and later in front and to the outer side of the pterygoid bone itself; and at the upper edge of this region the Vidian nerve bends over it from the lateral to the median side, running between the palate bone and the central stem of cartilage, which now is being enclosed by periosteal bone (the primordium of the basi-sphenoid).

The Os pterygoideum (Pls. 2, 9) (*Parasphenoid of Gaupp*).—This interesting bone lies behind and medial to the hinder part of the palate bone; further, it is placed lateral to the hindmost part of the ductus naso-pharyngeus. For the most part it consists of membrane bone, but encloses everywhere, save below, a very large cartilaginous nucleus (Pls. 2, 9), the basis of the hamulus around which the tendon of the tensor palate muscle turns into the soft palate. The contained nucleus in coronal section is pear-shaped in form, with the stalk of the pear reaching up almost to make contact with the pterygoid process of the ala temporalis, only a very thin lamella of bone intervening. The bone which envelops this cartilage from above is fused at this time at its upper end with the post-sphenoidal ossification, and in the angle between the two is seen the Vidian nerve. Lateral to cartilage and bone of the pterygoid the belly of the tensor tympani may be seen, and the central skin in this region is almost devoid of cartilage, that having been absorbed for the most part.

The Alisphenoid (Pls. 2, 4, 5) is partly a covering and partly a substitution bone—formed mainly in the perichondrium along the anterior edge of the ala temporalis; it also extends along the outer edge of that cartilage as far as the tip of its posterior lateral process. Invading the anterior limb of the fissure in the processus ascendens of the ala temporalis, it on leaving this expands widely as an ossification of the representative of the membrana obturatorum; it comes next to lie over and form a covering bone to the orbito-parietal commissure, along which it reaches anterior to the squama of the os squamosum. It does not, however, at this stage reach by a considerable distance the lower margin of the frontale. Viewed as a whole from the front in the model, the alisphenoid is seen to consist of two limbs—one horizontal, which lies along the anterior border of the ala temporalis, from which the musculus pterygoideus internus arises; the other almost vertical, from which the musculus pterygoideus externus arises. The upper edge of this part is overlapped by the squama of the os squamosum.

The Os tympanicum (Pls. 4, 6), a somewhat horseshoe-shaped membrane or covering bone, open behind, may be described as having two limbs, viz. an upper and a lower, which join just below and lateral to the cupula cochlæ. The upper limb lies below and lateral to the hind end of Meckel's cartilage, and on its medial side the goniale is seen lying below Meckel's cartilage. The lower limb, more cylindrical, follows very much the inferior contour line of the first turn of the cochlæ, from which it is separated by a comparatively small interval. From the close relation of the hinder end of the upper limb of the tympanicum to Meckel's cartilage, it may be looked upon as a covering bone to that cartilage. The manubrium mallei is projected into the middle of the area enclosed by the two limbs of the tympanicum.

The Goniale (Gaupp) or *Prearticulare* (Pls. 5, 6) is a flat membrane bone of some size, placed on the under aspect of the hinder end of Meckel's cartilage, immediately medial to the hind end of the upper limb of the tympanicum, between which it stretches, and the tensor tympani muscle, lying just dorsal to the tympanic cavity. It is perforated from above downwards by the chorda tympani nerve rather nearer its lateral than medial side, and much nearer its posterior extremity than its anterior one. It ends behind in a pointed extremity which is in close contact with the lower aspect of Meckel's cartilage, and its backward extent is somewhat greater than that of the upper limb of the tympanicum. Only a small part of the bone has much relation to Meckel's cartilage—in fact, little more than its outer edge. The great part of the bone is spread over the cavity of the tympanum (mucous membrane), and it reaches so far towards the tensor tympani muscle as to give one the impression that this muscle has some connection with it. In cross section the goniale in its best-developed part is of wavy outline, thin and concave upwards in its outer half, thick and concave downwards at the inner half, and subtended on its inner side by dense connective tissue in whose concavity the tensor tympani muscle lies.

The Mandibula (Pls. 2, 4, 9).—This, by far the largest bone of the skull, is composed of two symmetrical halves. Each half consists of a body which along a large part of its course divides in the upward direction to form two alveolar laminæ, one medial, the other lateral, which are widely separated from one another, but at this stage no alveolar septa are formed between the teeth contained. Posteriorly the body divides into three branches, of which the middle one, mainly represented by cartilage, passes backwards to the glenoid fossa of the squamosum; another, the ascending branch, is the coronoid process, which passes upwards under cover of the os zygomaticum; whereas the third or remaining process, formed of cartilage, forms the large backwardly divided angular process.

Both the condylar cartilage and the angular one are closely invested by perichondrial bone continuous with the bone belonging to the neighbouring parts of the mandible, but both cartilages, when traced backwards, emerge from this investing bone and become surrounded by a thick covering of dense connective tissue. As the condylar cartilage is traced to its proximal extremity, its cells which are most proximal are seen to be in a much younger condition than the more distal ones, and they ultimately merge into the surrounding fibrous tissue; above this connective tissue a joint cavity is present, and above that a connective-tissue interarticular plate, and above this again another joint cavity is visible. There are no cartilage cells in the interarticular plate or disc, and the external pterygoid muscle is in part inserted into its medial edge.

As has been before mentioned, the main body of the jaw divides into two lamellæ, viz. a median and a lateral; these two are the alveolar processes or walls. The inner alveolar process at its hinder end is fused with the inner side of the root of the coronoid process to form a bridge under which the inferior dental nerve runs from behind to enter the common alveolus. At its hinder end a plate of cartilage is developed in the inner alveolar wall (Pl. 9), a condition I have not observed in any other animal. Two tooth buds occupy the common alveolus, and opposite the more anterior of these Meckel's cartilage, which at first lies in a groove on the median side of the mandible, now becomes entirely enclosed within a bony canal which, at first fenestrated, so that the cartilage is here and there visible from the inner aspect, becomes soon complete. Further forward Meckel's cartilage once more appears on its medial side, uncovered by bone, and so runs forwards to meet and fuse with its fellow along a somewhat extensive symphysis. At the extreme anterior end of this symphysis each cartilage ends freely in a small-pointed extremity. By the side of the anterior symphyseal region of the two cartilages of Meckel, there is developed in the inner alveolar wall of the inferior incisor tooth socket an accessory cartilage which is thick enough to extend to both medial and lateral surfaces of this wall. It is partly ossified, and that by invasion from the surrounding membrane bone.

The alveolus of the large inferior incisor tooth, as might be expected, is of enormous size, and although complete behind, is laterally for a considerable distance—in fact as far as the anterior extremity of the mandible—deficient.

Above and behind the incisor alveolus an oval mental foramen is seen through which the mental branch of the inferior dental nerve emerges.

A word or two may be said regarding the inferior dental nerve, and its relation to the mandible. This nerve, after becoming free of the main mandibular nerve trunk, passes downwards and outwards between the external pterygoid muscle and Meckel's cartilage, the latter to its medial side, and on reaching the cartilage the nerve to the mylo-hyoid muscle is given off which reaches the mylo-hyoid muscle between the lateral aspect of Meckel's cartilage and the angular mass of cartilage. The main trunk of the inferior dental nerve, associating itself more with the medial lower edge of the condylar cartilage, enters the mandible through the inferior dental canal formed, as already mentioned, by union of the inner alveolar wall with the root of the coronoid process; proceeding outwards, it gradually sinks in level, until it more nearly approaches the angular cartilage and Meckel's cartilage, and when the common alveolus is reached it lies under the fibrous floor of that hollow some considerable distance below the hindmost tooth bud. Later it is in fairly close relation with the medial side of the angular cartilage; later it lies between Meckel's cartilage and the outer alveolar wall, and opposite the foremost tooth bud it divides into two terminal branches, of which the uppermost, the mental branch, rises upwards and forwards and leaves the mandible through the mental foramen; the other branch runs forwards in the mandible to supply the incisor tooth.

The Vomer (Pl. 2).—This bone reaches from a point almost immediately behind the medial palatine process of the incisivum, but at a plane somewhat dorsal to it, on the medial aspect of the upper half of the medial lamella of the paraseptal cartilage; in section it is here V-shaped, and may then be said to lie below the septum nasi and the two paraseptal cartilages. The connective tissue in which it lies, and which is of the same form in coronal section, stretches upwards and laterally to reach on each side of the septum the fibrous tissue suspending the paraseptal cartilage from the septum; further back the vomer is Y-shaped in section, the stem of the Y being downwards, and lying in the narrow fissure between the bilaminar parts of the paraseptal cartilages, and the two limbs reach out and upwards almost as far as the suspensory ligament of the paraseptal cartilage on each side. Further back, where the paraseptal cartilages have lost their lateral lamella, all the limbs of the Y-shaped vomer (in section) have thickened. Still further back, where the paraseptal cartilages have been reduced to narrow rods, the vomer has again been reduced to a V-shaped form, and each limb of the V now surrounds completely the corresponding paraseptal cartilage; and it is interesting to note that the fusion of the two limbs at the apex of the V is very imperfect, only here and there, in fact, hinting at a possible ontogenetic double origin of the vomer in Microtus. When the paraseptal cartilages have been traced back to their fusion with the lamina transversalis posterior, the vomer is still continued back, but now in two separate halves along the medial edge of the corresponding lamina transversalis posterior, and the cartilage here is much altered in character, presenting the appearances associated with commencing ossification in cartilage. Each half comes to an end shortly before the cupula posterior is reached, and here each half is separated by an appreciable interval from the cartilage of the lamina transversalis posterior. In the model the anterior V- and Y-shaped parts of the vomer, being so closely wedged in between the paraseptal cartilages, could not be shown.

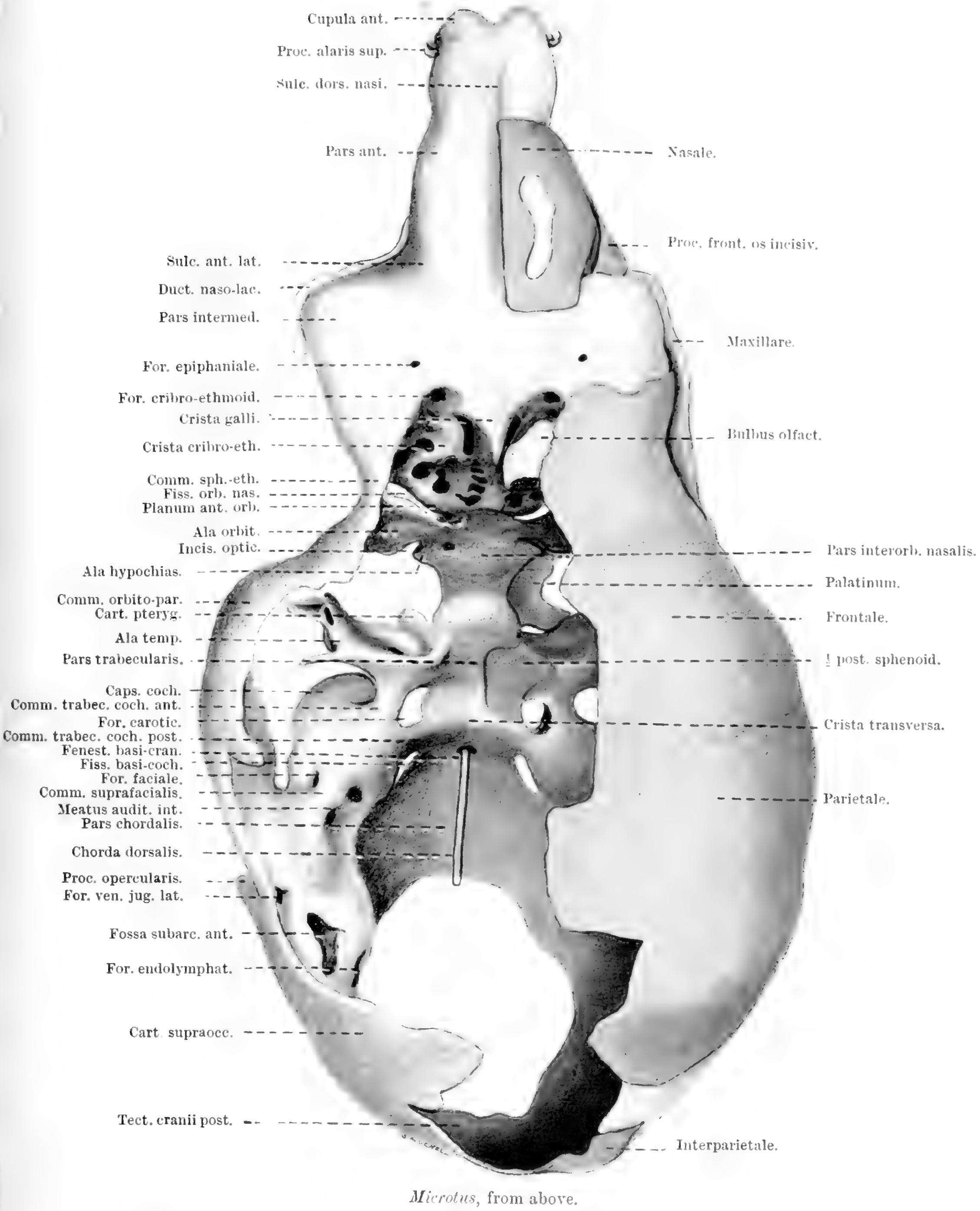
MIXED BONES (ENTOCHONDRAL AND SUBSTITUTION BONES).

Os sphenoideum.—This is only ossified so far as the ala temporalis and post-sphenoid are concerned. The ala temporalis is only slightly invaded by perichondrial ossification along its anterior margin and along its lateral edge. This ossification is in continuity with the alisphenoid membranous ossification. At its root part, where its median ventral process (see description of ala temporalis) is found, perichondrial ossification large in amount connects it at once with the os pterygoideum and with the ossifying post-sphenoid. The os pterygoideum is therefore at an early period fused with the post-sphenoidal elements. The post-sphenoid is chiefly ossified from the investing perichondrium of the pars trabecularis. On each side of the remnant of the cranio-pharyngeal canal it is easy to see that the cartilage is in process of absorption, and it is doubtful if the cartilage here forms anything more than a framework on which perichondrial bone is deposited. As this region is followed backwards under the lobes of the pituitary body, the cartilage of the pars trabecularis is complete, and ossification of its perichondrial investment is only apparent on its upper and lateral aspects; and by the time that the basi-cranial canal through which the notochord dips down to the region of the pharynx is reached—in other words, when the hindmost limit of the pars trabecularis is reached—the post-sphenoidal ossification ceases. The post-sphenoid, then, is essentially an ossification in connection with the pars trabecularis. I do not know if it arises by two centres corresponding with the two trabeculæ, as I long ago confirmed in man, and which, as a matter of fact, was well known; but it is possible that it may be so. At all events, double ossification of the post-sphenoid can be satisfactorily explained on the ground of its trabecular origin. No trace of pre-sphenoidal nor of orbito-sphenoidal ossification existed at this stage, nor have I any information regarding what happens in Microtus regarding these parts.

Os occipitale.—The basi-occipital and the exoccipital and the supra-occipital are in process of ossification. The basi-occipital ossification stretches from the anterior margin of the foramen magnum almost as far as the basi-cranial canal. It is to a large extent perichondrial, but does not reach out to the lateral limit of the chordal plate. The chorda dorsalis lies immediately under the perichondrial bone of the dorsal surface of the chordal plate in its whole length. This basi-occipital ossification is narrow behind at its commencement, but widens much as it is traced forwards. The exoccipital centres are primarily perichondrial, and envelop those cartilages above, in front and below but not behind, immediately lateral to the hypoglossal canals. Ossification does not reach out as far as the paracondyloid process; not further out, in fact, than the lateral margin of the upper ganglion of the vagus nerve. Behind the hypoglossal canals it invades slightly the condyle, and beyond the posterior limit of the condyle perichondrial as well as entochondral ossification is continued up along the side of the foramen magnum; later it is entirely perichondrial. This ceases opposite the level of fusion between the posterior pole of the auditory capsule and the exoccipital cartilage.

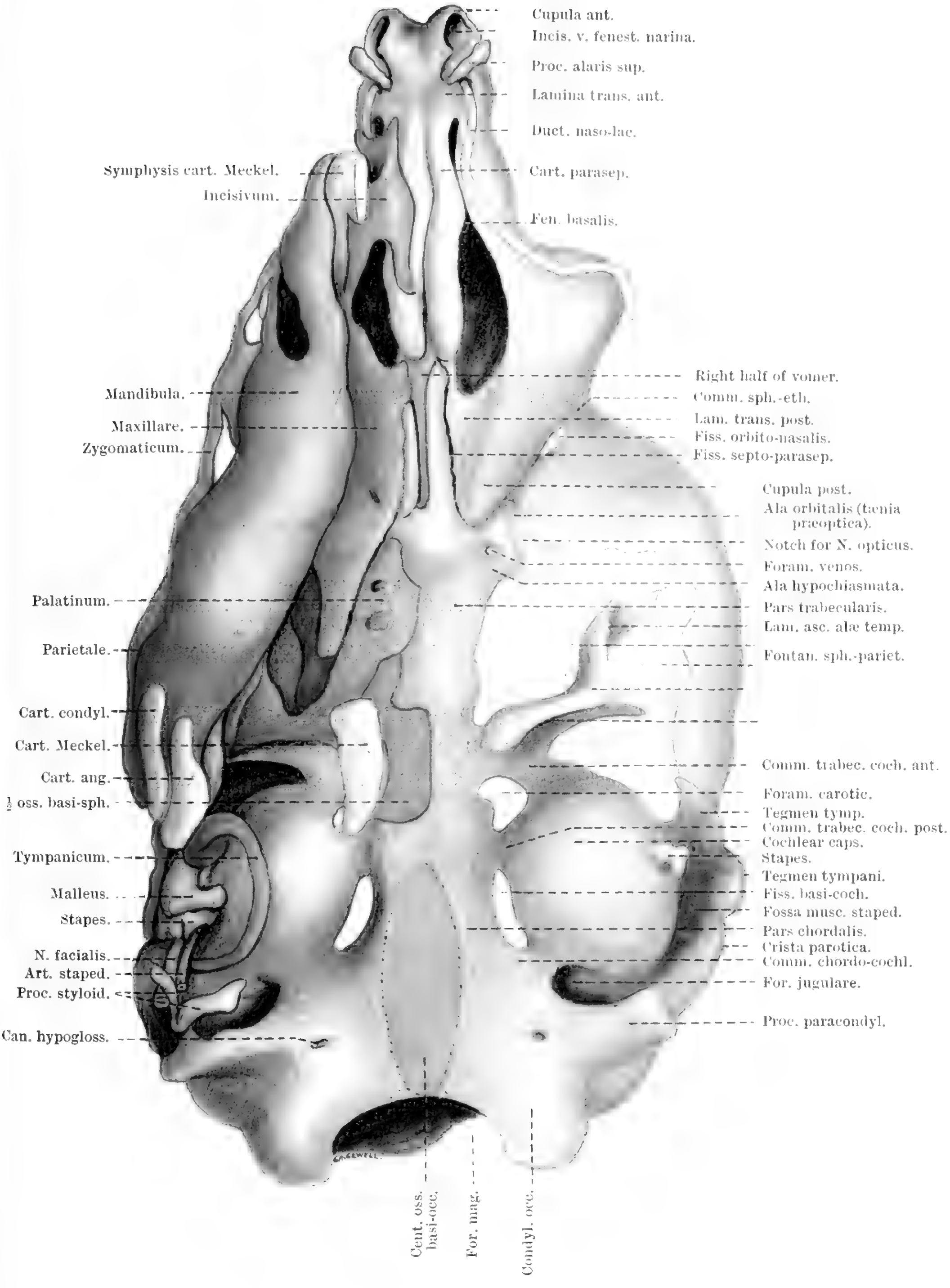
The supra-occipital is in process of ossification mainly perichondrial, but owing to the plane of section being coronal it is impossible to determine satisfactorily its limits.

