Human embryology and morphology.

Contributors

Keith, Arthur, Sir, 1866-1955.
University of Leeds. Library

Publication/Creation

London : Edward Arnold, 1913.

Persistent URL

https://wellcomecollection.org/works/w8yhh68k

Provider

Leeds University Archive

License and attribution

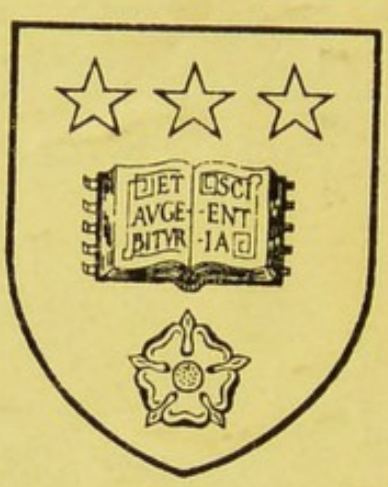
This material has been provided by This material has been provided by The University of Leeds Library. The original may be consulted at The University of Leeds Library. where the originals may be consulted.
Conditions of use: it is possible this item is protected by copyright and/or related rights. You are free to use this item in any way that is permitted by the copyright and related rights legislation that applies to your use. For other uses you need to obtain permission from the rights-holder(s).

wellcome collection

Wellcome Collection
183 Euston Road
London NW1 2BE UK
T +44 (0)20 7611 8722
E library@wellcomecollection.org
https://wellcomecollection.org

Unable to display this page

Library of the School of Medicine
University of Leeds



From the library of
The Right Honourable Lord Moynihan
of Leeds
1865 — 1936
Professor of Surgery

STACK
QS604
KEI
STACK
MEDICAL LIBRARY

To Sir Berkeley Moynihan
with Albert's very
kindest regards.
Feb 7. '17

30106 004160148

HUMAN EMBRYOLOGY AND MORPHOLOGY

Digitized by the Internet Archive
in 2015

https://archive.org/details/b21506851

HUMAN EMBRYOLOGY AND MORPHOLOGY

BY

ARTHUR KEITH, M.D.

LL.D.(ABERDEEN), F.R.C.S.(ENG.)

CONSERVATOR OF THE MUSEUM AND HUNTERIAN PROFESSOR,
ROYAL COLLEGE OF SURGEONS, ENGLAND

FORMERLY EXAMINER IN ANATOMY, UNIVERSITY OF ABERDEEN, UNIVERSITY OF LEEDS, AND IN THE NATURAL SCIENCE TRIPOS, UNIVERSITY OF CAMBRIDGE

THIRD EDITION, REVISED AND ENLARGED

ILLUSTRATED WITH 442 *FIGURES IN THE TEXT, OF WHICH* 126 *ARE NEW IN THIS EDITION*

LONDON

EDWARD ARNOLD

41 AND 43 MADDOX STREET, BOND STREET, W.

1913

36e7 691680

UNIVERSITY
OF LEEDS
MEDICAL LIBRARY.

PREFACE TO THIRD EDITION

DURING the eight years which have elapsed since this book was last revised, our knowledge of the development and evolution of the human body has made rapid progress. Especially is this true of the early stages in the formation of the human embryo. It is now possible to take up the story from the beginning and trace the rise of the human embryo from the ovum, the foetus from the embryo, and give a consecutive account of those marvellous changes which permit a human being to pass the first nine months as a parasite in the mother's womb. Advantage of this great advance has been taken to recast the whole form of this work; in place of beginning with an account of a well-known part of the body, such as the face, the history begins with the formation of the embryo from the fertilized egg, and is continued in subsequent chapters by an attempt to give a consecutive picture of the origin of the human body, and of the several systems which make the body a physiological whole.

Experience has confirmed the author in his earlier opinion that the facts of embryology are barren and meaningless until they are interpreted in the light of our knowledge of the evolution of the human body—a knowledge which must be founded on a wide study of comparative anatomy and physiology. Hence, in the present edition an attempt has been made to give not only a descriptive history of the development of the body, but to make these descriptive facts intelligible by bringing our knowledge of evolution to bear on them.

No attempt has been made to rival the great standard text-books—such as Oscar Hertwig's *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere*, Keibel and Mall's *Handbuch der Entwicklungsgeschichte des Menschen* (1910-1912), or Bryce's "Embryology" in Quain's *Anatomy* (1908). Indeed, this new edition is essentially a reflection of the knowledge which the author has found useful in his daily work, and in his attempts to understand the nature of the human body and of the diseases and malformations to which that body is subject. It is primarily intended to represent the investigations and opinions of British anatomists, but these investigations

are necessarily expanded and opinions modified by the knowledge which flows in upon us from the laboratories of the East and of the West. Ten years ago, when this work first appeared, we looked to the continent of Europe—especially to Germany—for new facts and for fresh inspiration, but we begin now to look towards America. The rise and progress of America in every form of Medical Research is one of the most striking manifestations of the last decade. As far as the development of the human body is concerned, the American influence is already manifest, and has affected this, as it must affect every text-book on Embryology.

In the preparation of this edition, the author has been frequently indebted to several excellent recent works. He must acknowledge especially Broman's *Normale und abnorme Entwickelung des Menschen* (1911); Vialleton's *Éléments de Morphologie des Vertébrés* (1911); Marshall's *Physiology of Reproduction* (1910); and Young's *Reproduction in the Human Female* (1911). The sections dealing with the brain proved the most difficult to revise; here the author followed the safe lead of Professor Elliot Smith, who has been good enough to revise the chapter dealing with the brain; but those who seek for fuller and more authentic information must consult the original documents referred to in the text.

The statements made regarding malformations of the body are chiefly founded on the Teratological Collection in the Museum of the Royal College of Surgeons, England. Fuller information will be found in the works of Ballantyne (*Antenatal Pathology*), of Ernst Schwalbe (*Morphologie der Missbildungen des Menschen und der Tiere*), and in Professor Wright's "Annual Summary of Teratological Literature" in the *Journal of Anatomy and Physiology*.

Over 120 illustrations have been added, several of the older figures have been replaced, and in spite of every endeavour this work has grown in size; but its utility to medical students and to medical men, it is hoped, has been enhanced. It will be thus seen that in many respects this edition may claim to be a new work rather than a mere revision.

ARTHUR KEITH.

Royal College of Surgeons,
England, *December* 1912.

CONTENTS

CHAPTER I.

PAGE

EARLY CHANGES IN THE DEVELOPMENT OF THE OVUM AND EMBRYO 1

CHAPTER II.

THE MANNER IN WHICH A CONNECTION IS ESTABLISHED BETWEEN THE FOETUS AND UTERUS - - - - - - - - - - 20

CHAPTER III.

THE ORIGIN AND NATURE OF CERTAIN EMBRYONIC STRUCTURES, AND THE GROWTH OF THE EMBRYO AND FOETUS - - - - - 29

CHAPTER IV.

THE SPINAL COLUMN AND BACK - - - - - - - - - 43

CHAPTER V.

THE SEGMENTATION OF THE BODY - - - - - - - - - 58

CHAPTER VI.

CENTRAL NERVOUS SYSTEM—DIFFERENTIATION OF THE SPINAL CORD 66

CHAPTER VII.

THE MID- AND HIND-BRAINS - - - - - - - - - - 77

CHAPTER VIII.

THE FORE-BRAIN - - - - - - - - - - - - 89

CHAPTER IX.

THE CRANIUM - - - - - - - - - - - - - 117

CHAPTER X.

DEVELOPMENT OF THE FACE - - - - - - - - - - 138

CHAPTER XI.

PAGE

The Teeth and Apparatus of Mastication - - - - - - 163

CHAPTER XII.

The Nasal Cavities and Olfactory Structures - - - - - 173

CHAPTER XIII.

Development of the Structures concerned in the Sense of Sight - - - - - - - - - - - - - - 184

CHAPTER XIV.

The Organ of Hearing - - - - - - - - - - - 204

CHAPTER XV.

Pharynx and Neck - - - - - - - - - - - - 221

CHAPTER XVI.

Organs of Digestion - - - - - - - - - - - 247

CHAPTER XVII.

Circulatory System - - - - - - - - - - - - 281

CHAPTER XVIII.

Respiratory System - - - - - - - - - - - - 324

CHAPTER XIX.

Urogenital System - - - - - - - - - - - - 342

CHAPTER XX.

Body Wall and Pelvic Floor - - - - - - - - - 391

CHAPTER XXI.

The Limbs - - - - - - - - - - - - - - 413

CHAPTER XXII.

Skin and its Appendages - - - - - - - - - - 450

Index - - - - - - - - - - - - - - - 463

HUMAN EMBRYOLOGY AND MORPHOLOGY.

CHAPTER I.

EARLY CHANGES IN THE DEVELOPMENT OF THE OVUM AND EMBRYO.

Chief Changes in the First Month of Development.—In the first month of human development changes take place very rapidly. In

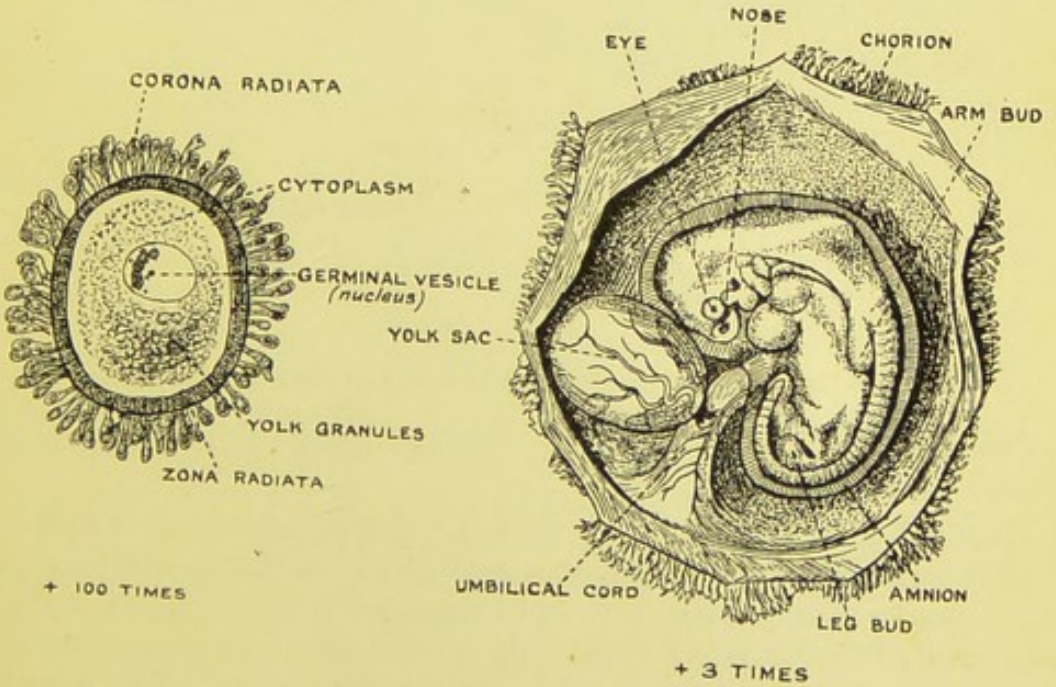


FIG. 1.—The parts of a Mature Human Ovum. (After Van der Stricht.)
FIG. 2.—Human Embryo and its Membranes at the end of the first month of development. (After Kollmann.)

that short time the fertilized ovum passes from the condition of a single cell, with a diameter of $\frac{1}{250}$ of an inch [1] to a fully formed human embryo about $\frac{1}{3}$ of an inch in length, and contained within a spherical

[1] Measurements are given at first according to our English standard, but throughout this book the more convenient metric system will be employed. One inch = 25·4 mm. One millimetre = 1000μ, or micromillimetres, or mikro.

envelope of embryonal membranes which measures nearly an inch in diameter (see Figs. 1 and 2). By the end of the first month the beginnings of all the parts of the adult body are recognizable—the head, the trunk, the limb-buds, the primitive segments, the eyes, the nose and mouth. A section across the abdominal cavity reveals the fact that the bases of the genital glands are already formed, and that certain cells have been set aside for the reproduction of another generation. Thus in a short month a cycle of developmental changes has produced

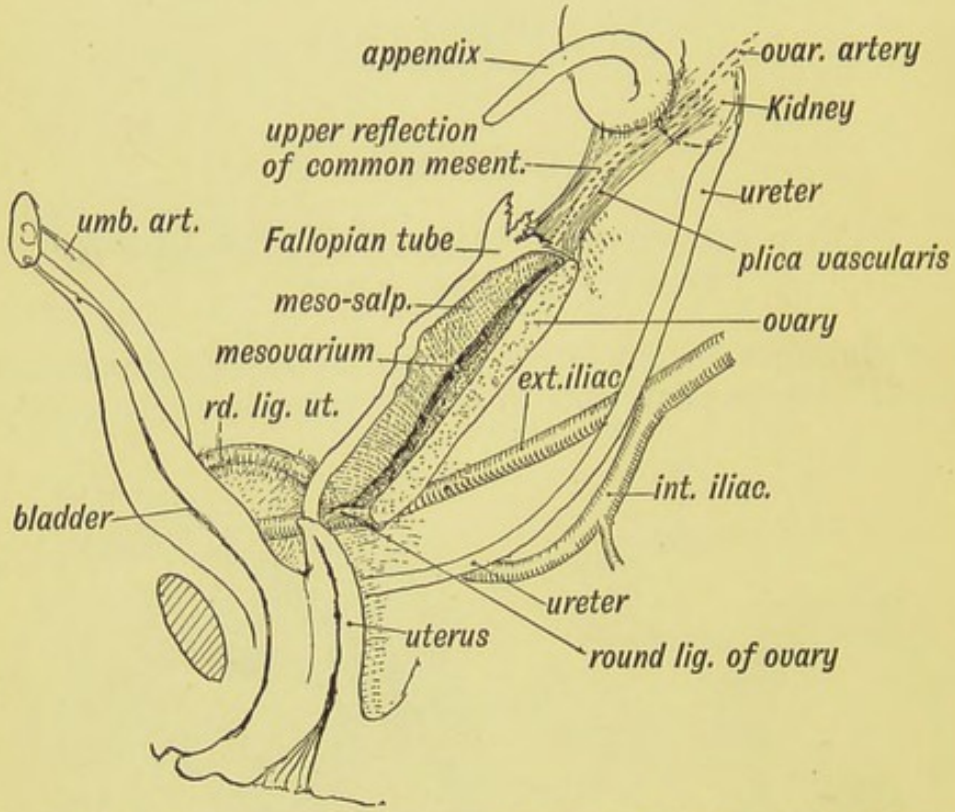


FIG. 3.—The position of the Ovary and Fallopian Tube in the 5th month.

a new generation of reproductive cells from the fertilized ovum of a former generation.

Descent of the Ovary.—In tracing the cycle of changes which lead from the fertilized ovum of one generation to the production of a reproductive gland in the next generation, we may begin our study at any point, but for many reasons it is convenient to commence with the condition of the ovary in a fifth-month foetus. The ovary is descending or migrating from the region of the kidneys where it was formed, and has reached the iliac fossa. In all primitive vertebrate animals the genital glands are stationed above the kidneys, but in mammals, for reasons to be explained afterwards, they descend to the lower part of the trunk—a change which is especially well seen in the human subject. In the fifth month the ovary is long and narrow, with an upper and lower pole ; it is three-sided in section—the surfaces being inner, outer and inferior or ventral (Fig. 3). The Fallopian tube

lies along the outer side of the ovary in the iliac fossa ; its upper fimbriated end terminates at, and is attached to, the upper or cephalic pole of the ovary (Fig. 3). As the parts lie on the iliac fossa, the tube and the ovary are supported each by its own mesentery, the **mesosalpinx** and **mesovarium.** The two mesenteries have, however, a common origin or attachment to the posterior abdominal wall, and to the common attachment the name of **common genital mesentery** may be given. The upper end of the common mesentery—the **plica vascularis** (Fig. 3), as it is reflected from the cephalic pole of the ovary and fimbriated extremity of the tube, is continued up towards the diaphragm and in it the ovarian vessels and nerves pass to the ovary and tube. The caudal pole of the ovary is joined to the uterus by its round ligament. The round ligament of the uterus, corresponding to the gubernaculum

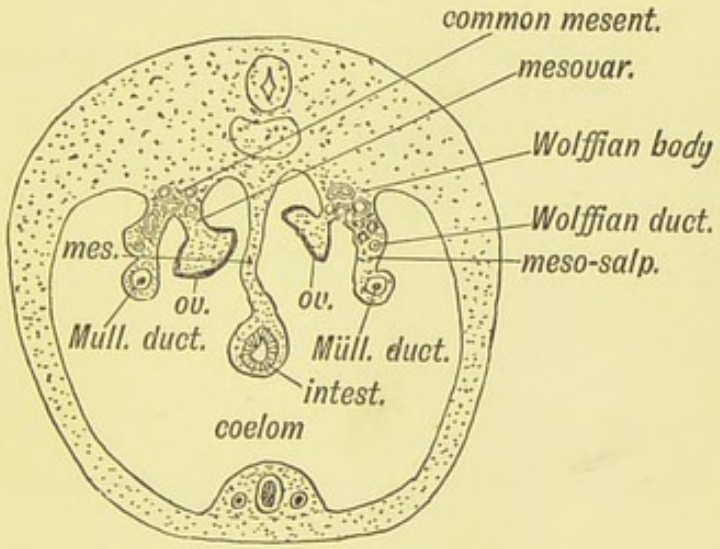


FIG. 4.—Diagrammatic Section of a Foetus at the end of the 2nd month, showing the attachments of the Ovary and Müllerian duct.

testis of the male, passes from the brim of the pelvis, where it is attached to the horn of the uterus, almost straight to the internal inguinal opening and assists in the descent of the ovary and tube.

By full term the ovary lies at the brim of the pelvis or partly within it ; after birth the ovary, uterus and rectum come gradually to occupy their adult positions within the pelvis. This is due to a relatively great growth in the pelvis, which becomes marked as the child learns to walk, and especially in the female at the time of puberty. The ovary, as is more frequently the case with the testicle, may be arrested in its descent.

In Fig. 4 an **earlier stage** is shown ; it represents the condition about the end of the second month The ovary and tube with the remnants of the Wolffian body—a primitive form of kidney—occupy the position in which they are developed. Both are suspended by mesenteries from the dorsal wall of the peritoneal cavity, at the side of the mesentery of the gut.

Normal Position of the adult Ovary.—When the ovary descends within the pelvis it usually occupies a definite triangle—the **ovarian triangle**—on the lateral wall of the pelvic cavity (Fig. 5). The ovarian triangle is bounded above by the upper half of the external iliac artery, below and behind by the internal iliac artery, with the ureter lying on the artery; in front by the reflection of the posterior layer of the broad ligament on the side of the pelvis. The peritoneum

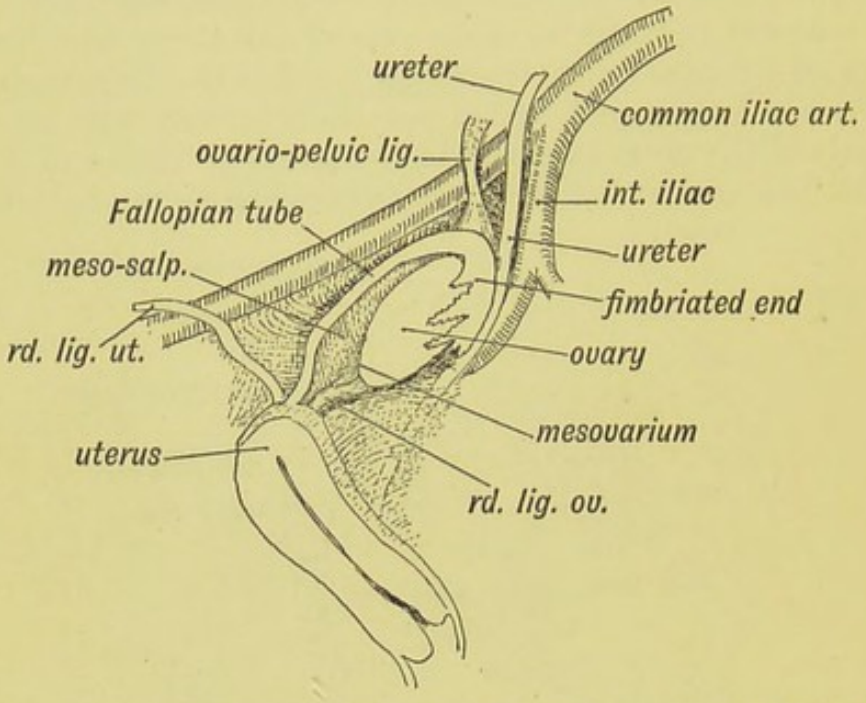


FIG. 5.—Showing the position of the Ovary on the lateral wall of the Pelvis and its relation to the Fallopian Tube.

covering the triangle forms a depression, or occasionally a pouch, for the ovary. The fimbriated end of the Fallopian tube is applied to the ovary, ready to receive the ripe ova and transfer them to the uterus. One of the fimbriae—the ovarian fimbria—tethers the tube to the ovary. It will be seen that, with the descent of the ovary, the meso-salpinx, the mesovarium, and the common genital mesentery have come to form the major part of the broad ligament. The upper end of the common genital mesentery now forms the ovario-pelvic ligament (Figs. 3 and 5). The ovary brings down with it, too, the ovarian arteries, veins, lymphatics and plexus of nerves. The nerves come through the aortic plexus from the 10th and 11th dorsal segments of the cord, and the lymphatic vessels carry the ovarian lymph to a group of glands situated high up in the lumbar region.

An Ovum.[1]—As the infantile ovary descends, it is laden with thousands of ova (over 10,000, T. G. Stevens; 100,000, F. H. A. Marshall). The ova are embedded in the stroma of the ovary, each being

[1] For fuller details and literature see Francis H. A. Marshall, *The Physiology of Reproduction*, London, 1910.

surrounded by a special layer of epithelial cells, which at first are flattened, but become columnar in shape as the ova ripen (Figs. 6 and 7). These cells which surround the ova, with a condensed layer of the stroma cells outside them, form a **Graafian follicle.** The ovary is covered by a layer of columnar epithelium, which is named the **germinal epithelium** ; at the hilum of the gland the germinal epithelium becomes continuous with the peritoneum on the mesovarium, the line of junction being sharp and quite apparent to the naked eye. Amongst and immediately beneath the columnar cells of the germinal epithelium larger cells occur during early foetal life. These are the **primordial ova** from which brood ova arise. The ova are carried within the ovary by tubular ingrowths of germinal epithelium. These tubular invasions of the ovary become broken up, the isolated masses of the germinal

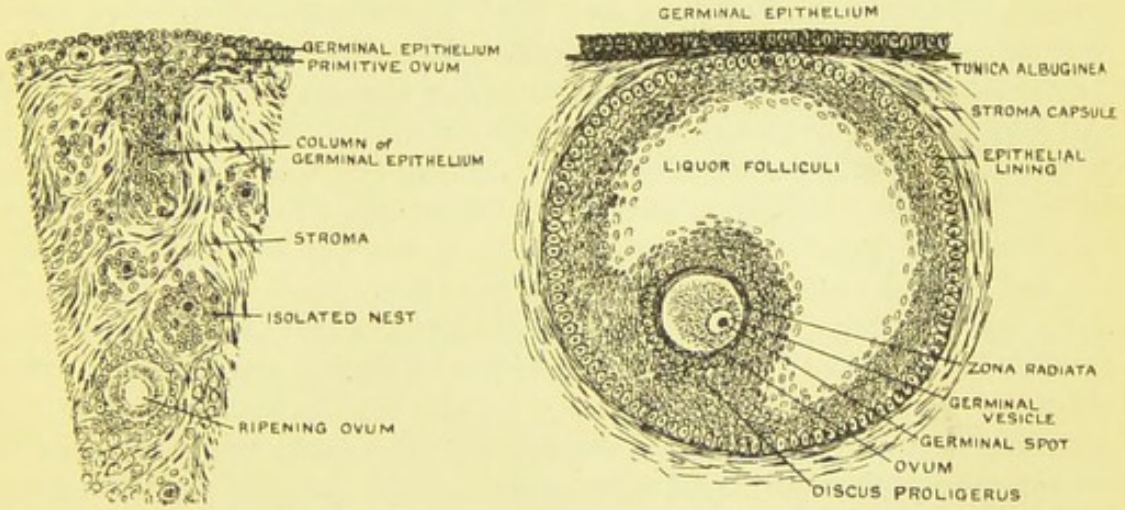


FIG. 6.—Diagrammatic Section of the Ovary of a fifth month Foetus, showing Nests of Germinal Epithelium and unripe Graafian Follicle.
FIG. 7.—Ripe Graafian Follicle at Puberty.

epithelium remaining to form the linings of the Graafian follicles. We shall see that another important constituent of the ovary also arises from the tubular incursions of the germinal epithelium—namely the **interstitial cells,** which are glandular in nature, and supply an internal secretion which regulates growth and development.

Discharge of the Ova.—At puberty especially, also before it, and for 30 years after it, one egg after another ripens ; the ovum enlarges ; so does its Graafian follicle (Fig. 7). The cells of the epithelial lining proliferate and a cavity appears within the follicle, due to a collection of fluid—the liquor folliculi—amongst the cells. The ovum remains attached to the wall of the follicle by a group of epithelial cells, the discus proligerus (Fig. 7). As the fluid collects, the follicle works its way to the surface of the ovary ; the tunica albuginea, which forms a capsule for the ovary, and the germinal epithelium, gradually atrophy over it, and at last it bursts and discharges the ovum. Many of the

immature ova are absorbed after birth and before puberty by the phagocytic action of the Graafian epithelium (T. G. Stevens).

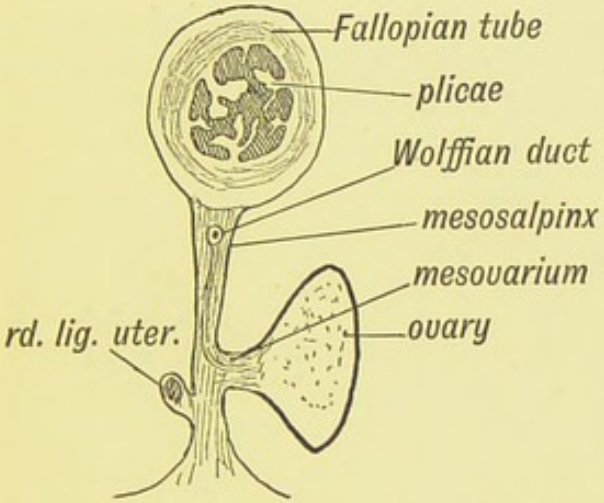
Two opposite opinions exist among gynecologists as to the period of rupture : (1) That it occurs at the onset of menstruation ; (2) that it has no relationship to the menstrual period. The truth is, probably, that both are right. The majority of ova, however, appear to be discharged during the menstrual period. Whether ova are discharged from both ovaries at once, or from only one, and whether one or more than one in a month, are points not yet settled ; but the usual opinion is that one ovum is shed each month, and only from one ovary. An ovum shed from one ovary may occasionally pass down by the opposite Fallopian tube.

The Graafian follicle, after rupture, fills up with blood ; a cellular tissue is soon developed within its cavity from the lining cells of the follicle. These contain lutein, and have a yellowish colour when seen in mass. If pregnancy does not occur, a **false corpus luteum** is formed, a formation which begins to disappear before the next menstrual period. If pregnancy occurs, however, the cellular mass continues to increase in size until it forms a glandular body as large as a pigeon's egg and is known as a **true corpus luteum.** It reaches its maximum size about the fourth or fifth month of pregnancy ; it is much reduced in size by the end of that period. Experiments have been made by Marshall and Joly and by Blair Bell which show that the secretion of the corpus luteum acts on the lining membrane of the uterus during the earlier stages of pregnancy. Both forms of corpus luteum lead to a cicatrix, which is seen on the surface of the ovary. The ovary of an old person is commonly covered with such scars. The Graafian follicles may become cystic and give rise to enormous ovarian tumours.

The Fallopian Tube.—When the ovum drops from the ovary it cannot easily escape the ciliated fimbriae of the Fallopian tube which surround and clutch the ovary. In Fig. 5 the relationship of the Fallopian tube to the ovary is shown. The tube may be demarcated into three parts : (*a*) the isthmus or arm directed outwards to the wall of the pelvis ($\frac{1}{2}$ to 1 inch) ; (*b*) the forearm or ampullary part, directed backwards on the lateral pelvic wall above the ovary ; (*c*) the hand, infundibular, or fimbriated part, folded backwards and grasping the free border and exposed surface of the ovary. The tube is fastened by one of its fimbriae to the cephalic pole of the ovary.

Course of the Ovum in the Tube.—The cilia on the fimbriae work towards the ostium abdominale, the abdominal mouth of the Fallopian tube, which is situated at the bases of the fimbriae, and carry the discharged ovum through the ostium within the tube. The ostium abdominale is shut when the tube is examined after excision ; the closure is probably due to reflex contraction of the tube muscle, caused by handling and cutting. In the infundibular and ampullary segments of the tube, the mucous membrane is thrown into long plicated

folds shown in section in Fig 8. They are covered with ciliated epithelium, which urge the ovum towards the uterus. Within the tube impregnation usually takes place. If the passage of the fertilized ovum is obstructed, which may result from an inflammation or cicatrization of the epithelial lining of the tube, development may proceed at the point of obstruction. When **tubular pregnancy** occurs, the growing ovum expands and ultimately perforates the tube—usually in the second month—an accident which is always attended by a grave haemorrhage.



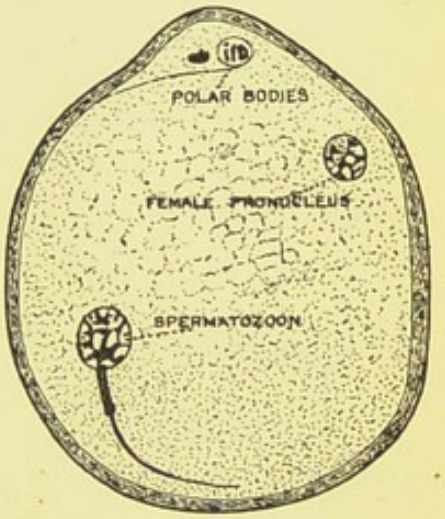


FIG. 8.—Diagrammatic Section of the Broad Ligament and Fallopian Tube.

FIG. 9.—Mature Ovum of Bat, showing the separated Polar Bodies, the Female Pronucleus and a Spermatozoön about to form a Male Pronucleus. (After Van der Stricht.)

The History of the Ovum within the Fallopian Tube.—When the ovum enters the Fallopian tube, it is a cell of very considerable size (250μ) with a cell wall—the zona radiata (Fig. 1), a nucleus—the **germinal vesicle,** and a nucleolus—the **germinal spot.** Then, or before then, the ovum prepares for fertilization by the extrusion from its nucleus of first one, then another **polar body,** and, with the extrusion, the germinal vesicle becomes the **female pronucleus** (Fig. 9). The polar bodies, which lie outside the protoplasm of the ovum, but within the zona radiata, are parts of the germinal vesicle, which are extruded with all the display of karyokinesis—the peculiar changes manifested by the nucleus when a cell is about to divide. What become of the polar bodies in the course of development of the fertilized ovum is not known, but they probably completely disappear. We shall see that the three polar bodies really represent three aborted ova—which have left their cell-bodies to enrich the principal ovum.

Karyokinesis.[1]—No one has seen the changes which take place in the human ovum either before or for some stages after fertilization;

[1] For literature and significance of Mitosis see C. E. Walker, *Essentials of Cytology*, London, 1907; Bashford and Murray, "Significance of Mitosis," *Proc. Roy. Soc.* 1909, vol. 73, p. 66; R. Fick, *Ergebnisse der Anat.* 1906, vol. 16, p. 1; S. Tschassownikow, *Anat. Hefte,* 1911, vol. 45, p. 197.

we infer that these do not differ materially from the prefertilization phenomena which we know to occur in the ova of invertebrates or from the postfertilization processes which take place in the higher mammals. The first and second polar bodies are the results of a primary and secondary division of the ovum. When an ordinary cell of the body is about to divide, the nucleus undergoes certain changes before cleavage takes place. The nuclear division precedes that of the whole cell. This mode of cell division or cell propagation is known as Karyokinesis or Mitosis. Two elements within the nucleus play a part in the process—the **chromatin,** which readily combines with certain staining reagents, and the **achromatin**, which does not absorb dyes. In the resting phase, the chromatin is scattered as minute particles in the network of the

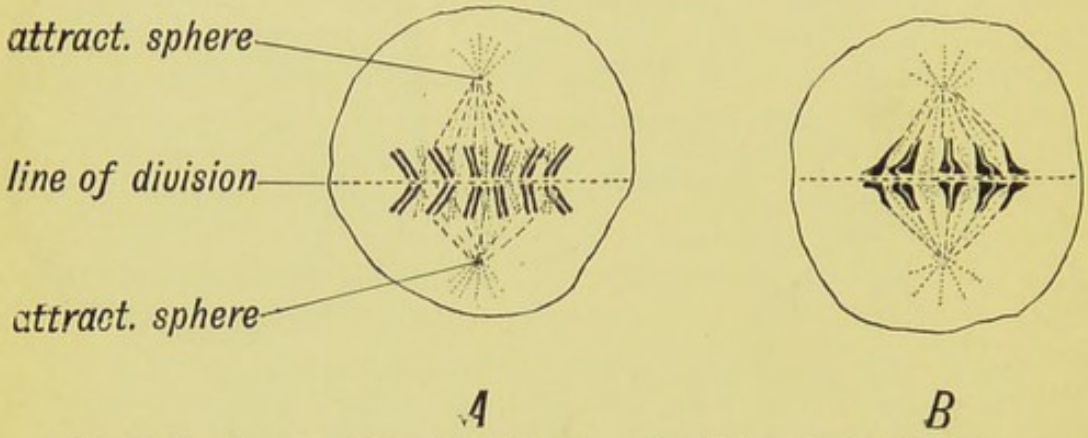


FIG. 10, *A*.—Diagram of Karyokinesis in a somatic cell (homotypical division). *B*.—Diagram of Karyokinesis during the production of matured ova and spermatozoa (heterotypical division). (After J. B. Farmer.)

nucleus, but when mitosis is to take place the particles unite into filaments ; the filaments break up into segments or rods, each rod being known as a **chromosome** (Fig. 10). The number of chromosomes that appears in each somatic cell is approximately constant for each species of animal ; in man twenty-four is the usual number (Broman). As the chromosomes form, an achromatin body appears outside the nucleus—the **centrosome,** which appears to yield a commanding influence on the division of the nucleus. The centrosome divides ; the two halves move apart until they lie at opposite poles of the nucleus where each forms an **attraction sphere** (Fig. 10). The attraction spheres become joined by a **spindle** of achromatin threads, the nucleus then appearing as if it were supported by the spindle between them. The chromosomes move towards the equatorial plane of the nucleus—midway between the attraction spheres ; during the movement each chromosome divides longitudinally, so that each is split into two, the two halves lying side by side, often bent into V-shaped forms (Fig. 10). As the nucleus divides in the equatorial plane 24 chromosomes pass into one half and 24 into the other. The attraction spheres fade away ; the division of the cell body is completed, each half having now its own

nucleus ; the chromosomes break up in the network of the daughter nuclei and the two cells enter a resting phase.