In conclusion, it may be stated that the main comparative statements made here concerning the very young stages are based on personal



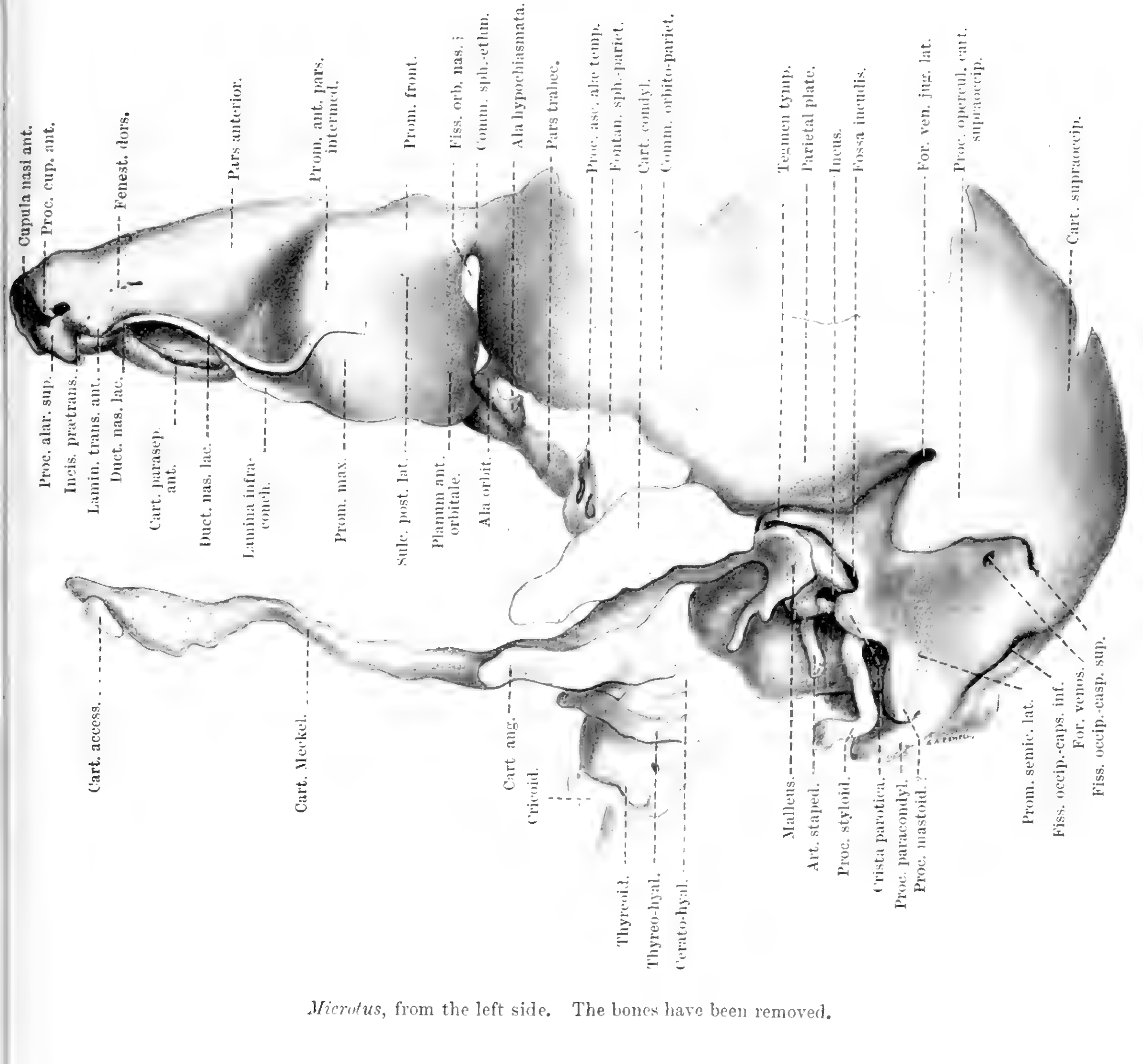
Microtus, from above.

Professor EDWARD FAWCETT.



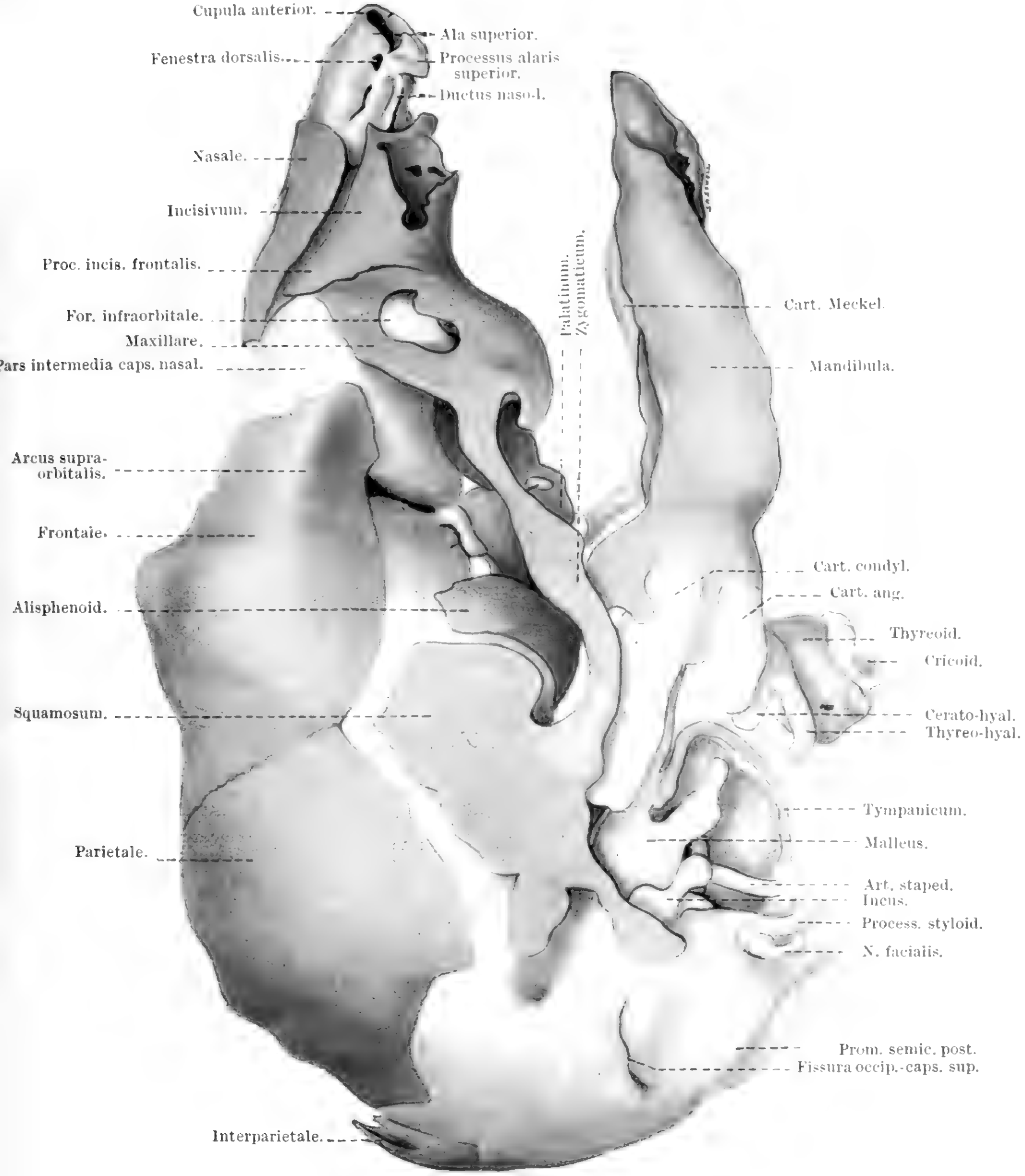
Microtus, from below.

Professor EDWARD FAWCETT.



Microtus, from the left side. The bones have been removed.

Professor EDWARD FAWCETT.



Microtus from right side, showing bones in addition to cartilage.

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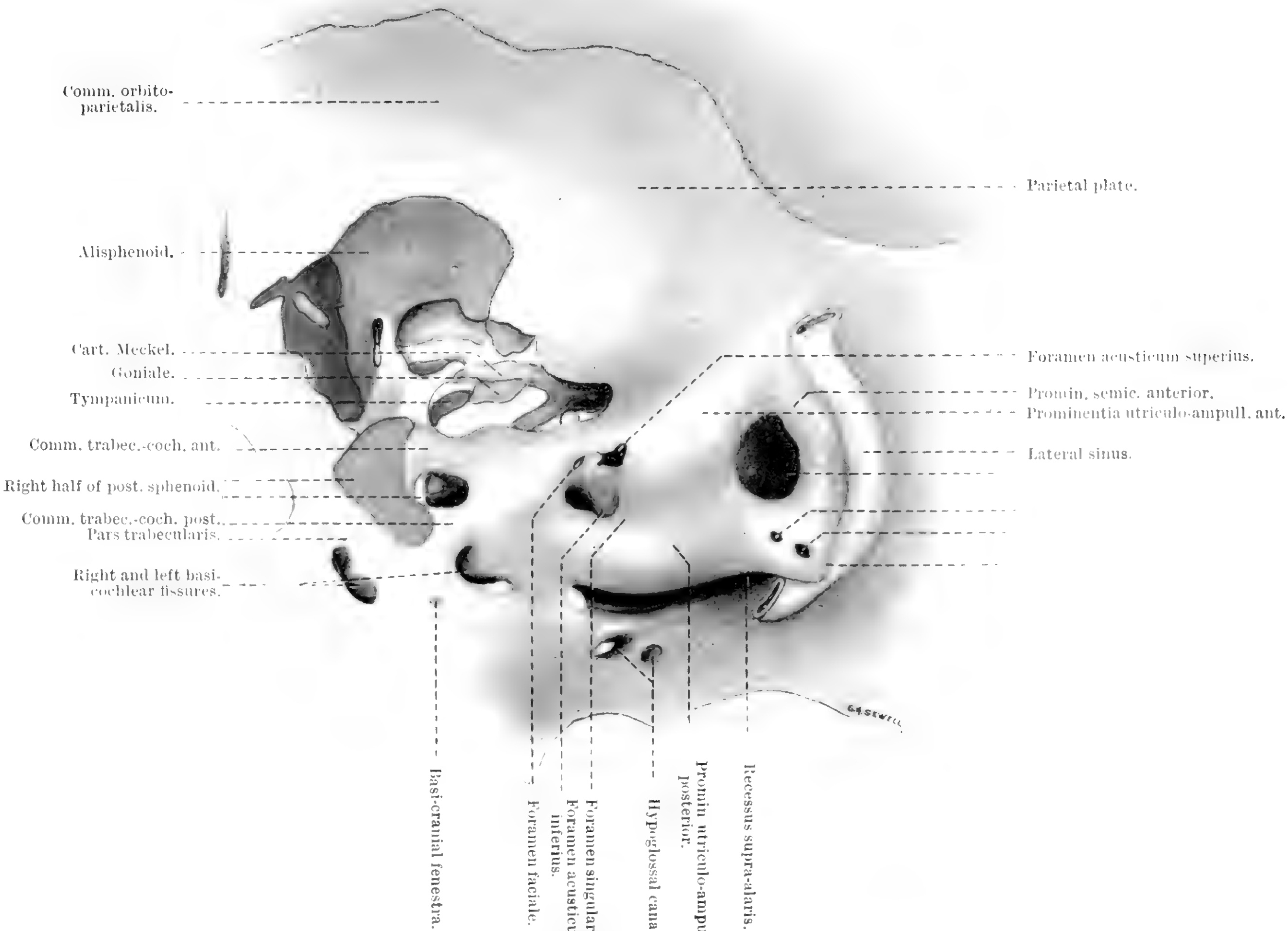
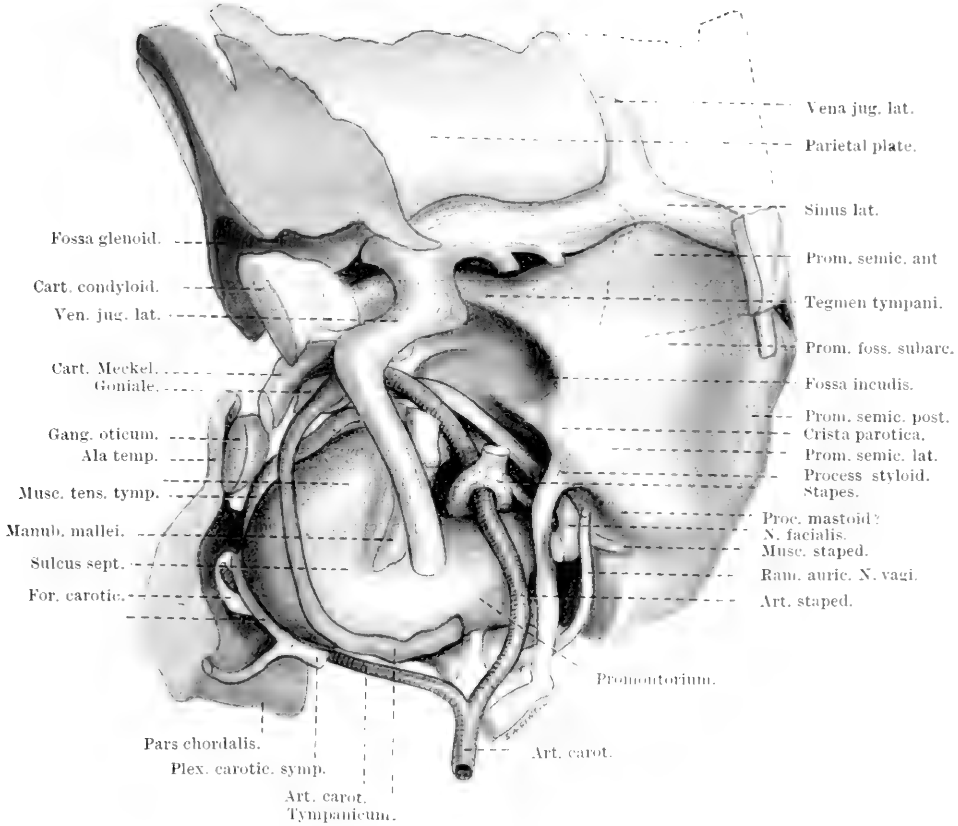


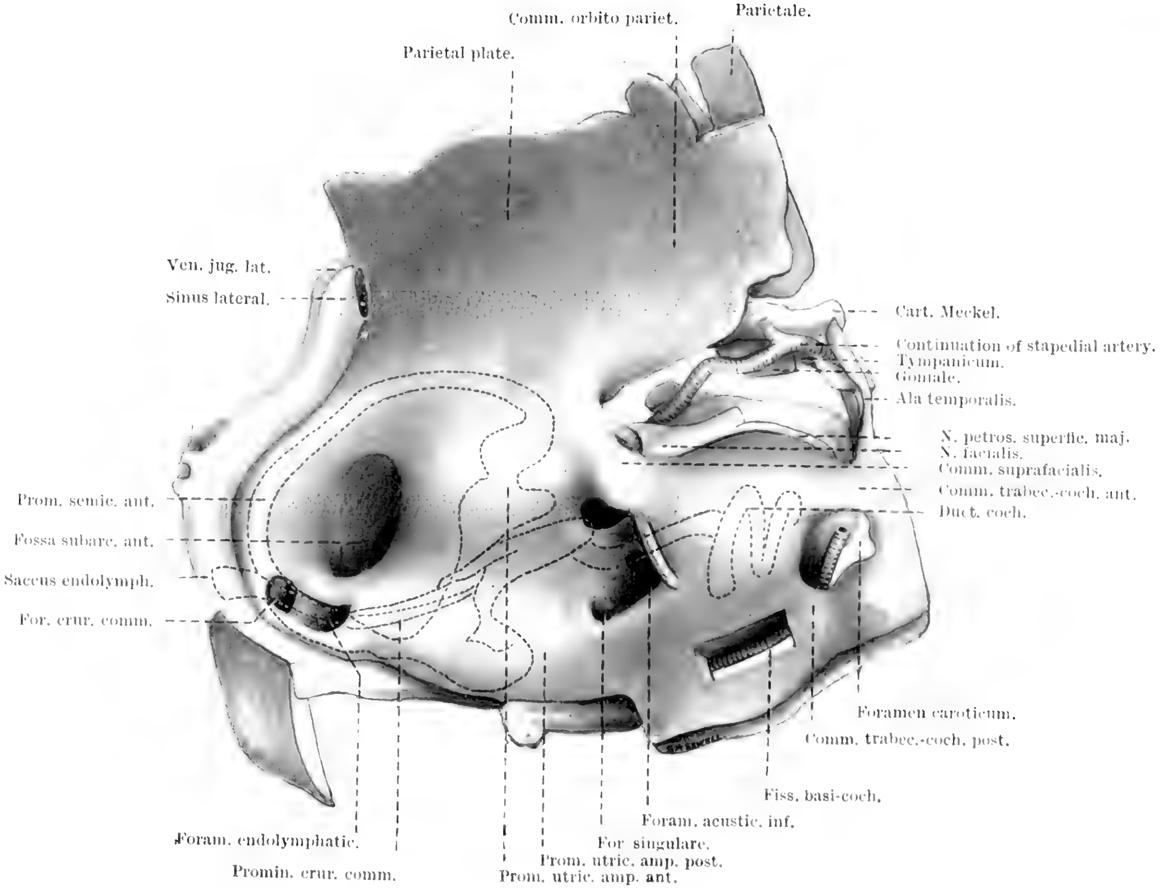
Microtus. The right auditory capsule and environs from medial aspect.

Professor Edward Fawcett.



Microtus. The left auditory capsule seen from the lateral aspect, with its environs. The area enclosed by an interrupted line is the supraoccipital cartilage, with its opercular process.

Professor EDWARD FAWCETT.



Microtus. Medial aspect of left auditory capsule, and the structures in relation with it.
The membranous labyrinth is shown by interrupted lines.

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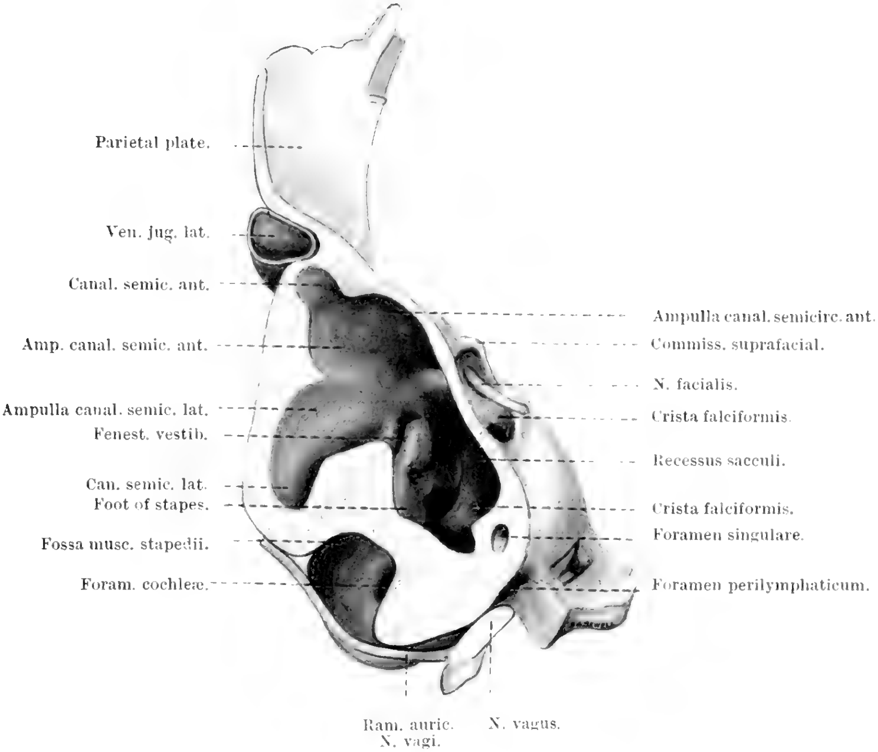
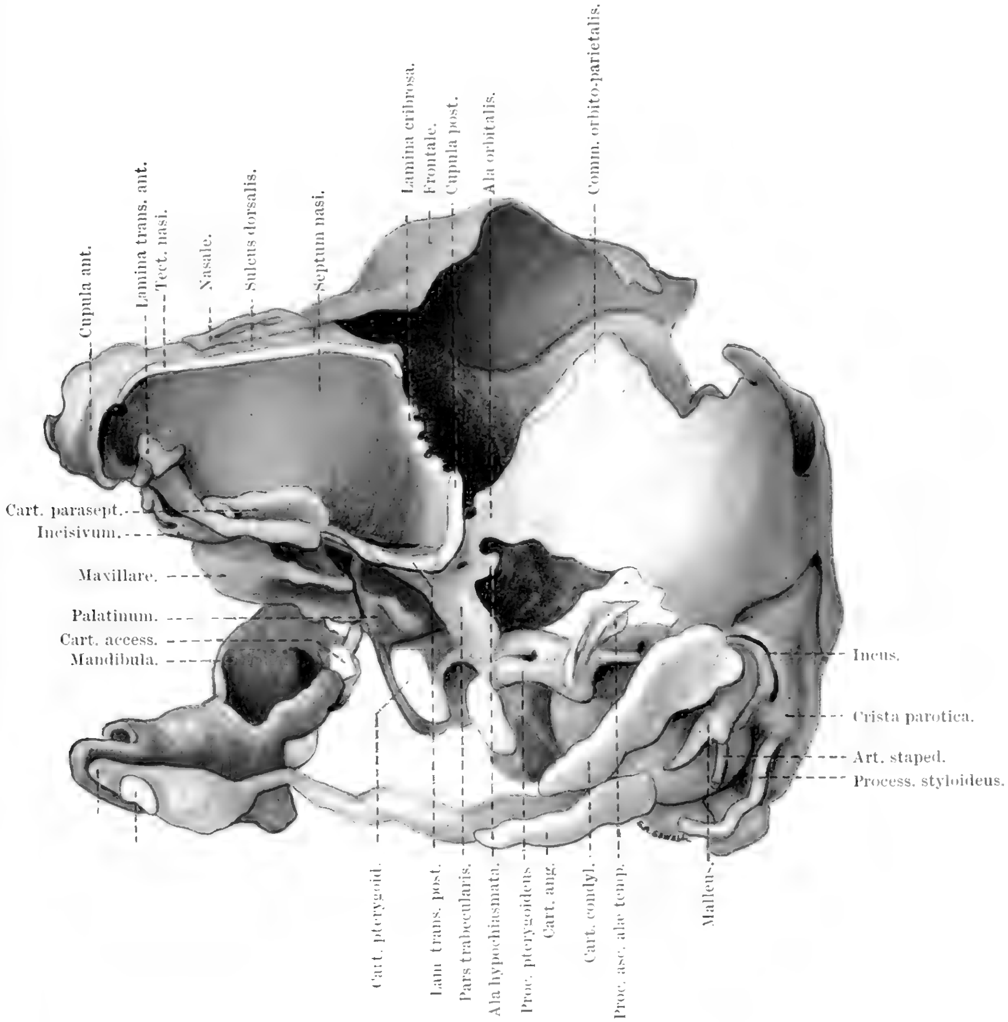


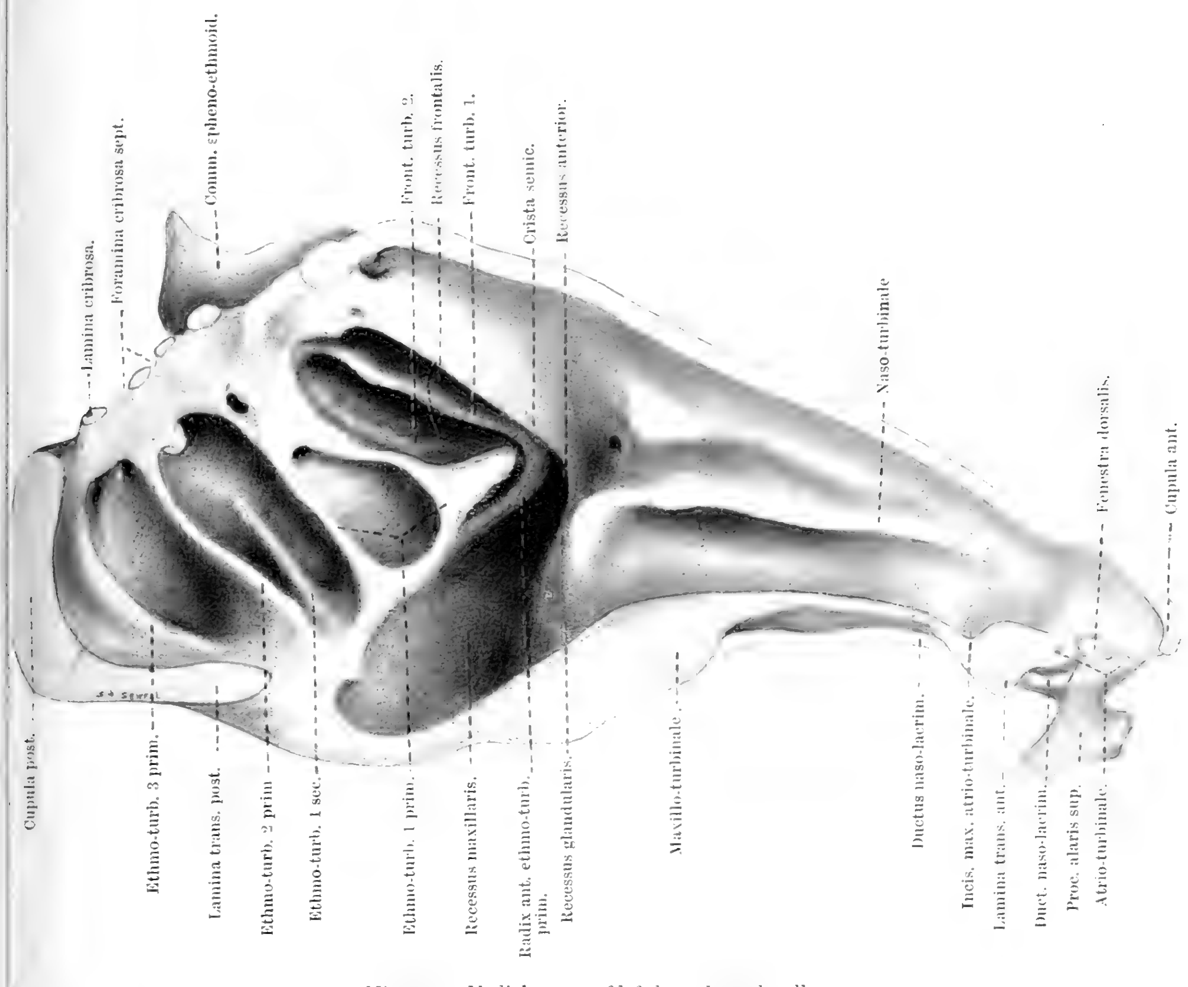
Microtus. Anterior half of coronal section of auditory capsule, viewed from behind.

Professor Edward Fawcett.



Microtus. Left half of nasal wall removed, to show especially the septum nasi and appended structures.

Professor EDWARD FAWCETT.



Microtus. Medial aspect of left lateral nasal wall.

Professor EDWARD FAWCETT.

investigations of those stages on specimens stained with thionin, as recommended first by Kallius (*Anat. Hefte*, vol. xxx., 1905, p. 9). It is by far the most delicate stain known to me for cartilage; in fact, tissue which would certainly be pronounced procartilage by hæmatoxylin stain stands out clearly as cartilage when stained with thionin. The tissue must be quite fresh and be well fixed. The stain is as delicate for cartilage as Mallory's stain for bone. This communication may be regarded as introductory to many others, hence but scant reference is made to literature, but it is my duty to refer here to the kindness with which my friends Professors J. P. Hill, F. Wood Jones, Arthur Robinson, and D'Arcy Thompson have placed material at my disposal; also to the invaluable help given me by my students, Misses Casson, Neville, Brown, Llewellyn, Richmond, and Messrs Tilsley, Datta, and White, in cutting out wax plates, etc. The main illustrations have been done by Mr S. A. Sewell, whilst fig. 3 I owe to my daughter Dorothy.

The expenses of this research were to a large extent defrayed by the University of Bristol Colston Society's Research Grant.

THE ACTION OF THE BICEPS FLEXOR CRURIS.

By Professor A. M. Paterson, *Liverpool.*

It is familiar to all anatomists that the great sciatic trunk is composed of three separate nerves—the peroneal, tibial, and nerve to the hamstrings,—enclosed in a sheath in that order from without inwards. The nerve to the hamstring muscles sends its branches to the muscles supplied in one, or more often two, bundles. It supplies the long head of the biceps: the short (femoral) head being supplied by the peroneal nerve.

It has further been shown that the short head of the biceps is closely related morphologically to the gluteus maximus. In Ruminants they form one muscle, the long vastus. In man they are occasionally supplied by a common nerve (the inferior gluteal) carrying the fibres (L. 5, S. 1, 2) for the supply of the short head of the biceps—as well as the gluteus maximus.

In view of these facts it is interesting to observe, as I have had the opportunity of doing recently, the effect of division of the peroneal nerve in gunshot wounds of the buttock. Cases are occasionally found in which only the outer part of the great sciatic trunk is divided, resulting in paralysis and anæsthesia in the area of distribution of the peroneal nerve alone. In such cases there is paralysis of the short head of the biceps, but the hamstring muscles, including the long head of the biceps, remain active.

The result of the elimination of the short head of the muscle is well seen when the patient lies on his face and flexes the knee. The long head of the biceps becomes taut in the early part of the movement, but when the limb is semi-flexed its function ceases and the tendon becomes flaccid—the reason being the absence of the aid derived in normal conditions from the contraction of the short head, which keeps taut the tendon of the muscle.

Furthermore, there is a hollow produced in front of the tendon of the long head during contraction, instead of a swelling due in the normal muscle to the contraction of the short head.

The movement of external rotation of the knee seems to be due to the agency of the long head of the muscle.

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THE FORM OF THE URINARY BLADDER.

By A. R. THOMPSON, Ch.M., F.R.C.S., *Surgeon in Charge of the Genito-Urinary Department, Guy's Hospital.*

DURING the past six years, as chief of the Genito-Urinary Department of Guy's Hospital, I have had reason to alter my conception of the form of the urinary bladder, and to consider that the descriptions usually offered in the text-books which deal with the subject are by no means adequate.

The following difficulties have occurred, in my own knowledge and experience, which are not adequately explained by the conception of a regular and symmetrical bladder occurring in the living subject.

The form of the bladder, in the living subject, is revealed by the cystoscope, which is a scientific instrument of precision. These are the difficulties:—

1. The asymmetry of the ureteric ridges, and the position of the ureteric orifices.
2. The difficulty of seeing, in some cases, the ureteric orifices, with the aid of the cystoscope.
3. The difficulty, in some cases, of completely draining a bladder, for a short or a long time, by means of a catheter.
4. A symmetrical stone, regular in outline, may be placed in an asymmetrical position as revealed by the X-rays, and the bladder sound.
5. The irregular passage of urine before, during, and after defæcation.
6. The apparent unwillingness of even expert surgeons to perform the operation of lithotrity, an operation which should not be attended with much risk, were the bladder symmetrical in form and position.

Before the war an investigation was begun by me into the shape of the bladder, with a view to demonstrating points in cystoscopy. The results of this investigation cleared up, in a satisfactory way, many of the difficulties, if not all, which have been enumerated. I thought it worth while, therefore, to bring these results before you at this meeting of the Anatomical Society (Friday, 1st December 1916).

For the results of this investigation I am indebted to the old-fashioned plan of the injection of plaster of Paris into the empty viscus in known amounts.

The bladders of subjects not long dead, and even in some cases with rigor mortis present, and in no case dead longer than twenty-four hours, were injected with plaster of Paris in a liquid state. Some of my latest specimens, *e.g.* Nos. 13 and 16, were injected within two hours of death.

The results of these investigations have convinced me that the form of the bladder is very variable. The shape of the casts resulting from the setting of the plaster fully explains, and agrees with, the shape of the living bladder revealed by the cystoscope.

In my collection of casts of the bladder there are twenty specimens. Only a few of the casts are complete, as it is very difficult to drain a bladder completely with a catheter, and a certain amount of fluid is left in the bladder unavoidably. This fluid does not mix with the injected plaster, and rises to the top of the bladder, and thus a flat surface of plaster is left. During catheterisation air also may enter the bladder.

This flat surface, however, helps us to place the cast in its true position. The bodies lay horizontally upon a metal table, and the specific gravity of the liquid plaster as shown by Hare's apparatus is 1·38.

It is possible that the flat surface is anatomical, and not accidental *e.g.* in No. 16.

The casts are numbered from 1 to 20, and have been grouped together according to weight.

GROUP I.—2½–4¼ ounces. Nos. 2, 3, 4, 5, 6.
GROUP II.—5½–8¼ ounces. Nos. 7, 8, 9, 10, 11.
GROUP III.—11 ounces. Nos. 12, 13.
GROUP IV.—13¼–15 ounces. Nos. 14, 15, 16.
GROUP V.—Infants and children. Nos. 1, 18, 19, 20.

DESCRIPTION OF INDIVIDUAL CASTS. UNDER GROUPS, RELATIVE TO ERECT ATTITUDE.

GROUP I.—2½–4¼ ounces.

No. 2.—Age not recorded—weight 2½ ounces. The specimen shows considerable asymmetry, extending forwards and to the left, and bulging backwards and to the right. The trigonal region, or base, is egg-shaped, being broader on the left side. There is a continuous ureteric ridge, not so well marked in the centre as laterally, near the ureteric orifices. The bladder is much broader at the base than at the fundus, and I imagine, from the usual shape of bladder retractors, that this specimen affords the average surgical conception of the form of the bladder.

No. 3.—Male, aged 21, displacing 3¼ ounces of water; shows, as rather a marked feature, the relative flattening and breadth of certain bladders.

No. 4.—Female, aged 61, displacing 3½ ounces of water; shows much more of the bladder situated upon the left side of the middle line. The flat surface is clearly accidental. The specimen shows a sacculus, situated on the left side, and in the line of the left ureteric ridge.

No. 5.—Young male subject, displacing 4 ounces of water. It is practically symmetrical. There is a very large entrance to the urethra. This last feature should be associated with the marked symptoms of vesical calculus in young people, and the relatively frequent occurrence of passage of calculi from the bladder into the urethra in young as compared with old people.

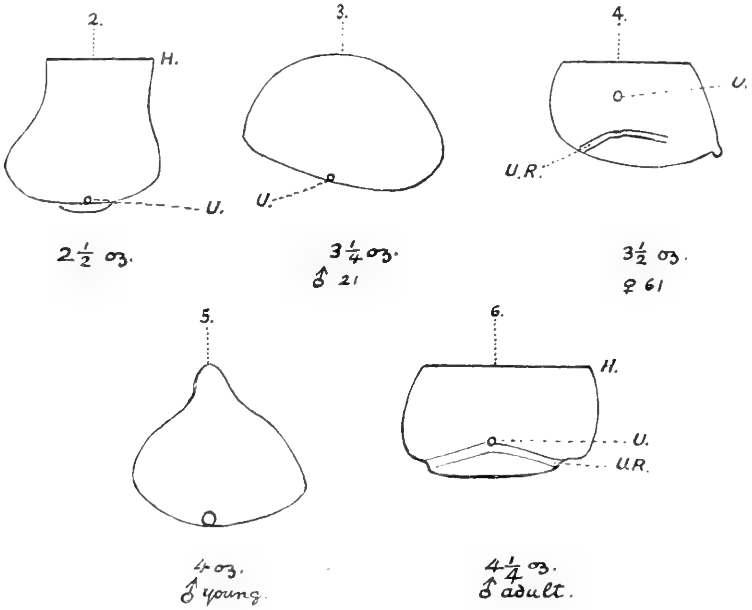


Fig. 1.—Group I. (Scale ⅓ nat. size.)

General references to diagrams.

H., horizon; U., urethral orifice; U.R., ureteric ridges; U.O., ureteric orifices; P.I., prostatic impression.

No. 6.—Age unknown, probably male, as there is a prostatic impression; shows relative flattening and broadening of the bladder. There is much more of the bladder on the left than the right side. The ureteric ridges meet at the neck of the urethra, without the intervention of a uvula.

Such cases are not uncommonly met with during a cystoscopic examination, and present difficulties in the passage of a ureteric catheter.

Apart from its asymmetry, this specimen follows closely Professor Dixon's masterly description of the bladder.

General Considerations of Group I.

The specimens lose some of their value owing to the flat surface mentioned in the introductory portion of this paper. Complete symmetry does not occur in any one of them. A greater part of the bladder is situated on the left side in three cases and on the right side in one case. The ureteric ridges are continuous, but show, in No. 2, a tendency to what I believe may be regarded as the infantile type (*vide infra*). In one case, No. 6, there is, strictly speaking, no area between the urethra and the ureteric ridges.

GROUP II.—$5\frac{1}{2}$–$8\frac{1}{4}$ ounces.

No. 7.—Age and sex not recorded, displacing 6 ounces of water.

This is a cubical-shaped bladder. The base is well marked, and shows, laterally, two symmetrical, well-marked depressions directed backwards and downwards, lying one on each side of the lower portion of the bowel. The ureteric ridges are of the infantile type, and the trigone is large. This is a symmetrical bladder.

No. 11.—Age and sex not recorded; shows an oblong bladder, displacing $8\frac{1}{4}$ ounces of water. Its longest axis is transverse. The lateral parts of the base are bulging slightly downwards. The base shows a strongly marked uvula. The ureteric ridges are not quite continuous, being separated by a slight groove. There is slight asymmetry of the bladder, more being on the right side of the middle line than on the left. The ureteric ridges are equal in length, but, owing to the asymmetry of the whole organ, the right does not extend relatively so far outwards as the left.

No. 8.—Male, aged 60, displacing 7 ounces of water; is a poor specimen, but is an accurate representation of the shape of the particular bladder. It shows the upper part of the bladder situated asymmetrically and to the left of the middle line. Its base is nearly symmetrical; the ureteric ridges are practically continuous with each other and a well-marked uvula. The base gives no indication of the asymmetry of this bladder. Doubtless if this bladder had become overfilled it would have passed upwards, and to the left of the middle line, and not to the right. Speaking from memory, I should say that bladders when overfilled in many cases do not keep accurately to the mid-line, but pass upwards to the right.

No. 9.—Male, aged 48, displacing $5\frac{1}{2}$ ounces of water; shows a typical bladder, with slight obliquity upwards and to the left. There is a small prostatic depression. The ureteric ridges are well marked and continuous. The trigone looks forwards as well as downwards.

No. 10.—A female, aged 52, displacing 5½ ounces of fluid; not quite complete at the fundus; the horizontal surface thus formed, and the direction of the catheter, help us to place the bladder cast in its correct position. In this specimen the adaptation of the shape of the bladder to the other pelvic viscera is particularly well marked. The lateral expansions outwards, downwards, and backwards are also particularly well marked. There is much more of the bladder situated on the right than the left side. The long axis of the bladder is directed backwards and to the right. There are signs of a ureteric ridge, and perhaps the ureteric orifice on the left

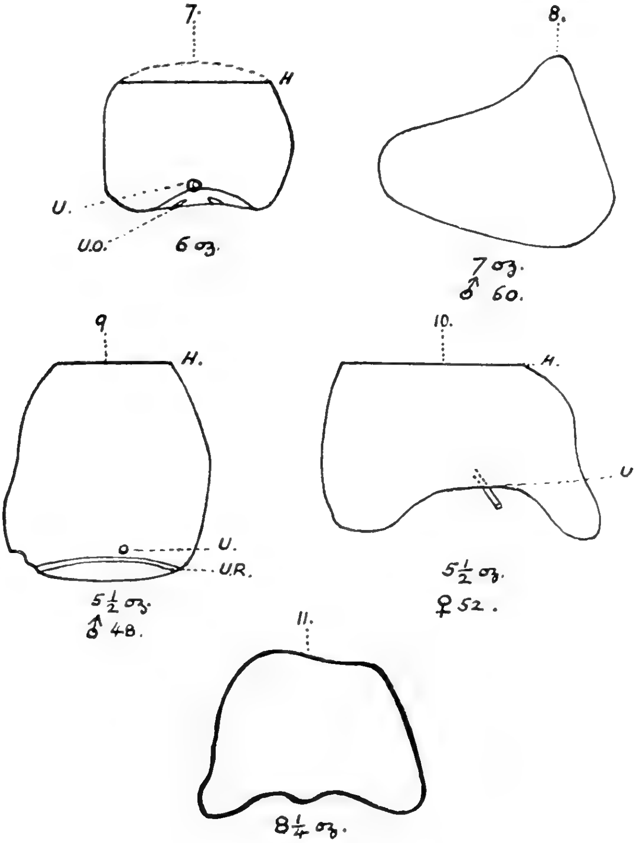


Fig. 2.—Group II.

side in actually looking outwards in what may be called the pararectal fossa of the bladder. I have no hesitation in regarding this cast as a true representation of the form of this subject's bladder. I have come across such cases clinically. They are difficult cases to cystoscope, and in whom to pass ureteric catheters. One could understand such a bladder causing great trouble to the obstetrician, gynæcologist, or surgeon.

General Considerations of Group II.

The bladders forming this group may be considered as holding the quantity of urine which usually produces the desire to micturate. It is therefore an important group. The direction in which the trigone looks is very variable, but it will be more convenient to consider this later. Only one, viz. No. 9, in any way corresponds to the shape usually described. Two of the bladders are cubical or oblong in general shape. One is quite irregular, as regards its fundus (No. 8), and one (No. 10) shows well-marked pararectal fossæ, which are also present, but much less well developed in Nos. 7 and 11.

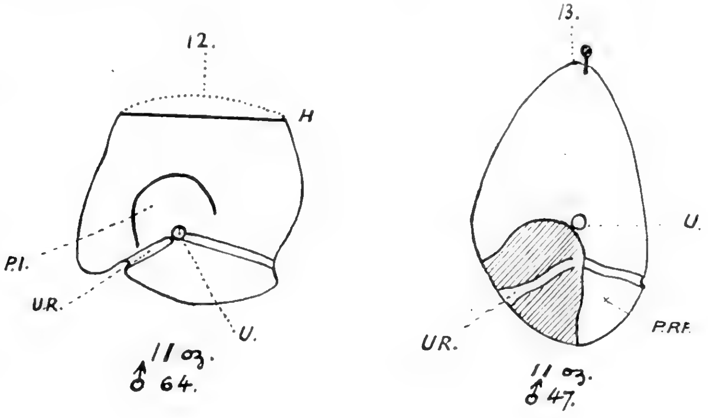


Fig. 3.—Group III.

Group III.—11 ounces.

This group consists of two specimens, and may be considered as holding a little more than the usual quantity of urine which necessitates micturition in the normal person. They are neither of them typical in shape, and both differ from each other very markedly. They both displace similar quantities of water, viz. 11 ounces.

No. 12.—Male, aged 64. This is roughly cubicle in shape, and asymmetrical, much more of the bladder being on the left side than the right.

There is a well-marked prostatic impression. The ureteric ridges are asymmetrical as regards size and position, the right being much higher and prolonged on to the posterior aspect of the bladder. There is no trigone, the ureteric ridges converging upon and meeting with each other at the urethral orifice. This would, I think, be a difficult bladder for one to cystoscope accurately.

No. 13.—Male, aged 47, displacing 11 ounces of fluid; has a hat-pin which was inserted into it vertically just above the pubes in the mid-line when the body was horizontal. This cast was made, the body being under four hours dead. The fundus is slightly to the right of the middle line. The outstanding feature of this specimen is the very large fossa on the left side directed backwards and slightly downwards. In spite of this large pararectal fossa, probably more of the bladder lies on the right side than the left. The ureteric ridges are symmetrical, and both are prolonged on to the lateral aspect of the bladder. The ridges are continuous with each other, but not very well marked. Neither of the bladders in this group may be considered typical in shape. No. 12, however, reproduces the cubical shape, previous specimens of this shape having been demonstrated.