The two karyokinetic divisions undergone by the ovum before fertilization differ in three particulars from the process as seen in a somatic cell : (1) Only 12 chromosomes are formed—each being really double ; (2) they are peculiar in shape and manner of division (Fig. 10) ; (3) the cell body divides very unequally—only a very minor part accompanying that half of the nucleus which is separated at the first and second divisions of the ovum and which form, when thus separated, the first and second polar bodies. A division of the first polar body accompanies the separation of the second polar body from the ovum. Thus the two divisions undergone by the ovum result in the formation of one matured ovum and three polar bodies. Three-fourths of the

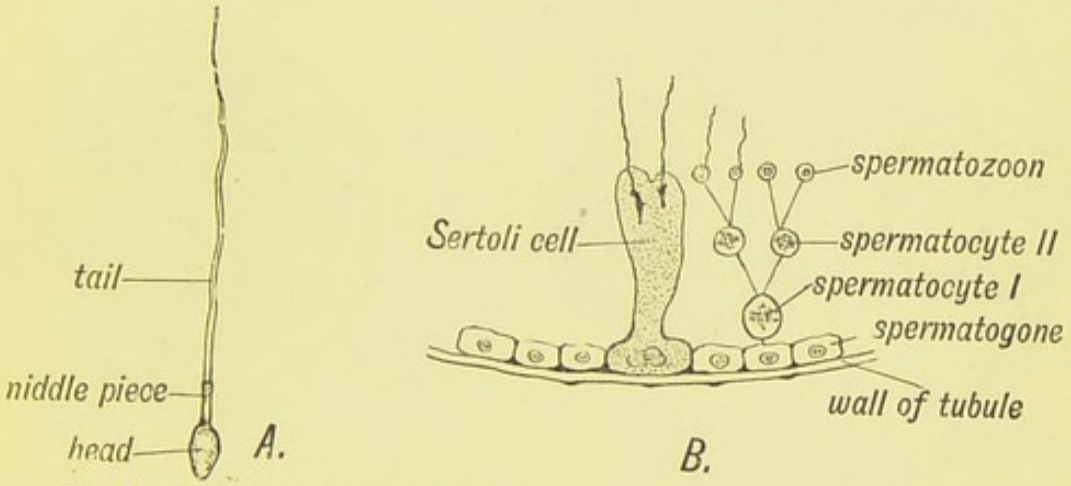


FIG. 11, *A*.—Diagram of a Spermatozoön.
B.—Diagram showing the origin of Spermatozoa from the lining cells (spermatogonia) of the tubules of the testicle.

chromatin in the nucleus of the original ovum are extruded in the polar bodies.

The cells of a malignant tumour frequently show in their divisions the peculiar mitotic changes which are seen in the preparation of the female pronucleus. Prof. J. B. Farmer regards such cells as essentially germinal in character. It has also been found that the heterotypical form of mitosis may occur in leucocytes and in inflamed tissues.

Formation of Spermatozoa.—Having thus described the maturation of the ovum, and followed it within the Fallopian tube, it is necessary to trace the history of its counterpart in the male—the spermatozoön. The manner in which a spermatozoön is produced by a primary and secondary division from a **spermatocyte** is very similar to the production of a **mature** from an **immature** ovum. The form of mitosis is the same (heterotypical), the chromosomes being reduced to 12 in number and peculiar in shape. The two divisions take place within the seminiferous tubules of the testis, and result in the production of four spermatozoa—corresponding to the matured ovum and three polar bodies (Fig. 11, *B*). The seminiferous tubules correspond to the ingrowths of

germinal epithelium which carry the primordial ova within the ovary. Lining the tubules are two kinds of cells—those of Sertoli (Fig. 11, *B*), large cells for nourishing the spermatozoa—representing those in the Graafian follicles—and other cells known as spermatogonia, corresponding to primordial ova. A spermatogone gives rise by division to a primary spermatocyte which corresponds to the immature ovum. The primary spermatocyte divides into two secondary spermatocytes, each of which again divides and thus four cells are produced, which become modified into spermatozoa (Fig. 11, *B*). The nucleus forms the head, the junctional part represents the centrosome, while the tail is all that remains of the substance of the cell body (Fig. 11, *A*). Gemmill has shown that spermatozoa can be kept alive for many days in nutritive media ; probably the secretions of the epididymis, vesiculae seminales,

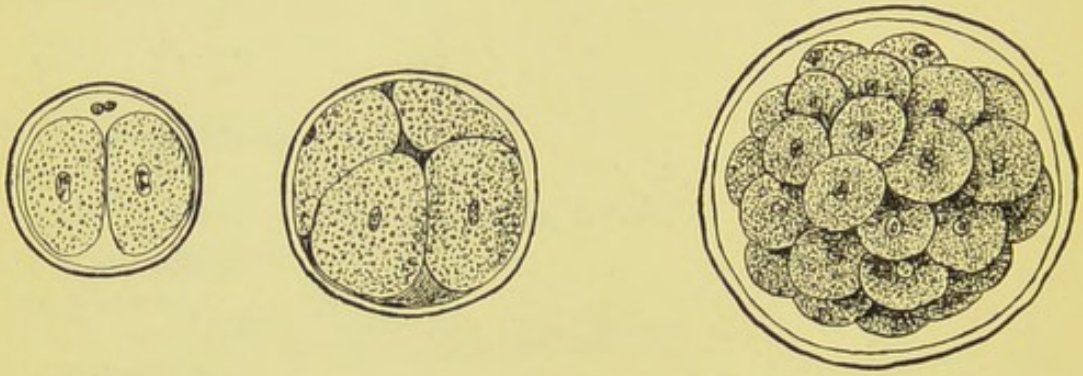


FIG. 12.—Showing the production of the Morula from the Ovum.
A. The Ovum after the first division. *B*. After the second. *C*. The Morula stage.

prostate and Cowper's glands are for this purpose. Beard has collected evidence to show that spermatozoa have no influence in determining the sex ; the sex of the ovum is predetermined before fertilization.

Fertilization.—In the course of fecundation thousands of spermatozoa are lodged in the genital passage ; many stem the adverse current of the uterine cilia, reach and live for days within the interlaminar grooves in the wider parts of the tube.[1] In the course of its descent within one of the grooves the egg may be fertilized. The spermatozoön bursts through the zona radiata, loses its tail, its head enlarges, and forms the **male pronucleus**. The male and female pronuclei unite, and from their union springs the nucleus of the fertilized ovum. This is the centre from which all future developmental changes start. In the pronuclei, it will be remembered that the chromosomes were reduced to half the usual number ; by their union the full complement of twenty-four is again restored in the fertilized ovum. By the process of fertilization the characters of two human individuals are mingled.

[1] For literature on fate of spermatozoa in the uterus see J. H. F. Kohlbrugge, *Roux's Archives*, 1912, vol. 35, p. 1.

The mixed chromosomes of the nucleus of a fertilized ovum are laden with the latent virtues and vices of both father and mother. They transmit the characters of the race from one generation to another. The ovum may be, but rarely is, fertilized in the ovary, or between the ovary and ostium abdominale, the result being a pelvic gestation. The length of time the fertilized ovum takes to reach the uterus is not known exactly, but probably it spends about eight or ten days within the Fallopian tube. The musculature of the tube, as well as

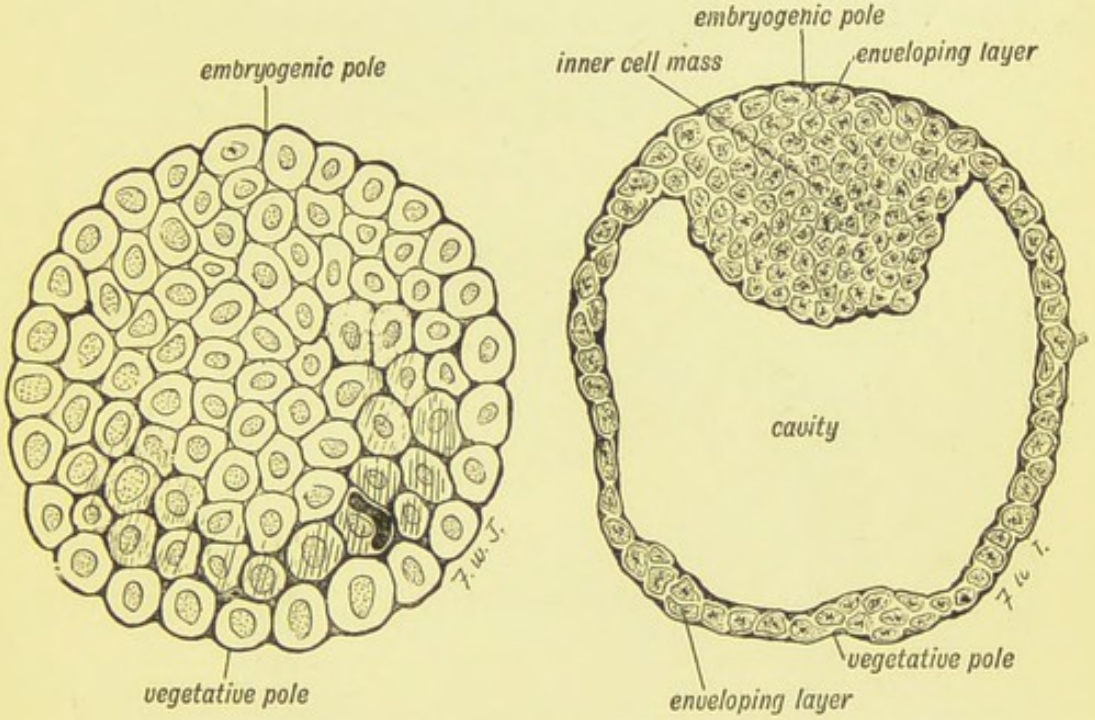


FIG. 13.—Stage I. The Blastula.
FIG. 14.—Stage II. The Blastocyst. (After Van Beneden.)

the action of the cilia, assists the fertilized and developing ovum in its progress to the cavity of the uterus.

Stages in the Formation of the Embryo.—In about fourteen days from the date of its fertilization the ovum passes through the following stages—the first and second probably taking place in the Fallopian tube, the others within the cavity of the uterus.[1]

Stage I.—The ovum, with a full display of karyokinetic changes of the ordinary somatic type, divides, subdivides, and grows within the zona radiata until a rounded mass of cells is formed—the morula or **blastula**. The cells are of unequal size and divide at unequal rates (Figs. 12 and 13).

Stage II.—This stage is produced from the first stage, by the collection of fluid within the mass of cells, a vesicle or **blastocyst** being

[1] For literature on early stages in the formation of the mammalian blastula see J. P. Hill, *Quart. Journ. Mic. Sc.* 1910, vol. 56, p. 1.

thus formed. The cells are then seen to be arranged in two sets—(*a*) an enveloping layer the **trophoblast** (Rauber's layer) in contact with the mucous membrane of the uterus (Fig. 14), and (*b*) a group of granular cells (the inner cell mass) attached to the enveloping layer at the *embryogenic pole* of the vesicle (Fig. 14). In Vertebrates with huge stores of yolk in their ova, such as birds have, the vesicle is filled by yolk-bearing cells, continuous with the enveloping layer at the *vegetative pole*, opposite to the inner cell mass.

Stage III.—The inner cell mass is differentiated into two parts. The inner cells become the **hypoblast** or **entoderm** (Fig. 15). They

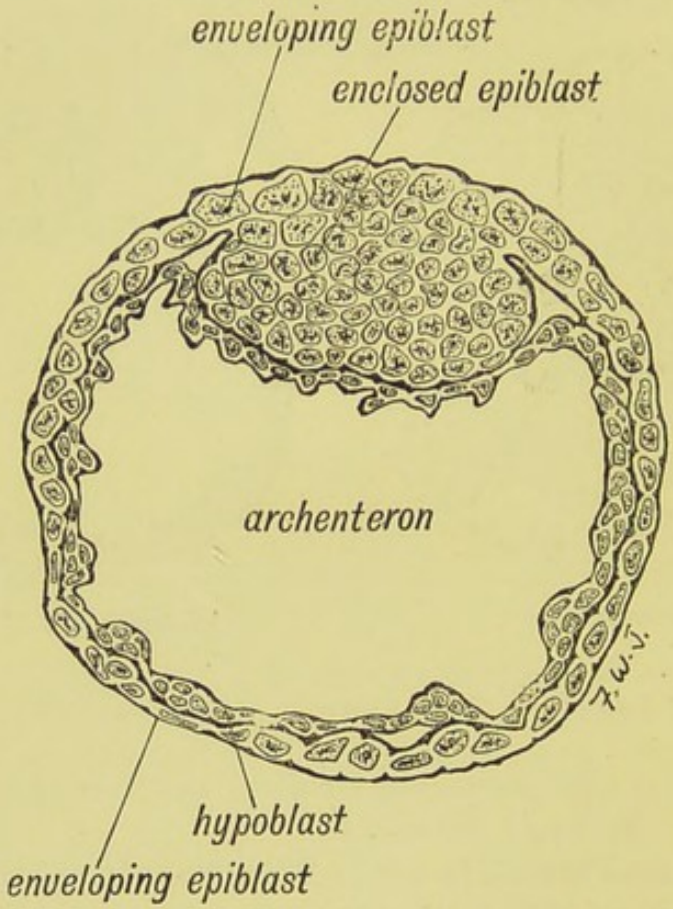


FIG. 15.—Stage III. Bilaminar Blastocyst. (After Van Beneden.)

spread out in the form of a single layer and enclose a cavity. To that cavity and its hypoblastic wall the term of Archenteron is applied. The outer cells of the inner mass are epiblastic in nature; they may be named the **enclosed epiblast** or **ectoderm.** The cells of the enveloping layer or trophoblast are also epiblastic in nature. At this stage, then, the ovum is differentiated into epiblastic and hypoblastic cells; the epiblast is further divided into an "enveloping" and an "enclosed" part. The three stages just described in the development of the human ovum have not yet been seen; they are inferred from what we know of the developmental stages in mammals nearly allied to man.

Stage IV.—During the last twelve years a number of specimens have been described which represent this stage.[1] The earliest form was that investigated by Teacher and Bryce in 1908; the cyst-like embryo measures 1·95 mm. in its longest diameter by ·95 mm. in its smallest, and is regarded as in the 13th or 14th day of development. It differs from the form represented in Fig. 15 in three particulars (see Fig. 16); (1) the hypoblast or entoderm is now separated from

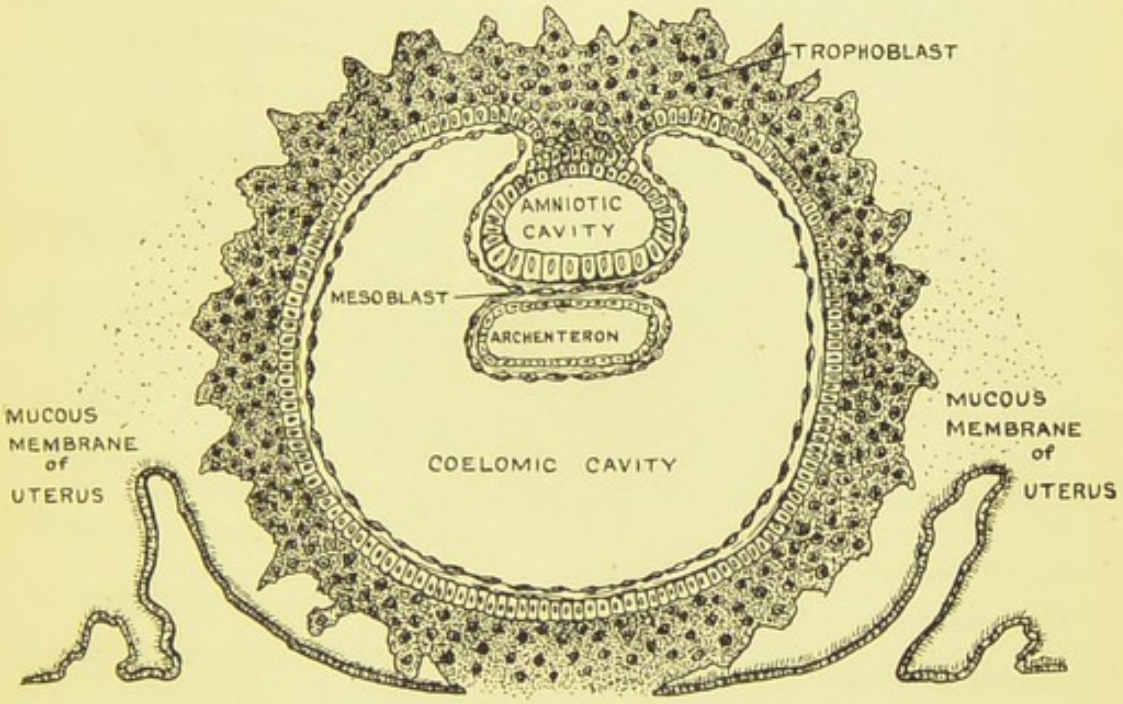


FIG. 16.—Showing the Origin of the Primitive Coelom, the Mesoblast and Cavity of the Amnion during the Development of the Human Ovum. (After T. H. Bryce.)

the "enveloping epiblast" by a wide space; (2) a cavity—the cavity of the Amnion—has appeared in the "enclosed epiblast"; (3) a third and new stratum of cells now lines the space between the hypoblast and epiblast (Fig. 16). The cells of this layer form the **mesoblast** or **mesoderm.** As the mesoderm spreads outwards from the cell mass it divides into two layers; while one covers the archenteron, the other lines the enveloping epiblastic layer. The cavity or space which exists between the outer and inner layers of mesoblast is named the **primitive coelom** (Fig. 16). The enveloping layer of the epiblast with its lining of mesoblast grows with an extraordinary rapidity (Fig. 17).

In 1899 Dr. Peters gave a full and clear description of a human ovum in a slightly more advanced state of development, but still in

[1] For literature on very early human embryos see T. H. Bryce and J. H. Teacher, *Contributions to the Study of the Early Development and Embedding of the Human Ovum*, Glasgow, 1908; James Young, *Reproduction in the Human Female*, Edinburgh, 1911; A. J. P. van den Broek, *Anat. Hefte*, 1911, vol. 44, p. 273; M. Herzog, *Amer. Journ. Anat.* 1909, vol. 9, p. 361.

the condition which is named here (Stage IV., see Fig. 17). The enveloping epiblast and its lining of mesoblast forms the main embryogenic mass; to this more advanced state of the enveloping layer the name **Chorion** is given. The hypoblast, enclosing the cavity of the primitive gut, or archenteron, remains of comparatively small size. The amniotic cavity, formed within the enclosed epiblast, is larger, and the cells

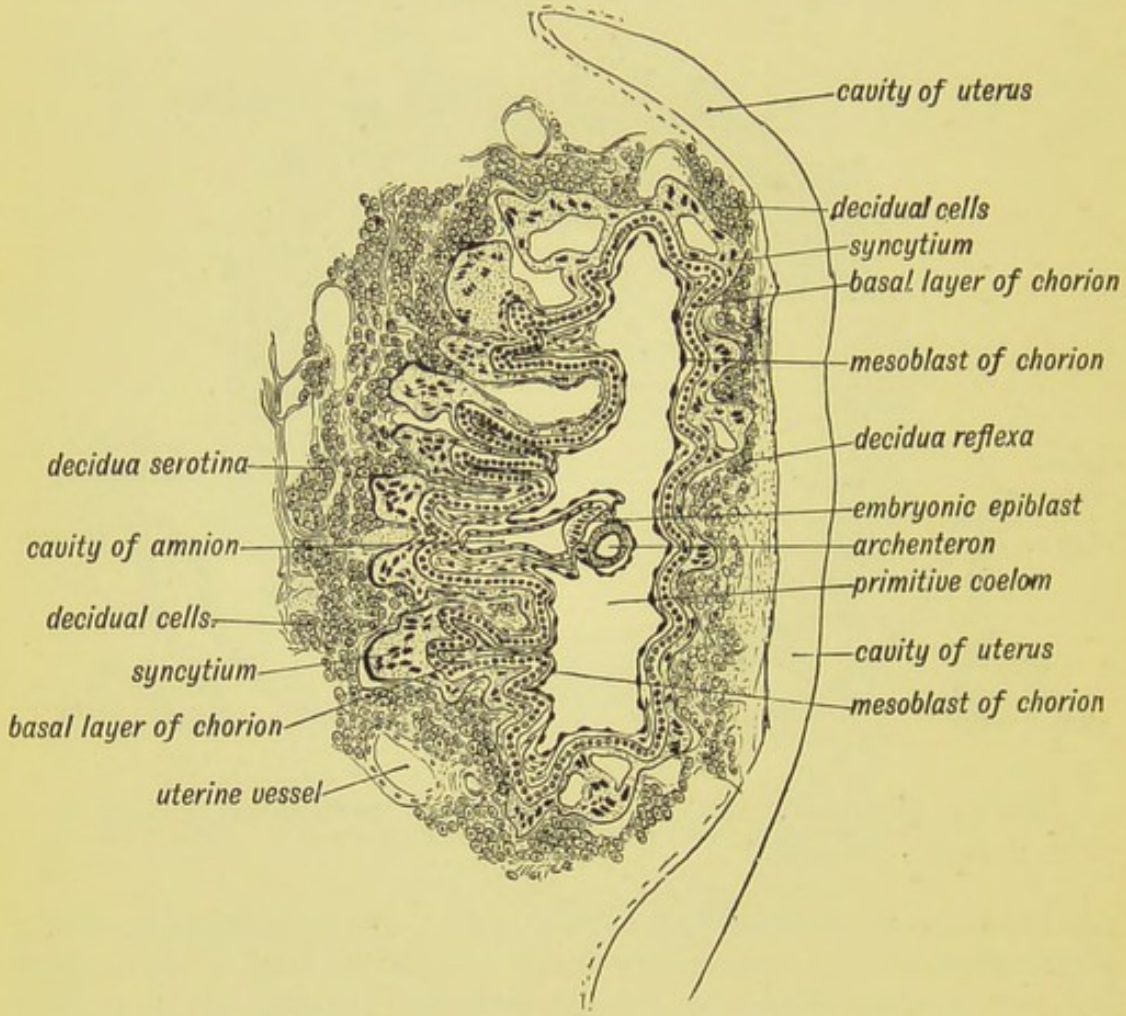


FIG. 17.—Stage IV. Section through the Ovum embedded in the wall of the Uterus. (Modified by F. W. Jones from figures given by Peters and Selenka.)

lining it have become differentiated into two kinds (Fig. 17). An area of columnar cells, forming the floor plate of the cavity, produces ultimately the epithelial covering of the body, and all the cells and fibres of the nervous system. The flatter cells which line the dome of the cavity will form the epithelial lining of the Amnion; the outer layer of mesoblast affords a covering to the amniotic epiblast (Fig. 17). Fluid collects within the cavity of the amnion; floating in the fluid, the human embryo develops. Thus the delicate embryonic tissues, being equally supported on all sides by the amniotic fluid, may pursue their developmental courses, unhindered by the influence of gravity, and uninjured by the pressure, to which the uterus within the abdomen

is subjected by the movements of respiration or bending of the trunk. If the fluid is deficient or absent then many forms of malformation may result.

It is in this stage (Stage IV.) that it becomes possible to detect the foundation or *Anlage* of the embryo. It is represented by the plate or lamina of tissues which separates the cavity of the archenteron from the cavity of the amnion (Fig. 17). The growth of the embryo remains in abeyance ; all the developmental energy is thrown into the upbuilding and expansion of the enveloping epiblast or **Trophoblast** as Hubrecht named it in 1889, for he recognized that its chief function was to provide the embryo with the means of nourishment (τροφός, a feeder). Thus in the earlier stages of development the actual embryo remains in abeyance, while the tissues which protect it and nourish it grow and develop with exceeding rapidity. Already, in Stage IV., it is seen that the epithelium forming the trophoblast has become differentiated into (*a*) a **Basal Layer** (Langhan's cells), (*b*) masses of cells, which have undergone multiplication without separation ; this formation is known as **Syncytium** (Fig. 17). The syncytium is chiefly developed on that aspect of the developing ovum which is directly in contact with the wall of the uterus. It is remarkable not only for the imperfect separation of its cells, due probably to the rapidity of its growth, but also for the extraordinary phagocytic power it exercises on the mucous membrane of the uterus. Processes of the synctium burrow within the thickened and vascular mucous membrane in a systematic and regulated manner ; they absorb the tissue with which they come in contact, and lay open blood vessels of the mucous membrane. The maternal blood escapes into spaces enclosed by the syncytial processes or into lacunae formed by the vacuolation of processes. In certain circumstances syncytial cells escape into the general circulation and form malignant growths. If the developing ovum be arrested in the Fallopian tube the synctium, owing to the extreme thinness of the lining membrane, quickly eats its way into and through the wall of the tube (H. R. Andrews).

Stage V.—The four stages just described are passed through in about 12 to 14 days ; in the beginning of the 3rd week a fifth stage is reached (Fig. 18). The embryonic plate is now more sharply differentiated ; it is composed of all three primary layers—epiblast, mesoblast and hypoblast, which at this stage is seen to lie in the floor of the cavity of the amnion (Fig. 18). The archenteron, with its covering of mesoblast, shows the beginning of a division into two parts —an intra-embryonic and an extra-embryonic part. The part outside the embryo forms the **yolk sac.** The part which will come to lie within the embryo shows a diverticulum forwards—into the head fold. It will form the **fore gut** from which the alimentary tract from the mouth to the second part of the duodenum is developed. A posterior diverticulum forms the cavity of the **allantois** and **hind gut.** There is a

communication between the cavity of the archenteron and that of the amnion (Fig. 18) which forms the blastopore or **neurenteric canal.** The trophoblast, now demarcated into basal layer and syncytium, with its mesoblastic lining, forms the **chorion.** Outgrowths which involve both the epiblastic and mesoblastic elements of the chorion spring out to form villi, which branch and rebranch. The villi become surrounded by the maternal blood within the syncytial spaces (Fig. 24, p. 23). The mesoblast which lines the chorion was derived, it will be remembered, from the inner cell mass, from which the embryo, amnion and

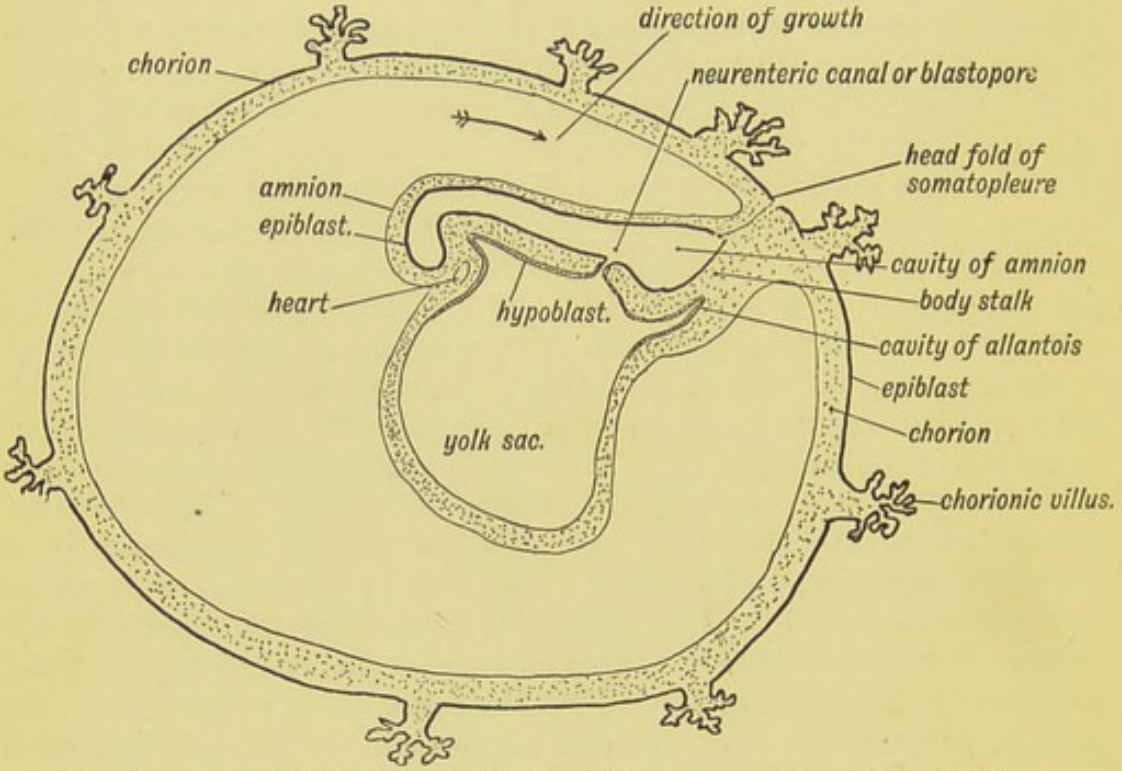


FIG. 18.—Stage V. Diagrammatic Section of the Human Ovum of the 15th day, showing its demarcation into embryo and membranes. (After Graf Spee.)

yolk sac were developed. The chorion is still bound to these three parts by a bond of tissue known as the **body stalk** (Fig. 18). Thus the ovum at this stage of development consists of (1) Embryo, (2) Yolk sac, (3) Amnion, (4) Body stalk, (5) Chorion.

Stage VI.[1]—By about the middle of the 3rd week, that is to say, about 16 or 18 days after the fertilization of the ovum, various parts of the embryo are becoming rapidly differentiated. The human embryo reconstructed from serial sections by Professor Thompson in 1907 shows the great advance made during the third week (Fig. 19). If transverse sections of embryos at the fifth and sixth stages be compared

[1] For description of embryos in the 3rd week of development, and for references to other descriptions see P. Thompson, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 159; F. Wood Jones, *Proc. Anat. Soc. Grt. Brit.* June, 1903; A. Low, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 237; W. E. Dandy, *Amer. Journ. Anat.* 1910, vol. 10, p. 85; Sussana P. Gage, *Amer. Journ. Anat.* 1904, vol. 4, p. 409.

(Fig. 20, *A*, *B*) it will be seen that the following changes have taken place: (1) A narrow plate of modified epiblast, stretching along what will be the median dorsal line of the body, becomes depressed, thus forming the floor of a groove; the lateral margins of the groove rise up, meet together and fuse along the middle line. Out of the **neural tube** thus enclosed are developed the spinal cord and brain. (2) In a somewhat similar manner a strip of cells along the median dorsal wall of the archenteron is separated as a tube to form the **notochord** (Fig. 20, *A*, *B*). Round the notochord are developed the spinal column and the greater part of the base of the skull. (3) Indications are to be seen

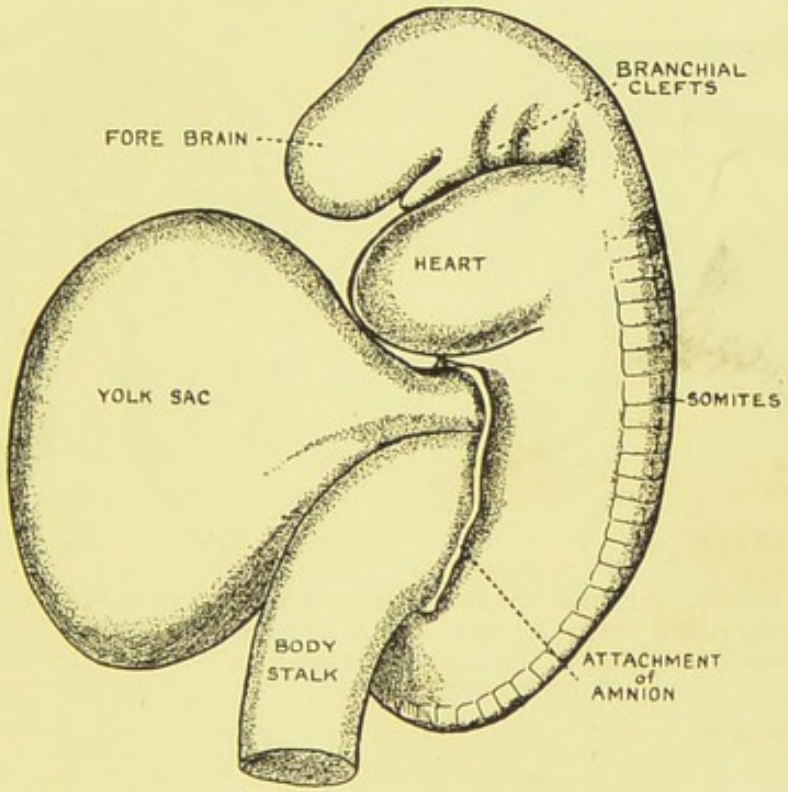


FIG. 19.—Human Embryo 2·5 mm. long, towards the end of the third week of development. (Professor Peter Thompson.)

of a separation of the archenteron into an intra-embryonic part, which will form the **alimentary tract,** and an extra-embryonic part, which becomes the **yolk sac.** (4) The mesoblast on each side of the embryo shows a division into four parts: (*a*) **paraxial mesoblast** (Fig. 20) from which the voluntary musculature, as well as other parts of the body system arise; (*b*) **intermediate cell mass** (Fig. 20, *B*, 5), in which the renal and genital organs are developed; (*c*) somatic mesoblast—this layer with the epiblast over it forms the **somatopleure,** the outer wall of the coelom; from the coelom are developed the pericardium, pleura and peritoneum; (*d*) the splanchnic mesoblast, which covers the intestine and yolk sac; the splanchnic mesoblast and hypoblast together form the **splanchnopleure.** (5) Indications can be seen of the division of the coelom into intra- and extra-embryonic parts (Fig. 20). When

the umbilicus contracts and closes, these two parts of the coelom are finally separated. It is also during the third week that the paraxial mesoblast becomes separated into primitive segments, or **somites**, formerly known as protovertebrae. In the embryo shown in Fig. 19 twenty-three somites are already separated.