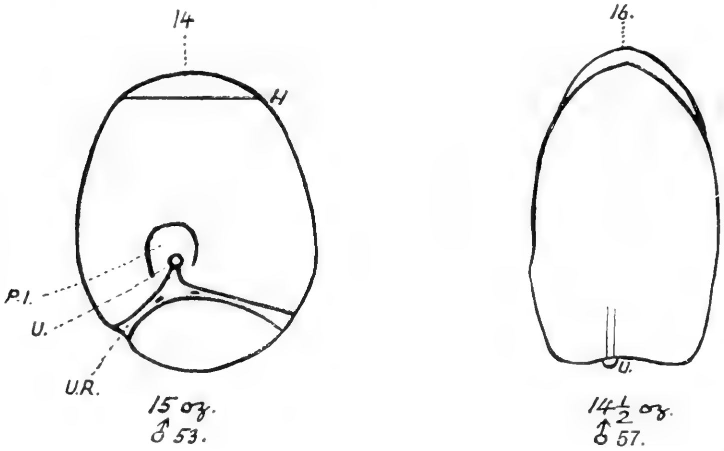


Fig. 4.—Group IV.

Group IV.—$13\frac{1}{4}$–15 ounces.

No. 14.—Male, aged 53, displacing 15 ounces of fluid; tends to reproduce the cubical shape described before. It is asymmetrical, more of the bladder being situated upon the left side. It shows a well-marked colic depression on its upper and back aspect. The ureteric ridges are well marked, and converge upon a very distinct uvula, half an inch long, proceeding forwards to the urethra. There is a well-marked prostatic impression.

No. 15.—Male, aged 44, displacing 13¼ ounces; except that it shows a well-marked pararectal fossa, is a cast of a cast, and therefore in itself calls for no special description. The reason of my thus neglecting any special description of it is explained by the following specimen, of which it forms a part.

No. 17 does not fall into any group, as it is a composite production. 150 c.cm. of liquid plaster were injected into the bladder and allowed to set. 150 c.cm of blue plaster were then injected through the right ureter. This was allowed to set, and then 150 c.cm. of red plaster were injected through the left ureter. Unfortunately the external casing was very thin in parts, and during the disorganisation of my department, consequent upon the beginning of the war, was smashed. The fragments were, however, preserved, and I was able to piece them together roughly and make the cast No. 15.

Nos. 15 and 17.

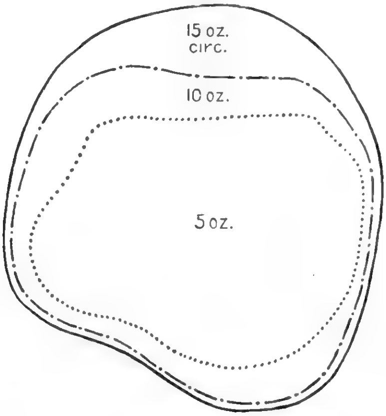


Fig. 5.—Bladder injected as described in the text.

A coronal section, probably directed downwards and slightly backwards, was made of the two inner casts, and the specimen coloured after being fixed in a plaster mount (fig. 5). It is an attempt to show changes which take place in the bladder as it is filled. The inside yellow cast represents a bladder holding about 5 ounces of fluid. A left pararectal fossa is obvious. When another 5 ounces is injected it will be observed, by reference to the blue cast, that the bladder fills up chiefly at opposite poles, viz. right upper pole and left lower pole. The latter is responsible for an increased development of the pararectal fossa. The outer cast, of which No. 15 forms an inadequate representation, showed with another 5 ounces of plaster injected very little increase of this pararectal fossa. This pararectal fossa is therefore not to be associated with the overfilling of a bladder.

No. 16.—Male, aged 57, injected within four hours of death; cast displaces 14½ ounces of water. It is of the shape usually described in text-books, although more of the bladder is on the left side. It is interesting as showing, with a few other specimens, that the typical shape of the bladder can be reproduced by these plaster casts, and that therefore the shapes other than typical which I have described cannot be disregarded. A pin driven in just above pubes in mid-line passed through the urethral orifice of the bladder.

Group V.—Young subjects.

No. 20 simply demonstrates that plaster will make a very good reproduction of the fasciculi of a small contracted bladder.

No. 1 is a cast of a bladder of a female aged four months, displacing 2 ounces of fluid. It affords a good demonstration of the very large part of the bladder contained in the abdomen in young subjects. The position of the brim of the pelvis is clearly shown. Generally speaking, the cast is symmetrical and typical, but the pelvic part shows distinct antero-posterior compression on the left side owing to the pressure of the pelvic colon.

No. 18.—Male, aged 11 months, displacing 3¾ ounces of fluid; shows the same features as No. 1, but in a more marked degree.

No. 19.—Female, aged 3 years, displacing 5 ounces of fluid; shows similar features. Pararectal fossæ, in addition, are well marked, especially on the left side.

Two of these specimens, No. 1 and No. 19, show small discontinuous crests upon which the ureteric orifices are situated, and in No. 18 the continuity of a ridge is by no means established. I am inclined to think these crests rather than ridges, continuous with each other, are more common in children than adults. The young bladder shows, therefore, ureteric crests; the adult bladder ureteric ridges continuous with each other.

Varying Direction of Base of Bladder.

Rough measurements of the angle of general direction in which the trigone looks, or failing this the base of the bladder, have been made in some of these specimens, and is found to vary according to the following diagram. The horizontal is taken with the subject in the dorsal position in order that the angles may be co-ordinated with cystoscope.

This variation of direction of the base, or trigone of the bladder, is of great importance in cystoscopy. The best view I ever had with a cystoscope was in an elderly man, in whom I held the cystoscope nearly vertical; on the other hand, in many cases it is necessary, in order to see the trigone, to hold the cystoscope below the horizontal.

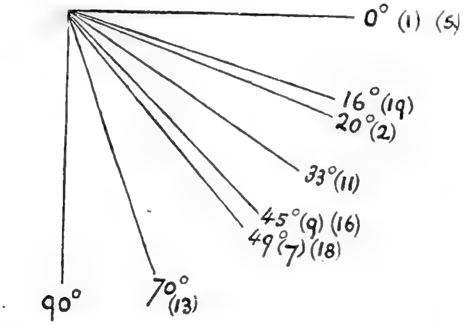


FIG. 6.—Represents the angle which the trigone, or base of bladder, makes with a known horizon.

The figures in brackets refer to individual casts.

The angle which the ureteric ridges or crests make with each other or the sagittal plane vary, but I have not had time to go into the measurements yet.

GENERAL CONSIDERATIONS RELATIVE TO THE FORM OF THE BLADDER IN THE ADULT.

Nos. 2, 3, 5, 6, 9, and 16 may be considered to belong to types usually described.

Nos. 7, 9 and 12 are more cubical in shape than types usually described.

Nos. 7, 10 (especially), 11, 13 (especially) and 15 show either unilateral or bilateral pararectal fossæ.

Nos. 3, 6, 7, and 11 are the only ones which are approximately symmetrical.

Nos. 4, 5, 6, 8, 10, 12 and 13, 15 and 16 show more of the bladder on the left side than on the right.

Nos. 9 and 11 show more of the bladder on the right side than on the left.

The following conclusions may therefore be deduced from the foregoing observations:—

1. The bladder is frequently asymmetrical in form and position.
2. The trigone may vary in superficial area, sometimes not existing at all. It may also vary in the direction in which it looks.
3. Prolongation of the bladder on one or both sides of the vagina and rectum, or rectum only, is not uncommon.

4. These departures from the type usually described offer an explanation of many of the difficulties met with in bladder surgery and treatment.

It would appear further that the same bladder, filled with different quantities of fluid, varies in shape, as depicted in the above diagram, constructed from X-ray photographs of a bladder filled with collargol and then photographed. Five successive photographs were then taken, with two ounces of collargol removed before each photograph. The change in form is quite apparent, especially when No. 5 is compared with No. 6.

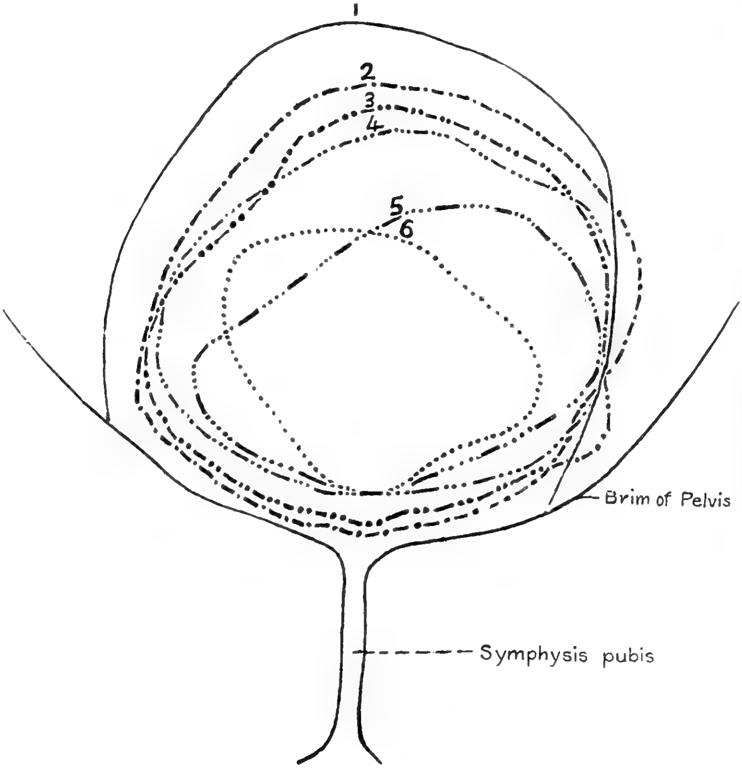


FIG. 7.—Living bladder injected with collargol from X-ray photographs, as described in text.

No. 1, represented by continuous line, holds 2 oz. more than
No. 2, " — · — · which " " "
No. 3, " — · · — · · — · · " " " "
No. 4. " — · · · — · · · — · · · " " " "
No. 5, " · · · · — · · · · " " " "
No. 6. " · · · · · · · · · · · · · ·

THE SUPRACONDYLOID TUBERCLES OF THE FEMUR.

By Y. G. Nadgir, M.S., F.C.P.S., *Grant Medical College, Bombay.*

In the October 1914 number of the *Journal of Anatomy and Physiology* Dr J. S. B. Stopford has described the supracondyloid tubercles of the femur. His observations are based on an examination of 286 adult femora, and his conclusions can briefly be stated thus:—

(1) The medial supracondyloid tubercle is a constant structure, being absent in only one out of 286 femora examined.

(2) In the series examined, it was sufficiently pronounced to make it possible to distinguish the medial aspect of the inferior extremity of the femur solely from its presence.

(3) It appeared as a nodular elevation in 80 per cent., a large projection in 8 per cent., and a slight elevation in 11·2 per cent. of the femora examined.

(4) Its position is constant, being proximal to the medial condyle and lateral to the medial epicondylar line.

(5) It is of diaphyseal origin, being present only in adult femora.

In order to verify these statements, I examined in all 177 adult femora from the anatomical collection of the Grant Medical College, and was surprised to find that the tubercle, so constant in European and ancient Egyptian femora, was absent in 130 out of the 177 bones examined. Further, in only 8 out of the 47 bones which showed the tubercle did it approach in size the average tubercle of Dr Stopford's series of bones. It was very slightly marked in 16 and fairly marked in 23. Thus it will be seen that in this series the tubercle was absent in 73·5 per cent., slightly marked in 9 per cent., fairly marked in 13 per cent., and well marked in 4·5 per cent.

The cause of this marked variation regarding the presence of the tubercle may probably be explained by the peculiar habits of the Indians. An average Indian is sitting tailorwise or squatting on the ground throughout the greater part of the day. In this position, the gastrocnemius is completely relaxed and there is no tension upon the points of its attachment. On the other hand, when a person is sitting on a chair or a stool, the gastrocnemius is not completely relaxed; and if in addition the heel be raised there is a decided tension upon the points of its attachment. Now, as in the average position the medial part of the muscle is under greater tension than the lateral part, it is probable that this continuous tension may be one of the factors in the development of the tubercle.

In regard to the situation of the tubercle and its absence in the young femora, I entirely agree with the observations of Dr Stopford.

A NOTE ON SOME CHARTS REPRESENTING THE RELATIONS OF CRANIAL LENGTH AND BREADTH.

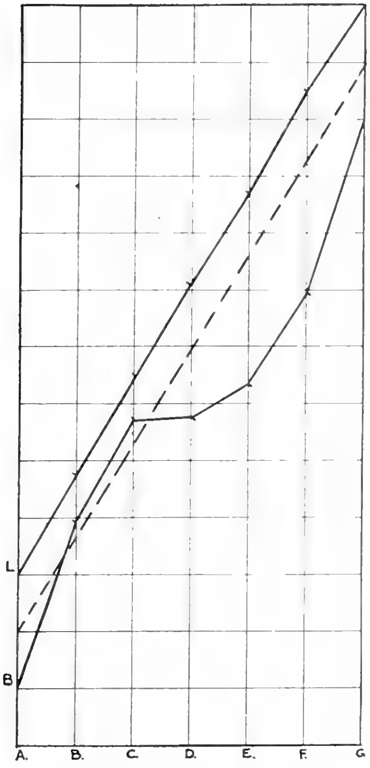
By W. L. H. Duckworth, M.A., M.D., Sc.D., *University Lecturer in Physical Anthropology, Cambridge.* (With Charts I. to XIX.)

In reporting upon measurements of dissecting-room subjects at the Cambridge Anatomy School (*cf.* this Journal, vol. li., January 1917, pp. 167 *et seq.*), I had occasion to discuss the grouping of the crania according to their length. The tabulation (Table IX. of the communication mentioned above) forms the starting-point of the present note. For this reason I reproduce the table here (as Table I., *infra*), with the addition of letters to distinguish the various subdivisions (called groups) of the series, and of columns in which the rate of increase is indicated by figures.

Table I.

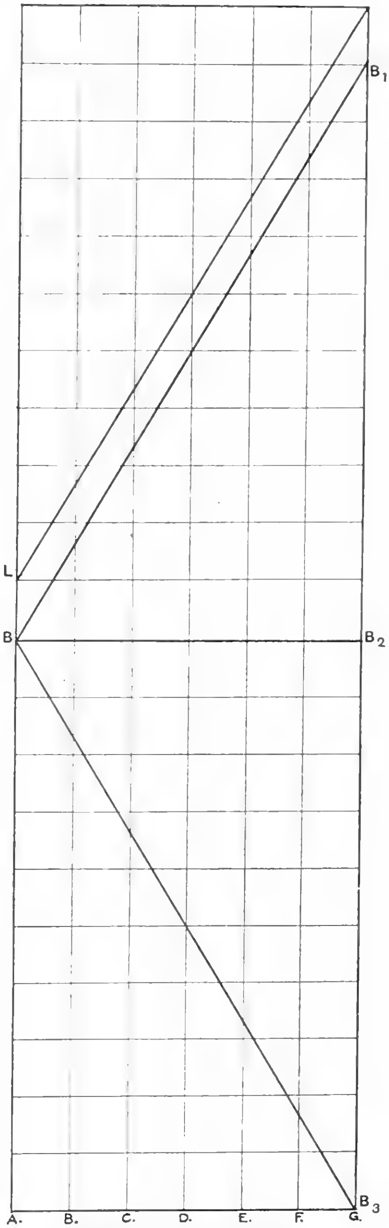
Grouping by length.	Group letter.	No. in group.	Mean length of group.	Increase in length on mean of preceding group.	Mean breadth of group.	Increase in breadth on mean of preceding group.	Mean breadth index of group.
Crania up to, but not exceeding 175 mm.	A	7	173·0	0	133·0	0	77·4
Crania from 175·1 to 180 mm.	B	15	178·0	5	138·6	5·3	77·6
,, ,, 180·1 to 185 ,,	C	23	183·0	5	141·7	3·1	77·3
,, ,, 185·1 to 190 ,,	D	42	187 8	4·8	141·8	·1	75·3
,, ,, 190·1 to 195 ,,	E	24	192·7	4·9	142·8	1·0	74·1
,, ,, 195·1 to 200 ,,	F	6	197·8	5·1	145·6	2·8	73·8
,, ,, 200·1 to 205 ,,	G	1	202·0	4·2	151·0	5·4	74·8
Totals . . .	...	118	..	29·0	...	17·7	...

The table (I.) shows that the increase in length amounting in all to 29 units is effected in a fairly regular sequence, the successive increments being nearly of equal value and approaching the arbitrary value (5) by which the groups (A, B, C, etc.) are separated. Reference to the corresponding data for cranial breadth shows successive additions, it is true, but the irregularity of the sequence (5·3, 3·1, ·1 as in Table I.) is striking, and the total increase amounts to 17·7 units (as against 29 for length).



CAMBRIDGE SERIES "DR." L/B. N=118.

CHART I.



THEORETICAL SERIES L&B.

CHART II.

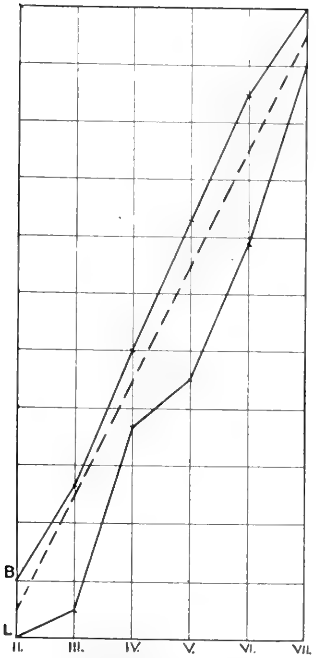
The present note gives the results of an inquiry as to whether the so-called sequences and the contrast between them are distinctive of the particular "material" (*i.e.* the series of dissecting-room crania, called Series "DR") under review. Diagrams for illustrating the comparison of one series with another were prepared as follows.

Each successive increment whether of length or of breadth is first expressed as a percentage of the total range of variation of the character in question. Thus in Series "DR" (Table I.) the length increases from 173 mm. to 202 = 29 units. The successive increments (5, 5, 4·8, etc.) are expressed in terms of 29 taken as = 100. A chart is prepared by subdividing a base-line into equal parts, the abscissæ corresponding in number to that of the subdivisions or groups (A, B, C, etc. . .) into which the series has been thrown. Ordinates erected in sequence represent the sum of successive increments of the particular dimension studied, and they vary in vertical extent from 0 to 100 units. The path followed by the dimension in its course from group to group through the series is traced by joining the ends of the successive ordinates. When this has been done in the cases both of length and of breadth, lines of length-increase and of breadth-increase are available for comparison (Chart I., L and B). For each dimension a separate base-line has been employed in Chart I., but this is a matter of convenience only.

But before proceeding with Chart I., I would direct attention to Chart II. This is theoretical, for it refers to no particular series though it represents lines of variation of two dimensions such as cranial length and breadth. Moreover, it is assumed that a series has been subdivided into groups according to the increasing value of one of the dimensions, *e.g.* the length. The increments in length being equal from stage to stage throughout, the length-line (L, Chart II.) ascends regularly from 0 to 100, its maximum value. I think three possible courses are open to the second line (B) representing the second dimension, and these possibilities may be thus described:—

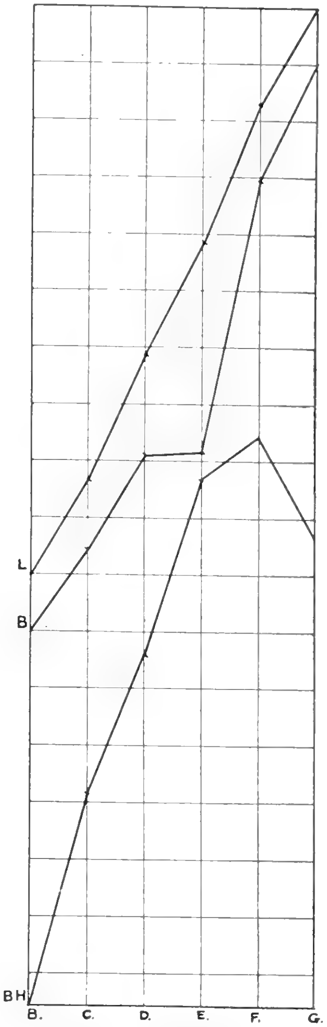
1. The breadth may increase with the increase of length. The increase may either be regular, *i.e.* uniform in amount, or irregular. So long as the second dimension increases with consistent regularity, its "indicator" or line will pass in the same direction as the length-line. And if regularity is maintained throughout the series, the second line will run parallel to that first drawn (*cf.* Chart II., L and BB_1), correlation will be perfect, and its coefficient = 1.

2. A second possibility is that the breadth remains unchanged throughout the series. The breadth-line will then coincide with the base-line (Chart II., BB_2), no correlation will exist, and the coefficient will = 0.



CAMBRIDGE SERIES
"DR". N = 118 ♂.
B&L. BREADTH AS BASIS.

CHART III.



SCOTTISH SERIES "K". [DR YOUNG].
♂. N = 100. L/B/BH.

CHART IV.