Origin of Ova and Spermatozoa.—Towards the end of the stage just described, the **genital ridges** arise from the intermediate cell mass and project into the coelom, one at each side of the root of the mesentery (Fig. 21). The mesothelial cells which line the coelom assume a columnar form over the genital ridges; between these cells

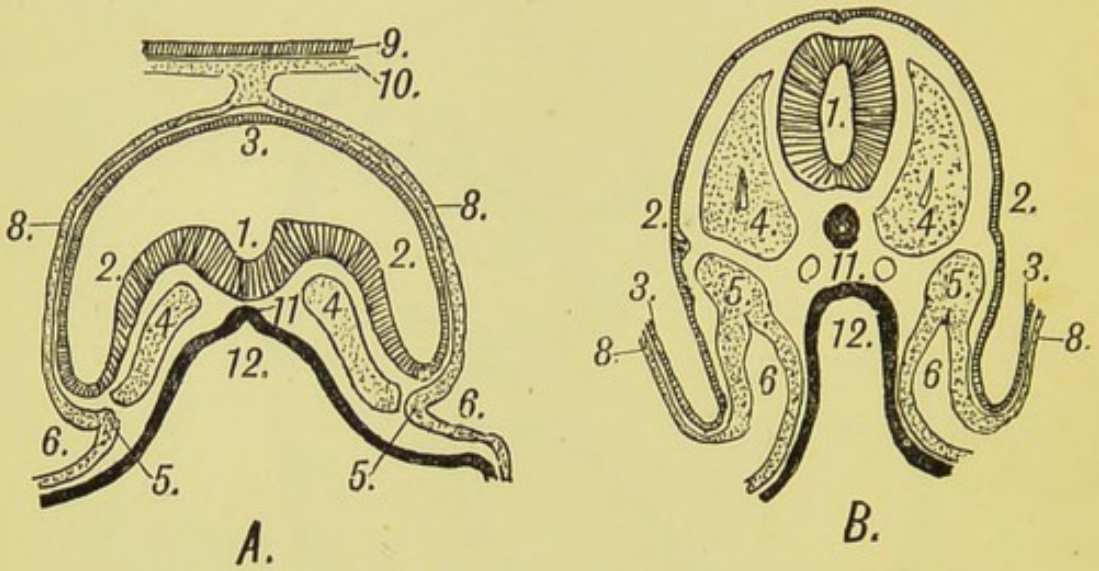


FIG. 20.—Schematic Transverse Sections of two Human Embryos.

A, About 12 days. (After Keibel.) *B*, About 15 days. (After Kollmann.)

The numbers are placed on corresponding points: Epiblast, shaded; hypoblast, black; mesoblast, stippled.

1. Neural groove and canal.
2. Epiblast of embryo.
3. Epiblast lining amnion. Only the attachment of the amnion is represented in *B*.
4. Paraxial mesoblast.
5. Intermediate cell mass.
6. Coelom, bounded by the somatopleure externally and splanchnopleure internally.
8. Mesoblast on amnion.
9, 10. Chorion.
11. Notochord.
12. Archenteron.

appear **primitive germinal cells** (primordial ova) characterized by their large size and reaction to certain stains. Hitherto it has been assumed that the germinal cells arose from the mesothelial columnar cells which cover the ridge. Beard, during a prolonged and accurate investigation of the development of fishes, especially of the skate, discovered that the germinal cells were not formed in the genital ridges but appeared at a very early stage corresponding to that described here as Stage I. When the coelom is formed they migrate towards the genital ridges. Those which fail to reach the suitable nidus, which the genital ridges afford, are absorbed, or, as Beard has suggested, they may give rise to these curious tumours known as teratomata. The manner in which the primitive germinal cells are carried within the genital ridge by tubular incursions of the mesothelium covering the ridge has been

already described, but we are ignorant of the circumstances which determine the production of spermatozoa and a testicle in one individual, and the formation of ova and an ovary in another.

Thus in the space of three weeks the fertilized ovum has given rise to (1) germinal cells which are endowed with the combined properties

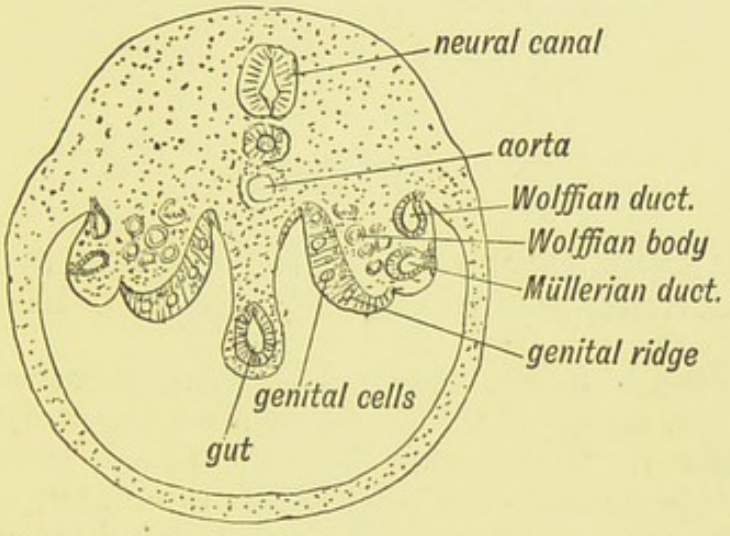


FIG. 21.—Diagrammatic Section of the Abdominal Region of the Coelom, showing the position of the Genital Ridges from which the Ovary or Testicle is formed.

of the ovum and spermatozoön from which they were produced; (2) an embryo in which these cells are nourished and protected; (3) membranes by which the embryo is protected and nourished during intra-uterine life. By the end of the fourth week (Fig. 2, p. 1) all these parts have progressed still further.

Having thus followed the chief developmental changes of the ovum, and seen how the embryo, the membranes and the reproductive cells are differentiated, we shall review in the next chapter the manner in which the ovum establishes itself in the cavity of the uterus and, for the space of nine months, passes a parasitic life there.

CHAPTER II.

THE MANNER IN WHICH A CONNECTION IS ESTABLISHED BETWEEN THE FOETUS AND UTERUS.

The Decidua.[1]—Every menstrual period, the mucous membrane which lines the cavity of the uterus becomes hypertrophied and its vessels congested. If the ovum be not fertilized, then the surface layer of the mucous membrane dies and is cast off, but if fertilization occur then the process of hypertrophy proceeds and the mucous membrane now receives the name of decidua. The formation of the decidua is characterized by (1) the origin of **decidual cells**—cells with a more or less rounded outline, large cell-body and relatively small nucleus—from the connective tissue cells which lie beneath the epithelial lining of the mucous membrane and between the tubular glands embedded in the mucous membrane (Fig. 17, p. 14); (2) the epithelial lining proliferates, the surface of the mucous membrane becoming rugose with pits and depressions; (3) the uterine glands become elongated; their mouths are closed by the growth of the decidual cells; their fundi, abutting against the muscular coat, undergo no change; the elongated bodies of the tubes, between their mouths and fundi form cavernous spaces; (4) the vessels of the uterus increase in size and the capillaries of its mucous membrane are dilated. In this manner the uterus is prepared to receive the fertilized ovum. It is highly probable that these changes are influenced by an ovarian secretion, for, when the ovaries are removed, these changes soon cease to occur.

Implantation of the Ovum.[1]—When the fertilized ovum reaches the cavity of the uterus it has already attained the blastocyst form (Fig. 16, p. 13). The inner cell mass, from which the embryo will arise, projects within the cavity and is protected by the enveloping layer or trophoblast of the blastocyst, the whole ovum measuring about 3-4 mm. in diameter. Implantation occurs in one of the pits of the mucous membrane usually on the posterior wall of the cavity near the fundus of the uterus, but it may occur anywhere, that form being especially dangerous in which implantation occurs in the neighbour-

[1] See references, p. 13.

hood of the internal mouth of the uterus. The area of the trophoblast in contact with the uterine pit divides rapidly and throws off proliferating masses of **syncytium** (Fig. 17, p. 14) which burrow into the decidua, thus embedding and anchoring the ovum and by the absorption of the decidual tissue, providing nourishment for it. The blastocyst is peculiar in man and the anthropoids in that it becomes completely buried in the decidua. The parts of the decidua are thus distinguished : (1) the **decidua serotina** or **basalis**, the part to which the ovum became

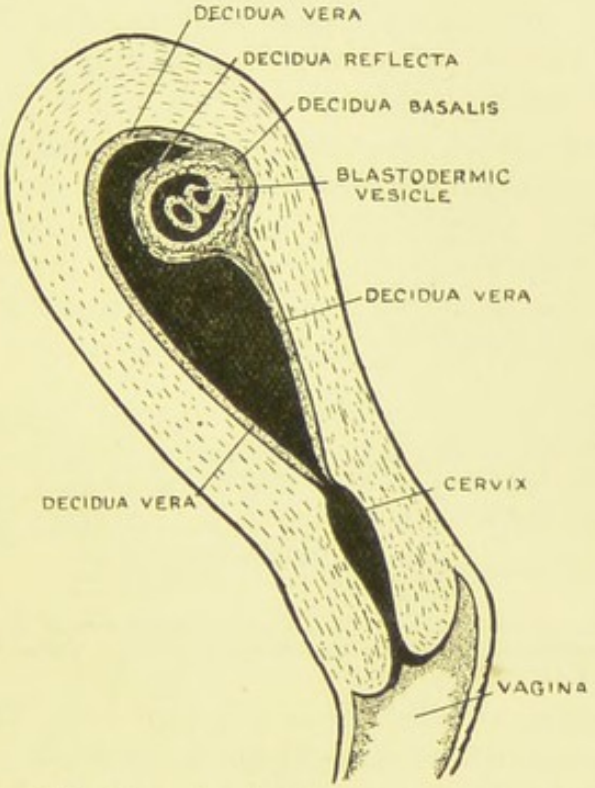


FIG. 22.—Section of the Uterus showing in a diagrammatic manner the Imbedded Ovum and the differentiation of the Decidua into Three Parts.

attached and into which the processes of syncytium grow (Figs. 17 and 22) ; (2) the **decidua capsularis** or **reflexa**, the part which covers the ovum and is stretched as the ovum grows ; (3) the **decidua vera**, which lines the rest of the uterus. The decidua vera ends at the internal os, the canal of the cervix producing no true decidual layer. With the growth of the embryo the decidua reflexa is brought in contact with the decidua vera. By the fifth month they have fused together, become flattened and partially atrophied. The decidua serotina, on the other hand, forms the basis in which the placenta is developed.

Nourishment of the Early Ovum.[1]—The ova of birds and reptiles are laden with yolk and on this the developing embryo lives—the yolk being absorbed by the hypoblastic cells lining the archenteron. Primitive forms of mammals, such as the Duckbill and Echidna, have also

[1] E. Emrys Roberts, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 192 (Embedding of Ovum and Nutrition—Guinea-pig) ; Emrys Roberts, *Proc. Roy. Soc.* May 21, 1908.

large supplies of yolk in their ova, but in all other mammals the ova contain only a small supply of yolk; hence the developing ovum has to draw its nourishment from the uterus. The secretion of the uterine glands contains a proteid (Emrys Roberts) which probably affords nourishment to the ovum. The decidual cells contain vacuoles of fat and glycogen (J. W. Jenkinson) and these cells and their contents are absorbed by the trophoblast and passed on to the growing tissue. At an early date the villi of the chorion grow into the trophoblast, and blood vessels are soon formed in them for the absorption of nourishment. The archenteron also enlarges, part of it forming the yolk sac. In the more primitive forms of mammals, as is also the case in birds and reptiles, the yolk sac takes an active part in nourishing the embryo.

The Yolk Sac.—Soon after the ovum is implanted and during the third and fourth weeks of development the yolk sac undergoes a very rapid increase (Fig. 18, p. 16). At the end of that period, when its growth becomes very slow or completely ceases, the yolk sac measures about 7 or 8 mm. in diameter; it has grown faster and is then larger than the embryo. The hypoblastic cells which line it appear to be

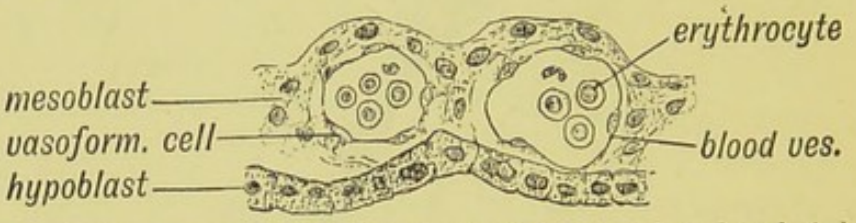


FIG. 23.—Section across the Yolk Sac, showing blood vessels and nucleated red blood corpuscles forming in its mesoblastic layer. (After Selenka.)

the seat of an active metabolism at this time (Fig. 23), they probably absorb and store nourishment from the uterine fluids which reach them through the enveloping layer of the blastocyst. In the mesoblast, which covers the yolk sac, a vascular network is formed (Fig. 23). The first circulation to appear is that which arises about the end of the second week in the yolk sac, the vitelline veins conveying the blood to the tubular heart while the aortae return it to the yolk sac. The yolk sac circulation is for the nourishment of the embryonic tissues and possibly it is also respiratory in its nature. By the end of the first month a constriction has occurred between the primitive gut and yolk sac (Fig. 20, *B*); the narrowed part becomes elongated and forms the **vitello-intestinal canal** (Fig. 19, p. 17). When the umbilical cord is fashioned, the canal is enclosed within it (see Fig. 2); later it becomes closed and disappears.

The Chorion.[1]—The origin of the chorion from a combination of two elements—the trophoblast (enveloping layer of epiblast) and an

[1] For details and literature see A. C. F. Eternod, *L'œuf humain*, Geneva, 1909; A. Eternod, *Compt. Rend. Congrès internat. d'Anat.* 1905, p. 197; *Compt. Rend. Assoc. des Anatomistes*, 1909, p. 1; A. W. Hubrecht, *Anat. Anz.* 1905, vol. 31, No 13 (Nature of trophoblast).

extension from the somatic mesoblast has been already traced (p. 14). The division of the trophoblast into a basal layer and syncytium was also mentioned. As soon as the ovum is embedded in the decidua, processes of syncytium invade not only the serotinal but also the reflected or capsular part (Fig. 17, p. 14). Villi, containing a core of mesoblast and a covering of the basal layer of chorionic epithelium, grow out into the syncytial masses (Fig. 24). The villi continue to divide and redivide thus becoming arborescent. About the end of the second week an extension from the circulation of the yolk sac spreads into the body stalk (Fig. 282, p. 293) and rapidly extends from the body

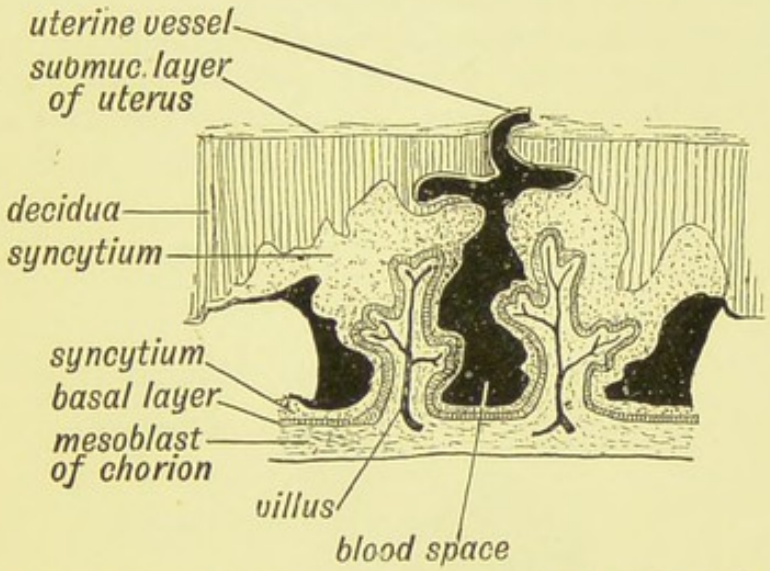


FIG. 24.—Diagrammatic Section of the Decidua Serotina (formed from the mucous membrane of uterus) and Chorion, to show the manner in which the placental blood spaces are formed.

stalk into the mesoblast of the chorion and of the villi. Direct prolongations of the two dorsal aortae now extend through the body stalk to the chorion—these extensions forming the umbilical arteries (Young and Robinson). The umbilical veins carry the blood from the chorion through the body stalk to the embryonic heart. The chorionic circulation replaces functionally that of the yolk sac. Through the chorionic circulation the embryo is nourished.

Formation of Placental Blood Spaces.—The decidual nutriment only affords a temporary supply. In the last few years the researches of a number of German investigators, but especially of Peters and Selenka, have shown that the maternal circulation is placed at the disposal of the choroidal villi in a simple manner. The syncytium, as it burrows into and replaces the serotinal part of the decidua (Figs. 22, 24), invades the blood vessels, and replaces their walls by its own tissue. The masses of syncytium between the main villi break down and thus form large spaces into which the decidual vessels, which were enclosed by the syncytium, freely open (Fig. 24). Through these spaces the maternal blood circulates, supplied by the uterine arteries

and carried away by the uterine veins. The trophoblast contains a ferment which prevents coagulation of the blood in the intervillous spaces thus formed (Young). The extension of the syncytium, the formation of villi and of blood spaces, go on until the 5th month. By that time the basal and syncytial layers of epithelium on the villi are replaced by a single flattened layer of cells. The vascular villi of the chorion hang within the blood spaces, and draw from the maternal blood oxygen and nutriment for the supply of the embryo. Processes and partitions derived from the syncytium remain to bind the chorion to the uterine wall.

The Allantois.—In the human embryo, as is the case in all Primate embryos, the allantois assumes a peculiar form, appearing as a diverticulum within the body stalk from that part of the archenteron which afterwards forms the posterior part of the alimentary canal and bladder (Fig. 18, p. 16). Its typical form may be studied in the developing

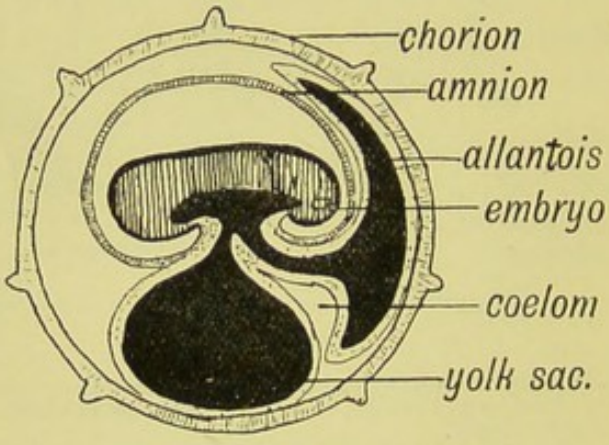


FIG. 25.—The primitive form of the Allantois. (After Turner.)

egg of the chick. It is a diverticulum from that part of the archenteron which afterwards forms the urinary bladder, the diverticulum being lined by hypoblast and covered by mesoblast (Fig. 25). Growing out into the cavity of the coelom, and carrying on it an extension of the vascular supply of the yolk sac, its expanded free extremity comes against the mesoblastic lining of the chorion (Fig. 25). The mesoblast of the allantois and chorion fuse and through the fusion the chorion of the chick becomes vascularized, and acts as a respiratory organ. In the unhatched chick the allantois acts as a reservoir for the secretion of the kidneys, and this is probably its primary function. Its respiratory function appears to be a secondary one. In the human embryo it is no longer required as a reservoir, for the excretory products of the embryo can be absorbed by the maternal circulation. Hence the smallness of the cavity of the human allantois. While its cavity remains so slightly developed in the human embryo, its mesoblastic element persists and takes an active part in establishing a circulation between the embryo and the chorion. Owing to the precocious develop-

ment of the enveloping layer or trophoblast of the human embryo, the mesoblast of the chorion and of the allantois are never separated, but remain in continuity through the body stalk (Fig. 18). The extension of the yolk-sac circulation to the chorion in the human embryo represents the outgrowth of the allantois seen in the chick. In fishes and amphibians neither chorion, amnion nor allantois are formed in the development of the embryo; in reptiles, birds and mammals all three structures are formed. The transformation of the embryonic bladder to form an allantois evidently occurred when water-living forms of vertebrates were being modified to live on land. The ovum then underwent a change, becoming large, yolk-laden, and enclosed within a special covering, within which the embryo was developed and matured.

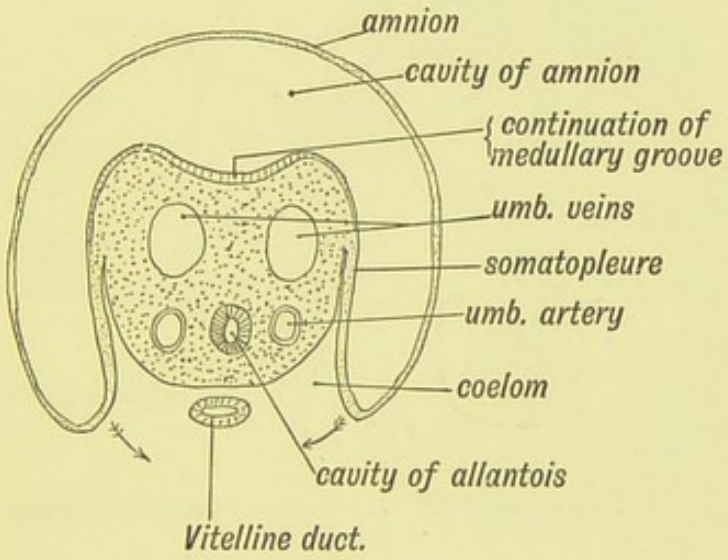


FIG. 26.—Section across the Body Stalk. (His.)

Formation of the Umbilical Cord.—At the end of the second week of development (see Fig. 18, p. 16), when the embryo forms a cap on the yolk sac and a plate in the floor of the amniotic cavity, neither umbilicus nor umbilical cord are differentiated. The **body stalk**, formed out of the posterior or caudal end of the embryo, then serves the purpose of the cord. A section across the body stalk (Fig. 26) shows that two umbilical arteries, two umbilical veins, and the canal of the allantois lie in its mesoblastic basis, and while its upper epiblastic surface projects, like the rest of the embryo, within the cavity of the amnion, its lower surface lies in the wall of the extra-embryonic coelom, in contact with the yolk sac (Fig. 18).

To understand the origin of the umbilical cord one must observe closely the attachment of the amnion at this early stage. It is attached to the circumference of the embryo and body stalk (Figs. 19 and 20); to the zone of somatopleure which unites the embryo and the amnion, the name of **junctional ring** may be given, with the clear understanding that the body stalk enters into the formation of the posterior part of

the ring. From the junctional ring the umbilical cord is developed. While the embryo grows rapidly and expands within the amnion the junctional ring retains its embryonic size (see Fig. 2). The parts of the yolk sac and coelom which are surrounded by the ring now appear to be constricted (Fig. 20). In the second month the junctional ring begins to elongate and form a cord-like structure, in which an umbilical and a placental extremity can be recognized. The amnion is attached

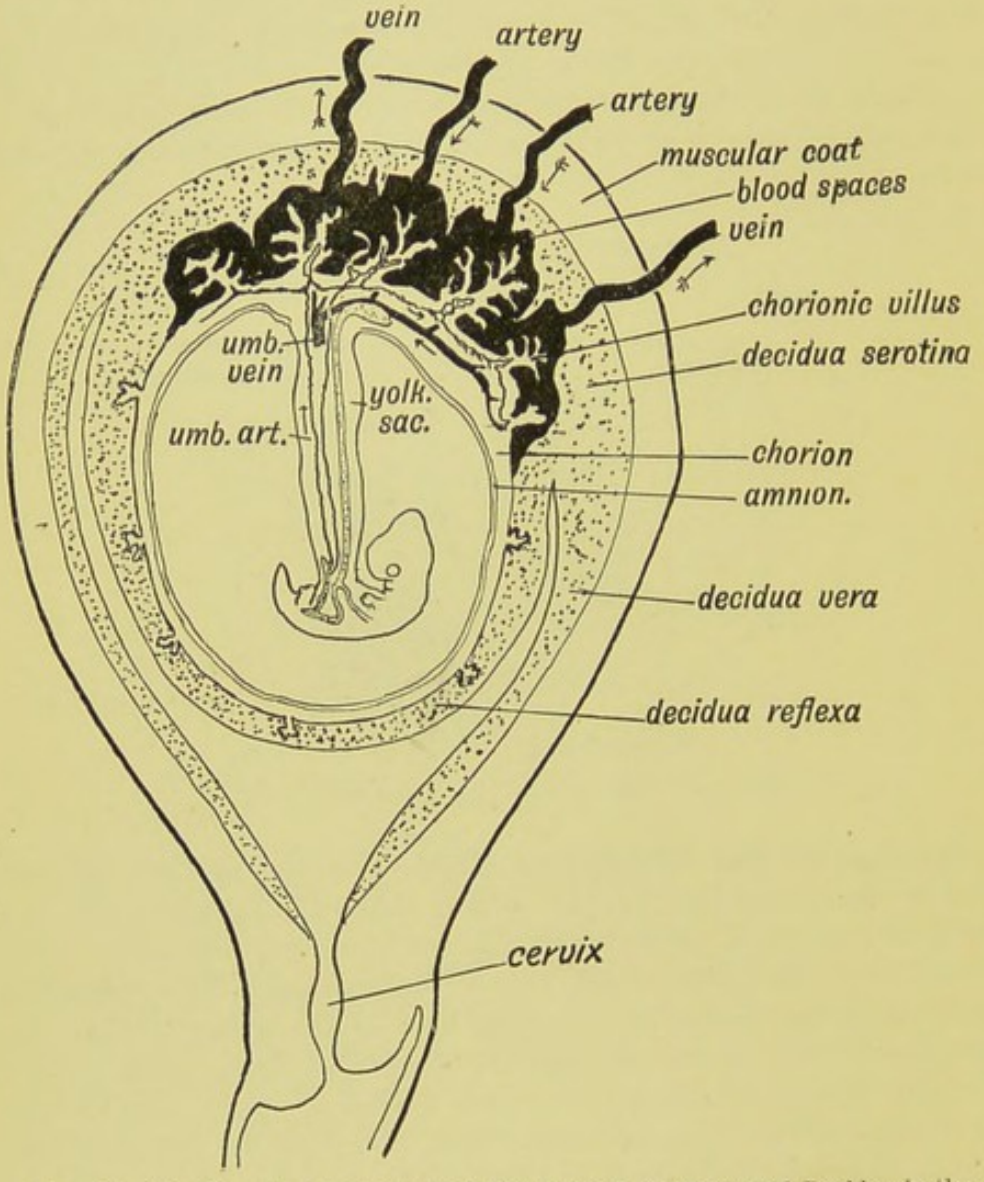


FIG. 27.—Showing the arrangement of the Amnion, Chorion, and Decidua in the 3rd month and the Formation of the Placenta.

at its placental extremity (Fig. 27). The mesoblast of the junctional ring forms the jelly-like tissue (Wharton's jelly) of the umbilical cord in which are embedded the umbilical arteries and one umbilical vein, formed by the fusion of the right and left vein. By the third month the cord measures 12 cm.; and 40 cm. by the ninth month. The elongation of the junctional ring to form the cord necessarily affects

all those structures which lie within the ring—the neck of the yolk sac (vitello-intestinal duct), the coelomic space, the cavity of the allantois. All of these are included within the cord, and are obliterated during its elongation. The coelomic or peritoneal space at the umbilical end of the cord closes at the beginning of the third month, but it may remain open and form the seat of a **congenital umbilical hernia.** As an exceptional occurrence, the intra-embryonic parts of the allantois or of the vitello-intestinal canal may remain patent as far as the umbilicus, and with the removal of the cord at birth give rise to a **urinary** or a **faecal fistula.**

Formation of the Placenta.—The condition of the membranes in the 3rd month (Fig. 27) differs from that of the 1st month (Fig. 18) by the formation of the placenta. In the first month the chorion is

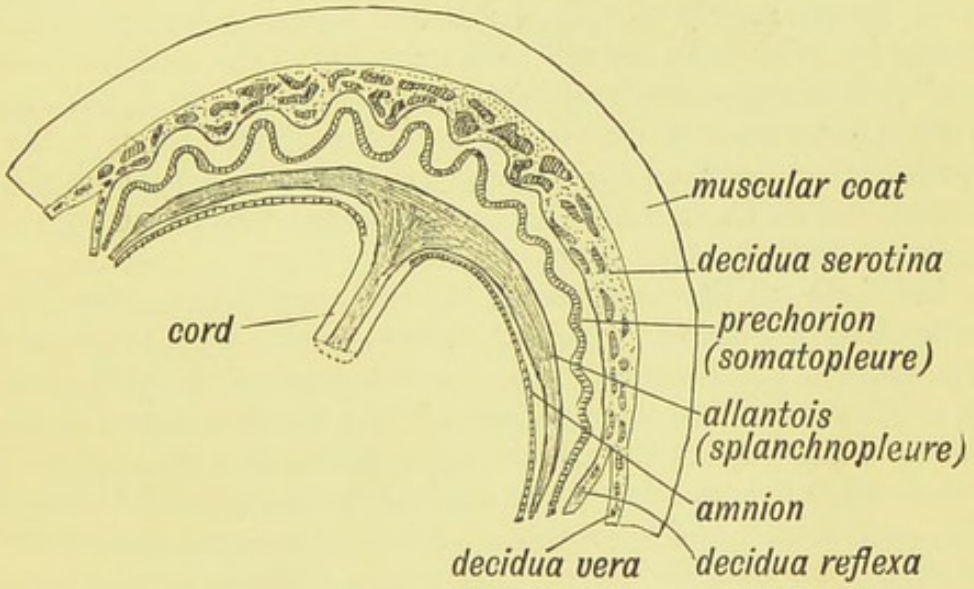


FIG. 28.—Diagrammatic Section to show the Elements which enter into the formation of the Placenta. The trophoblast on the outer side of the prechorion has been omitted for the sake of simplicity.

uniformly covered by shaggy villi, this being the permanent condition in low primates (Lemurs). In man the chorionic villi which project within the decidua serotina hypertrophy, while those within the decidua reflexa atrophy, and in this way the discoidal placenta of man is formed (Fig. 27). In lower primates (Monkeys) there are two discs (bi-discoidal), and this form occasionally occurs in man.

The elements entering into the formation of the placenta are diagrammatically shown in Fig. 28. They are :

1st. The decidua serotina, formed from the mucous membrane of the uterus. It is almost completely replaced by the syncytium and choroidal villi.

2nd. The chorion, or, strictly, prechorion.

3rd. An allantoic element which is fused with the mesoblast of the chorion in the human ovum.

4th. The amnion, which becomes applied to the inner surface of the chorion, thus obliterating the extra-embryonic coelom (Figs. 27, 28). Thus it will be seen that almost the entire placenta is produced from the ovum and is truly a part of the foetal structures. The decidua, the only maternal element, merely affords a nidus or suitable bed for the development of the foetal structures.

From the inner surface of the fully-formed placenta, the amnion, a thin transparent membrane, is easily stripped off. Its outer or uterine side is rough, shaggy, being mainly composed of the greatly hypertrophied villi developed from the serotinal or attached area of the chorion. The villi are grouped in clumps or cotyledons, between which are fibrous strands and partitions, which pass through the whole thickness of the placenta and thus maintain its fixation to the uterus. The manner in which the trophoblast covering the villi becomes changed until it forms merely a thin epithelial covering has been already described (p. 24). Into the villi pass branches of the umbilical arteries, ultimately forming a fine capillary network, from which the arterialized blood is returned to the foetus by the umbilical veins. The villi project within great blood spaces formed in the decidua serotina (Fig. 27). The ovarian and uterine arteries end in these blood sinuses, and the ovarian and uterine veins begin in them.

At full term all the membranes of embryonic origin come away in the after-birth ; also the decidua, except a thin, deep layer next the uterine muscle, which contains the deepest parts of the uterine glands. From this layer the mucous membrane of the uterus is regenerated.

The establishment of the developing ovum within the uterus of the mother constitutes one of the most marvellous chapters of Embryology. It is apparent that in the evolution of the higher mammals the young have become modified to pass the first stage of life as uterine parasites. In this chapter we have seen that the ovum has already reached a considerable degree of development when it enters the uterus from the Fallopian tube. All the earlier steps in development are directed towards the formation of the structures necessary for the protection of the embryo—the chorion, amnion, yolk sac, allantois and placenta. In the following chapter we propose to enquire into the origin of these and other obscure embryonic structures.

CHAPTER III.

THE ORIGIN AND NATURE OF CERTAIN EMBRYONIC STRUCTURES, AND THE GROWTH OF THE EMBRYO AND FOETUS.