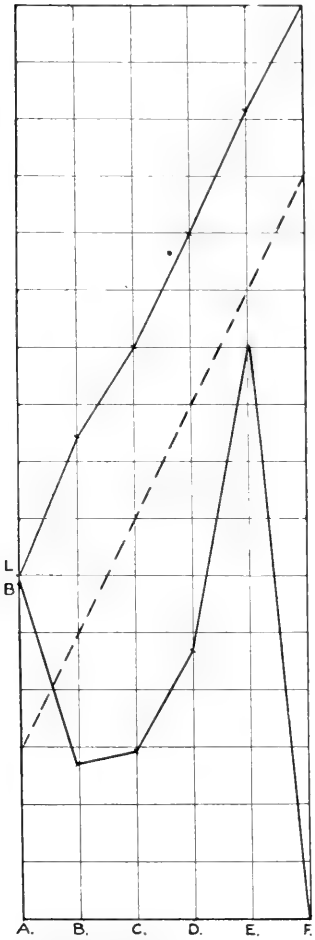
3. Lastly, the breadth may decrease while the length increases. Then the breadth-line will diverge from the length-line (Chart II., BB_3), correlation will be of the negative order, and if the decrease be consistently regular from end to end through the series, correlation will again be complete though the coefficient will $= -1$.

Chart II. shows one method of representing these possibilities. Combinations of the three modes must be almost infinite in number, and indeed the later charts show some of the variants. I wish to emphasise the point that I make no attempt to provide a measure of correlation, my prime object being to exhibit the actual fluctuations of cranial dimensions within a series, and to compare the behaviour of cranial breadth in relation to length in the several series actually studied. But I have mentioned the coefficient of correlation because I suppose it to be of the nature of a "mean" or average struck between a number of quantities of very different value. And though the charts do not provide a measure of correlation, yet I think they do indicate the range of variation summarised in the coefficient.

Returning to Chart I., and having regard to the breadth-line (B), the outstanding feature to be noted is a tendency to local "interruption" of correlation, so that the latter is for a stage almost obliterated. This inference is drawn from the tendency to assume a horizontal direction presented by the breadth-line between ordinates C and D. Apart from this feature, I would remark only that I see no evidence of any "compensatory" decrease in breadth, even when the upper extreme in length is reached.

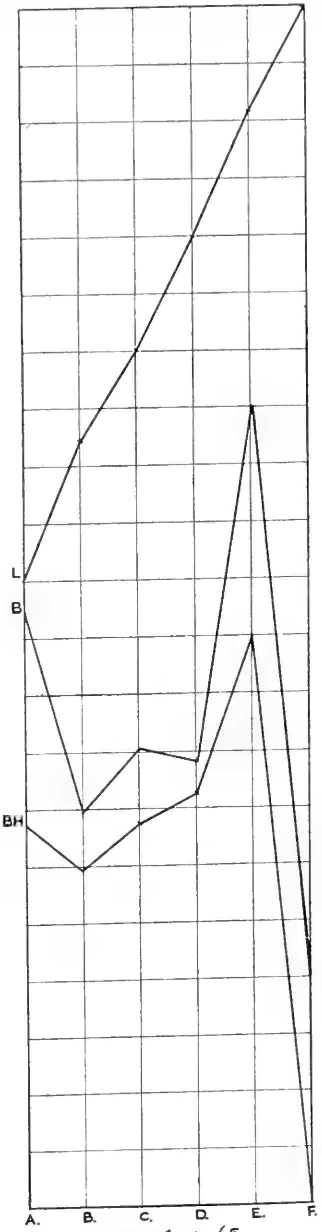
I prepared for comparison a number of charts based upon data published for other series, endeavouring to use those including about one hundred male crania. For special reasons, two series falling short of that number are included. Also I have made a few observations on cranial height, treating this dimension in the same way as cranial breadth, and using either basi-bregmatic (basal) height (BH), or auricular height (OH) for that purpose. The identity of the tracings is indicated with sufficient clearness in the several charts (IV. to XV.). In two instances (Charts III. and XII.) cranial breadth is employed as the basis of comparison. Subsidiary observations restricted to length and breadth relate to the subdivision of a particular group within a series (Chart XVI.), or again to the complete subdivision of a series into groups separated not as in the preceding examples by 5 mm. of length but by 1 mm. of that dimension. The groups are then increased greatly in number (Chart XVII.).

Finally, some observations of a general order are appended with Charts XVIII. and XIX.



SARDINIANS. ♂. N = 70. L/B.

CHART V.



SARDINIANS. ♂ N = 65.
L/B/BH.

CHART VI.

The Charts (IV. to XV.) prepared for comparative purposes are based upon data from the following series:—

No. of Chart.	Designation of series.	No. of examples.	Literary reference.
IV.	Scottish "K."[1]	100	Young, *Trans. Roy. Soc. Edinburgh*, vol. li. part ii. No 9.
V., VI., VII.	Sardinian (modern).[1]	70	Duckworth, *Zeitschrift für Morphologie und Anthropologie*, Band xiii. Heft 3.
VIII., IX., X.	Naqada (Egypt).[1]	143	Fawcett and Lee, *Biometrika*, vol. i. No. 4.
XI., XII.	Australian aborigines.[1]	132	Turner, "*Challenger*" *Expedition: Zoology*, vol. x., "Human Crania," 1884. Basedow, "Der Tasmanierschädel," *Zeitschrift für Ethnologie*, Heft 1, 1910. Duckworth, *Journal of the Anthropological Institute*, 1894.
XIII., XIV.	Zürich.[2]	66	Czekanowski, *Inaugural Dissertation*, *Zürich*, 1907.
XV.	Tübingen.[2]	108	Ranke, *Die Anthropologische Sammlungen Deutschlands*, xvi., Tübingen, 1902.

The study of the charts thus obtained leads me to the following conclusions:—

1. While the line of length (representing the mode of increase in length) pursues an almost regular (*i.e.* uninterrupted) course in all the series, yet the line representing the accompanying change in breadth is always more or less irregular. In some instances the amplitude of the oscillations exhibits clearly the high degree of variability within a series. And although this conclusion may be formed from the study of columns of numerical data, yet the impression left by the inspection of the chart is likely to be deeper and more lasting. The chart serves as a summary of and as a substitute for the large numbers of data to which it owes an origin.

2. As a net result in every series, an increasing length carries with it increased breadth. Yet the latter dimension may pursue a course of extreme irregularity, even though the general result is such as is thus described. Of the series studied, the crania of Sardinians and of the aborigines of Australia exhibit this irregularity in the highest degree. These series possess only a low degree of correlation of length and breadth. But it is easy to understand that out of such a series as either of these a particular group of skulls might be selected which when investigated separately would provide indications of a much higher degree of correlation than the parent series taken as a whole.

3. The occasional and irregular occurrence of a fall in breadth (or height)

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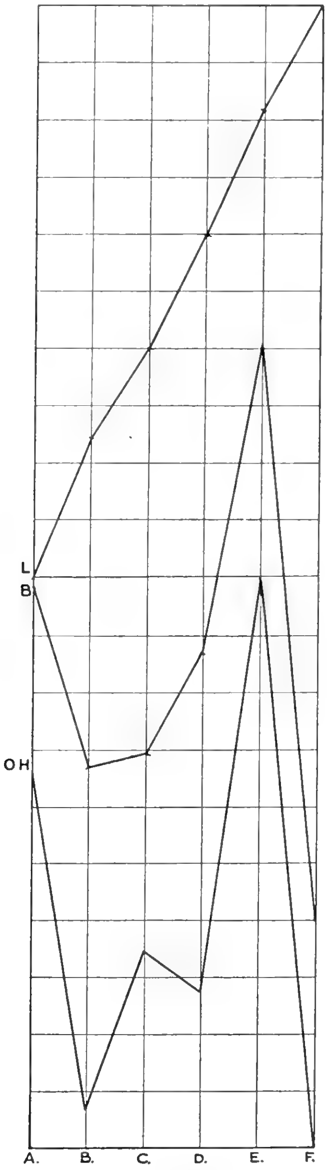
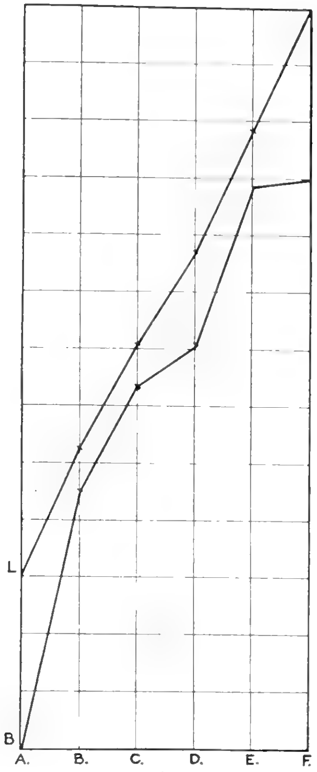
[1] Dolichocephalic series.

[2] Brachycephalic series.



SARDINIANS. ♂. N = 70.
L/B/OH.

Chart VII.



NAQADA. ♂. N=143 L/B.

Chart VIII.

(shown in a particular part of a series with a continually increasing length) may be claimed as evidence of "compensation." But unless the decrease

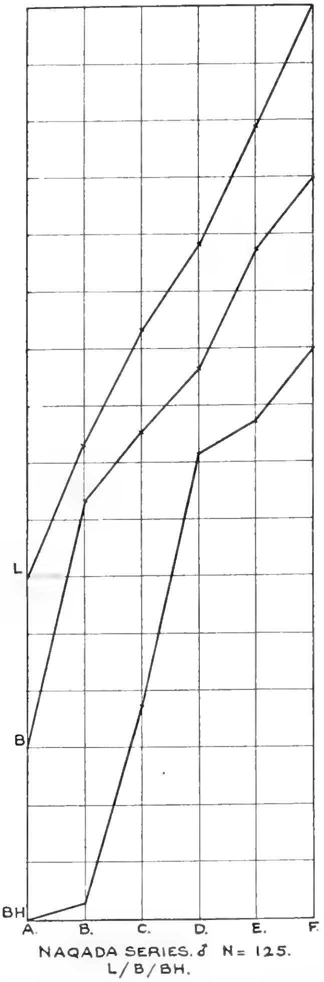


CHART IX.

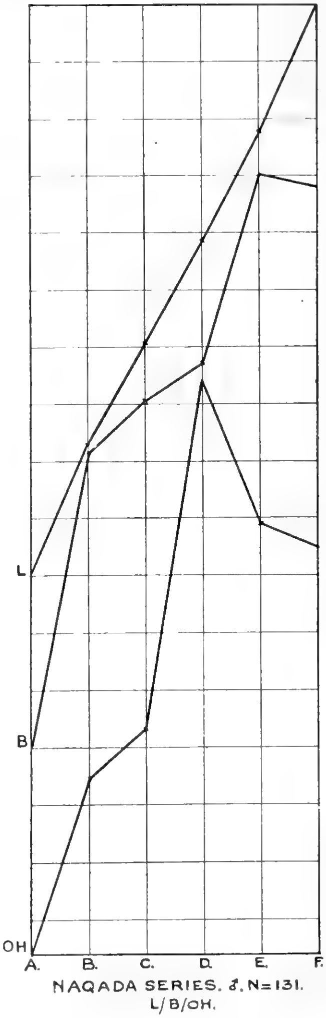
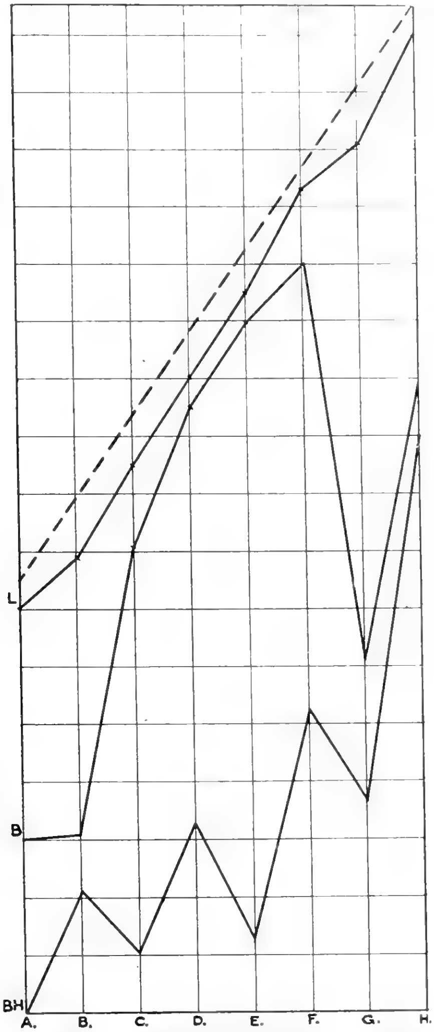


CHART X.

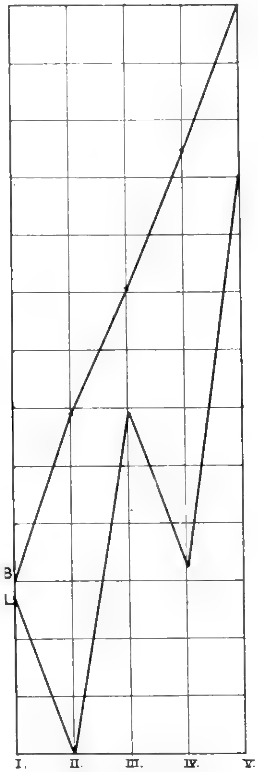
is uniformly exhibited, "compensation" can only be indefinite and vague in its reference. In the various series examined, such "compensatory" diminutions as are seen (and certainly the diminutions do occur) continue for a brief space and are limited.

4. No specific distinction has been detected as between brachycephalic and dolichocephalic series. But the brachycephalic series brought here into comparison provide indications of a more regular progression in respect of breadth-increase than do the dolichocephalic series.



AUSTRALIAN ABORIGINES. ♂. N.= 132. L/B/BH.

CHART XI.



AUSTRALIAN ABORIGINES
B.L.B. AS BASIS. ♂. N = 132.

CHART XII.

5. Irregularities are more pronounced at the limits (upper or lower)

of a series. The Sardinian series (Charts V., VI., and VII.) is distinguished from all the rest by the fact that the lowest terms of breadth and height coincide with the highest term of length.

6. In some instances (*e.g.* Chart I., Series "DR," Groups C to D), a temporary interruption of correlation appears, for breadth remains constant in two successive groups (though length varies). But within the group of individuals concerned the several data can be reviewed, and a chart (*e.g.* Chart XVI.) can be constructed with reference to the particular group. The chart shows that therein correlation may still be observed. Consequently it is concluded that the method of grouping, viz. taking the average of successive groups whose lengths differ by 5 units, tends to mask variations which really exist. A simpler but more laborious mode of division is employed in the construction of Chart XVII., where the data provided by series "DR" have been employed again. In Chart XVII. the crania have been ordinated in groups corresponding to increments of

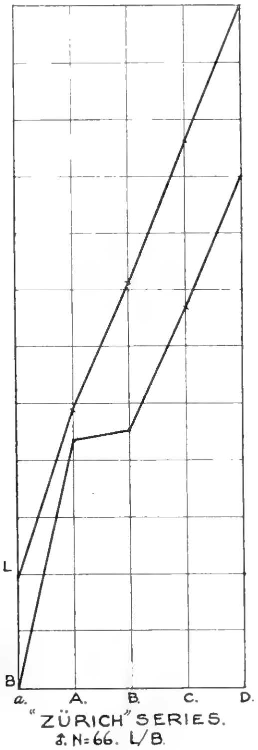


CHART XIII.

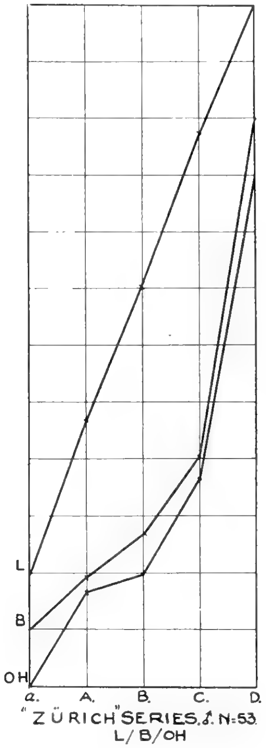


CHART XIV.

1 mm. of length. It is likely that this mode of division will prove more satisfactory than that actually applied in the majority of the charts, but so far it has been used in the case of Series "DR" alone.

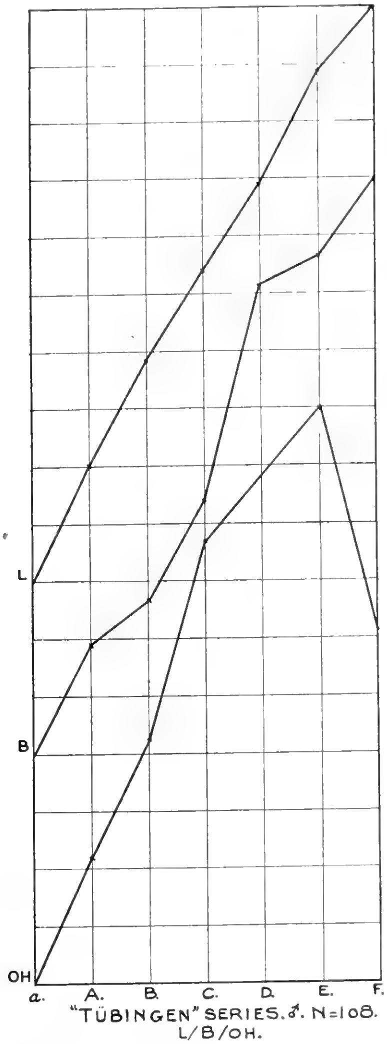


Chart XV.

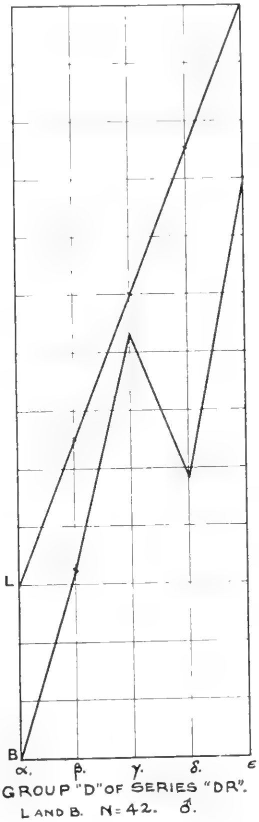
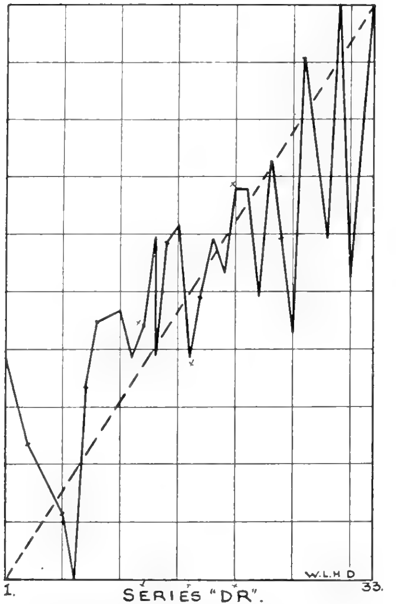


Chart XVI.

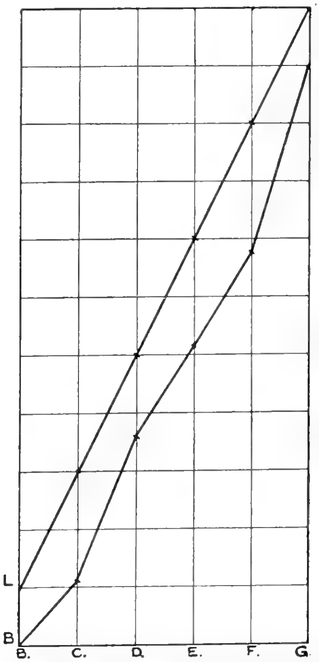
7. Sudden alterations in the direction of the "breadth-line" have been traced in numerous instances to particular specimens. These may be termed "aberrants" in contrast with their congeners. The charts show

how effective a small number of "aberrants" may be in determining the mean value of the group in which they fall Evidently they will be more potent when they occur in a "terminal" group, *i.e.* at one or other end of a series, for here they find fewer associates to counterbalance their peculiarities. But they may occur in any part of a series, and their further investigation seems important or at least worthy to be undertaken.



SERIES "DR".
CHART OF VARIATION IN CRANIAL WIDTH IN 33 GROUPS, OF WHICH CRANIAL LENGTH INCREASES UNIT BY UNIT FROM 169mm TO 202mm.
N = 118. ♂.

CHART XVII.

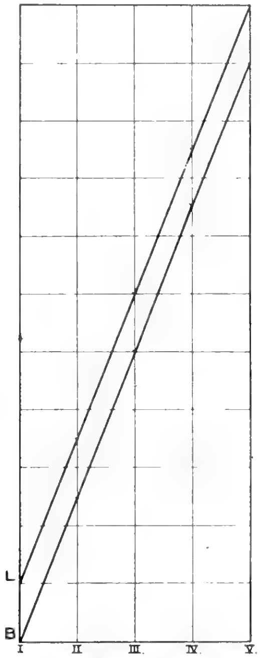


SWEDISH CONSCRIPTS (HEADS).
L & B. N = 5267.
[FROM RETZIUS, FÜRST AND JOHANNSEN].