Law of Recapitulation.—The pioneers of Embryology began in the hope of discovering the stages in the evolution of the human body by an accurate study of its development. It was expected that the ovum, as it became transformed into the embryo, and the embryo as it changed into the foetus, would recapitulate man's evolutionary history. From what has been related in the two previous chapters it is plain that we see no resemblance between the successive stages of the human embryo and the succession of types which compose the scale of the Animal Kingdom. Those who expected the law of recapitulation to hold true in all its details forgot that the human embryo is radically modified in order that the first nine months of development may be spent parasitically in the womb of the mother. The storage of yolk in the ovum, the precocious development of trophoblast, chorion, amnion and allantois, have transformed the orderly manifestation of evolutionary stages. Yet to a certain degree the law remains true; the human body begins as a single cell, similar in constitution to the simplest form of animal life—a protozoon; it becomes a globular cluster of cells in its morula stage, similar to the simple forms of multicellular organisms. Further, there are numerous features seen during the development of the embryo which can only be explained by supposing that the human body, in the course of its evolution, has passed through those stages which we see represented in simpler Invertebrate forms—such as the Hydra and the worm. The first of these obscure embryonic manifestations is the primitive streak and groove.

The Primitive Streak and Groove.—In the second week, before the medullary groove has been folded in to form the neural tube, a linear furrow is seen to commence between the hinder ends of the medullary folds and run backwards in the median dorsal line to terminate on the body stalk (Figs. 29, 30). At its anterior end the neurenteric canal opens, thus establishing a communication between the archenteron

and dorsal surface of the embryo (Fig. 18, p. 16). When the medullary folds unite, the anterior end of the groove is included in the neural tube (Fig. 29). Since the body stalk, on which the groove ends behind, is included in the formation of the umbilical cord, it is plain that the posterior parts of the body, which lie on each side of the median line, from the lumbar region on the dorsal aspect to the umbilicus in the ventral,

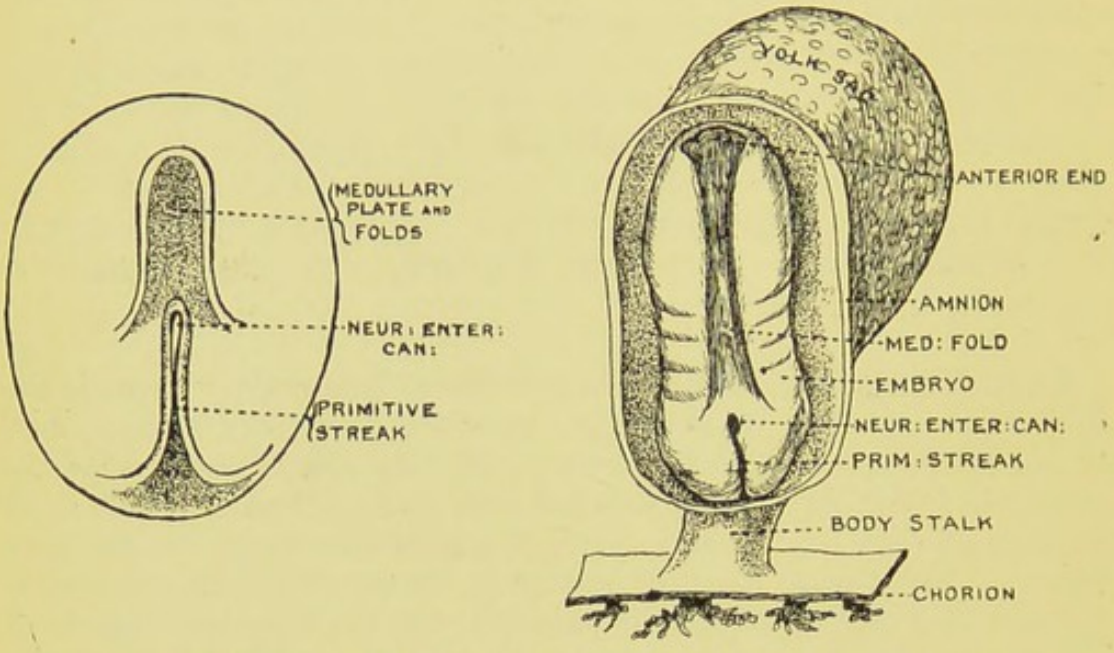


FIG. 29.—Diagram of the Embryogenic area of a Bilaminar Blastocyst viewed from above.

FIG. 30.—The Medullary Plate and Primitive Streak on an Embryo of the 3rd week. (After Graf Spee.)

must arise from the margins of the primitive groove.[1] The openings of the rectum and uro-genital passage are formed in the line of the groove.

The primitive streak probably represents the fused margins of a **primitive mouth** or **blastopore.** In an early stage of segmentation,

[1] For some of the recent literature dealing with the significance of the primitive streak and of gastrulation see:

R. Assheton, *Guy's Hosp. Reports*, 1907, vol. 61, p. 345 (Teleostean Development).
,, *Guy's Hosp. Reports*, 1908, vol. 62, p. 209 (Homology of Germinal Layers).
,, *Archiv. fur Entwicklungsmechanik*, 1910, vol. 29, p. 46 (Gastrulation).
,, *Quart. Journ. Mic. Sc.* 1910, vol. 54, p. 221 (Trophoblast); p. 631 (Gastrulation).
,, *Proc. Roy. Soc.* 1905, Ser. B, vol. 76, p. 393 (Ungulate Placenta).
,, *Anat. Anz.* 1905, vol. 27, p. 125 (Growth Centres).
J. T. Wilson and J. P. Hill, *Proc. Roy. Soc.* 1903, vol. 71, p. 314 (Gastrulation).
J. T. Wilson and J. P. Hill, *Phil. Trans.* 1907, Ser. B, vol. 199, p. 31 (Development of Ornithorynchus).
A. C. F. Eternod, *Bull. Soc. Vaud. Sc. Nat.* 1906, vol. 42, p. 197.
J. W. Jenkinson, *Proc. Manchester Phil. Soc.* Jan. 12th, 1906 (Lamination of Embryo).
G. Schlater, *Anat. Anz.* 1907, vol. 31, p. 312 (Origin of Mesoblast).

the ovum of Amphioxus forms a hollow sphere (Fig. 31, *A*) ; one part of the sphere becomes invaginated to form the hypoblast or entoderm, the uninvaginated or outer layer becoming the epiblast or ectoderm. The brim of the bilaminar flask (gastrula or cup) thus formed serves as a mouth or blastopore to the cavity of the hypoblast (archenteron) (Fig. 31, *B*). The primitive streak and groove seen in the embryos of all vertebrates are believed to arise from a linear fusion of the lips of the blastopore. The neurenteric canal is a part of the blastopore which retains its patency for a few days only in the human embryo. The process of invagination or gastrulation, which is seen to occur in

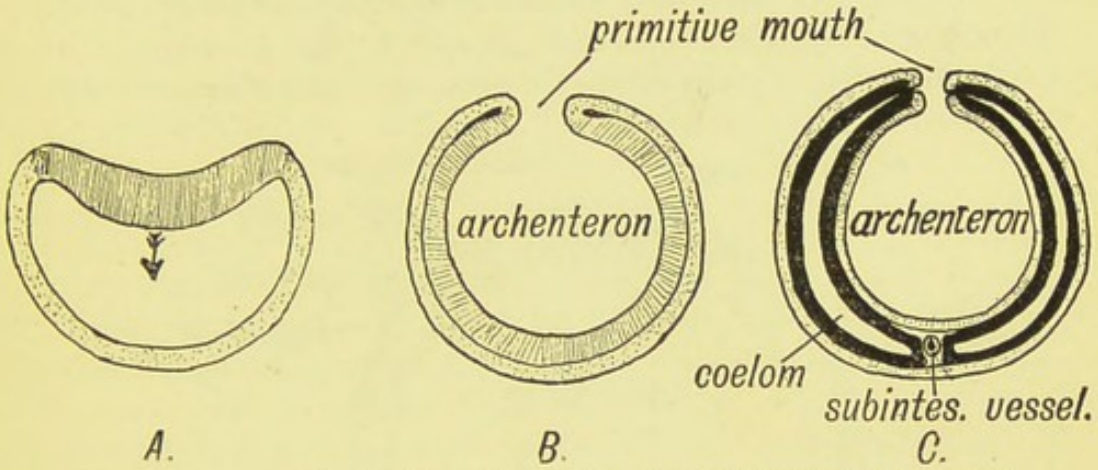


FIG. 31.—Diagram showing three stages in the early development of Amphioxus.
A. Invagination of the hypoblast (shaded) within the epiblast (stippled).
B. Formation of archenteron and primitive mouth (blastopore).
C. Origin of mesoblast (black) and coelom from margin of primitive mouth, with formation of a ventral mesentery round the subintestinal vein. (After Robinson.)

the development of amphioxus—by far the most primitive of vertebrate forms—has become masked and obscured in the embryos of higher vertebrates. The process has been profoundly modified by the accumulation of yolk in the ovum and the precocious development of the embryonic membranes. The bilaminar blastoderm of the human embryo may be regarded as the modified gastrula stage of amphioxus and the primitive streak as a modified blastopore. We shall see that some of the primary processes of development are initiated at the margins of the primitive streak.

Origin of the Mesoblast and Coelom.—In the developing ova of higher vertebrates the mesoblast is known to originate at each side of the primitive streak, but it is difficult to follow the exact manner of its development. In amphioxus it arises as a bilateral series of diverticula from the margin of the gastrular mouth or blastopore, along the line at which the epiblast and hypoblast are continuous (Fig. 31, *C*). The diverticula expand and their cavities fuse together between the two primary layers to form the coelom ; the right and left series of diverticula meet below the archenteron and form a ventral median mesentery (Fig. 31, *C*). In higher vertebrate ova, the epiblast and

hypoblast are fused together along the primitive groove just as round the primitive mouth of a Hydra. The mesoblast arises from the line of union (Fig. 32), and spreads outwards between the two primary layers. The coelom is formed, not as a diverticular cavity, but by a cleavage of the mesoblast, into outer and inner layers. In the human embryo the mesoblast is formed at an extremely early stage; at the beginning of the third week it is already present, a trilaminar stage being thus formed (Fig. 16, p. 13). The primitive streak is thus the chief, if not the only, centre at which mesoblast is produced, but the opinion is also widely held that mesoblast may arise from the two primary layers at other points as well as along the primitive streak.

Notochord.—In its origin the notochord, the forerunner of the spinal column, is closely related to the primitive streak. At the

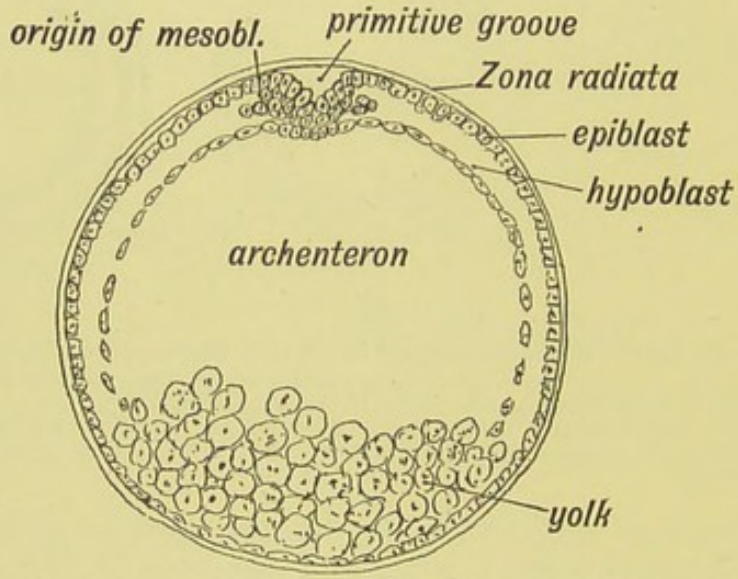


FIG. 32.—A Diagrammatic Section of a Bilaminar Blastoderm made across the primitive streak.

anterior extremity of the streak the tissues of the embryo—epiblast, hypoblast and mesoblast, are produced at an extremely rapid rate in the earlier part of the 3rd week. The rapid growth at the anterior end of the representative of the blastopore leads to the primitive streak being pushed more and more towards the caudal extremity of the embryonic plate. Amongst the structures produced at the end of the primitive streak, where the epiblast turns into to join the hypoblast is a plate of cells which come to lie along the median line on the roof of the archenteron or primitive gut-cavity. Presently the plate becomes folded off from the roof of the archenteron (Fig. 33) to form a rod of peculiar cells—the notochord. The posterior part of the notochord never forms part of the gut-cavity, but is developed in the lateral margins of the primitive streak. It will be thus seen that the first representation of a skeleton is produced at an extremely early date, and that it appears at the anterior end of the primitive streak.

Its continuity with the primitive gut seems accidental, for it is hard to believe that a mesoblastic skeletal structure such as the notochord could have been evolved from the alimentary system.

The Medullary Plate.—We have already seen that the primitive streak lies within the posterior folds of the medullary plate—the first indication of a central nervous system (Fig. 30). It will be evident that the growth at the anterior end of the streak also adds to the length of the medullary plate; indeed, the greater part of the plate is thus produced. A study of the mammalian embryo suggests that the great central nervous system of man has been evolved from a simple epidermal plaque of nerve cells originally situated on the anterior or cephalic side of the blastopore, and that the plaque has been extended until it formed the great medullary plate, an underlying, supporting rod of cells—the notochord—being produced at the same time.

Nature of the Yolk Sac.[1]—It is plain, when one examines a human embryo of the third week (Fig. 19, p. 17) that at no stage of evolution could there have been a human ancestor furnished with a correspondingly large extra-abdominal yolk sac. It has been produced from the alimentary canal to suit the needs of the embryo. To understand its origin one must remember that the amount of yolk stored in an ovum exercises a marked influence on the early developmental processes. The yolk is taken up by cells of the hypoblast, and, if in great amount, the invagination of the hypoblast, so plainly seen in amphioxus, will be hindered or absent in ova—such as those of reptiles and birds—in which the yolk is abundant. In the ova of fishes and amphibians, which can draw nourishment from the water in which they develop, the yolk is relatively small in quantity; in reptiles and birds, developed within shells, the yolk must be in large amount to provide means of nourishment. The yolk sac is to be regarded as a part of the alimentary canal which undergoes an altogether precocious and temporary development to supply the developing embryo with the means of growth. The human ovum contains practically no yolk, but the yolk sac develops and absorbs nourishment from the maternal fluids.

The Amnion and Chorion.—It is difficult to account for the origin of the amnion and chorion, but it is clear that no adult form of animal could exist enwrapped in membranes, and we must infer that they arose, like the yolk sac, as precocious and special developments of certain parts of the body. When the formation of the chorion and amnion is studied in animals in which the processes of development have been less modified than in man, it becomes quite apparent that these two structures arose as developments from the body wall. The part of the body wall set aside for their formation was the part which

[1] For literature see: J. Norberg, *Anat. Hefte.*, 1912, vol. 45, p. 611 (Yolk sac).

contains or surrounds the yolk sac (Fig. 33). Thus the embryo and foetus lie enclosed with a double fold of their own body walls.

The amnion, which contains a fluid in which the embryo floats, occurs only in those vertebrates which are not developed in an aqueous medium. The developing ova of amphibians and fishes are equally supported by the water in which they grow; with the evolution of air-breathing vertebrates, a fluid medium was retained by the formation of the amnion. A great development of the yolk sac evidently caused a similar enlargement of the embryonic body wall (somatopleure) (Fig. 33). In the amphibia the skin serves a double purpose—it is

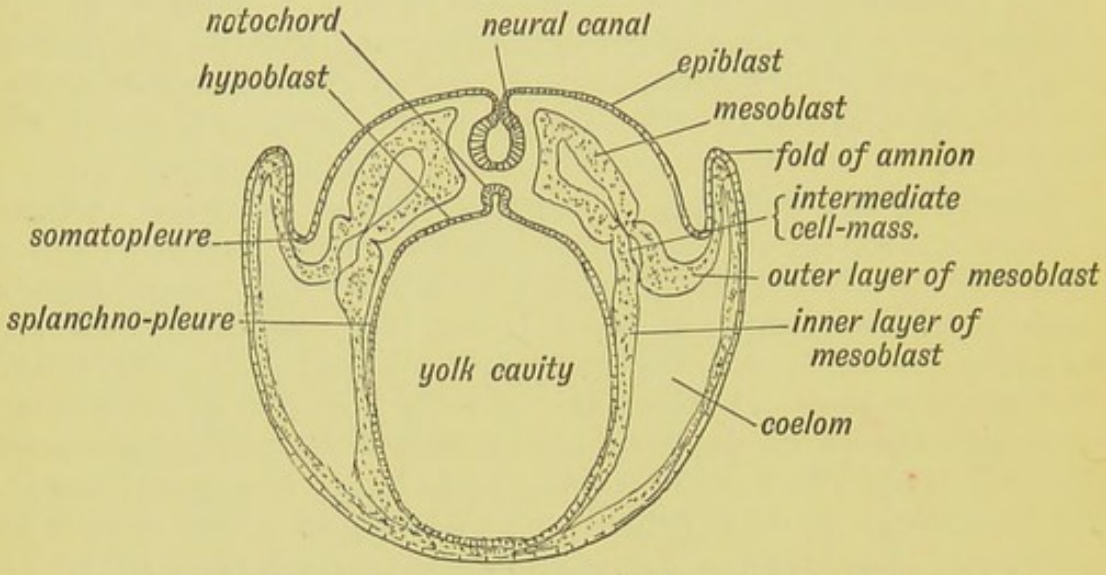


FIG. 33.—Diagrammatic Section of a Developing Ovum showing (1) the origin of the neural canal, (2) the origin of the notochord, (3) the ingrowth of the mesoblast, and (4) the formation of the coelom.

respiratory as well as protective in function. The body wall of the chick embryo serves a similar purpose. As the embryo sinks within the yolk sac, a fold of somatopleure rises up and covers it in (see Figs. 33 and 34). The inner layer of the folds forms the amnion, the rest the chorion, or to be more accurate, the prechorion (Figs. 34 and 35). In man and in all primates the process, although the same, is modified by the fact that the formation of the chorionic part of the somatopleure has been still further accelerated. This part is developed in them before every other structure, enveloping the inner mass of cells which gives rise to the amnion, yolk sac, and embryo (Figs. 16, 17). Further, the epithelium is modified to form the trophoblast, the cells of which have many points in common with cancer cells. There can be no doubt that the mammalian ovum was evolved from one which was laden with yolk and developed outside the maternal body. Intra-uterine gestation required and obtained a much earlier development of the chorion.

Origin of the Allantois.—The allantois was developed concurrently with the amnion and chorion. No allantois is present in

amphibian or fish embryos, yet it was certainly from such forms that allantois-bearing embryos were produced. The allantois represents an outgrowth of the embryonic bladder which is derived from part of

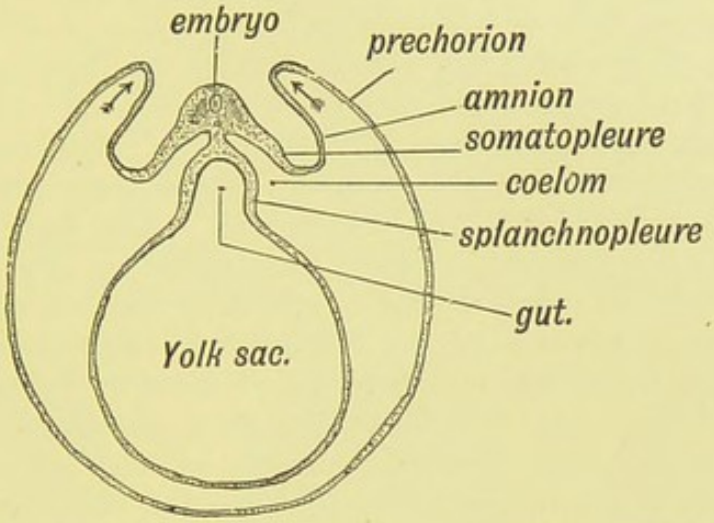


FIG. 34.—Diagram of a Developing Bird's Ovum separating into Embryo and Membranes.

the archenteron. At first it probably served as a receptaculum for the pent up secretion of the kidneys (Fig. 25, p. 24). Later it became respiratory in function. The vascular system of the yolk sac extended within it, and thus the allantois became a highly vascular structure.

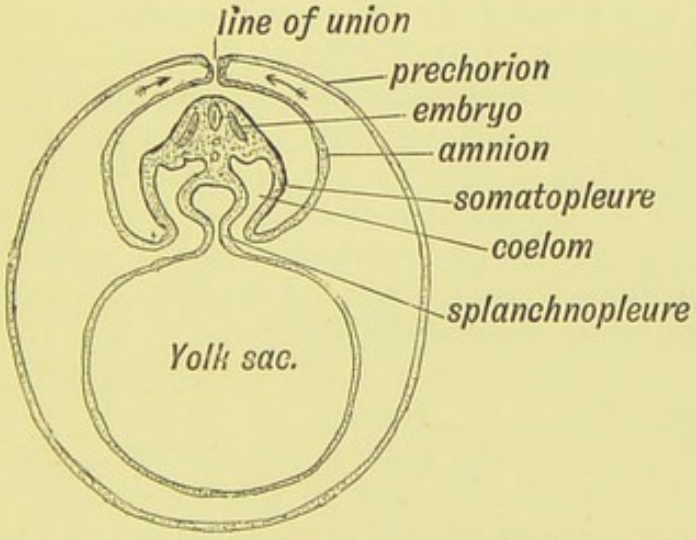


FIG. 35.—Showing the folds of the Somatopleure in a Bird's Ovum uniting over the embryo and becoming demarcated into Amnion and Prechorion.

By the application of the over-grown allantois to the inner surface of the chorion, and later still when the vascular system of the allantois invaded the chorion, the allantoic blood was aerated through the pores in the shell of the egg or directly from the maternal blood.

Segmentation.—At the beginning of the 3rd week the important process of segmentation commences in that region of the embryonic

plate which will form the cervical part of the body. So quickly does the process extend that, by the end of the 3rd week, thirty segments which go to form the cervical, dorsal, lumbar and sacral regions are marked off. In the 4th week three occipital segments appear, and in the 5th week as many as eight or ten coccygeal or caudal segments are present. The process of segmentation affects neither the epiblast nor hypoblast, only those parts of the mesoblast which lie on each side of the notochord—the paraxial masses (Fig. 20, p. 18). Segmentation occurs in all the vertebrata and also in many of the invertebrate forms of life—such as the annelids and crustaceans. The body, at an early stage of evolution, appears to have been made up of a succession of segments which were very similar in structure and function. At first the segments or somites of the mammalian embryo resemble each other in constitution, but in the course of development each becomes modified to enter into the formation of a particular part of the body. The somites are the real elements of our system, and it is possible, in the adult human body, to trace the final destiny of each somite.

Experimental Embryology.—In recent years those who study the development of the body have resorted to experiment in order to obtain a more direct knowledge of the laws and conditions of development. Loeb has shown that the ova of some invertebrate animals may be stimulated to development by chemical substances which thus simulate the action of spermatozoa. Dareste, fifty years ago, discovered that eggs hatched at abnormal temperatures often gave rise to malformed embryos. In more recent years it has been discovered that the addition of certain salts produce one form of malformation, while another group of salt solutions added to the *developing* water, in which the embryos of invertebrate animals are being hatched, will produce another set of abnormalities. It has been found that embryonic structures can be transplanted or grown on artificial media. In embryonic structures thus transplanted the development of nerve and other cells has been successfully studied. It has also been found that by dividing the ovum at an early stage after fertilization, or by separating the cells, it is possible to produce, in lower animal forms, an embryo from each part or cell separated, but the embryos so produced are small in size, and do not reach adult life. In other cases the cells thus separated only produce part of an embryo. Those who wish to obtain information on this important branch of embryology will find some of the more recent papers by Harrison, Lewis and others in the *American Journal of Anatomy* and *Anatomical Record*.

Twins, Perfect and Imperfect.[1]—The study of early stages in the development of the ovum throws some light on the manner in which

[1] For literature on malformations of the body see: J. W. Ballantyne, *Antenatal Pathology*, London, 1904; *Die Morphologie der Missbildungen des Menschen und der Tiere*, edited by Ernst Schwalbe, Jena, 1909-1912; Reports on Recent Terato-

twins arise, and especially on the production of human monsters by the incomplete separation of twins. Three theories are held concerning the production of Twins: (1) There may be two or more ova shed and fertilized. (2) That each of the cells produced by the first division of the ovum gives rise to an embryo. Assheton found two inner cell masses in the blastocyst stage (Stage II.) of a sheep, each of which would have formed an embryo. A blastocyst is necessarily the product of one ovum. (3) Beard regards the cells formed by the early divisions of the ovum as indeterminate in nature—a **thallus** from which a brood of germinal cells are produced. One of these germinal cells becomes the embryo, in the genital ridges of which the

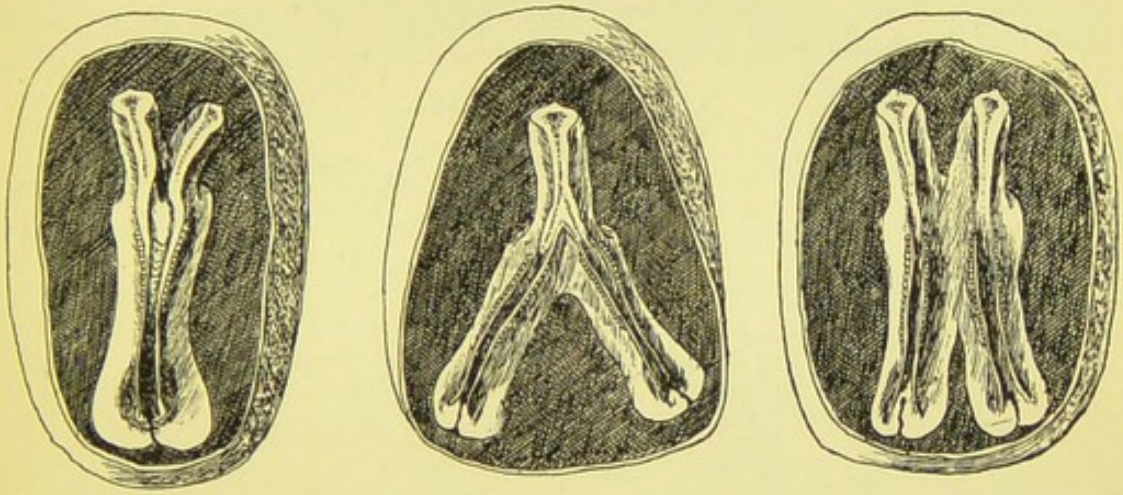


FIG. 36.—Division of the Embryonic Area, forming imperfect twins. *A*, Anterior dichotomy; *B*, posterior dichotomy; *C*, intermediate union.

remaining germ cells find a nidus and form ova or spermatozoa. If two of these germinal cells become embryos, twins are produced, if three, triplets.

"Identical" twins[1] are produced by the division of a single ovum. They are contained within the same enveloping membranes, are of the same sex and so alike in features that, to the casual observer, they are hard to distinguish. In the production of identical twins, the embryonic plates (see Figs. *A*, *B*, *C*) may remain unseparated, and in this manner most of the numerous forms of human monsters are produced. The embryos may remain attached to a common yolk sac, thus forming a "Siamese" twin—the two individuals remaining attached in the region of the umbilicus. The union may affect only the lower body and limbs, or only the upper part and arms. All kinds

logical Literature in *Journ. Anat. and Physiol.* by Professor William Wright; "Literatur" published periodically in the *Anatomischer Anzeiger*; see especially F. P. Mall, *Journ. of Morphology*, 1908, vol. 19, p. 3 (Description of a large collection of malformed human embryos with references to the more recent literature on the causation of the various kinds of maldevelopment).

[1] D. Berry Hart, *Proc. Roy. Soc. Edin.* July 1909; J. F. Gemmill, *Teratology of Fishes.* Glasgow. 1912.

and degrees of union occur—head to head, buttocks to buttocks, but the most common is a ventral union effected through a common yolk sac. In some cases one twin becomes a " parasite," and dependent on the other—the " host " twin—for its circulation and nourishment. Only part of the parasitic twin may develop, and then remains attached as an appendage to the body of the host twin. At an early stage of development the parasitic twin, arrested and delayed in development, may become included within the body of the host twin. There are two examples of this condition in the Museum of the Royal College of Surgeons, England.

Duplication and Atrophy of Parts.—Parts of the body, such as a digit or the penis may be duplicated. In such cases we suppose that the group of cells which give rise to the part undergo a division

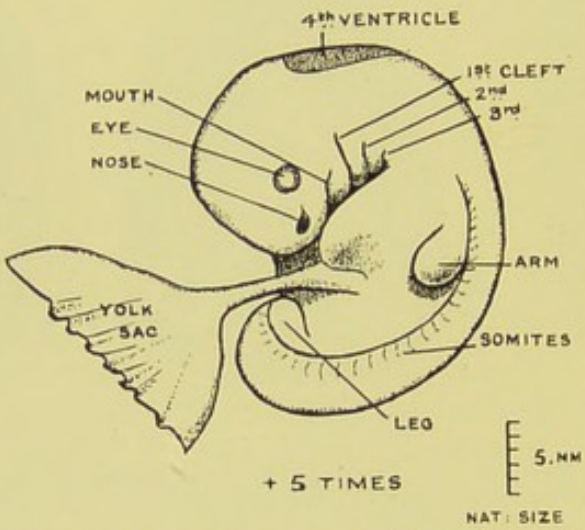


FIG. 37.—Outline of a Human Embryo 5 mm. in length, and in the 4th week of development. (Reconstructed by Professor Keibel and Dr. Elze.) (Magnific. × 10.)

or dichotomy. Those parts of the body which arise as outgrowths, such as the nasal processes, the extremities, or segments of the extremities may be partially or completely arrested at a very early stage of development. The embryo itself may be retarded in development or completely blasted while the membranes go on developing, giving rise to the developmental product known as a " mole." It is known that if eggs are incubated in abnormal conditions as regards temperature or atmosphere, such malformations occur more frequently than usual. Practically nothing is known of the circumstances or influences which give rise to abnormalities in the Human Embryo. We know that such abnormalities tend to occur in certain families; they are hereditary, but we do not know the circumstances which give rise to them.

Changes in External Appearance during the Fourth and Fifth Weeks.[1]—If the outlines of the human embryos, represented in Figs.

[1] Recently described specimens are J. L. Bremer, *Amer. Journ. Anat.* 1905, vol. 5, p. 459; C. Elze, *Anat. Hefte*, 1907, vol. 35, p. 409; N. W. Ingalls, *Archiv. f. mikros. Anat. und Entwick.* 1907, vol. 70, p. 506; L. Frassi, *Ibid.* p. 492.

37 and 38, be compared it will be seen that changes in external appearances occur rapidly at the end of the first and beginning of the second month of development. Even in the 4th week (Fig. 37) the branchial arches and clefts, which reach their clearest differentiation about the end of the 3rd week, are in a process of change ; by the end of the 5th week, while the first cleft, in the upper part of which the external ear will be developed, remains distinctly marked behind the first or mandibular arch, the other clefts are indicated merely by the depression known as the cervical sinus (Fig. 38). These changes in the 4th

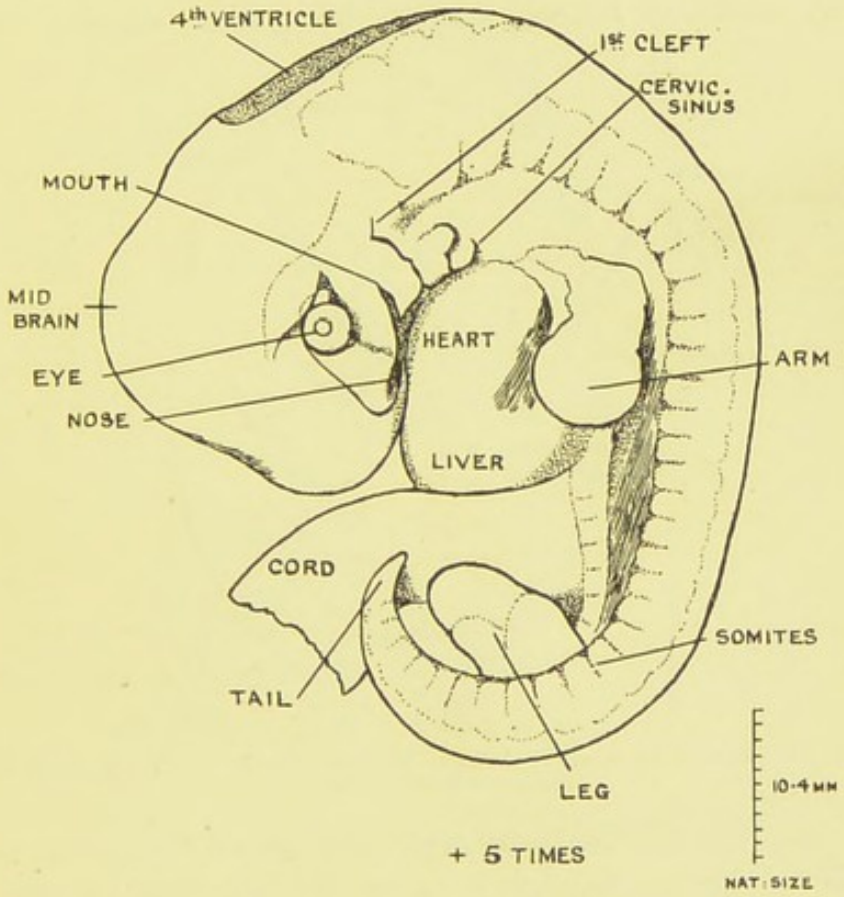


FIG. 38.—Outline of a Human Embryo 10·4 mm. long, and in the 5th week of development. (After Broman.) (Magnific. × 5.)

and 5th weeks can only be accounted for by supposing that they represent the transformations which occurred during the evolution of an air-breathing from a water-breathing form. The elevation caused by the heart is well seen in the 4th week below the visceral clefts ; in the 5th week an elevation caused by the formation of the liver has also appeared. The limb buds, already present in the 4th week, begin to show traces of a division into segments in the 5th week. In the 5th week the somites are all formed, and the free tail is already undergoing a process of atrophy. Other changes will be observed in the development of the nasal pits, in the eye and rudiments of the face.

It is also quite clear that the neural tube in the head region has undergone an elongation and a greater degree of curvation, but even in the 5th week the cerebral vesicles are small, the prominence on the crown of the head being formed by the mid-brain.

Embryo—Foetus.—At the end of the 2nd and beginning of the 3rd month those changes occur which transform the embryo into a foetus. In the embryo the various parts of the adult body are only indicated; in the foetus these parts have assumed their definite form. These changes are represented in Figs. 39 and 40. The chief parts affected are the face and neck. During the last week of the 2nd month all evident traces of branchial clefts have disappeared; the nasal,

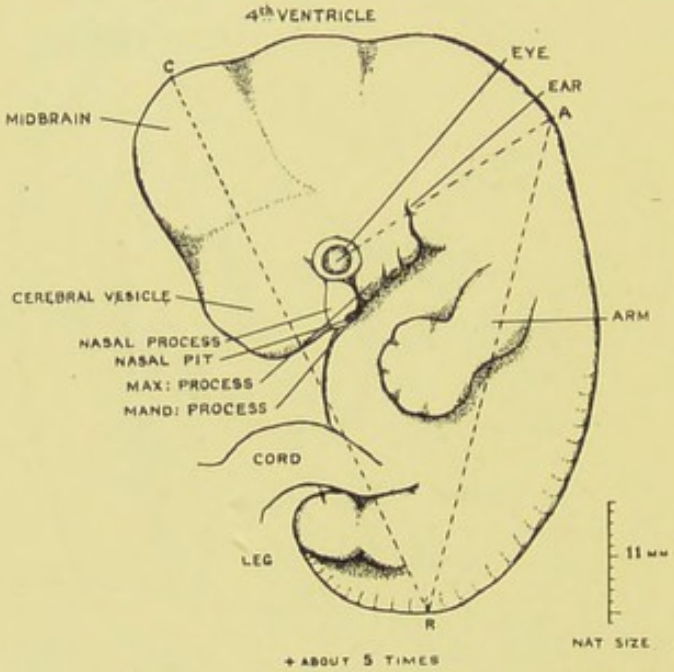


FIG. 39.—Outline of an Embryo 11 mm. long, and in the 6th week of development. (After Broman.)

maxillary and mandibular processes have grown out and united to form the face; the ear has arisen round the first cleft; a neck is now indicated by a process which has produced an extension or backward curvature of the head on the trunk. The mid-brain, even at beginning of the 3rd month, still projects on the crown of the head, but the cerebral vesicles are now large and growing backwards over it. The trunk is definitely marked (Fig. 40), but a loop of intestine remains within the root of the umbilical cord. The parts of the arm are developed—upper-arm, fore-arm, hand and fingers, and the corresponding parts are seen in the lower extremities. The external genital organs are represented by the genital tubercle and cleft.

Estimation of Age.[1]—It is difficult to estimate the precise age of an embryo or foetus, because the exact date at which fertilization

[1] F. P. Mall, *Anat. Record*, 1907, vol. 1, p. 129 (On Measuring Embryos); C. M. Jackson, *Amer. Journ. Anat.* 1909, vol. 9, p. 119 (Prenatal Growth and Proportions).

occurred can, as a rule, be only guessed. It is usual to presume it occurred soon after the last menstrual period, for conception arrests the process of menstruation. If no history is available, we must estimate the age of the developing ovum, embryo or foetus from its size, but it must be remembered that embryos, like children, show considerable variations in the rate of growth. The most accurate method of measuring the embryo is that used by Professor Mall, and is indicated in Figs. 39 and 40. The maximum length of the embryo and foetus is measured from " C," the crown of the head, to " R " the

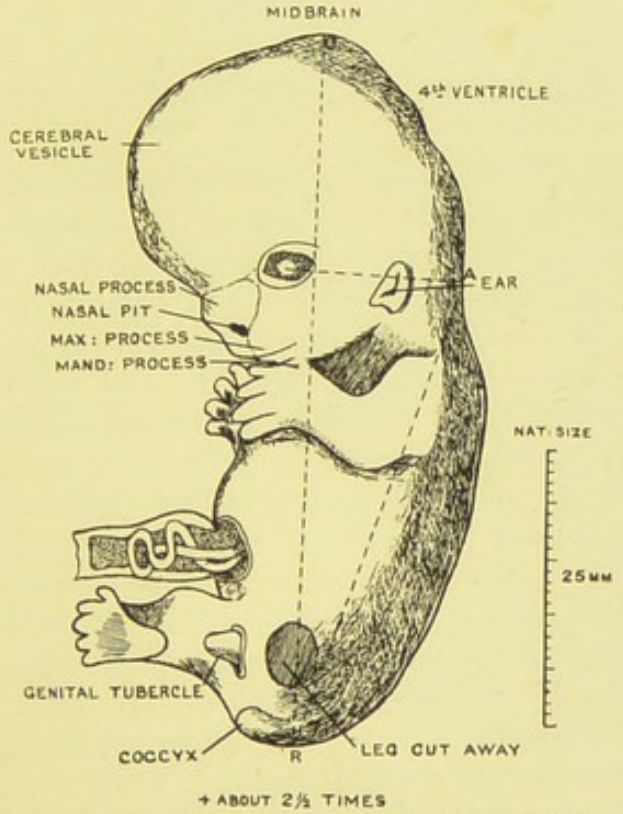


FIG. 40.—Outline of a Foetus 25 mm. (one inch) long, and at the beginning of the 3rd month of development. (After Broman.)

rump, and represents the " sitting " height of the adult. The length of the vertebral column is measured from "A" to "R" (see Figs. 39, 40). The point "A," corresponding to the atlas, is found by drawing a line from the eye backwards through the ear or upper end of the first cleft. When this line is continued backwards, it usually crosses the vertebral axis near the beginning of the spinal column. In the embryo the " C–R " line lies in front of the eye, while in the foetus it crosses behind the eye. The change is due to the formation of the neck and extension of the head. In estimating the age of embyros and of foetuses under 100 mm. (4 inches) the formula employed by Professor Mall will be found very useful:

$$\sqrt{100 \times \text{length in mm.}} = \text{age in days.}$$

For foetuses measuring from 100–220 mm. in " C–R " length, the

length in mm. represents approximately the age of the foetus in days.

The following table may be convenient for purposes of reference, if the reader may wish to estimate the age of an embryo from its total or standing length :

Length.	Age.
3 mm.	2½— 3 weeks.
5 mm.	3 — 3½ ,,
8 mm.	4 — 4½ ,,
20 mm.	6 — 6½ ,,
30 mm.	8 — 8½ ,,
80 mm.	12 —12½ ,,
140 mm.	4th month.
220 mm	5th ,,
320 mm.	6th ,,
370 mm.	7th ,,
420 mm.	8th ,,
460 mm.	9th ,,

CHAPTER IV.

THE SPINAL COLUMN AND BACK.

Stages in the Development of the Spinal Column.—In the three previous chapters the main facts relating to the development of the human body during the first and second months have been briefly sketched. We now turn to the consideration of particular parts of the human body, and naturally take up first the vertebral column—the main axis of the body. The most primitive form of axial support—the notochord—appears in the embryo during the third week. In amphioxus the notochord forms a permanent structure; in all vertebrate animals it is replaced by a segmented or vertebral axis. In the evolution of the spinal column three stages are recognized: (1) one in which the skeletal segments were composed of cellular or fibrous tissue; (2) a cartilaginous stage, in which the cells of the fibro-cellular stage become modified into cartilage forming or chondrogenous cells; (3) a final stage where the cartilage is replaced by bone. In the human embryo we see those three stages appear in succession; at the beginning of the second month the membranous foundation of the vertebera is being laid down; in the middle of that month the cartilaginous change has commenced; by the beginning of the third month ossification has commenced. In only certain groups of fishes is the cartilaginous stage the permanent one.

Stages in the Evolution of the Human Spinal Column.—In nearly all mammals the vertebral column serves as a horizontal axis or arch, which is supported on the fore and hind limbs. In a small group, however, which includes the anthropoid apes and man, the spinal column no longer forms a horizontal but a vertical axis or column. These higher primates are upright or **orthograde** when they move, in contradistinction to the ordinary four-footed mammals which are **pronograde.** There is no doubt that the orthograde posture was evolved from the pronograde. Although the anthropoid apes are orthograde, yet they use their arms in locomotion, to assist their lower extremities in supporting the weight of their bodies. Man is also orthograde, but he differs from the anthropoids in supporting the

weight of his body entirely on his lower extremities. Hence we find that the spinal column of man, although similar to that of the anthropoids, shows many peculiar adaptations to his manner of locomotion. These adaptations become especially manifest as the child learns to walk, and are best realized by a survey of the pyramids and curves of the spine.

The Pyramids of the Spine.—The spine, when viewed from the front, is seen to be made up of four pyramids : (1) Cervical ; (2) upper

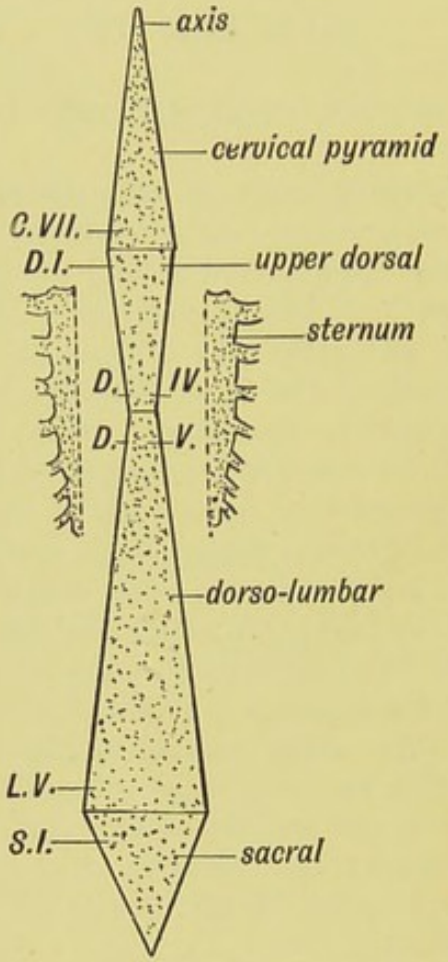


FIG. 41.—Diagram of the Pyramids of the Spine.

dorsal ; (3) dorso-lumbar ; (4) sacro-coccygeal (Fig. 41). The bases of the two upper pyramids meet at the disc between the 7th cervical and 1st dorsal vertebrae ; the bases of the lower two at the disc between the 5th lumbar and 1st sacral vertebrae. The apices of the two middle pyramids meet at the disc between the 4th and 5th dorsal vertebrae, which have therefore the narrowest bodies of the vertebral series. The narrowing in the upper dorsal region is due to the fact that the weight of the upper half of the trunk is partly borne by, and transmitted to, the lower dorsal region by the sternum and ribs which thus relieve the spine to some extent (Fig. 41). At the sacrum the weight

is transferred to the pelvis and lower limbs, hence the rapid diminution of the sacrum and coccyx. A well-marked thickening or bar in each ilium runs from the auricular surface to the acetabulum and transmits the weight to the femora.

The Curves of the Spinal Column.—There is only one curve—an anterior concavity—until the 3rd month (Fig. 42, *A*). About the beginning of the 4th month the sacro-vertebral angle forms between the lumbar and sacral regions (Fig. 42, *B*). At birth the cervical and sacral curves have appeared, but the sacral not to a pronounced extent

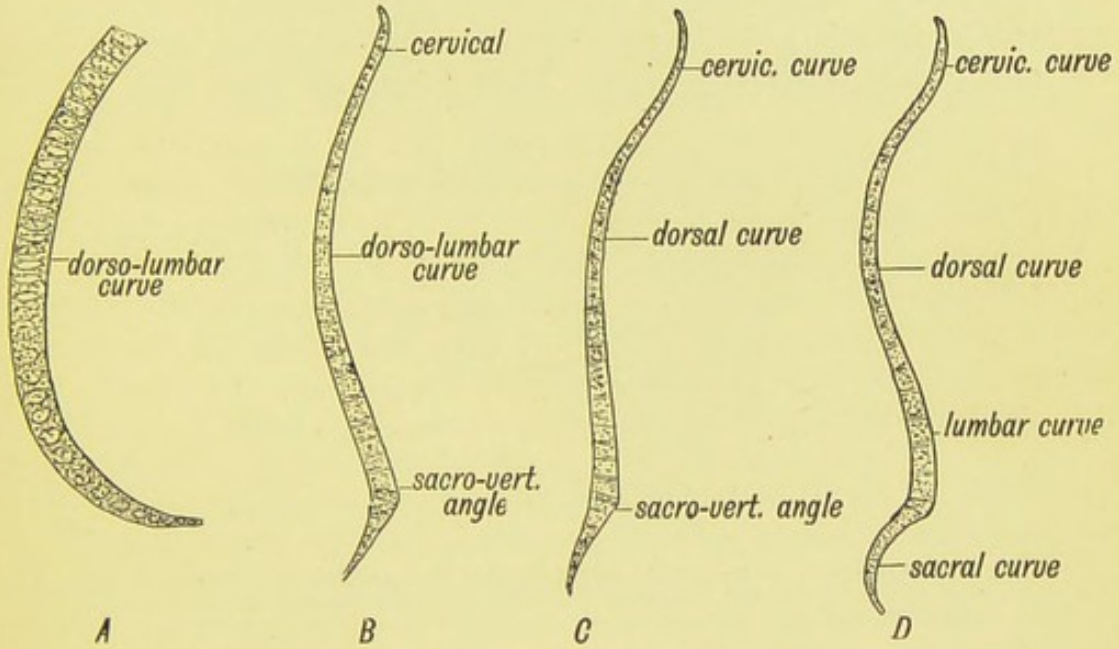


FIG. 42.—Diagram of the Curves of the Spinal Column.

A. At the 6th week of foetal life. *B*. At the 4th month of foetal life. *C*. Curves present at Birth. *D*. Curves present in the Adult.

(Fig. 42, *C*). The lumbar curve appears as the child learns to walk. It is produced to allow the body to be brought vertically over the lower extremities. The sacral and cervical curves also become at that time more marked (Fig. 42, *D*). The dorsal curvature and the sacro-vertebral angle are the primitive curves and are present in all mammals. The others are adaptations to the upright posture. The lumbar curve is most pronounced in the highly civilized races.

Proportion of Cartilage and Bone.—The intervertebral discs form one-third of the total height of the spine; the proportion of cartilage is greater in the lumbar than in the dorsal region and greater in the dorsal than in the cervical. The lumbar and cervical curvatures are due chiefly to the shape of the discs (H. Morris). In the lumbar region, which is convex forwards, only the lower three vertebrae are deeper in front than behind. This is true only for the higher races of mankind, for as Cunningham has shown, in lower races, as in the

gorilla, only the last lumbar vertebra is deeper in front than behind, and thus helps to maintain the lumbar curvature.

Unstable Regions of the Spine.[1]—In about 90 % of men there are 7 cervical, 12 dorsal, 5 lumbar, 5 sacral and 4 caudal vertebrae, making 33 in all. In the remaining 10 % there is some departure from the normal arrangement and these departures affect certain definite regions. The regions affected are those which lie at the junction of one section of the spine with another—at the cervico-dorsal, dorso-lumbar and lumbo-sacral junctions. At an early stage of development all the vertebrae have a similar form; at a later stage the vertebra of each segment assumes its peculiar form, but it is not uncommon for one vertebra to assume some or all of the characters of the one before it or behind it. Thus variations arise, and by the

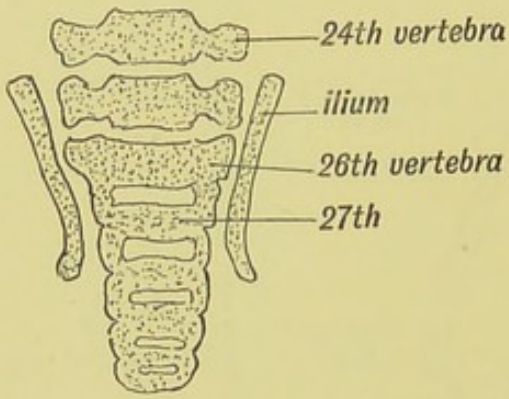


FIG. 43.—A Section of the Lumbo-sacral Region of the Spine in a Foetus at the end of the 2nd month, showing the 26th vertebra forming the 1st Sacral. (After Rosenberg.)

accumulation of variations new forms may be produced. Such variations are frequent, and are often of clinical importance.

I. **The sacro-lumbar.**—The 25th vertebra in 95 % of people forms the 1st sacral; in 1 % the 24th, and 3 % the 26th. These percentages are drawn from the observations of Paterson, Rosenberg, and others who have made researches on this subject. The vertebral formula is not fixed. Rosenberg's investigations showed (Fig. 43) that it is the 26th vertebra that forms the first of the sacral series in the early embryo; later the 25th throws out great lateral masses, and thus forms a con-

[1] For recent literature on variations of vertebrae: Bardeleben, *Ergebnisse der Anat.* 1905, vol. 15, p. 119; 1906, vol. 16, p. 191; 1908, vol. 18, p. 71. A. Fischel, *Anat. Hefte*, 1906, vol. 31, p. 459. E. Rosenberg, *Morph. Jahrbuch*, 1907, vol. 36, p. 609. F. Wood Jones, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 377 (Influence of Nerve-plexuses in determining Development of Costal Processes). C. R. Bardeen, *Amer. Journ. Anat.* 1904, vol. 4, p. 163 (Development of Vertebrae). E. Barclay Smith, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 144. T. Manners Smith, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 146. A. F. Le Double, *Bull. et Mem. Soc. d'Anthrop.* 1911, Ser. 6, vol. 2, p. 413 (Lumbar Ribs); p. 428 (Cervic Ribs). F. Wood Jones, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 249 (Cervical Ribs). T. W. Todd, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 244 (Cervical Ribs).

nection with the ilia. Bardeen has not been able to confirm Rosenberg's observations; he found that the vertebra which was to form the first sacral—whether it was the 24th, 25th or 26th in the vertebral series—took on a predominance at its earliest appearance. In the lower primates (monkeys) the 27th forms the 1st sacral; with the evolution of man the 26th, then the 25th underwent sacral modifications, the trunk being correspondingly shortened. The lumbar region of the human spine elongates much more rapidly after birth than either the cervical or dorsal region, in order to form an elongated flexible pillar for the support of the upper part of the body. In the anthropoid apes the lumbar region is relatively short as in the child at birth. It will be seen that the number of lumbar vertebrae in man is not definitely fixed. The anterior point of attachment of the ilium fluctuates from the 24th to the 26th vertebra. With the sacral transformation of the 25th and 26th (lumbar) vertebrae, there was a corresponding movement forwards of the sacral plexus.

II. **Sacro-coccygeal.**—The 30th vertebra forms the 1st coccygeal; not uncommonly this vertebra is sacral in type and forms part of the sacrum. On the anterior or pelvic aspect of the 1st coccygeal vertebra a rudiment of the **haemal arch** is usually to be found during foetal life. The haemal arches are well developed on the proximal caudal vertebrae of tailed monkeys, and represent developments from the hypochordal or intercentral element of a vertebra.

III. **Dorso-lumbar region.**—This region is also liable to variation; the 20th vertebra instead of forming the 1st lumbar, may simulate the last dorsal in the type of its articular processes, and may bear ribs, probably a reversion to an ancestral condition, or, on the other hand, the 12th dorsal vertebra (19th) may not carry ribs. About 2 % of bodies show the latter kind of variation—a reduction of the costal series, and about 6 to 8 % the former kind, in which the costal series is increased (see also Chap. XIX.).

IV. **Dorso-cervical.**—The 7th vertebra may carry ribs; rarely the 8th vertebra has no ribs attached to it and is cervical in type.

In Fig. 44 is represented the condition of the seventh cervical vertebra, as seen in 72 human skeletons. In the foetus, the costal element is always apparent (Fig. 42, *C*); in the adult it may vanish or fuse with the transverse process. In about 1 % of individuals it assumes the development shown in Fig. 44, *E*; it may, in occasional cases, assume all the characters of a first dorsal rib, with its anterior end implanted on the presternum. Recently Dr. Wingate Todd has published a series of observations, which are confirmed by the statements made here. A cervical rib may fuse with the costal element of the first dorsal vertebra, thus giving rise to a **bicipital** rib (Dr. Wood Jones). The lower trunk of the brachial plexus crosses a **cervical rib**, and hence in such cases symptoms of nerve-pressure may arise.

V. **Cervico-occipital Region.**[1]—The occipital or posterior part of the skull represents three united vertebrae. Very rarely the last of these may partly assume a vertebral form, but it is by no means rare to see

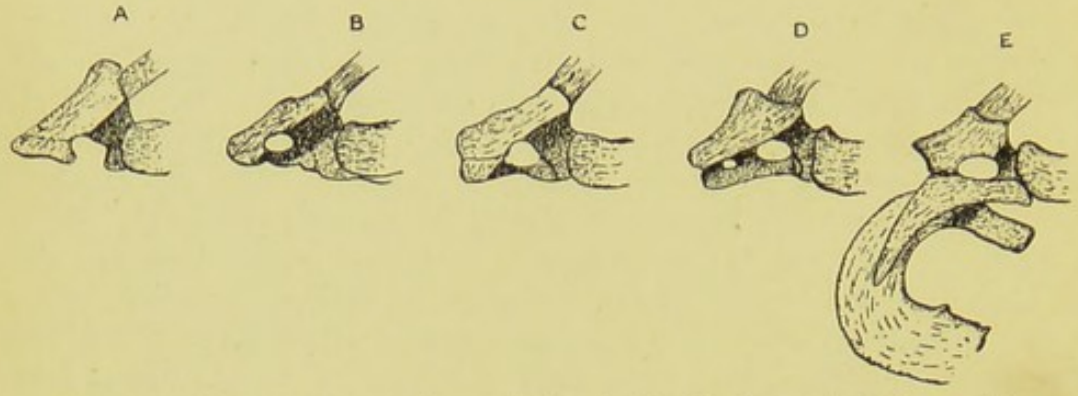


FIG. 44.—Diagram showing the variation in the development of the costal element of the seventh Cervical Vertebra in 72 skeletons. In *A* and *B* the costal element is partly fused with the transverse process; in *C*, *D* and *E* it remains free.

the atlas or first cervical vertebra partly fused with the occipital bone, representing a tendency to add a fourth vertebra to the occipital series.

The Notochord.—It has already been seen that the notochord is formed at a very early stage by a tubular evagination from the roof

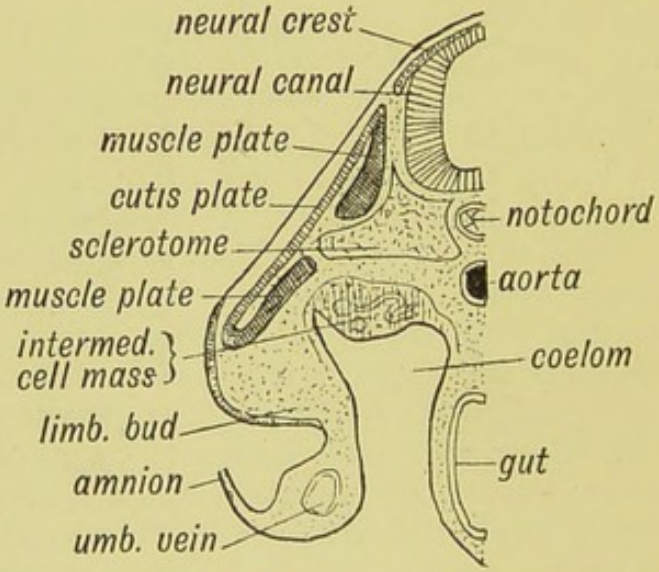


FIG. 45.—A Schematic Section of an Embryo to show the sclerotome, muscle plate and skin plate which arise from each segment of the paraxial mesoblast. (Compare with Fig. 57, p. 59.)

of the archenteron and lies along the ventral aspect of the neural canal (Fig. 33, p. 34). The notochord, with the mesoblastic tissue round it, represents the most primitive type of spinal support. It is hollow

[1] For reports of recent cases of fusion of atlas: Schumacher, *Anat. Anz.* 1907, vol. 31, p. 145 (Homologies of Occipital Bone); K. Weigner, *Anat. Hefte*, 1911, vol. 45, p. 81 (Assimilation of Atlas); Glaesmer, *Anat. Anz.* 1910, vol. 36, p. 129.

—the canal of the notochord runs from end to end, and into its posterior part the neurenteric canal opens. Afterwards it becomes a solid rod composed of cells of a peculiar type. A sheath is formed round the notochord by cells of the paraxial mesoblast (Fig. 45), which grow inwards and surround it. These cells form the **sclerotome** and spring from the inner parts of the primitive segments or protovertebrae into which the paraxial mesoblast is divided (Fig. 45). At the same time the cells of the sclerotome also grow up and gradually surround the neural tube. From these cells which grow inwards and surround the

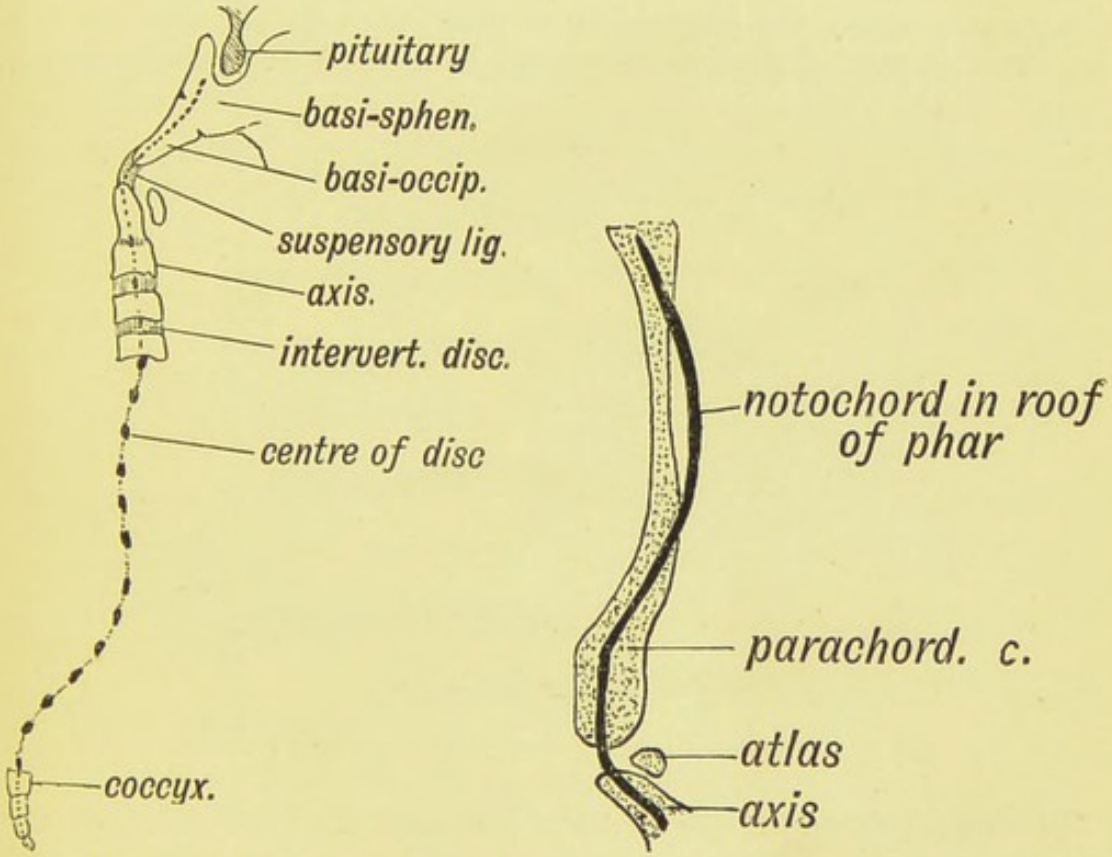


FIG. 46.—Where Remnants of the Notochord may occur in the Adult.
FIG. 47.—The relationship of the Notochord to the parachordal cartilages of the human embryo. (Robinson.)

notochord and neural canal, the membranous basis of the spinal column is formed and also the basi-occipital and part of the basi-sphenoid bones of the skull (Fig. 46).

What becomes of the Notochord.[1]—In the second month of foetal life the notochord begins to disappear ; the bodies of the vertebrae and parachordal cartilages form round its sheath and constrict it. The parachordal cartilages are transformed into the basi-occipital and basi-sphenoid—the basal part of the skull—behind the pituitary fossa.

[1] Recent papers on notochord : A. Bruni, *Anat. Hefte*, 1912, vol. 45, p. 307 (Involution of Notochord) ; A. Linck, *Anat. Hefte*, 1911, vol. 42, p. 605 (Dev. of Notochord) ; L. W. Williams, *Amer. Journ. Anat.* 1908, vol. 8, p. 251.

As they form, the notochord is obliterated between them. Eternod, however, found the anterior part of the notochord on the dorsal wall of the pharynx in the human embryo; Robinson has shown that in man the parachordal cartilages are developed in part on its dorsal aspect (Fig. 47). The odontoid process represents the body of the atlas, and the suspensory ligament the disc between the occipital bone and atlas. A remnant of the notochord is enclosed in the suspensory ligament. The centrum of each vertebra is formed round the notochord, and at first each contains an hour-glass canal surrounding the notochord. Within each centrum or body the notochord ultimately disappears, but in the intervertebral discs it swells out and forms a considerable part of the central mucoid core which each disc contains.

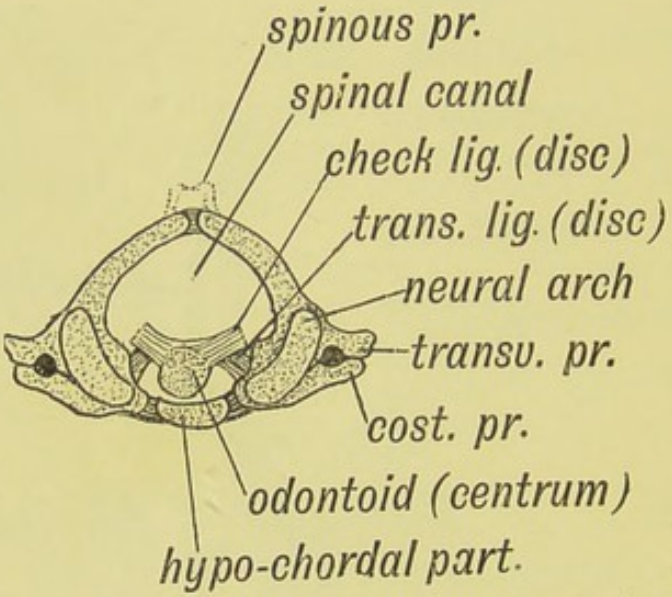


FIG. 48.—The Morphological Parts of the first Cervical Vertebra.

Protovertebrae or Primitive Segments.—Protovertebrae are not the forerunners of the vertebrae; they are the primitive segments or somites into which the mass of mesoblast at each side of the neural canal and notochord divides (Figs. 45; 57, p. 59; 19, p. 17). The process of division or segmentation begins at the occipital region towards the beginning of the third week, and spreads backwards until 35 or more body segments or somites are isolated. Each segment thus separated forms its own muscles (from its muscle plate or myotome), has its own nerve (spinal nerve), its own artery (intercostal), its own cutis plate or dermatome, and the basis for its skeletal tissue (sclerotome) (Fig. 45). The **intersegmental septum** separates one protovertebra or segment from another. Ribs, transverse and spinous processes, are formed in the intersegmental septa. Hence an intercostal space with its muscles, vessels, and nerves, with the corresponding intervertebral structures, represents a differentiated protovertebra. In the ventral aspect of the neck and loins, some of the intersegmental

septa disappear. In the head nine segments are recognized, but their recognition rests on observations made, not on the human embryo, but on the embryos of lower vertebrates.

Morphological Parts of a Vertebra.—The constituent parts of a vertebra, although much modified, may be best recognized in the atlas (see Fig. 48). These parts are (1) the **centrum,** which forms the odontoid process ; (2) the right and (3) the left half of the **neural arch** ; (4) the **hypochordal part,** which forms the anterior arch or bow. Besides the four chief elements there are three secondary processes, all of which spring from the neural arch. These are (*a*) spinous, (*b*) transverse, (*c*) costal processes. In the dorsal region the costal processes become separated from the neural arches by articulations ; in other vertebrae they retain their continuity with the arch. Howes found that the hypochordal element formed the inter-centra in Sphenodon. To the hypochordal element of a typical vertebra Gadow has given

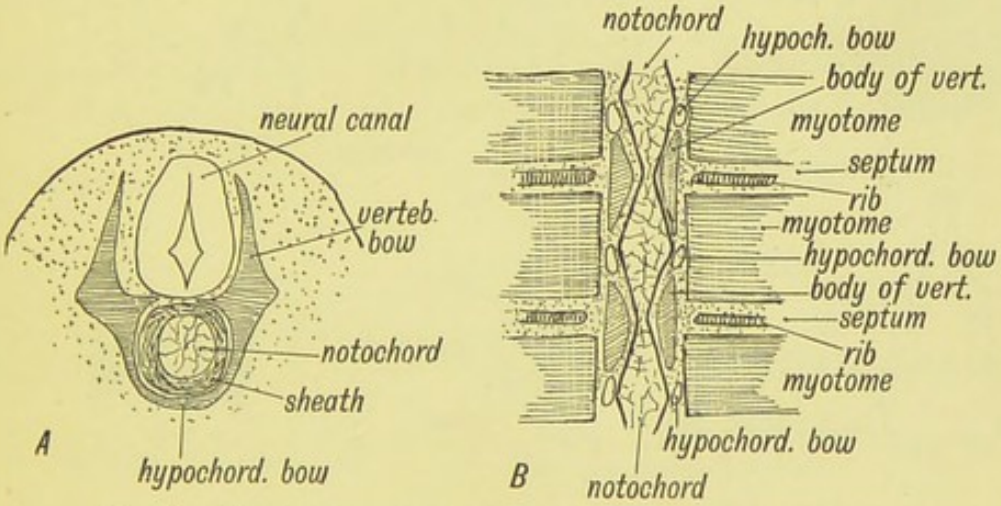


FIG. 49.—The development of the Membranous Basis of a Vertebra.
A. In transverse section. *B*. In horizontal section showing the relation of the vertebra to the Primitive Segments. The section is viewed from the dorsal aspect.

the name of **basi-ventralia,** the centrum or body proper being named the **inter-ventralia**.