CHART XVIII.

8. The mention of the counterbalancing of individual peculiarities by the levelling mass of a large number of associated specimens leads to the consideration of the effect of actual numbers upon the appearances shown by the charts. Numbers are not always capable of "smoothing" a curve in these instances, and this is well illustrated by the contrast of the breadth-lines in Charts XI. (Aboriginal Australians) and XIV. (Zürich), where the more irregular line is associated with a much larger collection of individual data than the more regular line (132 as against 53).

Notwithstanding this consideration, I endeavoured to find a much larger series than any examined above. And remembering that some of the points I had been investigating (though they are not described here) are dealt with by Professor Johannsen in a paper published some years ago, I returned to the study of that memoir (Johannsen, "Über Dolichocephalie und Brachycephalie" in *Archiv für Rassen- und Gesellschafts-Biologie*, Marz–April 1907). There I had the good fortune to discover data supplied by Professors Retzius and Fürst relating to several thousand Swedish conscripts. The data include head-length and head-breadth, and are published in such a form that the construction of a chart was easy. This chart (XVIII.) summarises observations on more than 5000 individuals, and the regularity with which the line of breadth mounts in conformity with that of length suggests strongly the damping effect of numbers. So far I have made no further tests of the kind.



JOHANNSEN'S BEANS. L & B.
PURE LINE "BB".
N = 2689.

CHART XIX.

But another reflection arises from the perusal of Professor Johannsen's paper. The regular and co-ordinate course of length and breadth in the large Swedish series may owe its regularity to the numbers taken into account, yet again it may be due to the individuals of which the series is composed possessing a degree of homogeneity not encountered elsewhere (in the present communication). And the question arises as to whether the charts can provide any suggestion of homogeneity of type, and purity of race (assuming that a pure race is homogeneous in respect of type). The well-known difficulty of finding an example of a pure human race is an absolute bar to the preparation of a length and breadth chart illustrative of its cranial dimensions. Consequently I have had recourse to Professor Johannsen's beans. The Professor cultivated these beans for many seasons, and established stocks which he named "pure lines." The title was awarded upon considerations of the constancy with which the offspring reproduced the special parental characters. Most of the characters were not suitable for comparison with the data of human craniometry. But Professor Johannsen measured large numbers of the beans. And as the latter were of "reniform" contour, they provided length and breadth and a breadth index. These dimensions seemed to me appropriate to the purpose of preparing a chart which is submitted herewith (Chart XIX.). It is based upon observations bearing upon one of four "pure lines" described by Professor Johannsen. The other three "pure lines" yield charts so nearly resembling Chart XIX. as practically to be identical with it. Perhaps it is too far a cry to pass from beans to human crania, but the suggestion provided by Chart XIX. seems worthy of remembrance in any extension of craniological investigations on the lines indicated in this note.

NOTE ON THE CHARTS I. TO XVII. AND XIX.

The abscissæ correspond to the groups into which the various series of crania have been divided, the mode of division being shown in Table I. in the text. Cranial length is employed as the basis of division in most of the charts.

In Charts III. and XII. cranial breadth is substituted for length as the basis of division, and the abscissæ I., II., etc., correspond to groups of crania of breadth not exceeding 125 mm. (I.), or between 125·1 and 130 mm. (II.), and so on.

In Charts XIII., XIV., and XV. a group of crania of length less than that denoted by the group letter A (*cf.* Table I.) has to be recognised, and is designated Group "a."

In Chart XVI., α, β, γ, etc., denote groups of which the respective lengths are 186, 187 . . . 190 mm.

In Chart XVII. thirty-three abscissæ correspond to cranial lengths rising from 169 mm. to 202 mm. inclusive, and increasing by 1 mm. at each stage. The sequence of lengths is indicated by the interrupted line, that of breadths by the continuous line in this chart.

In Chart XIX. the abscissæ correspond to lengths from 9 mm. to 13 mm. inclusive.

Throughout the charts, L denotes the course pursued by cranial length, B that pursued by cranial breadth, BH that pursued by basi-bregmatic height, and OH that pursued by auricular height in the several series.

ABSENCE OF PRE-MAXILLA. By Cranston Walker, M.D., Ch.B., B.Sc.

(from the General Hospital, Birmingham).

The subject of this communication is a boy of fourteen years. He presented himself at the Casualty Department of the Birmingham General Hospital for a pain in the side, which proved to be due to herpes zoster. A somewhat broad and low bridge to the nose led to an examination of the face, and it was at once perceived that the pre-maxillary portion of the palate, with the incisor teeth, was absent (see figs. 1, 2).

The two front teeth presenting in the upper jaw are the canines—conical in shape. Behind them on each side are the two bicuspids and two molars, the third molars can be seen in the radiograph, not yet erupted. On the left side there is a persistent milk molar between the permanent canine and the bicuspid. There are thus five functional teeth on each side.

The biting surface of the upper teeth on each side is not level, but convex downwards, and the apices of the canines are 5 mm. higher than those of the bicuspids. The whole upper jaw is short. The mesial borders of the two canines are only 6·5 mm. apart; their apices are 19 mm. apart. The four upper incisors are absent. In the mesial plane there is a narrow cleft, which can be traced for 5 mm. above the level of the canine-gum.

The arch of the palate is rather high and narrow, but is completely closed. Radiography shows that there is apposition of the bony parts of the two alveolar processes in front, but not actual union. There are three well-marked palatal ridges on the left, and two on the right. The nose is flat and broad (fig. 1), and is unusually flexible. The nasal septum is complete, but can be seen radiographically to be incompletely ossified (fig. 2).

No other abnormality has been found. The upper lip is well shaped, with a fully developed vertical ridge on each side of the nasal septum.

The upper teeth do not overlap the lower in front, but meet them irregularly and incompletely; the boy was not conscious of any inconvenience. Neither his face nor his voice would strike a lay observer as unusual, and no abnormality had been suspected by his parents or his schoolmasters.

Anatomically, the abnormality consists of a deficient ossification of the nasal septum and a complete absence of the pre-maxilla (fig. 2). The latter deficiency has partially been made good by the two maxillary processes growing forwards and inwards, meeting in the mesial plane and bearing the two canines almost into the position of the central incisors.

The anatomical deficiencies are situated in what was the mesial nasal process of the embryo; other portions of the same process, such as the tip of the nose and the middle portion of the upper lip, show no deficiencies.

As to the origin of the defect, the available history is an uncertain guide. It is as follows:—

Fig. 1.

The mother was unconscious of any abnormality. When pressed for memories, however, she thinks the first teeth to erupt were the two upper front ones; she does not remember the order of the remainder. When three years old the boy had measles, and was seriously ill. He then pulled a tooth, or it may have been one or two teeth, with some "flesh" attached, out of his mouth, and handed it to her; she promptly threw the article away. Soon after this he was admitted to the Sick Children's Hospital, Birmingham. The mother does not remember any remark having been made there about his teeth, and the case cannot be traced among the hospital records. There is no history of any injury. There are two brothers and one sister younger, all normal. No case of hare-lip or cleft-palate is known in the family.

So far as any reliance can be placed on this history, it suggests that the pre-maxilla was not congenitally absent, but that it sloughed away during an attack of measles—a very unusual event. In this case, the embryonic defect might be of the nature of a double cleft palate, without hare-lip, and with a deficiency of the nasal septum which allowed the pre-maxilla to separate from its upper attachments, and which also prevented the nasal septum from ossifying to the normal extent. There is no ready alternative explanation of a child of three handing teeth out of his mouth, since this age is too early for the shedding of milk teeth. The mother's notion that the upper front teeth were the first to be cut is consistent, since if the original upper front teeth had been the canines, their eruption would have been preceded by several months by the lower incisor teeth. However, the growth and eruption of teeth in a pre-maxilla, which must have had very slender attachments to its surroundings, presents some difficulties.

Fig. 2.

A cast of the upper jaw and palate has been placed in the John Humphreys Odontological Museum of the Birmingham University. My thanks are due to Mr G. H. Teal for very kindly obtaining an excellent dental cast, and to Dr Emrys-Jones and the Radiographic Staff of the Birmingham General Hospital for facilitating the radiography and photography of the case.

SUMMARY.

1. The case shows complete absence of the pre-maxilla, with the four upper incisors, and deficient ossification of the nasal septum. Other malformations are absent.

2. The two maxillary processes have grown forwards and inwards, have met each other and the nasal septum in the mesial plane, carrying the canines into the incisor position, and have filled the space left by the pre-maxilla.

3. The history of the case is open to doubt, but it suggests that the pre-maxilla was sloughed at the age of three during an attack of measles. A previous deficiency of attachment must be supposed. Congenital defect of the mesial nasal process is evidenced by the condition of the existing nasal septum.

SOME NEW FACTS IN THE ANATOMY OF CERTAIN MOVEMENTS. By Edgar F. Cyriax, M.D. Edin., *London.*

The treatment by Swedish medical gymnastics, as is well known, consists to a large extent of localised movements of joints, which may be passive, purely active, or resisted. The study of these movements, whose number is practically unlimited, has brought forward a number of new facts, some of which I present herewith.

Shoulder-joint.

The part played by the scapula during abduction and adduction of the shoulder-joint does not seem to be understood; the part played by it during flexion and extension of the shoulder-joint seems to be entirely ignored. In both these sets of movements the behaviour of the scapula is practically identical; it will therefore be necessary to refer only to one of them.

Modern anatomists are still somewhat at variance regarding the mechanism of abduction and adduction. It used to be laid down that the first half of the movement up to the horizontal was accomplished at the gleno-humeral joint, the scapula being fixed, and that the second half depended solely on rotation of the scapula. This is manifestly incorrect; it implies that the scapula rotates through an angle of 90°, so that at the conclusion of the movement its vertebral border is horizontal, which is not the case. At a later period certain observers stated that the scapula rotated most during the first half of the movement, and least during the last quarter.[1]

As a matter of fact, there are two methods of performing the movements of abduction and adduction of the shoulder:—

(*a*) As during everyday life, the scapula not being fixed.

(*b*) As during active gymnastic exercises (whether applied medically

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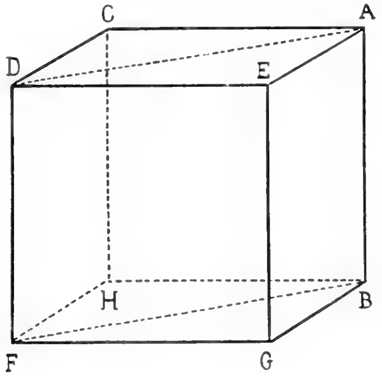
[1] See, for example, Cathcart, *Journ. Anat. and Phys.*, 1884, xviii. 211; Cleland, *ibid.*, 275; Cleland and Mackay, *Human Anatomy*, 1896, pp. 155, 267; Dalla Rosa, *Physiologische Anatomie des Menschen*, 1898, vol. i. p. 283; Mollier, *Statik und Mechanik des menschlichen Schultergürtels unter normalen und pathologischen Verhältnissen*, 1899; Steinhausen, *Arch. f. Anat. u. Phys.*, Phys. Abth., Suppl., 1899, 403; Thöle, *Arch. f. Psych.*, 1900, xxxiii.; du Bois-Reymond, *Ergebn. d. Physiol.*, 1903, pt. ii., 621; Demeny, *Méchanisme des mouvements*, 1904, 39; De Laroquette, *Rev. internat. de méd. et de chir.*, 1910, xxi. 193.

or educationally), the scapula being kept drawn inwards and backwards as much as possible during the entire time of execution of the movement.

In the former of these cases, the facts are that the scapula rotates most during the first quarter, less during the second, still less during the third, and least during the last quarter. In the latter case, during the first half the scapula remains practically immovable, the movement taking place only at the gleno-humeral joint. After the horizontal has been reached, the movement is continued almost exclusively by rotation of the scapula; this soon begins to diminish, the movement being resumed by the gleno-humeral joint, so that at the final stage of the movement it is almost exclusively the latter, just as it was at the commencement.

I should also like to say a few words concerning the number of movements possible in the shoulder-joint. This joint is of the ball-and-socket variety, and therefore permits of angular movement in every direction, as well as rotation. This may be represented graphically as follows:—Let A represent the shoulder-joint, and AB the longitudinal axis of the humerus when the arm is dependent, and AC the same axis when the humerus is abducted through a right angle. Complete the cube ACDFGB, and draw the diagonals AD, BF. Then movements of flexion and extension of the humerus will take place in the plane ABGE, movements of abduction and adduction in the plane ABHC, and a combination of the two in an intermediate plane such as ABFD; rotations will take place in the line AB, or any other line radiating from A. Now, suppose the humerus to be first flexed to a right angle so as to assume the direction AE, and then to be moved in the plane AEDC, so that it ultimately assumes the direction AC, we have in this and then the reverse back to AE a movement of the humerus which at present is not recognised, and has no



name in anatomy books, although in Swedish gymnastics it is known as arm carrying outwards and inwards. In ordinary life this movement is of frequent occurrence, as, for example, when transferring books from one place to another on the same shelf.

ELBOW-JOINT.

I wish to make some remarks on the muscles involved in flexion and extension of this joint; they are best studied by performing these movements against resistance applied over the wrist or its neighbourhood. As regards the muscles of the upper arm that aid in these movements, the biceps and brachialis anticus act in flexion, and the triceps and anconeus in extension, and this holds good whatever the position of the radio-ulnar joints. Variations in the latter, however, very greatly modify the action of the forearm muscles, *e.g.*:—

(*a*) When the forearm is completely pronated. Flexion is assisted by the *extensors* on the back of the forearm together with the supinator longus, the tension being felt most in the latter muscle and the extensor carpi radialis longior. Extension is aided by the *flexors* on the front of the forearm, the tension being felt most in those on the ulnar side.

(*b*) When the forearm is in the mid-position. Flexion is assisted by the extensors and flexors on the radial side of the forearm, the tension being felt most in the supinator longus. The extensors and flexors on the ulnar side of the forearm are in action during extension.

(*c*) When the forearm is completely supinated. The flexors of the forearm assist in flexion, and the extensors in extension, as ordinarily stated; the tension is, however, felt most in the muscles of the upper arm, not in the forearm, as in the case of pronation or the mid-position.

WRIST-JOINT.

I cannot remember ever having seen an anatomy text-book refer to the movement of rotation of the wrist-joint, although they all mention such rotation as being present in the joints of the phalanges. This movement at the wrist-joint can be readily demonstrated; the radius and ulna are fixed by the surgeon's one hand; the other, grasping the patient's hand in the same manner as if to shake hands, rotates it first in one direction and then the other. The amount of such rotation obtainable is about through 45° to 60°. This of course represents the amount of passive rotation; active rotation is impossible.

ANKLE-JOINT.

The calf muscles—gastrocnemius, soleus, and plantaris—are generally considered as being the muscles that are active in extension of the ankle-joint. This is not true of every position of the foot. If the subject sit on a table so high that the lower leg does not touch the ground, and then extend his foot as much as possible, none of the calf muscles are placed in action, the tendo Achillis not even being rendered taut. The only active muscles appear to be the tibialis posticus and peronei.

LUMBAR VERTEBRÆ.

Anatomy text-books either state that there is no rotation at all in the lumbar vertebræ, or else assert that it is present in such small amount as to be a negligible quantity. No book that I have met attempts to describe a *modus operandi* of testing for this movement. The simplest way is to lay the subject on his face, and, while firmly fixing the lowest dorsal vertebræ with one hand, lift up the anterior superior spine of one side with the other. Normally it ought to be quite easy to raise it about two inches without the dorsal vertebræ participating in the movement. This is effected by rotation which takes place exclusively in the joints of the lumbar vertebræ, and roughly speaking corresponds to about 10°.

NEW PUBLICATIONS.[1]

GIORNALE PER LA MORFOLOGIA DELL' UOMO E DEI PRIMATI. Edited by Professor G. L. SERA, University of Padua. 1917. Vol. I. Part I.

WE extend a most hearty welcome to this new journal, which is to be devoted to papers and researches connected with the morphology of Primates, with man as the central figure. The editor, Professor G. L. Sera, indicates the exact scope of the journal in a preliminary article. Three papers appear in the first number: (1) On the Penis of Macacus, by O. de Beaux; (2) Marsupial Features in the Human Mandible, by C. Pelizzola; (3) The Biological Value of Sera's Empirical Curve, by A. Giardina. There is also included a review of Pilgrim's recent paper on the Siwalik Primates.

THE BASLE ANATOMICAL NOMENCLATURE (B.N.A.). By E. B. JAMIESON, M.D., M.B., Ch.B. (Edin.), Lecturer on Anatomy, University of Edinburgh. 1916. Green & Son, London and Edinburgh. (Price 6s.)

DR JAMIESON has performed a very useful service in preparing an alphabetical list of terms showing the old terminology, the B.N.A. terminology, and the suggested English equivalent. In a majority of cases the old terminology seems to us preferable to the new.

APPLIED ANATOMY: THE CONSTRUCTION OF THE HUMAN BODY CONSIDERED IN RELATION TO ITS FUNCTIONS, DISEASES, AND INJURIES. By GWILYM G. DAVIS, M.D., Professor of Orthopedic Surgery in the University of Pennsylvania. Fourth edition. Lippincott & Co., Philadelphia and London. 1916. (Price 24s.)

THIS profusely illustrated work on applied anatomy first appeared in 1910, and is now in its fourth edition. In its latest form some new matter has been added to the text, while several of the illustrations have been improved.

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[1] The Editorial Committee would welcome notes on new publications.

INDEX

PRINTED IN GREAT BRITAIN BY NEILL AND CO., LTD., EDINBURGH.

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

DECEMBER 1915.

THE ANNUAL GENERAL MEETING of the Society was held on December 3, 1915, at the London Hospital Medical College. The President, Professor **HOWDEN**, occupied the chair.

(1) Professor E. **FAWCETT** demonstrated several models of developing chondrocrania, among which were those of calf embryos of 25 and 19 mm., ferret embryos of 25 and 19 mm., and a mole of 19 mm.

A summary of Professor Fawcett's contributions will be found at the end of the *Proceedings*.

(2) Dr W. C. **M'KENZIE** demonstrated his paper on "The Attachments of Duodenum and Transverse Colon."

Among the Marsupials three folds are noted :—

1. *Mesial Fold*, well marked in koala, and connecting the colon to the pyloric region. This corresponds to the separation of the colon into right proximal, or mesenteric, and left distal, primary, or mesocolic colon. As showing its connection with the ventral mesentery, in the chameleon this fold is noted crossing the pylorus to be continuous with the gastro-hepatic omentum or ventral mesogaster. There is also evidence of this in Macropodidæ and Cheiroptera.
2. *Left Lateral* (lieno-mesocolic fold).—This is well seen in the platypus. It passes from the shorter left posterior process of the spleen to the left aspect of the mesocolon of the left colon. On this fold is suspended the left, frequently the greater, part of the pancreas.
3. *Right Lateral* (duodeno-mesocolic or duodenal fold).—This is well developed in koala and the opossum. Where we have a definite duodenal loop developed this fold passes from the ascending duodenum to the right

aspect of the mesocolon. Where the loop is not developed, the right fine extremity of the fold corresponds to the termination of the duodenum, *i.e.* a part defined by an inequality of growth between the mesoduodenum and the common mesentery, as is well shown in the Tasmanian devil. Between the duodeno-intestinal flexure, root of mesentery, and the upper margin of the fold is the primary duodenal fossa, which can be demonstrated through the Mammalia up to Platyrrhini.

1. *Mesial Fold.*—From the selection point of view, this fold is of prime importance in colon development. Proximity of the colon to the pylorus is associated with colon development to the right, *i.e.* on the mesentery. Failure of this proximity, *i.e.* poor development or absence of the band, is associated with small development of colon to the right. The extremes in Marsupialia are the koala and the carnivorous dasyures, and throughout the Mammalia varying intermediate grades are seen. The right colon —like the mesial hepatic lobe—is the experimental colon. Here we find large and small cæca-appendices—coils and loops. The somewhat complicated right colon of Rodents is simplified in the Lemuroidea, and the human type appears in the platyrrhines. In the Tasmanian devil there is no development of the colon on the mesentery, but at the junction of the small intestine and the colon (left, mesocolic) some direct branches are traced from the right vagus to the gut. Furthermore, there is evidence in Mammalia of a direct branch or branches of the right vagus to the colon on the right of the pyloric relation, *i.e.* corresponding to the division into right and left colons. It is interesting to note, as seen in Lemuroidea, platyrrhines, catarrhines, and great Anthropoids, that the fixation of the right colon, *i.e.* shortening and dorsal fixation of its common mesentery, takes place from above downwards, *i.e.* begins at the mesial attachment.

The selection sequences from the "human" point of view would be expressed as follows:—

(1) Presence of a mesial fold causing approximation of the commencement of the left, distal, or mesocolic colon to the pyloric region.

(2) Associated with this a good development of colon to right, on the common mesentery.

(3) The coils and loops seen in Rodentia and Lemuroidea are used as Nature's means for shortening the colon.

(4) Definite shortening and simplification precede fixation essential for the erect attitude.

(5) Fixation dorsally of the right colon, and so increase of the base of mesentery commences from the mesial fold, *i.e.* above downwards.