Development of a Typical Vertebra—the 6th Dorsal.[1]—(1) **Membranous Stage** (4th and 5th weeks). The vertebra then consists of 1st a centrum surrounding the notochord, formed from its sheath (Fig. 49, *A*), and 2nd a horse-shoe shaped **vertebral bow** (Fig. 49, *A* and *B*). The bow consists of a hypochordal part and two lateral limbs, united by the hypochordal part ventral to the centrum, the right and left parts representing the limbs of the neural arch.

[1] For an account of the differentiation and development of vertebrae : C. R. Bardeen, *Amer. Journ. Anat.* 1904, vol. 4, p. 163 (Thoracic Vertebrae) ; also p. 265 ; 1908, vol. 8, p. 181 (Cervical and Occipital Regions).

(2) **Cartilaginous Stage** (Fig. 50).—It commences in the 5th week. The fibrous basis of the whole vertebra is transformed into cartilage. In each lateral half of the cellular basis of a vertebra three centres of chondrification appear—one for the neural arch, one for the costal process, and one for each half of the centrum, but those of the centrum soon fuse together. In the process of chondrification the cells derived from the sclerotome are directly transformed into cartilage cells. In the atlas the hypochordal part of the bow becomes cartilaginous and subsequently ossified ; in all the other vertebrae, excepting the cervical segments just behind the atlas (Fig. 52), this element never passes beyond the membranous stage of development. It should be

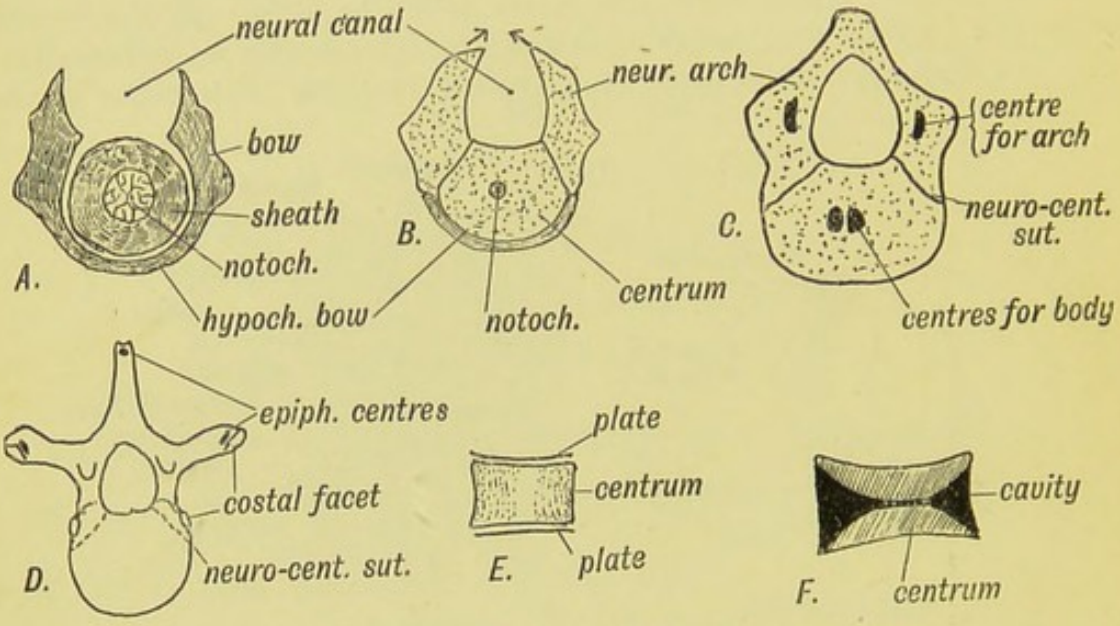


FIG. 50.—Showing the Stages in the Development of a Vertebra.
A. In the Membranous Stage. *B*. In the Cartilaginous Stage. *C*. The appearance of Ossific Points. *D*. The appearance of Secondary Ossific Centres. *E*. The epiphyseal plates of the centra. *F*. Section of an amphicoelous vertebra.

noticed (Fig. 49, *B*) that the vertebral bodies are formed round the notochord, *opposite* each intersegmental septum. Hence each vertebra belongs to two segments. The intervertebral disc is situated opposite the middle of a segment (Ebner). The lateral limbs of the cartilaginous bow meet behind (dorsal to) the neural canal in the 4th month, thus completing the neural arch.

(3) **Bony Stage.**—The centrum and neural arch elements of the cartilaginous vertebra fuse and give rise to the condition shown in Fig. 50, *C*. In the 7th week two centres appear in the centrum, but quickly fuse ; one appears in each limb of the neural arch (8th week) ; at birth the ossific centres of the centrum and neural arch have met. The central and neural ossifications meet at the neuro-central suture, and unite at the 4th or 5th year, the **body** being formed by (1) the centrum, (2) basal

parts of the neural arch (Figs. 48, 50). The neural ossifications fuse behind (where the spinous process is produced) in the 1st year. The spinous and transverse processes are formed by outgrowths of cartilage into the septa between the protovertebrae or primitive segments. The ribs are also formed by outgrowths from the vertebrae. In the cervical lumbar and sacral regions they fuse with the transverse processes, but in the dorsal region they remain as separate elements. In typical ribs the head corresponds to the intervertebral disc, because according to Gadow the rib was originally evolved from an intervertebral element—the intercentral or hypochordal. In atypical ribs—the 1st, 11th and 12th—the head of the rib articulates only with the vertebra behind its own disc. Epiphyseal centres for the ossification of the transverse and spinous processes appear about puberty.

The Bodies of Mammalian Vertebrae are peculiar (1) in the development of an upper and lower epiphyseal plate; (2) in that no trace

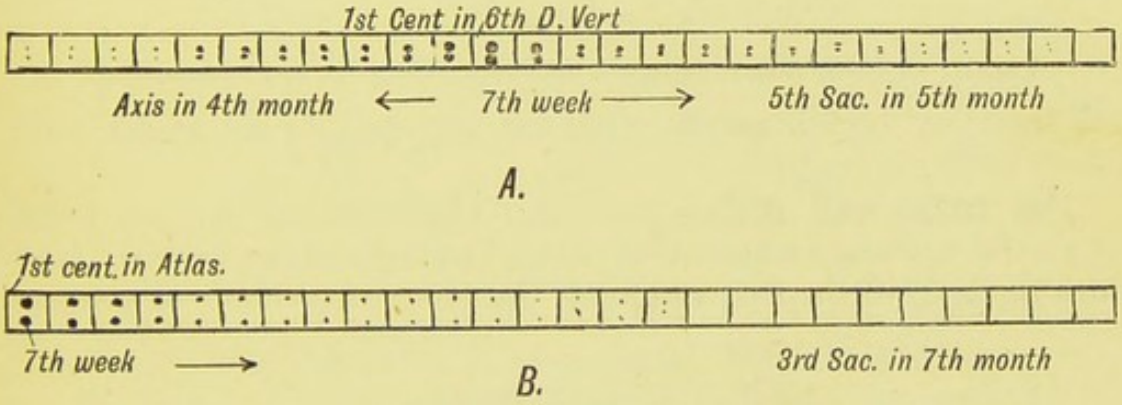


FIG. 51.—The Order in which the Centres of Ossification appear in the Bodies (*A*) and in the Neural Arches (*B*) of the Spinal Column.

of the notochord remains within them. In Fishes, as in the early human or mammalian foetus, the bodies are hour-glass shaped (amphicoelous, Fig. 50, *F*); in Amphibians they may retain a concavity in front (procoelous) or behind (opisthocoelous), but in mammals both ends are filled up.

It will be observed (Fig. 51, *B*) that the **centres of ossification** [1] for the neural arches appear first in the anterior end of the spine (1st cervical), the date becoming later the more posterior the vertebra. In the 1st sacral they appear about the 4th month; in the 2nd sacral, in the 5th month or later; in the 3rd they may not appear. In the 4th and 5th sacral and 1st coccygeal vertebrae only vestiges of the neural arches are formed. These vertebrae retain the early foetal type shown in Fig. 50, *B*. In the remaining coccygeal vertebrae only

[1] See F. P. Mall. *Amer. Journ. Anat.* 1905, vol. 5, p. 433 (Centres of Ossification before end of 2nd month); E. Fawcett, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 172 (Costal Epiphyses).

the centres for the bodies appear. The centres for ossification of the bodies of the vertebrae appear first in the mid dorsal region (6th dorsal). From that point they spread forwards and backwards, the centres for the odontoid process appearing at the 4th month, and that for the

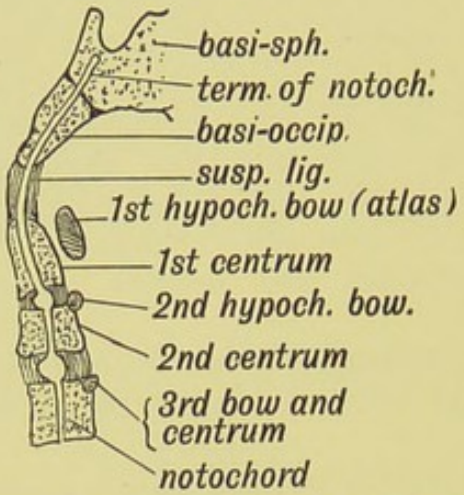


FIG. 52.—A Diagrammatic Section of the Foetal Axis, Atlas, and Basi-occipital.

5th sacral at the 5th month, while the coccygeal do not appear until about birth.

The Atlas and Axis.—The atlas represents the completed bow of the 1st cervical vertebra (Fig. 48). The body of the vertebra fuses with the body of the 2nd, and forms the odontoid process. A remnant

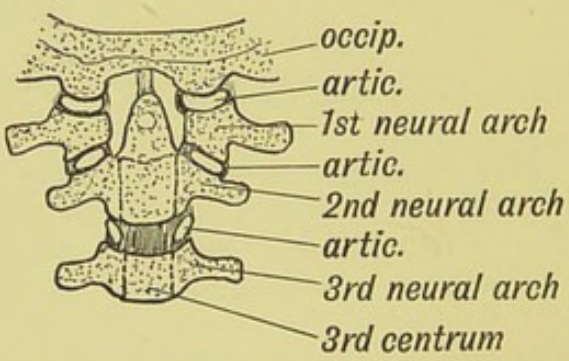


FIG. 53.—The nature of the Atlanto-axio-occipital Articulations.

of the disc between the 1st and 2nd vertebrae can sometimes be seen when the odontoid is split open. The suspensory and check ligaments are the representatives of the disc between the last occipital segment and the 1st cervical (Figs. 48 and 52).

Occipito-atlanto-axial Articulations.[1]—In the intervertebral discs of the cervical region there is at each side, between the lateral lips of the vertebral bodies, a small articular cavity (Fig. 53). It is situated between the part of the body formed by the neural arches and lies

[1] O. Jackel, *Anat. Anz.* 1912, vol. 40, p. 609 (Morphology of Atlas).

in front of (ventral to) the issuing spinal nerves. Between the axis and atlas this articulation is greatly enlarged. At it the rotatory movements of the atlas on the axis take place. The atlanto-occipital joint, which separates the atlas and the last occipital segment, is of the same nature. The atlas has neither the upper nor the lower articular processes of the other vertebrae. Hence the 1st and 2nd cervical nerves appear to issue behind the articular processes. At one time the single median occipital condyle seen in birds and reptiles was regarded as very different in nature from the double condyles of mammals. Recently Symington has shown that in the lowest mammals (monotremes), the occipital condyles are fused in the middle line, and that all foetal mammals also show this condition. The articular facets on the upper surface of the atlas are also continuous over the hypochordal element. In the human skull a remnant of this median fusion of the

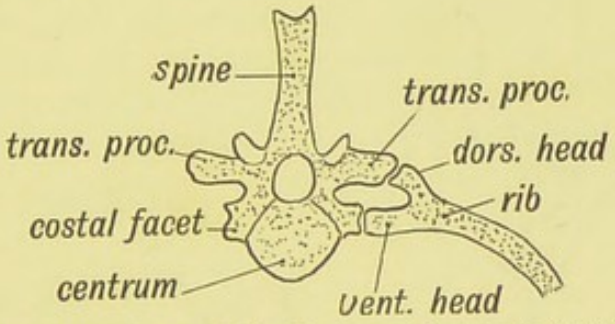


FIG. 53A.—The Bicipital Rib of a Lower Vertebrate (crocodile).

condyles is frequently seen on the anterior margin of the foramen magnum ; it is named the third or **median occipital condyle.**

The Ribs are developed as vertebral processes in the septa between the dorsal primitive segments. In lower vertebrates (birds, reptiles, etc.) each rib has two heads, a dorsal and ventral (Fig. 53A). The tuberosity of the human rib represents the dorsal head ; the ventral head is well developed in man, as in mammals generally. The rib articulates with the neural arches only (Fig. 50, *D*). The **conjugal ligament** is made up of fibres which cross in the posterior aspect of the intervertebral disc and unite the heads of the pair of ribs which are opposite. The conjugal ligament which is strong in some animals is weak in man (Sutton). The transverse ligament of the atlas may belong to the conjugal series.

Vestigial Ribs.—Although the ribs are only fully developed in the dorsal region, yet a representative—a **costal element**—is present in every vertebra. In the **cervical vertebrae** (Fig. 48) the anterior part of the transverse processes represents a costal process, but only in the 6th (sometimes) and 7th is the costal process formed by a separate centre of ossification. The costal process of the 7th, usually represented by a mere vestige, may develop into a rudimentary or even a fully formed rib which reaches the sternum. In the **lumbar vertebrae** only

the first shows a separate centre for the formation of the costal process ; it fuses with the transverse process in the later months of foetal life ; in the other lumbar vertebrae the tips or perhaps the whole of the transverse processes represent costal processes. The 12th dorsal rib varies widely in size ; it may be six or ten inches long or reduced to a mere vestige. In quite 40 % of women the 12th rib cannot be palpated because it does not project beyond the outer border of the erector spinae.

In the **1st, 2nd and 3rd sacral vertebrae** the costal processes are large and have their own centres of ossification.[1] Their cartilaginous bases fuse early to form the greater part of the lateral masses of the sacrum. The part of the lateral mass formed by the costal processes is shown in Fig. 55. The costal processes are absent in the 4th and

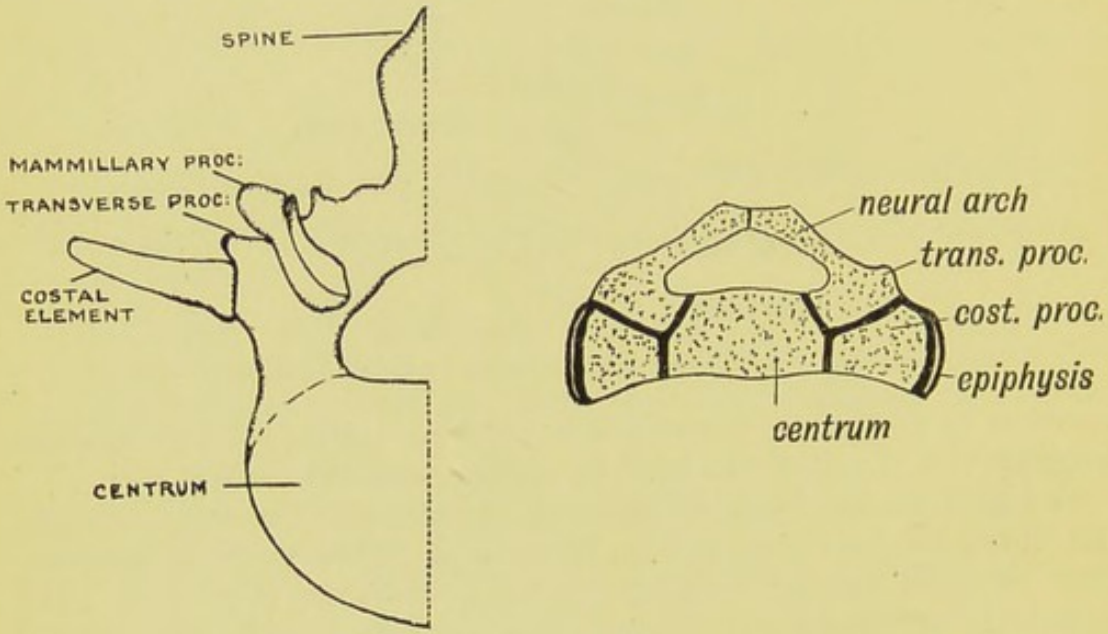


FIG. 54.—Half of a first Lumbar Vertebra showing a separate costal element.
FIG. 55.—A Section to show the Nature of the Elements composing the Sacrum.

5th sacral and in all the coccygeal vertebrae. The two lateral epiphyseal plates on each side of the sacrum are new and independent formations.

The Accessory Processes are found in the lumbar and lowest two dorsal vertebrae. They are developed at the base of the transverse processes and are for the attachment of slips of the longissimus dorsi. The **mammillary processes** are developed on the articular processes of the lower two or three dorsal and all the lumbar vertebrae. They give attachment to tendons of origin of the multifidus spinae. In a recent

[1] References to recent papers on sacrum : E. Fawcett, *Anat. Anz.* 1907, vol. 30, p. 414 (Sacral Costal Epiphyses) ; Otto Petersen, *Anat. Anz.* 1905, vol. 26, p. 521 ; D. E. Derry, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 202 (Sacral Accessory Articulations) ; L. Bolk, *Anat. Anz.* 1912, vol. 41, p. 54.

paper (*Journ. Anat. and Physiol.* 1912, vol. 47, p. 118) Dr. Wood Jones points out that these two muscular processes, the mammillary and accessory, are fused together in the dorsal region, but in the lumbar region they are separated by a groove containing the inner branch of the posterior division of the corresponding spinal nerve.

The Transverse and Spinous Processes grow out from the vertebral bow (Fig. 50, *A*) into the septa between the primitive segments. Each transverse process is pierced, while still in the fibrous condition, by a branch of the corresponding segmental (intercostal) artery. In only the cervical region do those perforating arteries and their foramina persist. In that region the perforating arteries anastomose, and out of the chain thus formed is developed the vertebral artery. Thus the foramina for the vertebral artery are formed independently of the costal element in each cervical transverse process. The spines are absent on the 1st cervical, 4th and 5th sacral and coccygeal vertebrae. They are slightly developed and united by ossification of the interspinous ligament in the 2nd and 3rd sacral vertebrae. The 2nd, 3rd, 4th, 5th, and 6th cervical spines are bifid in Europeans ; but in lower races, as in anthropoids, the 5th and 6th spines are usually undivided.

CHAPTER V.

THE SEGMENTATION OF THE BODY.

Segmentation of the Body.[1]—The human body or trunk consists of 33 or 34 segments. Each segment is fundamentally of the same type, but the resemblance is obscured owing to extensive modifications which the somites undergo to form the cervical, dorsal (thoracic), lumbar (abdominal), sacral (pelvic) and caudal regions of the body. The outgrowth of the limbs also renders it difficult to recognize in the adult the simple system of segments which can be seen in the embryo at the end of the third week (Fig. 403, p. 416).

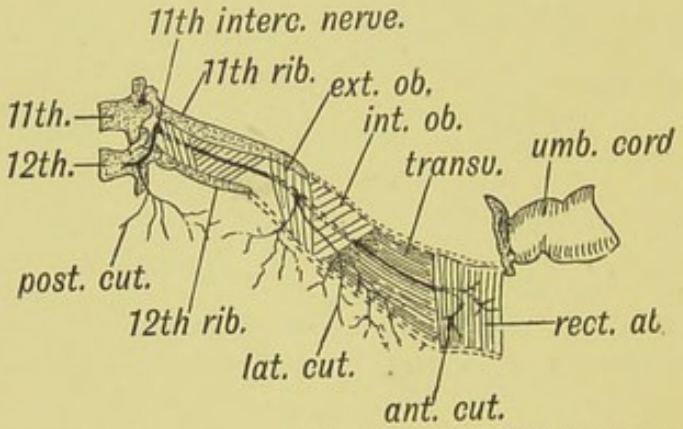


FIG. 56.—Some of the structures derived from the 11th Dorsal Segment of the Right Side.

Until lately the segmentation of the human body was a matter of only speculative importance, but recent advances in our knowledge of the distribution of nerves, has shown that it has a direct bearing on diagnosis and treatment.

Constitution of a Typical Segment (11th Dorsal).—It is better to study the development of a typical body segment, and from that

[1] For recent papers on segmentation see: G. van Rynberk, *Ergebnisse der Anat.* 1908, vol. 18, p. 353; A. L. J. Sunier, *Onderzoekingen verricht in het Zoolog. Lab. Univ. Groningen*, 1911, Leyden (Differentiation of Myotome). See also references under Bardeen (p. 46); under Lewis (p. 411).

the student will be able to note for himself the modifications which have taken place in the more highly differentiated segments of the body. By the end of the third week, the process of segmentation, which began in the cervical region a few days previously, has spread backwards and separated the 18th body segment (11th dorsal) from those in front and behind. As already explained, the process of segmentation affects chiefly the paraxial block of mesoblast which lies on each side of the neural canal and notochord, and also the inter-

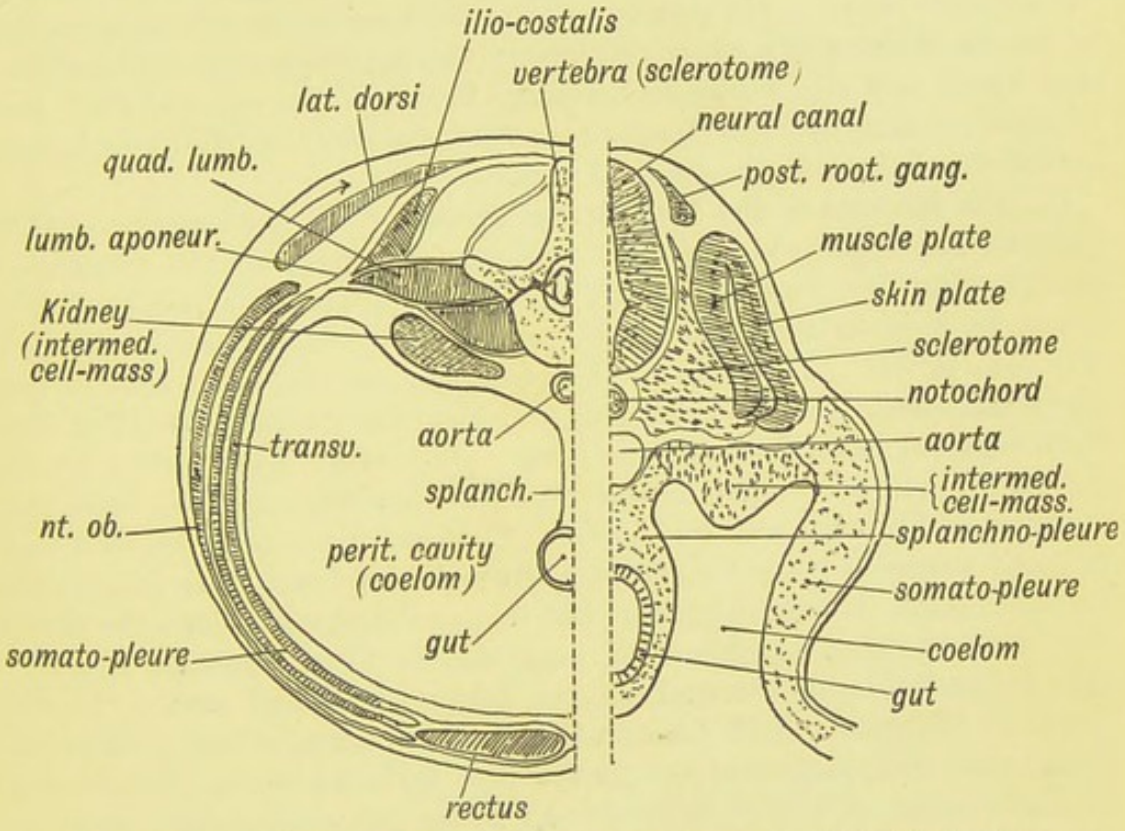


FIG. 57, *A*.—A Transverse Section showing the Elements of the 1st Lumbar Segment in the Adult.

B.—A corresponding Section of an Embryo about the end of the 3rd week (diagrammatic).

mediate cell mass. In Figs. 57, *A*, *B*, a segment is represented in the adult and in the embryonic condition.

The following elements make up the 11th dorsal segment: (1) Its skeletal basis; (2) Muscular element; (3) Renal element; (4) Vessels; (5) Nerves; (6) Neural segment; (7) Cutis plate. Although the epiblast and hypoblast are never segmented, yet a definite area of each is associated with every body segment. The origin of each element will be taken separately.

I. The **skeleton** of the 11th dorsal segment is represented by the adjacent halves of the 11-12 dorsal vertebrae and the disc between them, for, as already pointed out, the vertebrae are intersegmental in their development (Fig. 49, *B*). The transverse processes, the

spinous processes and 11th and 12th ribs are also formed in the septa in front of and behind the 11th segment (Fig. 56). The septum in the rectus muscle a little below the umbilicus represents the intersegmental septum corresponding to the 11th rib. Sometimes another septum occurs in the rectus, midway between the pubes and umbilicus, marking the lower limit of the 11th segment. The linea alba separates the segments of the two sides.

In the linea alba or ventral median line of the thoracic region, the sternum is developed. The intersegmental septa are well marked in the thoracic region ; the ribs and their cartilages are developed in them. In the neck the septa are almost lost ; the intermediate tendon of the omo-hyoid and the septa occasionally found in the sterno-hyoid and -thyroid, complexus and trachelomastoid muscles are the only representatives of them in the cervical region.

II. **The Muscles of the 11th Dorsal Septum.**—All the muscles of this segment are developed from the muscle plate (myotome) of the primitive segment (see Figs. 56 and 57). There is a cavity, which probably arises as a diverticulum of the coelom, in each primitive segment (Fig. 33, p. 34). The cells of the mesoblast on the inner side of the segmental cavity become columnar and form the muscle plate (Fig. 57). Each segment has its own muscle plate. The cells of each plate increase rapidly in number ; they spread into the somatopleure, and form the muscles of the body wall and limbs. Each cell becomes elongated and directed across its segment from septum to septum. The intercostal muscles retain this arrangement, but in the abdominal region the fibres fuse with those of neighbouring segments to form muscular sheets—the external oblique, internal oblique, transversalis and rectus. In the foetus of the fifth month traces of these septa may be seen ; Bardeen found that the intercostal nerves retained their segmental distribution in the muscles of the belly well. In fishes the embryonic segmental arrangement of the musculature persists. The manner in which the final groups of muscles are derived from the muscle plates is not accurately known, but in the typical segment with which we are at present dealing it will be seen that the musculature falls into two groups (see Fig. 57, *A*) : (1) **epaxial**, the erector spinae, etc. ; and (2) **ventro-lateral** or body-wall muscles (intercostals, rectus, oblique muscles, etc.). The musculature of the limbs is derived from the ventro-lateral group (Figs. 399, p. 412 ; 408, p. 421).

The ventro-lateral sheet separates into a **ventral longitudinal** band and a lateral transverse-oblique stratum. Each of these divides into an inner and outer **primary** layer ; the outer and inner **secondary** layers arise as delaminations of the primary layers, thus making four in all. The internal oblique and transversalis, and internal intercostal are derived from the internal primary layer ; the external oblique and external intercostal from the external primary layer. The rectus abdominis represents the deeper of the two layers derived from the

external primary. Parts of the deepest layer of the lateral sheet, represented in the adult by the transversalis, have migrated inwards to form the subvertebral or **hypaxial** muscles—the quadratus lumborum, crura of the diaphragm, longus colli, rectus capitis anticus major and minor, and the levator ani. When muscles migrate they invariably carry with them the nerves of the body segments in which they are developed. Hence the nerve supply affords the clue to the segments from which a muscle or part of a muscle arises. The middle layer of the lumbar fascia is developed between the epaxial and ventro-lateral musculatures.

Many of the ventro-lateral muscles (trapezius, rhomboids, and

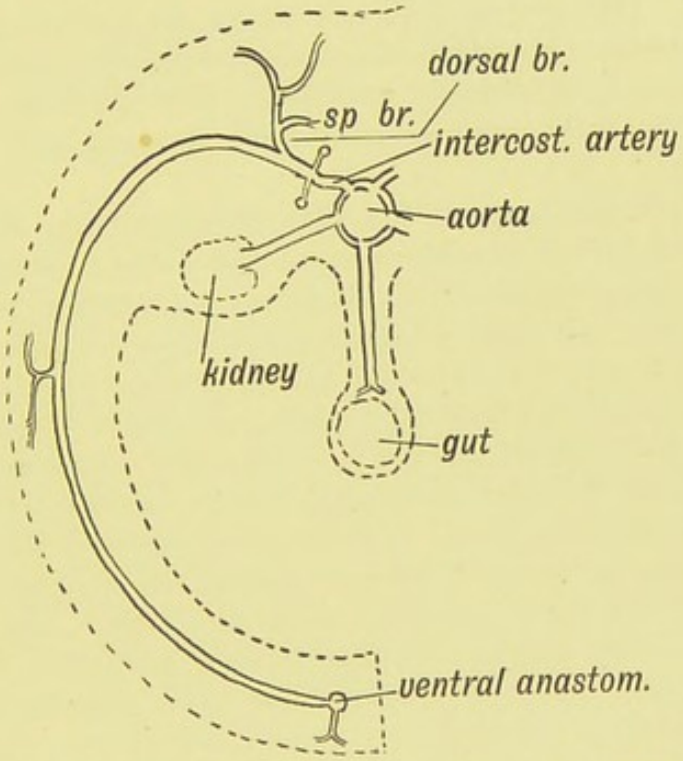


FIG. 58.—The distribution of a typical Segmental Artery.

latissimus dorsi), migrate dorsalwards over the epaxial muscles, and take origin from the spines of the vertebrae (Fig. 57, *A*).

Each muscle fibre is a cell derived from the endothelial cells which make up the muscle plate. The protoplasm of each cell is converted into a living contractile substance (myosin), which reacts to nerve stimuli. The nuclei of the fibres come to lie near the surface of the original cell. The number of fibres is complete at the 5th month; after then fibres grow in size only.

III. **The Arteries of the 11th Segment**[1] (Fig. 58).—The 11th intercostal is the artery of the segment. It gives off a dorsal branch to supply the epaxial muscles, the spinal column, spinal cord and mem-

[1] For segmental origin of arteries see: J. Broman, *Ergebnisse der Anat.* 1906, vol. 16, p. 639.

branes, and skin. The segmental artery joins at its termination with a ventral longitudinal vessel, the deep epigastric. The primitive arrangement in vertebrates appears to have been one with a dorsal and ventral longitudinal vessel, the segmental artery passing from the dorsal to the ventral vessel. The vertebral, ascending cervical, deep cervical, ascending lumbar and lateral sacral arteries are examples of the anastomoses that may arise between segmental arteries.

Segmental arteries also arise from the aorta to supply the structures formed from the intermediate cell mass (the kidney, testis, ovary, etc., Fig. 58). As a rule only one renal segmental artery persists, but frequently accessory renals are seen. These may be persistent embryonic vessels of the several segments from which the mesoblast of the kidney arose. The splanchnopleure shows no certain traces of segmentation ; hence its vessels (coeliac axis and mesenteric) if of segmental origin have become profoundly modified. Lately Broman has demonstrated that the splanchnic arteries have a segmental arrangement in the embryo.

IV. **The Nerve Elements of the 11th Segment** (Fig. 59).—Although the spinal cord during development of the human embryo shows no clear sign of being definitely divided into segments corresponding to those of the body, yet from what we know of its condition in embryos of other animals and from clinical evidence there can be little doubt that such a segmentation does take place, and that it possesses segments corresponding to those of the body. From each segment four groups of cells arise : (1) Somatic motor, (2) somatic sensory, (3) splanchnic motor, (4) splanchnic sensory. The motor groups for the greater part remain within the spinal cord, but many enter the sympathetic ganglia ; the sensory groups form ganglia outside the cord. The nerve fibres connected with the somatic groups have a diameter varying from 9-18μ ; those with the splanchnic, 2-9μ. The **somatic motor** group, in the anterior horn, sends out processes to all the muscles of the primitive body segment in which it is situated. The anterior root of a spinal nerve is formed by the somatic motor fibres. The **splanchnic motor** cells, in the lateral horn, send out processes within the splanchnopleure which reach viscera through the white rami communicantes and sympathetic system (Fig. 59, *A*).

At the point where the medullary plates are cut off from the epiblast to form the neural canal, a crest, **the neural crest,** grows out on each side (Fig. 59, *B*) composed of the cells which formed the junctional line between medullary plates and epiblast. A group of these neuroblasts—the **somatic sensory** group—grows into each segment and forms the **posterior root ganglion.** Each neuroblast within the ganglion sends out a process which bifurcates, one branch or fibre growing into the cord and ending in the posterior column and cells of the posterior horn, the other passing to the skin, muscles, etc., of the segment. The posterior nerve root is thus formed by the ingrowing processes from

the cells of the posterior root ganglion, and thus the body segment in which the outgrowing processes are distributed is brought into sensory communication with the central nervous system (see also p. 75). The anterior and posterior roots unite to form a spinal or segmental nerve. Like the artery, it divides into a posterior division for the epaxial part of the segment and an anterior for the ventro-lateral part (Fig. 59, *A*). The **splanchnic sensory** [1] groups are situated in the posterior root-

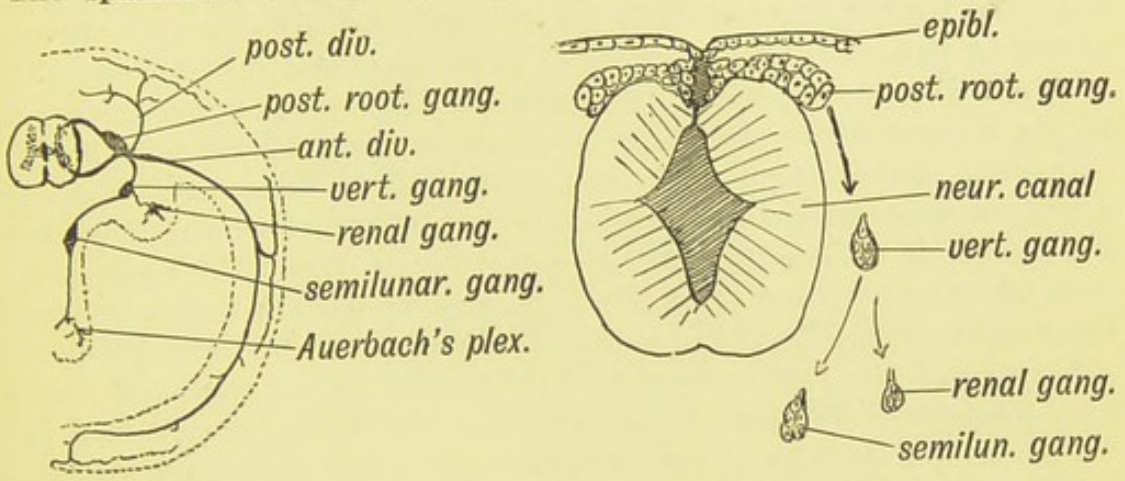


FIG. 59, *A*.—Diagram of the Nerve System of the 11th Dorsal Segment.
B.—A diagram showing the derivation of the Parts of the Nerve System of the 11th Segment in the Embryo.

ganglia, and probably also in the various ganglionic masses of the sympathetic system. These sympathetic cells are derived, with the posterior root ganglion, from the neural crest, and at first form a continuous paravertebral column (in 4th week). From the paravertebral column are differentiated :

(*a*) The prevertebral ganglion situated on the vertebra (in the gangliated chain), ventral to the exit of the spinal nerve ;

(*b*) A group to the intermediate cell mass (renal ganglion) ;

(*c*) Another to the splanchnopleure (in the semilunar ganglia) ;

(*d*) To the viscera (cells of Auerbach's plexus, etc.).

Groups (*c*) and (*d*) show no trace of segmentation in their arrangement, but, clinically, evidence is to be found that every viscus or part of a viscus is connected with certain segments of the spinal cord. The cells of the posterior root and sympathetic ganglia throw out axis-cylinder processes, which are connected with the spinal cord by fibres in a white ramus communicans and posterior root, and act as sensory pathways from the viscera. The distal end of the axis-cylinder process ends in a viscus. In this manner certain segments of the spinal cord are brought into touch with certain parts of the viscera. The vaso-motor supply of each body segment passes to it from the sympathetic ganglion by a grey ramus communicans.

It will thus be seen that all the parts of a segment—body wall (somatopleure), kidney (intermediate cell mass), and a part of the

[1] See Gaskell's original paper in *Journ. of Physiol.* 1886, vol. 7, p. 1.

abdominal or thoracic viscera (splanchnopleure) are connected by nerves to a corresponding segment of the spinal cord. In diseased conditions of any part of a body segment the corresponding spinal segment of the cord is disturbed. Such a disturbance is referred along the somatic sensory fibres, for the brain has no power to assign to their source impressions travelling inwards by the splanchnic sensory fibres. Thus, for instance, a stone in the pelvis of the kidney (which is supplied from the 10th, 11th, and 12th dorsal segments) is frequently accompanied by pain which the brain refers along the 11th and 12th intercostal nerves. The skin supplied by these nerves may become hyper-aesthetic. In the central nerve system as in the muscular, the primary simple segmental arrangement has been disturbed by enormous changes which have occurred in the process of evolution. In order to secure a harmonious co-operation of the various segments of the body, communications have been established, by means of nerve tracts, between the various segments of the spinal cord and between the segments of the cord and the higher centres of the brain. These communications have obliterated well nigh all traces of the primitive segments, and yet we see in the ganglia of the posterior roots and in the prevertebral ganglia of the sympathetic chain clear evidence that each segment of the body was originally provided with its own semi-automatic nerve mechanism. Clinical observation has supplied evidence that certain viscera—such as the heart, the liver, the kidneys—have a nervous correlationship with certain segments of the body, and we may infer that these organs have been evolved in connection with certain definite segments of the body.

Segments from which Splanchnic Fibres Escape.—The small medullated or splanchnic fibres do not arise from every spinal segment. Bishop Harman found that in man such fibres escape only by the roots of the dorsal nerves and first lumbar; occasionally splanchnic fibres come out in the roots of the last cervical and second lumbar. These fibres enter the gangliated chain, and are distributed to the viscera. Splanchnic fibres also escape by the 3rd sacral, frequently too from the 2nd or 4th, to form the nervi errigentes for the pelvic viscera. The greater part of the 9th, 10th and 11th cranial nerves is made up of splanchnic fibres. There are thus three visceral centres—an anterior or medullary, a middle or dorsal, and a posterior or sacral. How these centres came to be thus separated is not known.

Abnormal Segmentation.—In certain pathological conditions the process of segmentation is disturbed, with the result that an irregular and asymetrical separation of the segments take place. In Fig. 60 part of the spinal column and ribs are shown of a foetus in which the effects of such an irregularity is well illustrated. The vertebrae of the 3rd and 4th cervical segments are fused on the left side; the succeeding segments show many abnormalities of a similar kind. The bodies of the 1st and 2nd ribs of the right side are fused. In the same foetus the

pectoral muscles were imperfectly developed. In such foetuses one or both of the shoulders are placed high in the neck (**congenital elevation of the scapula**). Imperfect separation of two adjacent vertebrae

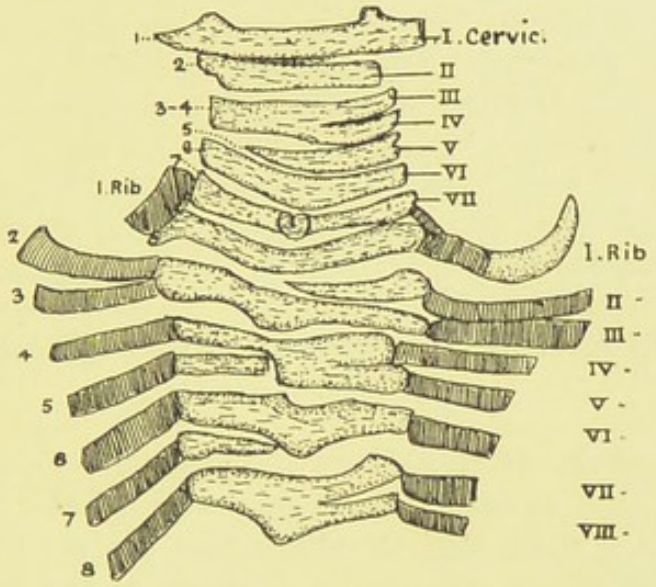


FIG. 60.—Cervical and dorsal parts of the Spine of a Human Foetus showing irregularities of segmentation.

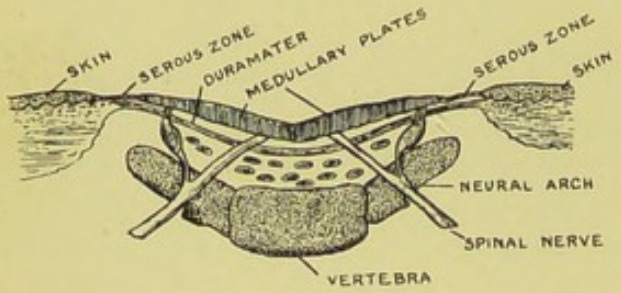
or ribs is occasionally seen—abnormalities due to a lesser irregularity of segmentation.

NOTE. While this edition was in press Professor Elliot Smith informed the author that he had evidence to show that the cells of the sympathetic ganglia which supply motor fibres to the visceral musculature are migrants from the anterior horn or basal lamina of the neural tube. The splanchnic motor fibres which escape by the anterior roots represent not root-fibres, but intraspinal tracts which have been drawn out in pursuit of their migrant motor cells.

CHAPTER VI.

CENTRAL NERVOUS SYSTEM—DIFFERENTIATION OF THE SPINAL CORD.

Evolution of the Central Nervous System.—To students who are familiar with the extraordinary complexity of the central nervous system of man it must seem incredible that it arose by the specialization of an area of the ectoderm or covering of the body. It is only on such a hypothesis that we can explain the fact that the medullary plates, out of which the whole central nervous system of the body is



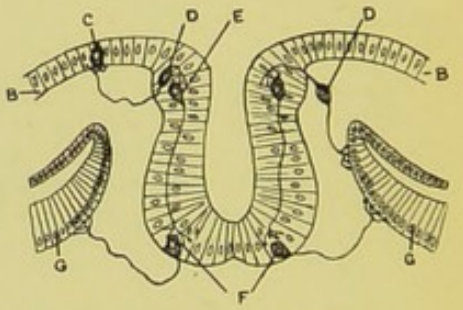


FIG. 61.—Diagrammatic Section across the Back of an Anencephalic Child in which the medullary plates were exposed on both head and spine.

FIG. 62.—Diagram to show how the ectodermal cells of the Medullary Plates are differentiated into nerve cells or neuroblasts and supporting cells or spongioblasts. (After Prenant.) The central canal is being enclosed by upgrowth of the medullary plates. *B*, *B*, ectoderm; *C*, sensory cell in ectoderm; *D*, *D*, cells which become enclosed in posterior root ganglion; *E*, *E*, nerve cells which connect the sensory and motor cells; *F*, *F*, motor cells in anterior horn; *G*, *G*, muscle plates.

developed, are exposed on the surface of the embryo during a part of the 3rd week of development. It occasionally happens that children are born, in which the medullary plates are exposed along the head and back as they are during very early embryonic life. The condition is shown in Fig. 61, and it is impossible to explain the condition except by supposing the medullary plates are modified parts of the ectoderm. When, however, one remembers the condition in the lower invertebrates, such as is seen in the organization of the Hydra, the explanation becomes more acceptable. The ectodermic cells of Hydra are not only

protective and secretory in function, but they also serve the purposes of nerve cells and muscle cells. One can understand how a specialization of function in the ectodermal cells may have occurred—some becoming purely contractile, others purely sensory, or secretory, or protective. In the cells of the medullary plate we see a further specialization (see Fig. 62); cells are specialized to connect the sensory with the contractile or muscle cells. Those connected with the sensory cells—the posterior root ganglia—arise near the lateral margins of the medullary plates; those connected with the muscle cells arise near their mesial margins. If this hypothesis is true, then the central canal is merely an enclosed tube of ectoderm and filled with fluid, because the form of animal in which the medullary plates were evolved was a water-living form. Dr. W. H. Gaskell has advanced the view that the

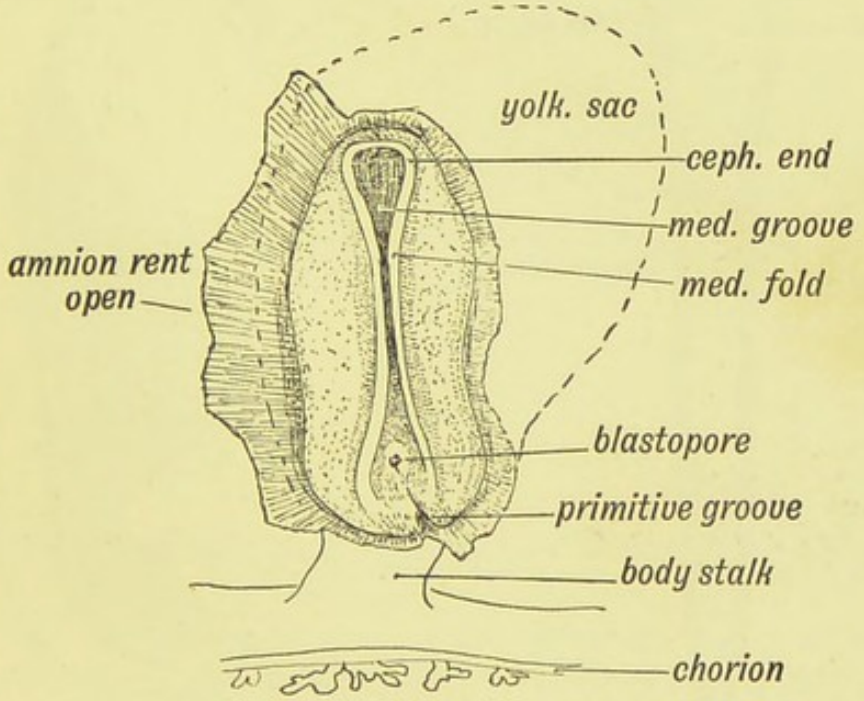
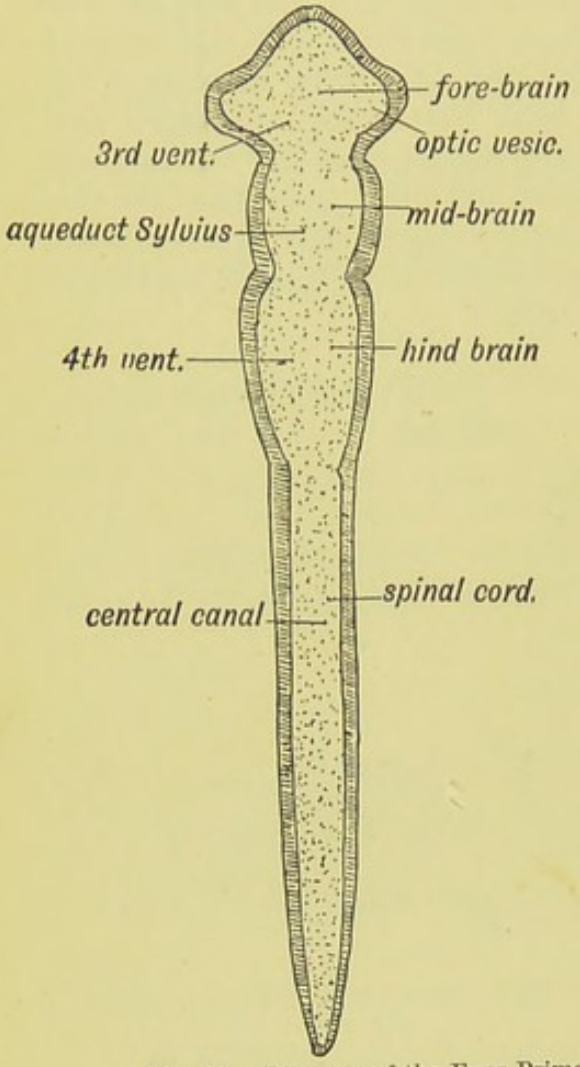


FIG. 63.—Medullary Folds uniting to form the Neural Tube in a Human Embryo of about 14 days. (After Graf Spee.)

central canal represents a former alimentary tube round which nerve cells have gathered. While Dr. Gaskell's hypothesis explains many facts, it leaves many more unexplained—especially the manner in which the central nervous system is developed.

Formation of the Central Canal.—The medullary plates of ectoderm, which form the spinal cord and brain, rise up, meet, and enclose a canal—the central canal of the spinal cord and brain (Fig. 63). The lips of the medullary plates meet and fuse together in the cervical region first (Fig. 63), the process of union spreading forwards and backwards, the last parts to be enclosed being the cephalic and caudal extremities. The opening at the anterior extremity—the **neuropore**—and the posterior or **caudopore** close towards the end of the 3rd week,

the neuropore closing first. The optic vesicles begin to grow out from the medullary plates before these have united to enclose the cavity of the fore-brain. It will be thus seen that the optic vesicle, which becomes the retina and optic nerve, is developed as a part of the medullary plate.



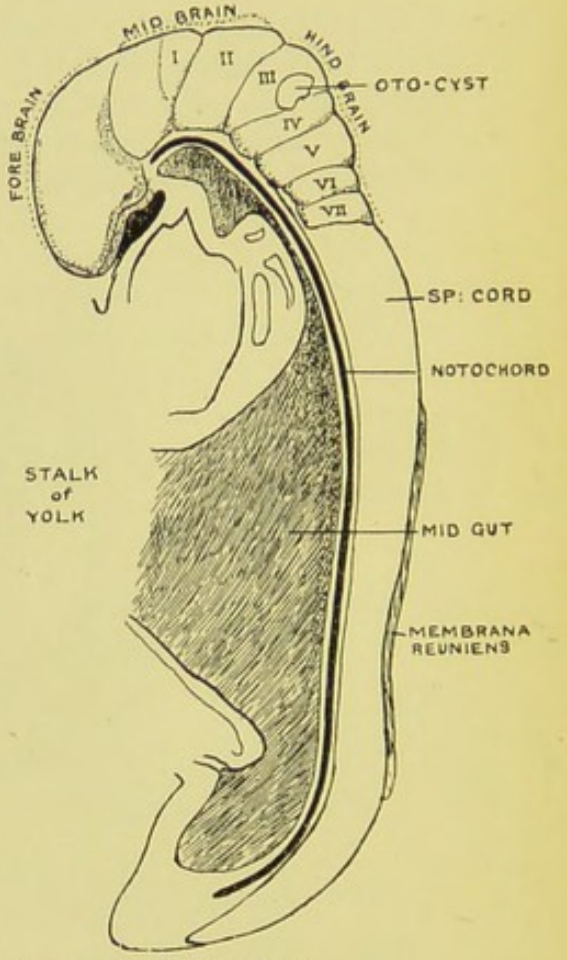


FIG. 64.—Diagram of the Four Primary Divisions of the Neural Tube.
FIG. 65.—Lateral View of the Central Nerve System of a Human Embryo of the 3rd week—3 mm. long. (Dr. Low.)[1]

Divisions of the Neural Canal (Figs. 64, 65).—At the end of the 3rd week the neural tube is divided into four parts. They are :

(1) An anterior dilatation, the fore-brain, which forms the 3rd and lateral ventricles and their walls.

(2) The mid-brain, which becomes transformed into the aqueduct of Sylvius, corpora quadrigemina and crura cerebri.

(3) The hind-brain, the basis of the 4th ventricle, pons, cerebellum and medulla.

(4) The central canal and spinal cord.

[1] For segmentation of hind- and mid-brain see : A. Meek, *Anat. Anz.* 1910, vol. 36, p. 560.

The Spinal Cord.—**The Spinal Cord** at first extends throughout the whole length of the spinal column. After the 3rd month the spinal column and canal grow more rapidly than the cord, and at birth its lower end has become withdrawn to the level of the 3rd lumbar vertebra. By the third year it only reaches the disc between the 1st and 2nd lumbar vertebrae. The results of this inequality of growth are :

(1) The roots of the lumbar and sacral nerves become enormously elongated, forming the cauda equina ; all the nerves are more or less drawn up, except the 1st and 2nd cervical ; the origins of the lower cervical nerves are drawn up 2 vertebrae (as indicated by the position of their spines) ; the upper dorsal, 3 ; the lower dorsal, 4 ; the lower

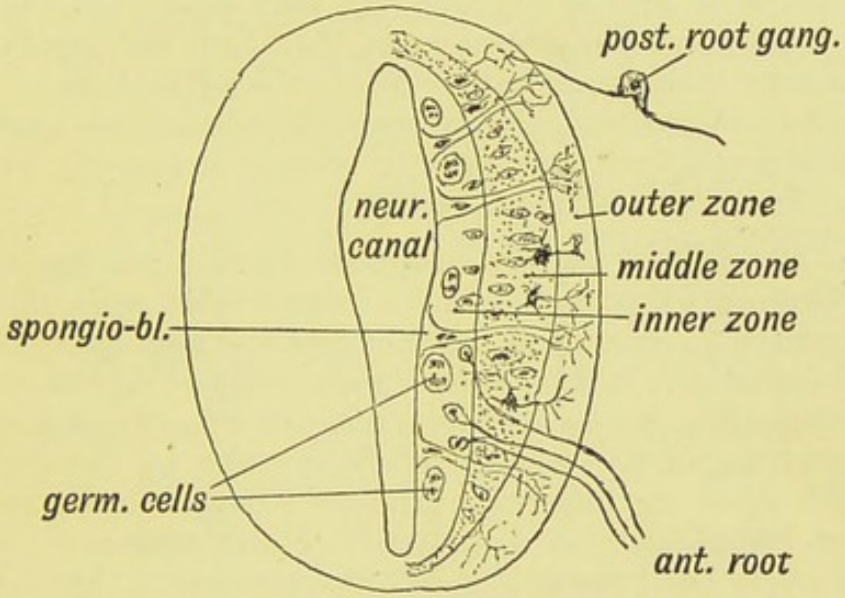


FIG. 66.—Diagrammatic Section showing the three Zones of the Spinal Neural Tube at the 6th week.

lumbar, 5 ; the coccygeal, 10. These statistics represent a broad expression of the observations made by Professor R. W. Reid.

(2) As the caudal termination of the neural canal is never separated from the epiblast over the coccyx, the posterior end of the cord with its pial covering (mesoblast) is pulled out into a fine string—the **filum terminale.** The neural canal extends for some way into the filum terminale, lined by a single layer of columnar epithelium and surrounded by pia mater, and in the foetus shows there a dilatation or ventricle. The arachnoid and dura mater, mesoblastic sheaths of the cord, do not suffer in the retraction of the cord ; they remain widely open to the level of the 2nd sacral vertebra.

Neurenteric Canal.—The caudal ends of the medullary plates fold over and include within the neural canal the blastopore (Figs. 63, and 18, p. 16). The blastopore occurs at the anterior end of the primitive streak and marks the point at which the cavity of the hypoblast (that part which becomes the hind-gut) opens on the epiblast. There is thus set up a communication between the neural canal and

the gut to which the name of neurenteric canal is given. The neurenteric canal also opens into the posterior end of the canal of the notochord. It is purely a temporary structure, having completely disappeared by the end of the 3rd week.

Differentiation of the Spinal Part of the Neural Tube.—When the medullary plates close in at about the 15th day, to form the neural tube, the single layer of elongated epithelial cells, of which they were originally composed, is already differentiating into several cells deep. By the **6th week** these cells have undergone the following changes (Fig. 66).

(1) Some become **neuroglia,** elongated and branched supporting cells; in the **outer zone** of the tube wall they form a mesh-work; in the **inner zone,** round the central canal, they form the ependyma; in the **middle zone** their interstices are filled with neuroblasts.

(2) The majority of the cells become differentiated into **neuroblasts.** These are produced from germinal cells lying in or near the inner zone (Fig. 66). Two points should be noted:

(*a*) That the cells in the **roof** and **floor** scarcely undergo any proliferation—they retain for a considerable time the simple embryonic shape, and form the **roof** and **floor plates** (Fig. 68).

(*b*) The neuroblasts in each lateral plate multiply rapidly and mass themselves in two great columns (see Fig. 68), and with this grouping of the cells, which is apparent by the end of the 4th week, the important primary division of each medullary or lateral plate into a dorsal, or alar **sensory** part and a ventral, basal **motor** part becomes apparent. One can be certain that all the neuroblasts and their processes or fibres which arise in the ventral part are efferent or motor in function; all in the dorsal part are afferent or sensory in nature. Further, the visceral or splanchnic neuroblasts come to lie in an intermediate position—between the dorsal and ventral zones. In each lateral plate the neuroblasts are grouped thus from anterior to posterior horn (1) somatic motor; (2) splanchnic motor, (3) splanchnic sensory, (4) somatic sensory. That order of grouping holds good from end to end of the neural canal. The neural crests, from which the spinal and sympathetic ganglia arise, clearly represent detached parts of the sensory lamina. By the end of the 4th week the neuroblasts of the anterior horn have commenced to form the anterior roots, and soon after the posterior roots arise from the spinal ganglia and enter the dorsal lamina.

The changes which occur in the Spinal Cord **after the 6th week** are mainly connected with the production of processes or fibres from the neuroblasts. By these fibres the neuroblasts are joined up with all parts of the body by means of nerves, while the various parts and seg-

ments of the central nervous system are linked and co-ordinated by nerve tracts. We have seen that the outer zone of the neural tube is composed chiefly of a fine sponge-work or scaffolding, along which the nerve tracts grow. The main developmental changes at this time are :

A. **In the Outer Zone :**

(1) Postero-mesial and postero-lateral columns are produced by the fibres developed from the ganglion cells of the posterior roots. They become myelinated about the 6th month.

(2) To the inner side and to the outside of the anterior horn, fibres are produced from cells in the anterior horn, which connect together neighbouring spinal segments (association fibres).

(3) Two tracts of fibres grow out from cells in the grey matter of the cord and go to the cerebellum. They are the direct cerebellar

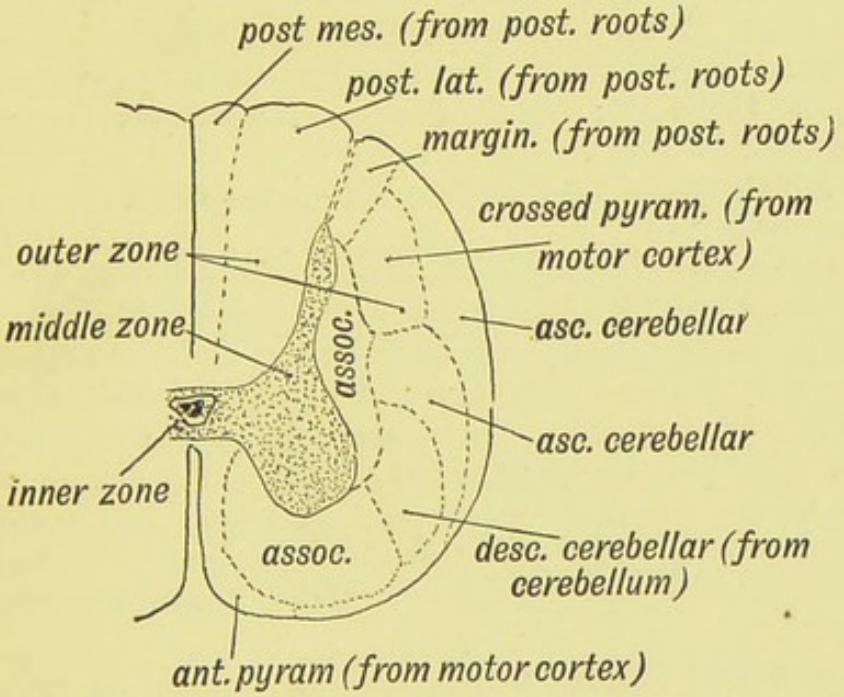


FIG. 67.—Diagrammatic Section of the Spinal Cord to show the Parts formed in the three Zones of the Embryonic Spinal Cord.

tract (Flechsig's) from the cells of Clarke's column, and Gower's tract from cells at the base of the opposite posterior horn.

(4) Fibres produced by the cells of the vestibular and olivary nuclei grow downwards outside the anterior horn (intermediate tract). All these tracts are medullated or myelinated before birth.

(5) The pyramidal tracts (crossed and direct) grow down from the cells of the motor cortex. They are not medullated until soon after birth.[1] The pyramidal tracts are the means by which the brain controls the motor cells of the cord. In man these tracts are remarkable,

[1] Florence R. Sabin, *Amer. Journ. Anat.* 1911, vol. 11, p. 113 (Model of Tracts medullated at Birth) ; J. P. Good, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 391

not only for their great size, but also that besides the crossed lateral tract, which is present in all mammals, there is also an anterior or direct tract. The anterior tract appears to be a recently evolved system; it is extremely variable in size. The only other animals which possess it are those nearest allies of man—the great anthropoid apes.

The white matter of the cord is thus entirely produced by the ingrowth of nerve fibres within the neuroglial network of the outer zone. The cerebral motor cortex, through the pyramidal tracts, comes to dominate the cord; sensory and cerebellar paths are formed, and intercommunications set up between the spinal segments.

The **Anterior Median Fissure** is produced by the growth of the white matter. The posterior median septum becomes apparent towards the end of the 2nd month. The central canal, between the sensory or dorsal laminae, becomes occluded by their apposition and fusion, the permanent canal of the cord thus representing only the ventral part of the original lumen of the neural tube. Some grey matter still remains round the canal; the anterior or white commissure is formed in the floor plate (Fig. 68).

B. The **Middle Zone**—filled with neuroblasts—forms the horns and grey matter of the cord.

C. The **Inner Zone** becomes the ependyma which lines the central canal and the gelatinous tissue which surrounds it. With the formation of the posterior columns, the grey matter of the dorsal laminae, at first united by the roof plate, becomes widely separated to form the posterior horns (Figs. 67, 68). At the same time part of the gelatinous tissue of the inner zone is separated to form a cap on the posterior horns (Fig. 68). In the gelatinous tissue congenital cysts may occur. The columnar cells which line the central canal are ciliated. The central canal retains the embryonic calibre while the wall increases enormously in thickness.

Segments of the Spinal Cord.—To that part of the neural tube and neural crest which corresponds in position to a primitive body-segment, the name of **Neuromere** is given. From the cells of a neuromere are produced the posterior and anterior root of a spinal nerve on each side. The extent of each neuromere is thus marked out by the attachments of its nerve roots. At no time are the medullary plates divided into embryological segments in the same sense as the mesoblast is divided, although the neural tube probably did arise from the fusion of a series of neuromeres or ganglia, each presiding over a definite segment of the body, subsequent evolutionary changes have led to their fusion. These changes are related to the combination of the various segments and systems in carrying out the functions of the

(Spina Bifida in Embryo Rabbit); J. Voigt, *Anat. Hefte*, 1906, vol. 30, p. 393 (Spina Bifida); A. F. Dixon, *Dublin Journ. Med. Sc.* 1907, July (Explanation of Crossing of Pyramidal Tracts).

body. The cervical and lumbar enlargements of the cord appear in the 4th month. They contain the neuroblasts connected with the body segments which gave rise to the upper and lower extremities. The neuroblasts are arranged, not according to the original neural

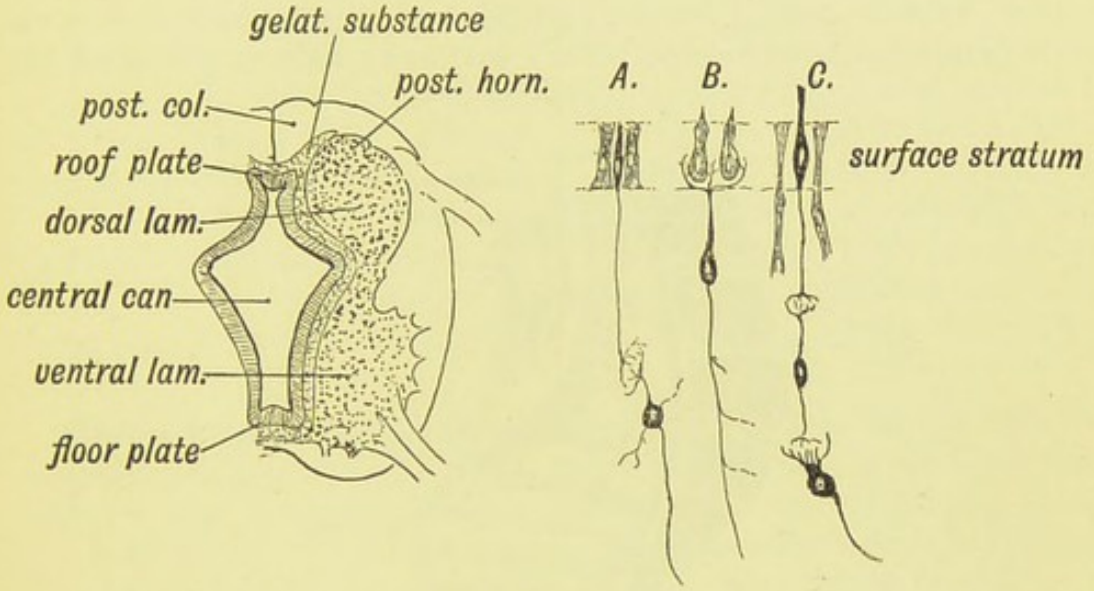


FIG. 68.—Diagrammatic Section of the developing Spinal Cord to show (1) the Roof and Floor Plates; (2) the Dorsal (alar) and Ventral (basal) Laminae; (3) the Gelatinous Tissue between the Middle and Inner Zones.

FIG. 69.—Showing Transformation of Cells of the Ectoderm to Sense Epithelium, Nerve Cells and Supporting Cells, in *A*, the Olfactory Plate, *B*, the Otocyst, *C*, the Retinal Layer of Optic Cup.

segments, but rather in relationship to the movements of the limb. The group representing the hand movements lie behind (distal to) those representing movements of the forearm.