2. *Left Lateral Fold.*—The importance of this fold is in connection with the fixation of the colon in the splenic region. My explanation of its origin is that it is a *pari-passu* development with the spleen and the great omentum (*cf.* platypus), the spleen originally having, as in certain Reptilia, lain obliquely in dorsal mesogaster and mesocolon. In others the spleen involves mesogaster only, and such a spleen would not be associated with the development of this process, as in koala. On this process diffuses the left part of the pancreas (below the level of the lesser sac). For selection purposes it would not be advantageous for the pancreas to be included in the lesser sac. It would not then easily conform to the abdominal law of dorsal fixation of solids. As evolution proceeds, the upper part of the great omentum (gastro-splenic) shortens inclining spleen dorsally. Pancreas also approaches the dorsum, and result is shortening of the fold and adhesion to the kidney (lieno-renal), first to the lower pole, then the upper. The fold was originally free of kidney and dorsal wall. Thus we have proximal the spleen, pancreas, colon, kidney, and adrenal, and grades are seen in platypus, opossum, wombat, and Anthropoids. The fixation of the left colon is now further aided by secondary inclusion of the gut and its mesocolon—between pylorus and spleen—by the great omentum; and grades of this can be seen in kangaroo, platyrrhines, catarrhines, and Anthropoids. Thus the mesial band is of further importance, as this inclusion begins on the right, and it is noticeable also that the fixation of the "descending" colon begins at the splenic region and extends downwards.

3. *Duodenal or Right Lateral Fold.*—The important question in connection with this fold is what part does it take—if any—in producing duodenal shape. If we regard this band and the so-called Treitz's fold as producing shape, then we assume that they dominate function. The peculiar shape of the duodenum is the result of function force, not traction force. Shape is response to a need. In the chameleon we have evidence of duodenal shape. At this early period the duodenum becomes defined as a distinct intestinal segment. There is a distinct tucking in, representing loop commencement. Yet no membrane is present traceable to the mesocolon, so that the point of view of a band between the two acting as a traction force is out of the question. At this early period there is an inequality of growth—a failure to develop of the dorsal mesentery for the commencement as compared with that for the rest of the small intestine. Apart from gut specialisation, this inequality of growth is influenced also by growth of pancreas, spleen, and great omentum. The result of this inequality of development in the dorsal mesentery is to produce a loop or bend in the intestines at the junction of the mesenteries,

i.e. mesoduodenum and common mesentery. Owing to the presence of the mesial fold, *i.e.* the pyloric relation of the beginning of the left colon, the mesentery of the small intestine is *ab initio* ventral to the mesoduodenum, and further development of the duodenum would be to the left and dorsal to the common mesentery. As is seen throughout the Mammalia, this development does take place, and the result is an adhesion between the duodenum and the mesocolon of the left or primitive colon. From this adhesion the duodenal fold so characteristic of the Mammalia up to the Platyrrhini develops. Pancreatic development is only a minor factor in helping duodenal shape. Furthermore, throughout the Mammalia the junction of the duodenum and small intestine is an important nerve-control area receiving direct branches from the right vagus and also mixed branches of the vagus and sympathetic; and one sees the advantage of the position of the flexure in Man, since it lies dorsally near the origin of the superior mesenteric vessels. Mechanical factors probably play a part in its good development in koala, where we have a large right colon and cæcum swung on the mesentery and supported at the pylorus. A minor and later function of the duodenal loop would be to form good attachment in the looping and fixing of the right colon. So far I have failed to find evidence of nerve-carrying function of this band, and only in the bandicoot, where it is continuous with the left lateral fold in front of colon, is there a suggestion that the band is not acquired, but biological. It can be stated that the nearer we approach the single mesentery type seen in the Tasmanian devil and ant-eater, the less defined becomes the duodenal fold. In the latter it is absent, and in the comparatively simple gut of the Virginian opossum, by dividing the elongate lax mesial fold and stretching the duodenal fold, we get practically the primitive condition of the ant-eater.

To sum up, duodenal shape is a response to function, and its specialisation is associated with the entrance of direct vagal branch or branches at its termination. This latter is a constant. The site of duct entrance is not as is shown throughout the Marsupials, but it is always proximal to the vagus relation. The fold is not a biological peritoneal fold, but a secondary one and result of adhesion (zygosis). It is seen throughout the Mammalia up to Platyrrhini, is the "primary" duodenal fold, and is associated with the "primary" duodenal fossa. With the dorsal fixation of the duodenum from peritoneal adhesions, associated with fixation of right colon and its mesentery, and especially pancreas, neither fossa nor fold is seen in Catarrhini or orang.

From the comparative point of view the human-gut segments can be regarded as follows:—

1. Duodenum. Pyloric sphincter to duodenal-jejunum flexure, where we have direct vagal control.
2. Small intestine. Duodenal-jejunum flexure to termination of ileum, where we have the valve and also vagus and vago-sympathetic control.
3. From ileo-cæcal valve to large gut in relation to pylorus, practically corresponding to the entrance of direct vagal branches, is right, proximal, or mesenteric colon. This signifies origin better than terms "ascending colon" and "hepatic flexure."
4. Colon to the left of that, *i.e.* from pylorus to pelvis, is left, distal, or mesocolic colon. This signifies origin better than terms "transverse colon," "splenic flexure," "descending colon," and "sigmoid.'

In conclusion, I may mention that my researches have failed to discover throughout the Mammalia up to great Anthropoids the presence of the so-called Jackson's membrane, Lane's band, and Treitz's band. So that in my opinion these can be regarded not as biological but acquired bands—associated in Man with the erect posture.

Professors J. P. HILL, ARTHUR KEITH, and Dr CUNNINGHAM took part in the discussion of this paper.

(3) Professor WILLIAM WRIGHT exhibited numerous models which he had prepared from the viscera of the elephant. The points upon which he particularly dwelt in his demonstration were the absence of a pleural space. the peculiarities of the great venous trunks of the heart, the relation of vessels to the lungs, and the very large amount of yellow elastic tissue found throughout the body of the animal.

Professor Wright was inclined to believe that the absence of a pleural cavity was a primary condition in the elephant. He also exhibited models of the peculiar "temporal gland," and discussed its structure and significance.

Professors ARTHUR KEITH and F. WOOD JONES discussed some of the points brought out in the paper.

JUNE 1916

IN place of the usual Summer Meeting of the Society an ordinary meeting, which extended over two days (June 2 and June 3), was held at the Royal College of Surgeons, London.

The meeting on Friday, June 2, commenced at 2.30 p.m. The President, Professor R. HOWDEN, occupied the chair.

The minutes of the previous meeting were read by the Secretary.

The PRESIDENT recalled to the Society the loss suffered by the death of Sir William Turner; and he dwelt with particular emphasis upon the human side of Sir William Turner's life, since this was an aspect with which he had been in contact during an association of very many years.

Professor Howden also reminded the Society that Mr Charles Stonham, whose death had been recently announced, was one of the founders of the Society, and one of its most valued members.

(1) Dr W. C. M'KENZIE gave a paper dealing with the biology of the spleen and biliary apparatus in Monotremes and Marsupials. Dr M'Kenzie illustrated the actual conditions present in a very wide series of species, and made an exhibit of a very large number of most interesting specimens. One of the most important points brought out in this paper was the extraordinary variability of the spleen in certain Marsupials, such as the wombat. In this animal both spleen and liver show an extraordinary number of different forms, and some of these forms exhibited were strikingly human.

By the aid of this material Dr M'Kenzie demonstrated clearly the evolutionary stages of the human spleen, which had resulted in producing the notches along its anterior margin. Another very extraordinary feature, which was well displayed in the material exhibited, was the wide variety seen in the method of termination of the bile and pancreatic ducts in the intestine. The ducts may enter separately or in company, near the pylorus or far from it.

Professors F. G. PARSONS and ARTHUR KEITH took part in the discussion of this paper.

(2) Professor F. G. PARSONS recorded a series of measurements made upon nearly 300 modern English clavicles, the age and sex of which were definitely known. The first portion of the demonstration consisted of determining the relation between the clavicular length and the shoulder width. Professor Parsons then showed the results which he had obtained in endeavouring to establish an average contour for the clavicle of the male and female of modern English people. The ideal or average clavicles were recorded as permanent models, which were exhibited. Professor Parsons found that the left bone exceeded the right in length in both sexes. The last part of the paper dealt with the possibility of sexing the clavicle, and, working along the lines which he had determined from an examination of his material, he concluded that a correct diagnosis could be arrived at in 88 per cent. of cases.

A very large number of specimens was exhibited, several points of interest being mentioned in connection with the many variations. In particular, Professor Parsons drew attention to the foramen, which not uncommonly perforates the bone.

Professor E. BARCLAY SMITH exhibited a specimen perforated by a foramen with the descending cervical nerves *in situ* in the canal, and he pointed out that, when such a condition was present, the emerging nerves appeared at the lower surface of the bone by passing through the nutrient foramen.

(3) Professor FAWCETT gave a further communication on the mammalian chondrocranium, illustrated by models. This contribution, with Professor Fawcett's other communications for 1916, is summarised at the end of the *Proceedings*.

(4) Mr V. Z. COPE gave a paper on "The Internal Structure of the Sphenoidal Sinus." It was shown that the sphenoidal sinus was by no means a simple cavity, and the presence of more or less constant septa and loculi was demonstrated. The sinus in its simplest form might occupy only a portion of the pre-sphenoid, or it might invade the post-sphenoid.

(5) Professor F. WOOD JONES gave brief abstracts of two papers. The first, dealing with the genitalia of the Cheiroptera, was subdivided into two parts, treating of the Megacheiroptera and Microcheiroptera respectively. Among the bats two main types of genitalia were described, the one having many points of affinity to that seen in the Primates, and the other reminiscent of that seen in Galeopithecus. The first type was found only among those New World bats comprised in the Phyllostomidæ. The second paper dealt with the genitalia of Tupaia, and in this animal a strange blend of almost Primate conditions with almost Metatherian features was demonstrated.

The meeting was resumed at 10.30 on the morning of Saturday, June 3, the PRESIDENT being in the chair.

(1) In the absence of Surgeon CECIL P. G. WAKELEY, a case of congenital atresia of the ileum was demonstrated by Dr R. GLADSTONE.

This anomaly occurred in a female full-term child, which was operated upon three days after birth for intestinal obstruction. At the operation a marked narrowing of the upper part of the ileum was found; the stomach and proximal part of the intestines were very distended. The rest of the small intestine beyond the constriction received its blood-supply from a pedicle of mesentery, in which the vessels were dilated and thrombosed. Owing to the bad condition of the patient nothing further was done, the child dying a few hours afterwards. The interest of these cases lies principally in the possibility of saving life by intestinal anastomosis. In the case recorded a gastro-enterostomy was contra-indicated on account of the rest of the small intestine having a defective blood-supply, its vessels being thrombosed. It would have been useless to have performed a jejunostomy, because the child could not have lived with merely a stomach and at most twenty inches of small intestine; moreover, the condition of the jejunum was very bad, and precluded any further operative procedure.

This specimen, and others in which a considerable length of the intestine is imperforate, suggests that a twist or blocking of the mesenteric vessels, resulting in a defective blood-supply of a part of the intestine, may in some cases be the immediate cause of the arrest in its development.

(2) Dr R. Gladstone also exhibited, on behalf of Dr E. A. Cockayne, a specimen showing accessory lungs and a congenital diaphragmatic hernia which was obtained from the body of a premature female infant. The diaphragmatic hernia was on the left side, and through the opening into the pleural cavity two separate groups of organs protruded. The first consisted of the stomach, first part of the duodenum, part of the gastro-hepatic omentum, a tongue-shaped lobule of liver attached to the under surface of the left lobe, the spleen, an accessory spleen, and part of the body and the tail of the pancreas; the second consisted of the ileum, cæcum and appendix, the ascending and transverse colon with the splenic flexure and commencement of the descending colon, and the mesentery and mesocolon. The right and left kidneys and suprarenal glands lay below the diaphragm. The right lung was perfectly developed, the left had an upper and lower lobe; it was much, but proportionately, reduced in size, and normal in shape. Between the base of the left lung and the stomach were two accessory lungs in no way connected with the rest of the pulmonary system. Each was completely covered by a layer of visceral pleura, and was attached by a pedicle to the pleura covering the anterior surface of the descending aorta. Each accessory lung was larger than the whole of the left lung. The pedicle of the upper accessory lung contained two arteries, one arising from the right and one from the left side of the aorta, two veins communicating with the vena azygos major, and nerves derived from the great splanchnic. The pedicle of the lower accessory lung contained an artery derived from the descending aorta, a vein which joined the vena azygos minor, and a nerve from the

great splanchnic. Neither pedicle contained a duct in communication with the respiratory system or the œsophagus. Microscopically, in the lower pedicle, incompletely developed striped muscle was seen surrounding and running parallel to the long axis of the artery. The lower accessory lung was divided into lobules separated by connective tissue in which branches of the artery ran surrounded by similar muscle fibres. In the largest mass of connective tissue, situated centrally, was a collection of lymphoid tissue and a bronchus lined by columnar ciliated epithelium and containing plates of cartilage in its wall. The lobules were composed of very numerous bronchioles lined by columnar ciliated epithelium and a variable number of alveoli lined by cubical epithelium. The interalveolar stroma was very dense. A section through the upper accessory lung at a point distant from the pedicle showed a similar arrangement of bronchiolar and alveolar tissue. The pedicle itself and the part near the pedicle were not examined microscopically.

(3) Professor J. E. S. **Frazer** demonstrated the formation of the pars membranacea septi.

In the earlier stages the bulbar portion of the heart cavity becomes continuous with the ventricular part altogether to the right of the position of the A.V. opening: subsequent alteration in relation is not the result of any change in the position of the opening, but is due to the disappearance of the bulbo-ventricular ridge and the associated left dorsal wall of the bulb. This is a necessary preliminary to the formation of the aortic vestibule, the dorsal channel made in the bulbar region by the meeting of the bulbar ridges and directed obliquely from the arterial end to the left ventricle across the fused A.V. cushions. The channel thus opens into the left ventricle through the original interventricular foramen. The pars membranacea is made from the fused A.V. cushions, the auriculo-vestibular part from the right end of the upper cushion, the interventricular part from the lower one, with some trabecular structure joining this with the proper interventricular septum. The true interventricular foramen does not close, but remains patent as the opening into the aortic vestibule from the left ventricle. The septum separating the cavities of aortic vestibule and infundibulum is made by the junction of two *bulbar ridges*, which join the free edge of the interventricular septum below: with them is a marked downgrowth of the fused lateral arterial cushions at the distal end of the bulb. Only the lower portion of the right auriculo-ventricular opening remains as the permanent opening, the upper part being closed and lying in the floor of the aortic vestibule: this upper moiety is cut off from the lower by the right bulbar ridge growing across the opening to meet the edge of the interventricular septum. It is doubtful whether the permanent left opening is the whole or only a part of the earlier one.

(4) Dr R. H. Robbins, as a preliminary to a communication on the condition in other animals, demonstrated the principal markings and connections of the human pisiform, "and the general conformation which could be identified in apparently dissimilar specimens." The continuity of the outer fibres of the flexor carpi ulnaris tendon was shown with those of the annular ligament along a well-marked oblique ridge on the radial aspect of the bone. It was pointed out that any impression due to the ulnar nerve must be palmar to this ridge. The well-marked hollow, forming one of the principal features of the pisiform, and confined to the proximal portion, lies for the most part, owing to the oblique position of the bone, under cover of the tendon, and is occupied by dense fatty tissue.

(5) Dr Matthew Young demonstrated, with the aid of a series of tables, the principal results derived from a research concerning correlation in a series of metopic skulls. The research was carried out on the West Scottish series of skulls preserved in the Anatomy Department of the University of Glasgow, which contains nearly eighty metopic skulls. These were subjected to intensive study by detailed external measurement, by working out correlations, and by analysis of the characters of the vault. The condition of the sutures was also determined.

The main results were that, with practically the same mean capacity, the metopic skulls, as compared with the normal, while retaining the same average breadth, were distinctly shorter and markedly lower. The mean capacity was maintained by increase in frontal width. The vault differed from the normal not only in the greater frontal width, but in the vertical character of the frontal region, with the bregma absolutely as well as relatively farther forwards, while there was a marked flattening behind, above, and below the lambda. Although not very decisive, the evidence regarding the sutures pointed to the closure of the sutures in the region of the lambda, at a period when all the sutures in the frontal region remained open. Metopism, therefore, is probably only one feature in a general change in the growth factors which, in the normal members of the series, determine a backward expansion, with increase in depth of the posterior part of the brain-case. The result is an exaggeration of brachycephalic characters in a brachycephalic series, and a nearer approach to the brachycephalic type in a dolichocephalic series. The evidence is against the view that the persistence of the suture is "compensatory." Metopism is not to be explained merely by an expansion of the frontal region of the brain, but more probably represents one factor in a general adjustment of the brain-case to its contents as a whole. The sum of the changes represents a second mode of attaining a given capacity in a series of uniform type. The rarity of metopism in primitive races suggests that it is a progressive phenomenon—evidence of an instability in the adjustment between brain-mass and brain-case, or between brain-type and a capsule of stereotyped form.

Professor KEITH expressed his satisfaction at the thoroughness of the investigation, and noted the interesting fact of the absence of metopism, even as an anomaly, in anthropoid apes.

(6) Dr T. WALMSLEY gave a demonstration of certain points in the mechanism of the hip-joint.

A contrast was drawn between the mechanisms of mechanical combinations and organic joints, and in reference to the latter the following were put forward as general principles:—

1. That sections of articular surfaces at right angles to their axes of movement are not mathematical arcs;
2. That the movements within the joint are not movements of simple rotation;
3. That the whole of either articular surface is not in contact with its complement in any position of the components, but is in part in action and in part inactive or at rest.

The last conclusion was demonstrated in sections of the hip-joint in different positions of the limb through the same axis of the femoral head.

The retinacula of Weitbrecht were shown in dissections to be related to the blood-vessels of the epiphysis of the head of the femur and of the metaphysis of the neck. The opinion was advanced that their function was to control the movements of the femoral synovial pads, and that no direct morphological comparison should be made between the inferior set and the mesentery of the ligamentum teres of reptiles.

In the discussion which followed this paper Professors KEITH, FRAZER, and WOOD JONES took part.

(7) Mr ALWYNE COMPTON gave a demonstration of the intrinsic anatomy of the large nerve trunks of limbs.

The paper dealt with the sciatic trunk.

The tibial and peroneal divisions of the sciatic trunk may be so closely applied to each other that the line of union is difficult to define. In such cases the inner two-thirds correspond nearly to the tibial, the outer third to the peroneal. The peroneal division lies on a plane slightly anterior to the tibial. No nerve fibres pass from one to the other. When the fibrous sheath has been removed, the trunk is seen to be marked by superficial longitudinal bundles. The posterior aspect of the tibial division is partly covered by a sensory tract, the posterior cutaneous nerve of the calf. The same aspect of the peroneal nerve is overlaid by another sensory tract composed of the lateral cutaneous nerve of the leg and the peroneal communicating nerve. Occupying the interior of each division in the middle third of the thigh is a plexus. The sensory tracts have little or no connection with the plexuses. All the motor bundles, however, take part in the formation of the plexuses, except the nerves to the hamstring muscles, which leave the sciatic trunk more proximally. The bundles composing the peroneal division are arranged spirally, whereas those of the tibial are practically vertical. There is no haphazard grouping of the bundles, but a definite arrangement associated with the relative position of the soft parts supplied by the bundles.

(8) Dr M. F. LUCAS exhibited and demonstrated a remarkably complete case of double inferior vena cava. The question of the underlying embryological channels involved in this anomaly was gone into, and Professor FAWCETT and Dr GLADSTONE further discussed the subject.

DECEMBER 1916

THE ANNUAL GENERAL MEETING was held at the London School of Medicine for Women on December 1, 1916. The greater part of the meeting was occupied by the Society's business. Professor HEPBURN occupied the chair. The following scientific communications were made:—

(1) Professor FAWCETT demonstrated some additional models of the developing chondrocranium, the findings from which are summarised later.

(2) Professor A. M. PATERSON gave a paper upon "The Action of the Biceps Flexor Cruris." A gunshot wound of the buttock, which divided the peroneal nerve, had produced paralysis of the short head of the biceps, while the long head, in common with the rest of the hamstrings, remained fully functional. Professor Paterson had made a series of observations upon the case, and he concluded that the long head of the biceps acted only until the limb had attained a position of semiflexion, the short head being then called on to complete the action.

(3) Mr A. R. THOMPSON read a short paper on "The Form of the Urinary Bladder." The paper was illustrated by several plaster casts made of

bladders shortly after death. The conclusions of the author's investigations were as follows:—

(1) The bladder is frequently asymmetrical.
(2) The bladders of individuals injected with the same quantity of plaster may vary very much from each other in shape and appearance.
(3) There is, in some cases, a well-marked bladder diverticulum on the side of the rectum. This diverticulum may be lateral or bilateral.
(4) The area and direction of the trigone vary in different bladders.

These anatomical conclusions are confirmed clinically by means of cystoscopic examination.

(4) Miss M. K. Lander contributed a paper entitled "The Pectoralis Minor: a Morphological Study."

The primitive condition of the pectoralis minor is generally considered to be represented by a large muscular sheet inserting on the lateral surface of the shaft of the humerus. The insertion is assumed to show a phylogenetic migration cephalad over the capsule to the coracoid process, as in man.

But this supposed secondary attachment of the coracoid is also to be found in such lowly mammals as Tatusia and Galeopithecus, as well as in Phascolomys and other Metatheria. The coracoidal insertion is not a purely functional one related to a digging fore-limb, as it is not found in rabbits, badgers, or Mustelidæ. It is therefore probably correlated with skeletal modifications.

The coracoid process is primitively a large flat element between the sternum and the scapula. It subsequently dwindles in size to a mere tubercle above the glenoid cavity of the scapula. If a muscle originally attached to this process is forced to migrate owing to recession of the process, it may move (1) upwards over the acromion, (2) downwards over the capsule, or (3) inwards on to the clavicle. The pectoralis minor is found to have tried each of these directions: (1) in the Ungulates, (2) in the Carnivora and most rodents, and (3) in a few rodents, in which case the sterno-scapularis is also found, probably an attempt to retain the influence over the movable fore-limb. Insectivora and Primates, having fair-sized coracoids, show a variable insertion of the pectoralis minor muscle, but the tendency is toward the downward humeral insertion.

Ontogenetically the early attachment to the coracoid, with subsequent descent over the capsule to the humerus, may be traced in fœtal kittens, and muscular fibres are sent down to the coracoid in early rabbit and calf embryos. Lewis describes caudad migration in the ontogeny of the human pectoral sheet.

In Monotremes there is no pectoralis minor, but rectus abdominis is inserted on to the coracoid process. In slightly less primitive mammals rectus is continuous, with a pectoralis minor going to the coracoid, save for the interposition of the lower costal margin or first rib. Humphrey has shown that the pectoralis major is merely rotated fibres of the superficial layer of rectus, and it is probable that pectoralis minor is a deeper layer rotated in a similar way owing to regression of the coracoid process laterally. In man connecting fibres between the insertion of rectus and the origin of pectoralis minor may frequently be demonstrated.

Pectoralis abdominis represents the lateral fibres of this upper part of rectus forced off the coracoid and down to the humerus, when the coracoid begins to diminish in size. Subclavius consists of the most mesial fibres forced back to the clavicle still earlier in myological history.

Anomalous arrangements of the deep pectoral sheet in man correspond to one of the three definitive conditions found in other animals. The size of the coracoid is very variable, and the pectoralis minor is in a condition of migration.

Professors THANE, FAWCETT, and KEITH discussed this paper.

(5) A paper by Professor AMIN ABDEL RAHMAN on "A Case of Complete Transposition of the Viscera" was, in the absence of the author, taken as read.

SUMMARY OF PROFESSOR FAWCETT'S COMMUNICATIONS ON THE DEVELOPING CHONDROCRANIUM.

Professor FAWCETT communicated, at the meetings held during 1914, 1915, 1916, the results of observations made on the developing chondrocrania of various mammals, and exhibited wax-plate models of them in illustration.

The models in question were:—mole, 19 mm.; nine-banded armadillo, 12 and 17 mm.; Australian native cat (*Dasyurus viv.*), 25 mm.; calf, 19 and 25 mm.; cat, 25 mm.; hedgehog, 25 mm.; water-rat, 25 mm.; ferret, 19 and 25 day. Many other stages of most of these animals had been examined in addition to those modelled, and he expressed his cordial thanks to the donors and loaners of the material, viz. Professors Wood Jones, J. P. Hill, and Arthur Robinson.

The results briefly summarised here will be published *in extenso* at a later date. Commencing with the basilar part of the chondrocranium, and first especially with those parts in the neighbourhood of the middle line, there are to be recognised from behind forward the following parts:—first, a part developed under the notochord—a hypochordal part; next, a part through which dorso-ventrally and caudo-rostrally the notochord runs until it comes into contact with the epithelium of the dorsum of the pharynx—a parachordal part; next, a part developed independently of the two previous parts which surround the pituitary body—the trabecular part. (In the mole of 9–10 mm. separate procartilaginous and cartilaginous trabeculæ are quite evident. In *Tatusia* of 12 mm. a single trabecula is laid down like a ring around the pituitary body.) A cellullar gap at first separates the parachordo-hypochordal cartilage from the trabecula, which evidently corresponds with the like space in, say, the reptile. Next follows an independently chondrified interorbito-nasal septum. This is quite clear both in the mole of 9–10 mm. and in *Tatusia* even as late as the 17-mm. stage; but the trabecula (formed by union of two lateral trabeculæ in mole) ends at the ventral-hinder extremity of the interorbito-nasal septum, exactly as in *Lacerta*—the two, however, being distinctly separate.

These three elements of the median basal line, viz. the hypochordo-parachordal, the trabecular, and the interorbito-septal, at a later stage fuse together to form a continuous cartilaginous stem from the anterior edge of the foramen magnum to the anterior end of the nose, and in the following manner the hypochordo-parachordal segment ends anteriorly in two lateral points; these elongate in a forward direction, and unite with backwardly directed and similar processes of the trabecula.

(In *Tatusia* the whole of the plate which I have designated hypochordo-parachordal is hypochordal, and the trabecula shifts in a caudal direction over the front end of this plate, so burying the notochord.) The trabecula fuses anteriorly with the lower edge of the interorbito-nasal septum.

It is interesting to note that the basi-cranial axis, including the lower border of the interorbito-nasal septum in the Metatheria, in the Edentates, the Ruminants and Rodentia and Insectivora examined and modelled, is particularly flat from behind forwards in the well-chondrified state, whereas in the Carnivora and Man it is bent in such a way that the nasal capsule is almost at right angles to the rest of the median basilar region. The flattening out of the axis, which is secondary in the edentate and probably also in the insectivore, has the effect of pushing the trabecular region backwards over the dorsal surface of the parachordal plate and so burying the notochord.

Development of Paramedial Structures from behind forwards.—From the hypochordal part of the hypochordo-parachordal plate more particularly an outgrowth takes place which forms that part of the occipital cartilage which belongs more especially to the exoccipital region, and this sends forwards under the auditory capsule a process which is identical with the jugular process of human anatomy. The twelfth nerve passes out through the occipital cartilage by either one or two foramina according to the species, and not infrequently species makes no difference. Anterior to the exoccipital region the auditory capsule is laid down, always chondrifying first around the semicircular canals, and finally around the cochlear duct. The manner of chondrification of the canalicular part of the capsule varies much with the species. In some, marked cartilaginous prominences are present on the surface, more particularly corresponding with the anterior and posterior semicircular canals, recalling the reptilian condition. In all cases a well-marked depression is found under the arch of the anterior semicircular canal—fossa subarcuata, or so-called floccular fossa. In no case save that of *Miniopterus* have I seen any flocculus lying in this fossa. The facial nerve always has a close relation to the division between cochlear and semicircular canal region, and a suprafacial commissure develops over the nerve, growing outwards from cochlea to vestibular and semicircular region over the nerve, as observed in the calf. In the mole an upwardly directed lamina of cartilage grows from the canalicular capsule to end freely—the operculum: this latter ossifies. In *Microtus amphibius* (water rat) the lateral aspect of the canalicular capsule in its upper half is hidden by the downgrowth of the tectum synoticum—of which later.

Anterior to the auditory capsule lies the ala temporalis, which in some marsupials is continued from the trabecula directly into the orbito-parietal commissure. In most it is laid down as an independent element in cartilage, which by its median end articulates for a time with the trabecula, and particularly in man at the 27-mm. stage the connection presents all the appearances presented by a developing diarthrodial joint. In the mole it seems to be chondrified in continuity with the trabecula. In *Tatusia* it is chondrified before the trabecula. In its relation to the branches of the fifth nerve it varies. The lower in the scale one goes, the more it tends to be associated with the mandibular division of that nerve, and not infrequently is perforated by it, *e.g.* calf. In ferret and man no immediate relation is presented to this nerve, but the ala is perforated by the maxillary division. In all cases it serves for the partial origin of the external pterygoid muscle. Anterior to the ala temporalis the ala orbitalis is met with. This is chondrified independently, and sends towards the hinder part of the interorbito-nasal septum one or two limbs: if one, that passes in front of the optic nerve; if two, then one passes anterior to the nerve, the other posterior to it. In the marsupial the posterior limb fails, so that the optic nerve passes through the same fissure as the other nerves of the orbit. The same condition is met with in *Microtus*. In *Tatusia* a foramen is met with lateral to the optic foramen, through which a blood-vessel passes from orbit to lateral cranial vein. This foramen recalls and is possibly homologous with the epioptic foramen of *Lacerta*, in which case the hind limb of the ala orbitalis is a true metopic tænia, as in *Lacerta*. I have not met with this foramen in other species, but the early chondrocranium of *Tatusia* is so extraordinarily like that of *Lacerta* that its presence is not surprising. Developed in connection with the hinder limb of the ala orbitalis and below the optic nerve is a muscular process—the so-called ala hypochiasmata. Naturally, where this hind limb fails the ala hypochiasmata likewise fails. It serves for the early attachment of the rectus system of muscles, especially the medial rectus of the eyeball. In the mole, where the eye muscles and eyeball are in a very rudimentary condition, the ala is wanting or extremely small. In *Tatusia* it seems to chondrify independently. In the hedgehog the margin of the optic foramen is almost tubular, and the eye muscles of the rectus system arise from this tube.

Anterior to the alæ orbitales is the nasal capsule. This in all the chondrocrania examined was divisible into three parts, viz. an anterior (Sakterwulst) or vestibulo atriæ; a middle part which might be called fronto-maxillary; and a posterior, the cupolar or ethmoidal part.

The anterior segment is separated from the middle one by a groove on the exterior—the antero-lateral sulcus, and a corresponding ridge in the interior—the crista semicircularis. The middle segment (fronto-maxillary) is separated from the posterior one by a sulcus on the exterior—the postero-lateral sulcus, which corresponds with a prominent ridge internally—the first ethmo-turbinal. This arrangement is constant throughout the series examined. In the fronto-maxillary segment two or three antero-posterior turbinals are formed, low in height. In the posterior segment three main turbinals project one behind another into the cavity of the nose, of which the most anterior, the first, is the first to develop and the others follow in succession; the first ethmo-turbinal tends to split into two somewhat divergent lamellæ. Between these main or primary ethmo-turbinals secondary ones are developed later and are much lower in height. The roof of the nasal capsule, divisible into two parts, viz. a hinder or subcerebral, and a more anterior, is only complete in its pre-cerebral part. The subcerebral part, until the formation of a cribriform plate, shows a large vacuity, opening more particularly into the hinder or cupolar segment and into the fronto-maxillary segment; and when the cribriform plate is later formed it is divided by an oblique stem of cartilage—the cribro-ethmoidal crest—into an antero-lateral group of foramina communicating in particular with the fronto-maxillary segment of the nose, and a postero-median part communicating with the cupolar or ethmoidal segment. At the anterior end of the cribro-ethmoidal crest a foramen, the foramen epiphaniale, runs through the capsule to the exterior for a short distance for the lateral branch of the nasal nerve.

In *Dasyurus*, in the mole and hedgehog and water-rat there is a well-marked flattened roof to the cupolar segment of the nasal capsule behind the cribriform plate. This is not met with in the remainder of the series. The floor of the nasal capsule exhibits varying degrees of completeness, according to age and species. In all there is formed anteriorly a lamina transversalis anterior. This may be almost horizontal or nearly vertical. In all save ferret and man it is prolonged backwards along the septum for a varying distance as the anterior paraseptal cartilage. Similarly, posteriorly, in the floor of the nose a lamina transversalis posterior is developed sooner or later, even in man. And this lamina transversalis posterior becomes connected by a narrow median piece along the septum, the posterior paraseptal cartilage with the anterior paraseptal cartilage, the junctional region being very narrow. The result is a complete common paraseptal cartilage, such as is seen in *Dasyurus viv.*, in the rabbit, in *Microtus*, and others, but this connection may not be brought about when, as in *Tatusia*, the mole, calf, ferret, hedgehog, and man, anterior and posterior paraseptal cartilages remain separate although connected with one another by fibrous tissue.

That the posterior paraseptal cartilage and lamina transversalis posterior are derived by thrusting back of the posterior wall of the nasal capsule, and at the same time the incurving and atrophy of the lower part of the median wall of the capsule, is evident and strikingly shown in specimens of progressive age of *Dasyurus*.

In the ferret and man the anterior paraseptal cartilage has lost its connection with the lamina transversalis anterior, and in the latter bears no immediate relation to the organ of Jacobson.

In man the lamina transversalis anterior is not formed, for the most part, only its median segment remaining as the processus lateralis ventralis. At no time are either common paraseptal cartilage, or its component parts, the anterior and posterior paraseptal cartilages, in cartilaginous continuity with the septum nasi.

The gap in the floor of the nasal capsule corresponding with the posterior choana is bounded in front by the lamina transversalis anterior, when that exists, by the lamina transversalis posterior posteriorly, by the lateral wall of the nasal capsule laterally, and medially by the common paraseptal cartilage or its representatives.

Anteriorly, in front of the lamina transversalis anterior a fenestra narina exists. This may be placed, as in the majority of cases, anteriorly, but in a few, such as *Dasyurus*, it is laterally placed, and a distinct cupola anterior is found at the anterior end of the nose. In man the fenestra narina and the choana communicate, owing to the lack of a lamina transversalis anterior, and a long rostro-ventral fissure is the result.

The nasal septum is the forward continuation of the interorbital septum. In the rabbit and in *Microtus* it shows a perforation in the cartilage or septal foramen. This is not far from the anterior end, and it recalls that of *Reptilia*. The whole form of the nasal capsule bears out the suggestion that it has been thrust back along the interorbital septum by the increase in size of the epithelial nasal sacs, and that its medio-inferior wall has remained only as the common paraseptal cartilage or its representatives in cartilage or fibrous tissue.

Lateral Structures in the Neural Part of the Chondrocranium.—Posteriorly at the most lateral extremity of the exoccipital cartilages on each side there is laid down a supra-occipital cartilage. This rapidly grows towards its fellow in the middle line, as seen in the calf. Later it sends forwards a process which connects it either directly with the canalicular part of the auditory capsule or with the orbito-parietal commissure (of which later). A gap is formed thus between the canalicular part of the auditory capsule and the supra-occipital cartilage, which has received various names. When fusion has taken place between the supra-occipital cartilages with one another in the mid-dorsal line, and anteriorly on each side with the canalicular part of the auditory capsule, the so-called tectum synoticum is formed. Its mode of formation is best illustrated by the calf and hedgehog. It would appear that it reaches its highest development in man, and in man a second tectum synoticum is formed anterior to the main one, but independently of it, and very much smaller. In man from the 30-mm. stage a well-marked processus ascendens grows forwards from the tectum posterius in the middle line, recalling the condition in *Lacerta*.

Antero-lateral to the tectum synoticum arises in the lateral membranous wall of the chondrocranium a plate of cartilage, the parietal plate, but whether by independent chondrification or by upgrowth from the canalicular part of the auditory capsule, the specimens examined do not show. But in all cases above quoted, save in man, this plate becomes connected sooner or later with the postero-lateral extremity of the ala orbitalis, and an orbito-parietal commissure results stretching from the ala orbitalis to the canalicular part of the auditory capsule. Small foramina for vessels create vacuities in this structure.

Anterior to the fusion of the ala orbitalis, the antero-lateral angle of the last-named cartilage grows forward to a process which has grown backward from the frontal part of the fronto-maxillary segment of the nasal capsule, and when fusion takes place a spheno-ethmoidal commissure is the result. The two stages are shown in the 19- and 25-mm. stages of calf. In the sheep, as is well known, the spheno-ethmoidal commissure is not complete.

With the formation of a spheno-ethmoidal commissure, an orbito-parietal commissure and a tectum synoticum, a complete lateral and posterior and at the same time somewhat ring-like cartilaginous wall is formed for the neural part of the chondrocranium.

Between the orbito-parietal commissure and the median structure, especially the trabecular region, a large gap is left which is partially broken up into two by the projection into it from the trabecular region of the ala temporalis. It is entirely divided into an anterior and posterior part in those marsupials in which the ala temporalis fuses laterally with the orbito-parietal commissure. That part behind the ala temporalis and over its outer extremity is filled with fibrous tissue, in which later the alisphenoid and squamosal are largely developed. The vacuity in front of the ala temporalis becomes to a great extent the sphenoidal fissure. The gap between the ala orbitalis and the nasal capsule, bounded laterally by the spheno-ethmoidal commissure, is the orbito-nasal fissure, and transmits the nasal nerve to the upper surface of the cribriform plate, and will ultimately be reduced to form the anterior ethmoidal canal.

Connections of the Median Structures with the Paramedian Ones.—The hypochordo-parachordal region becomes twice connected with the auditory capsule, first by exoccipital fusing with the canalicular part of the capsule to form the jugular process; secondly, with the cochlea, to form a parachordo-cochlear commissure. This is clearly seen in the mole and in the cat.

The trabecular region is doubly connected with the cochlear region once medial to the internal carotid artery and once lateral to it. The lateral connection, the so-called ali-cochlear commissure, clearly belongs to the trabecula, as is shown in *Tatusia*. Between the hinder trabeculo-cochlear commissure and the parachordo-cochlear commissure a basicochlear fissure remains permanently in the chondocranium of the mole and cat; but if such exist in the others examined, it must have been obliterated at a very early stage, for in none of them examined is such a basicochlear fenestra present, but a continuous fusion exists along the median aspect of the cochlear with the median structures. In the nine-banded armadillo a basicochlear fissure or fenestra exists first, but it closes up as development proceeds.

In man at the 27-mm. stage my specimens show that the so-called ali-cochlear commissure (anterior trabeculo-cochlear commissure) is in direct continuity with the cochlea lateral to the internal carotid artery, so the resemblance to the mole, cat, and other animals is here quite complete. This continuity may be—and, so far as I know, is—given up later, and the anterior trabeculo-cochlear commissure chrondifies independently in man, but this may be regarded as a secondary condition and of no morphological value. No sufficient reason seems to support the view that the mode of entrance of the internal carotid artery to the skull is different from that in the *Reptilia*; in fact, the conditions described seem to harmonise the two.

Visceral Skeleton.—Nothing of importance was noted at variance with the now usually accepted views as to its formation so far as concerns the first arch. In the second arch much the same may be said; the stapes was perforated by the stapedial artery in all save *Dasyurus*, and in the young *Tatusia* distinct evidence was obtained of the medio-hyal and latero-hyal divisions of the posterior end of the hyoid arch, the latero-hyal in the usual manner being fixed at the lower end of the tegmen tympani (crista parotica). In some it was unchondrified, in others chondrified.

The third arch was in all cases of comparatively small size, and clearly formed the so-called greater cornu of the hyoid; it was usually connected with the posterior end of the next or fourth arch by a cartilaginous bridge.

The fourth arch in all formed the thyroid cartilage from *Dasyurus* onwards, deepening as the animal rose in the scale: the foramen in the side of the thyroid cartilage, sometimes looked upon as an indication of its formation from the fusion of fourth and fifth arches, being merely produced by folding over of the hinder part of the fourth arch to meet the more anterior part, as shown in the two *Tatusia* models. The fifth arch in all cases formed the cricoid cartilage. In *Dasyurus* the upper end of the trachea was so formed as almost to simulate a sixth arch, but in this as in all other cases the position of the arytenoid cartilages stamped the cricoid or fifth arch, if anything else were indeed required. From Metatheria onwards, then, the thyroid cartilage was formed from the fourth arch, and that alone.

Accessory Cartilages in the Chondrocranium.—These are cartilages which develop in certain bones without any connection with the primordial chondrocranium. They were found in connection with the mandible, usually in the condylar and angular regions, but in *Microtus* a pair existed near the anterior end of the mandible on its medial side and close to, but not in any way connected with, the corresponding Meckel's cartilage; and in addition another was found at the hinder end of what is often but erroneously designated splenial. This has not been observed in any other animal examined. The one near the anterior end recalled the symphysial cartilage found in man. In connection with the maxilla and with the palate bone at the medial edge of the palatine process, it seemed to be the usual thing to find an accessory strip of cartilage, but this was absent from *Microtus*, and is not present in man; but in man a cartilage appears in the outer alveolar wall and root of the malar process of this bone which was not elsewhere observed. In *Microtus* an accessory cartilage appears at the hinder end of the post-auditory process of the squamosal, and in the 35-day ferret the lower edge of the squamosal also develops such a cartilage.

The cartilage forming the hamulus or its representative for the pterygoid bone was found in all save *Dasyurus*, and in all was accompanied by such bone, save in the mole.

The above is a condensed, brief, and perhaps, without illustration, almost unintelligible account of the results of the researches carried out. It does not contain any references to work previously done, all of which will appear when the various chondrocrania are described *in extenso*, but the more important points which it seems to settle are the establishment of the existence of separate trabeculæ and interorbito-nasal septum, the presence of a hypochordal segment too of the basilar part of the chondrocranium, the mode of formation of the various commissures, a more concise account of the manner of formation of the nasal region, and especially of the paraseptal cartilages, the significance of the ala hypochiasmata, and, with reference to the visceral skeleton, the origin of the thyroid cartilage. Finally, new accessory cartilages are introduced.

Many interesting points were also brought out with reference to the mode of origin of the covering bones of the chondocranium, but these will be dealt with later.

Professor Fawcett expressed his indebtedness to the following students, without whose help he could not possibly have attempted to make the numerous models which illustrated these communications:—Miss Salter, Miss Casson, Miss Richmond, Miss Neville, Miss Brown, Miss Llewellyn, Mr R. P. White, Mr G. E. Pilsley, and Mr Datta.

Journal of anatomy

1916-17