Origin of the Medullary Plates and Nerve Cells.—The medullary plates like the olfactory plates which give rise to the sense-epithelium of the nose, the otocyst from which the auditory organ is developed, and the retina are derived from the ectodermal covering of the embryo. The olfactory plate retains to the greatest extent the features of the ectoderm (Fig. 69, *A*). Its cells are of three kinds: (1) protective, (2) secretory, (3) sensory, the latter being essentially surface nerve cells in nature. A process or axis cylinder is produced from each sense cell; from its opposite extremity a sensory process is produced (Fig. 69, *A*). In worms, sense epithelial cells sink beneath the protective and secretory cells, the sensory process being drawn out to form a fibre. In the otocyst, the sensory cells produce no axis-cylinder process, but a ganglionic cell—produced from the ectoderm through the neural crest—comes into connection with it (Fig. 69, *B*). From the ganglionic cells are produced (1) a chief process or **axis cylinder**; (2) a branching process or processes—**dendrites**—from the opposite pole, which end in an arborescence round the sensory cells. To a nerve cell

and all the processes developed from it the name of **Neuron** is given. In the retina, as in the olfactory plate, three types of cells are seen: (1) protective or supporting which form the fibres of Müller, (2) secretory over the ciliary processes, (3) the sensory cells, which produce an axis cylinder on one side, and a rod or cone on the other (Fig. 69, *C*). Further, by a process of division, bipolar and ganglionic cells are produced from the retinal sense cells. In the medullary plates of the

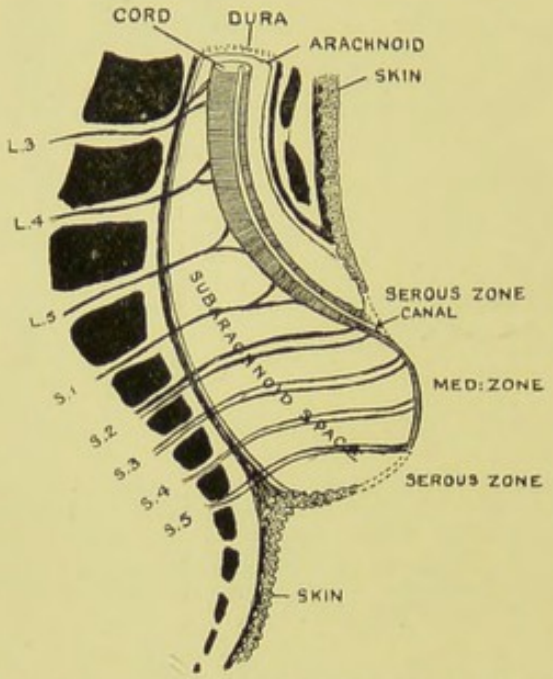


FIG. 70.—Vertical Section of the Lumbar Region to show the arrangement of parts in a typical case of cystic spina bifida.

spinal cord the representatives of the original ectoderm form the ependymal and neuroglial cells, the first of which may be regarded as both secretory and supporting; the neuroblasts arise by a process of division from the primary ectodermal cells. Each neuroblast gives rise to a neuron. Their axons or axis cylinders are in many cases two feet or more in length; for instance, the motor and sensory fibres which pass from the lumbar enlargement to the muscles and skin of the foot. The nerve cells in the basal laminae are peculiar in that their axis cylinders end on muscle cells.

Malformations of the Neural Canal.[1]—The fact that children are occasionally born with the medullary plates open and exposed on the head and back has already been mentioned (see Fig. 61). **Total Rachischisis,** as the condition is named, is rare; it is much more usual to find only one part of the neural tube open—either the anterior or cephalic part, giving the condition known as **Anencephaly**—absence

[1] Malformations of neural tube; see references on p. 72.

of brain, or the posterior or lumbo-sacral part, giving the condition known as **cystic spina bifida.** The latter condition is shown in Fig. 70. As the spinal cord is followed down, it is seen to enter a cystic structure formed by a dilatation of the subarachnoid space, across which the roots of the lumbo-sacral nerves pass. The projecting dome of the cyst is formed by the expanded medullary plates; hence the spinal cord appears to end on the wall of the cyst, and spinal nerves actually arise from it. The lumbo-sacral parts of the neural tube and of the spine have never been enclosed; the cerebro-spinal fluid collects in the subarachnoid space, and the unresisting medullary plates are raised up to form part of the wall of a cystic tumour. Another form of pathological dilatation may appear after the neural tube is completely closed. In chicks hatched at abnormal temperatures fluid may collect in certain parts of the tube, thus dilating it and giving rise to cystic conditions.

Membranes and Vessels of the Cord.—When the neural tube is enclosed towards the end of the 3rd week by the upgrowth of mesoblast in the medullary folds, mesenchymal cells become applied to the neural tube. They form the primary sheath of the neural tube. The sheath receives a vascular supply from each dorsal branch of the segmental arteries and veins. Branches of the vessels perforate the nerve tissue, and thus a vascular mesoblastic element is added to the epiblastic neural laminae. By the middle of the second month the primary sheath has become cleft into an inner or pial layer, and an outer or arachno-dural layer. The cleft becomes the subarachnoid space, which is apparently of the nature of a lymphatic space.

Development of Nerves.[1]—In lower fishes Kupffer found that nerve fibres were formed by the union of a chain of cells—probably ectodermal in origin, and many suppose that the nerve fibres of all vertebrates are formed in this manner, the nuclei of the chain-cells becoming the nuclei of the neurilemma. On the other hand His and Kölliker concluded that every nerve fibre is produced as a continuous outgrowth from one nerve cell, and that the cells of the sheath are mesoblastic in origin. It is possible that both interpretations of the appearance presented by developing nerves are right, and that one kind of nerve fibre is produced in the first manner and another kind in the second manner. The opinion generally held at the present time is that an axis cylinder is the product of one nerve cell or neuroblast, and that the cells which surround the growing fibres and form their sheaths are derived from the neural crests, and are therefore ectodermal in origin. It is maintained by Dr. John Cameron that these surrounding cells assist in the deposition of an achromatic substance at

[1] Recent papers on histogenesis of nerves: R. G. Harrison, *Amer. Journ. Anat.* 1905, vol. 5, p. 191; W. H. Lewis, *Amer. Journ. Anat.* 1906, vol. 6, p. 461; J. Cameron, *Journ. Anat. and Physiol.* 1905, vol. 41, p. 8.

the growing points of nerve fibres (*Journ. Anat. and Physiol.* 1906, vol. 41, p. 8). Dr. Ross Harrison found that when small parts of the medullary plates of tadpoles were transplanted or maintained alive in artificial media the outgrowth of the neurons as processes from single cells could be witnessed (*Anat. Record*, 1908, vol. 2, Nos. 9, 10).

Another theory receives support from Graham Kerr's recent investigations on Lepidosiren, viz. that nerve fibres are formed by the stretching of original protoplasmic connections which exist between nerve and muscle cells.

CHAPTER VII.

THE MID- AND HIND-BRAINS.

When the neural tube is traced forwards into the head region, it is seen to undergo a marked change in form—a transformation due to a change in function. In the spinal cord the nerves arose in two rows—a dorsal sensory and a ventral motor; here the dorsal and ventral series are still represented, but a third or intermediate series has been added. This series is represented by the spinal accessory (XI), vagus (X) and glossophangeal (IX, VII, V) nerves. They arise from an intermediate column of cells representing in an exaggerated degree the splanchnic or visceral nerve columns of the spinal cord. Further, the central canal becomes enlarged to form the 4th ventricle. Part of the roof of the neural tube becomes reduced to a membranous lamina, forming the medullary velum and choroid plexus—a secretory mechanism. Part of the roof is specialized to form a complex mechanism (the cerebellum) for the co-ordination of the motor cells of the spinal cord. This high degree of specialization almost obliterates the original simple nature of that part of the neural tube which forms the mid- and hind-brain. In the human embryo of the 3rd week (Fig. 65, p. 68) it is seen that this part of the central nervous system retains its tubular character, and shows a segmentation into seven neuromeres, two of which form the mid-brain, while five are included in the hind-brain. On each side of the floor of the hind-brain there are to be seen, during embryonic life, a series of six transverse grooves. Their meaning is not quite clear (see Streeter, *Anat. Record*, 1908, vol. 11, p. 111). Further, the neural tube in the regions of the mid- and hind-brain, as in the spinal cord, lies over the notochord (Fig. 65). The notochord ceases at the junction of the mid- and fore-brains.

That part of the neural tube which forms the hind-brain (Fig. 64) becomes transformed into:

(1) The Medulla Oblongata.
(2) The Pons Varolii.
(3) The Cerebellum.

The Fourth Ventricle.—The cavity or neural canal of the hind-brain becomes the fourth ventricle. In its floor are developed, out of the **basal** or **ventral** and **alar** or dorsal **laminae** (Fig. 71) of the medullary plates, the pons and medulla. In its roof are developed the cerebellum and the superior and inferior medullary vela.

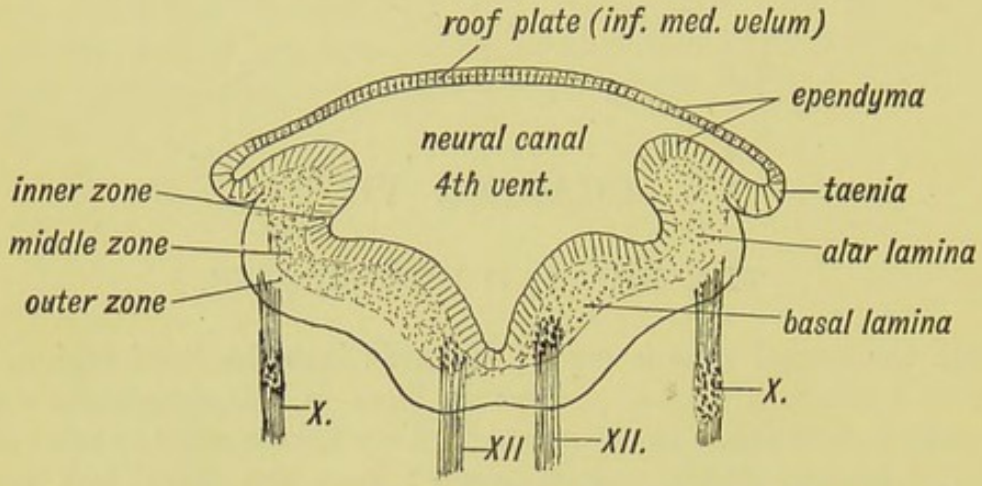


FIG. 71.—Section across the Hind-Brain of a Human Embryo in the 5th week.

Basal and Alar Laminae of the Medulla.—The basal and alar laminae of the neural tube become flattened out to form the floor of the hind-brain. The nuclei formed within them which are connected with motor and sensory *splanchnic* nerves, become highly developed and can be distinguished by their position from other nuclei which are connected with the *somatic* sensory and somatic motor nerves. The nuclei [1] connected with the splanchnic motor and sensory nerves (VII, VIII, IX, X, XI) are situated in the adjacent parts of the basal and alar laminae (Fig. 72, *A*) ; the nuclei connected with the somatic motor (XII) and somatic sensory (V) lie in the median part of the basal lamina and the lateral part of the alar laminae (Fig. 72, *A*). This primary relationship is obscured by the occurrence of : (1) a folding over of part of the alar lamina (Fig. 72, *B*) which buries the sensory roots of the splanchnic (ascending root of the IX and X) and somatic nerves (descending root of V) ; (2) migration of cells from the alar laminae to form the olivary bodies and probably also the nuclei of the pons in the basal laminae ; (3) development of cerebral and cerebellar tracts in both laminae.

Inferior Medullary Velum.[2]—When a section is made across the posterior half of the hind-brain of a fifth week human embryo (Fig. 71),

[1] G. L. Streeter, *Anat. Record*, 1908, vol. 11, No. 3 ; *Amer. Journ. Anat.* 1909, vol. 4, p. 83 ; C. R. Essick, *Amer. Journ. Anat.* 1912, vol. 13, p. 25 (Dev. of Pontine Nuclei).

[2] Some recent papers dealing with the development and morphology of the hind-brain are : J. T. Wilson, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 210 (Junction of Central Canal and 4th ventricle) ; G. Elliot Smith, *Rev. Neurol. and*

the same parts are seen as in a section of the cord. The only difference is that the roof plate, which in the cord is narrow (Fig. 68), is here very wide and thin. In the roof plate over the anterior half of the 4th ventricle is developed the cerebellum and superior medullary velum; over the posterior half, the roof plate forms the inferior medullary velum.

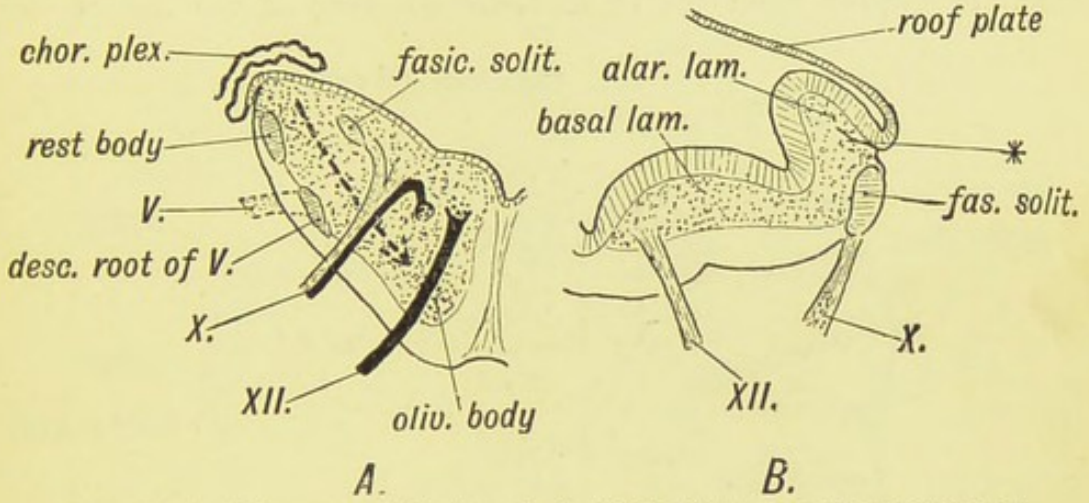


FIG. 72, *A*.—Diagrammatic Section of a Foetal Medulla to show the relative positions of the Nuclei connected with the Somatic and Splanchnic Nerves, and the Origin of the Olivary Body. The Motor Nerves, both Somatic and Splanchnic, are represented black. The arrow indicates the route of migration of the Cells of the Olivary Body.

FIG. 72, *B*.—The Alar and Basal Laminae of the Hind-Brain at the beginning of the 6th week to show the superficial position of the sensory root of the Vagus. (Compare with *A*.) The point at which the root of the 5th Nerve and Restiform Body will be formed is indicated by an asterisk. (After His.)

As shown in Fig. 73, the velum is continuous with the cerebellum above and the roof of the central canal of the cord below. In the posterior margin of the cerebellar rudiment are developed: (1) the nodule, (2) the flocculus, (3) the peduncle of the flocculus between 1 and 2 (Figs. 74, 77). Hence the inferior medullary velum ends above in these structures.

The obex and ligula, thickenings or ridges found on the margins of the 4th ventricle, mark the attachment of the roof plate or velum to the alar laminae of the medullary plates. They represent the attached margin of the velum. The velum is also attached to the restiform body which is developed in the upper margin of the alar lamina. Over the opening of the central canal of the spinal cord into the 4th ventricle there is often a fold formed by the union of the alar laminae (see J. T. Wilson, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 210).

The velum is to be regarded as a part of the neural tube, specially modified for the purpose of secreting the cerebro-spinal fluid which

Psych. 1903, vol. 23, p. 368 (Morphology of Cerebellum); O. Charnock Bradley, *Journ. Anat. and Physiol.* 1905, vol. 40, p. 1 (Dev. of Cerebellum), J. W. Langelaan, *Anat. Anz.* 1908, vol. 32, p. 421; P. Thomson, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 134 (Foetal Brain of Cat).

fills the central canal and subarachnoid systems. This fluid may help to support the central nervous mass in a mechanical sense, but its rapid secretion, its circulation and chemical composition point to some more important nutritive or regulatory influence on the neural centres. The ectodermal cells retain the primitive columnar type, and form an epithelial covering over inflections and processes of the pia mater which is derived from the mesoblastic covering of the neural tube.

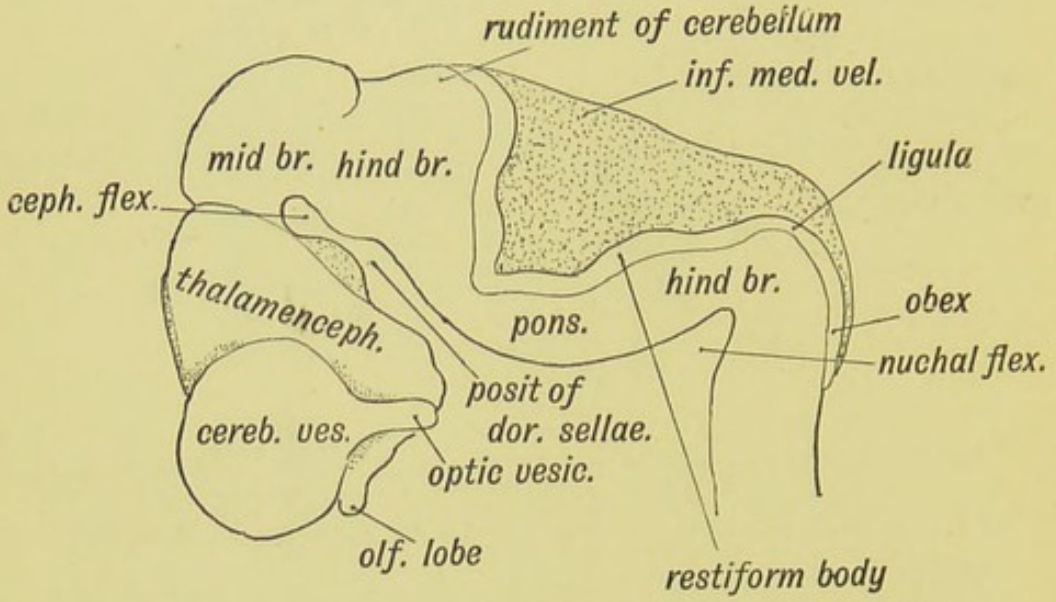


FIG. 73.—Lateral View of the Cephalic Part of the Neural Tube in a 5th week human embryo. (After His.)

The foramen of Majendie and openings at the lateral recesses of the 4th ventricle are produced secondarily by outgrowths of the choroid plexuses into the neighbouring subarachnoid spaces. By means of these openings the lumen of the neural tube is brought into communication with the subarachnoid spaces. As will be seen from Fig. 73, the neural tube is bent with its convexity forwards at the pons. His has suggested that this bend may have something to do with the production of the wide roof plate of the 4th ventricle, for if a piece of tubing be bent so, the part in the concavity of the bend becomes widened out.

Cerebellum.[1]—The basis of each half of the cerebellum is developed as a plate or fold from the dorsal laminae of the anterior part of the hind-brain. The lateral cerebellar plates fuse on the anterior part of the roof plate or velum of the hind-brain—the bridge thus formed becoming the vermis. The condition of the cerebellum in a 4th week human foetus resembles that of the Frog (Figs. 74 and 75). It is then merely a thickened transverse band in the anterior part of the roof plate of the 4th ventricle. Towards the end of the 3rd month the cerebellar plate becomes demarcated into **anterior, middle,** and **posterior**

[1] I have followed the accounts of the cerebellum given by Elliot Smith, Charnock Bradley, Kuithan, Bolk and Stroud (see references, p. 78).

primary lobes, these being separated by two transverse grooves or fissures—the first and second fissures (Elliot Smith). Since these three primary divisions are to be recognized in nearly all mammalian cerebelli, they must be of fundamental importance. Quickly succeeding these two primary fissures there appear two others, one which

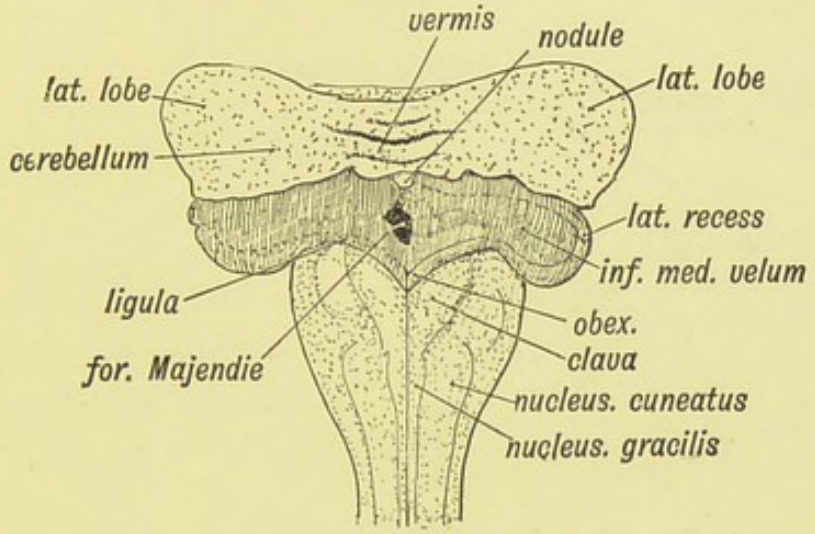


FIG. 74.—Diagram of the Attachments of the Inferior Medullary Velum in a 5th month foetus. (After Kollmann.)

divides the median part of the posterior lobe—the post-nodular fissure —and the other the anterior lobe (Figs. 76, 77). The post-nodular fissure may appear in the human brain before the *fissura secunda.* Thus, in the fifth month four fissures are seen to be developed in the

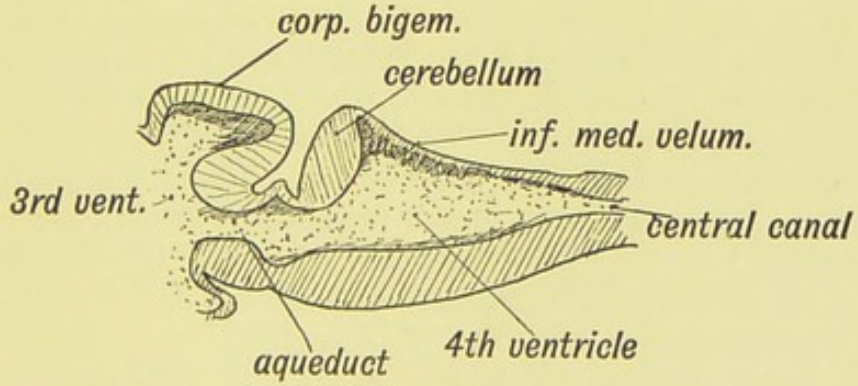


FIG. 75.—Medium Section of the Cerebellum and 4th Ventricle of a Frog.

human cerebellum (Fig. 76). The rapid growth of the cerebellum, with the pressure of the cerebrum above or in front, and the resistance of the occipital bone below or behind cause the plate-like form to be replaced by one which is wedge-shaped in section, with an upper and lower surface. The minor sulci and fissures of the cerebellum appear between the 5th and 7th months of foetal life.

Parts derived from the Posterior Primary Lobe (Figs. 76, 77, *A*, *B*).—From the median part arise the nodule and uvula separated by the post-nodular fissure. From the lateral parts arise the flocculus and para-flocculus, which represent the oldest of all the distinctive parts of the cerebellum, and the first to become differentiated in the human organ. The para-flocculus, part of which fills the subarcuate fossa in

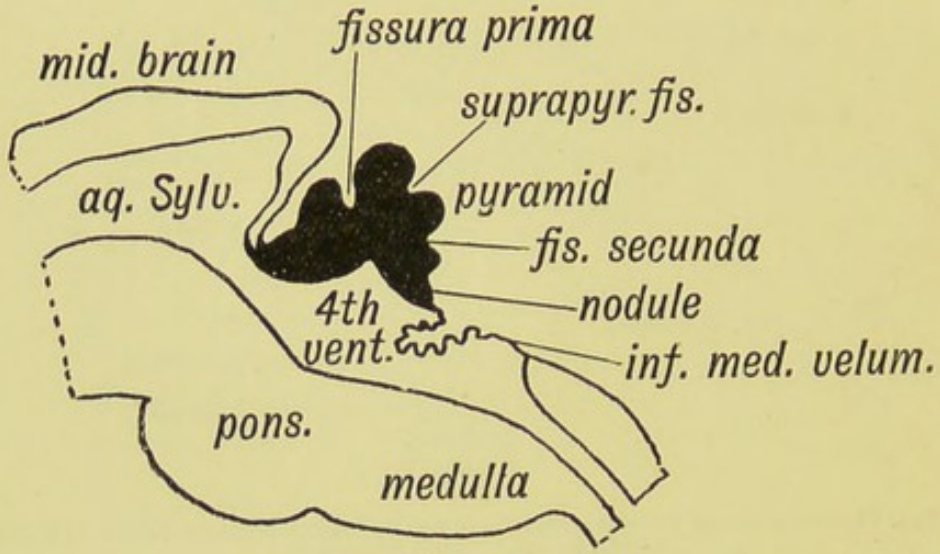


FIG. 76.—Diagrammatic Section of the Cerebellum of a Human Foetus about the end of the 4th month showing the folding of the Cerebellar Plate. (After Kuithan and Elliot Smith.)

the temporal bone (p. 217), becomes reduced to a vestige in man and the anthropoids (Fig. 77, *A*).

Parts derived from the Anterior and Middle Primary Lobes (Figs. 76, 77, *A*, *B*).—From the anterior primary lobe arise the lingula, central lobe, and alae, the culmen and the anterior crescentic lobes. The rest of the cerebellum, comprising by far its greater part, arises from the middle lobe. The median part forms the pyramid and the clivus, separated by a deep fissure. The lateral parts undergo an enormous development in higher primates. In man the tonsil and biventral lobe attain a very great size. The great development of the lateral parts of the middle primary lobe leads to the formation of the great horizontal fissure (see Figs. 77, *A* and *B*).

The **Superior Medullary Velum** is part of the roof plate of the 4th ventricle which remains between the superior peduncles. The vestigial laminae which cover it form the lingula (Fig. 76).

The three Peduncles of the cerebellum are produced thus—probably during the latter half of intra-uterine life :

(1) The **Superior.**—Fibres grow from the cells of the dentate nucleus of the cerebellum—probably also from the cortex—to the red nucleus and optic thalamus on the opposite side of the brain. Some of the ascending antero-lateral cerebellar fibres from the cord probably enter

the cerebellum by the superior peduncles. In this manner the cerebellum is connected with the sensory ganglia at the base of the brain.

(2) The **Middle Peduncles** are formed by processes which grow from the cortical cells of the cerebellum to the nuclei of the pons, and also by processes from the cells of the pontine nuclei to the cerebellum.

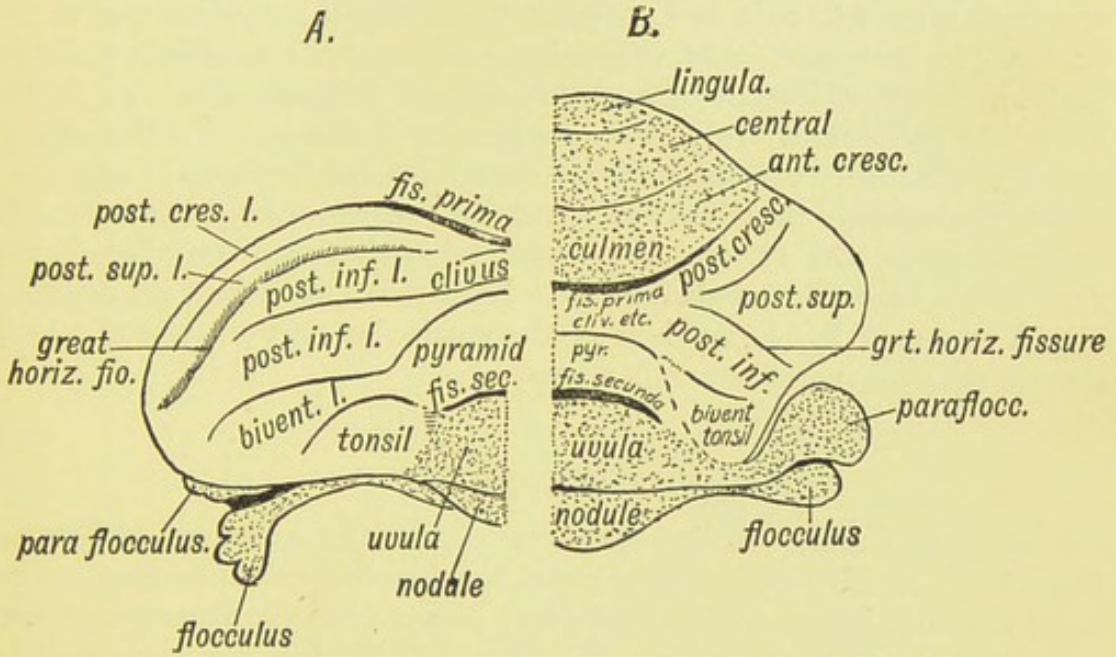


FIG. 77, *A*.—Left half of the Cerebellum of a Foetus of 5 months, seen on its inferior aspect. Only the middle and posterior primary lobes are exposed. The parts forming the posterior lobe are stippled. (After Elliot Smith.)

B.—Right half of a typical Mammalian Cerebellum, spread out so as to show the anterior, middle and posterior primary lobes. The anterior and posterior lobes are stippled. The fissures and parts are indicated by the terms used in human anatomy in order that the peculiar features of the human cerebellum may be made evident. (After Elliot Smith.)

They are probably connected indirectly with the frontal lobes through the fronto-cerebellar fibres which lie in the inner third of the crusta.

(3) The **Inferior Peduncles** are formed by :

(*a*) Processes from the cerebellar cortex to the cord (descending cerebellar tract) ;

(*b*) Processes which end in the opposite olive ;

(*c*) Processes which grow in from Clarke's column (direct cerebellar) ;

(*d*) Processes from the cells of the sensory nuclei of the postero-mesial and postero-lateral tracts (nucleus gracilis et cuneatus) ;

(*e*) Processes from the nuclei in which the vestibular nerve ends.

Three points in connection with the development and comparative anatomy of the cerebellum are especially worthy of attention :

(1) It arises from the alar laminae, which are directly connected with afferent or sensory nerves only ; further, the nuclei in the mesencephalon, pons, and medulla, with which it is connected, arise from the alar laminae.

(2) The part of the neural tube from which the cerebellum arises is that connected with the hyoid segment of the head. The vestibular ganglion, connected so closely with the function of balancing, arises from the neural crest of the hyoid segment of the hind-brain.

(3) The cerebellum reaches its greatest development in primates amongst mammals; it is also greatly developed in swimming vertebrates. In primates, as in swimming mammals, the equilibrium of the body is finely adjusted. On embryological grounds alone we would infer that the cerebellum is part of a sensory mechanism. Clinical and experimental observations indicate that its main function is to co-ordinate the various muscles of the body in performing definite acts. It is therefore on the afferent nerve system arising from muscles, joints and bones, that the cerebellum has been developed, but its position was determined by the nucleus of the vestibular nerves, cells of which invade the embryonic cerebellar plate.

THE MID-BRAIN.

The central canal of the mid-brain forms the **aqueduct of Sylvius** (Fig. 76). In its roof are developed the corpora quadrigemina. The basal and alar laminae of its medullary plates form the tegmentum and crusta of the crura cerebri. In lower vertebrates the mid-brain is larger and more important than the fore-brain. In its roof or dorsal plate the most of the fibres of the optic tract terminate. Other afferent fibres from the ear and sensory nerves of the body also terminate in it. The roof plate contains an expansion of the central canal (Fig. 75). In mammals the mid-brain is overshadowed by the fore-brain; the dorsal lamina becomes divided into anterior and posterior corpora quadrigemina, which are connected with the sensory tracts from the eye and from the ear. The 3rd and 4th cranial nerves represent the motor nerves of its two segments. From the 3rd month onwards the mid-brain becomes the highway for developing nerve paths which unite the fore-brain with the nerve centres lying in the hind-brain and spinal cord. Since the notochord ends beneath it, and further because the first truly segmental nerves arise from it, the mid-brain may be regarded as the anterior end of the primitive neural tube. All the parts of the brain which lie anterior to it may be regarded as developments from or additions to the primitive neural tube (see Fig. 65, p. 68).

The Three Neural Flexures (see Figs. 65, 73).—The **pontine flexure,** a convexity forwards of the pons, has already been mentioned; the **nuchal flexure** is concave forwards and occurs between the medulla and cord. Both of these are of small import, but the **anterior flexure,** whereby, in the third week of foetal life, the fore-brain appears as a downward and forward development until it comes to lie on the ventral aspect of the cephalic end of the notochord, leads to a great alteration

in the form and relationships of the fore- and mid-brains, and is of great importance. Even in the embryos of the lowest vertebrate forms the expansion and bending of the anterior end of the neural tube is apparent (Fig. 73). The mid-brain, by this flexure, comes to be, for a short time, the most anterior part of the neural canal; the fore-brain is doubled back under the notochord (Fig. 73). Round the projecting end of the notochord—projecting between the mid- and fore-brains—are developed the posterior clinoid processes and dorsum sellae (Fig. 65, p. 68). The dorsum sellae marks the position of the anterior flexure in the adult brain. The tentorium cerebelli is developed between the mid-brain and fore-brain, and lies at first at right angles to the axis of the mid-brain, but the subsequent great growth of the cerebrum forces it backwards and downwards until it becomes a

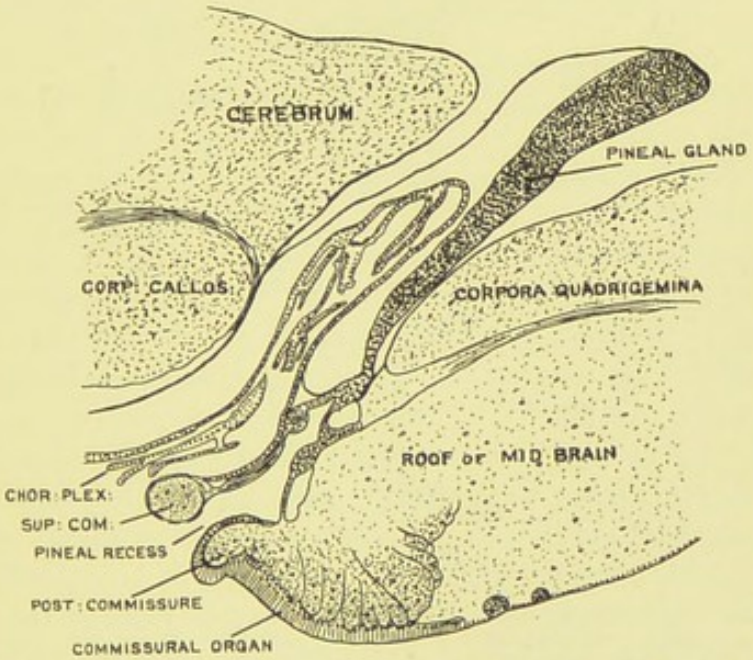


FIG. 78.—Section of the anterior part of the Roof of the Mid-Brain of a Cat to show the subcommissural organ. (Dendy and Nicholls.)

horizontal partition between the cerebellar and cerebral chambers of the skull.

Subcommissural Organ.—For some time it has been known that the ependyma on the roof of the mid-brain of lower vertebrates, immediately behind the posterior commissure (see Fig. 78), is modified to form a peculiar area of high columnar cells. The cells are related to a certain very large fibre (Reissner's fibre), which descends ventral to the central canal of the spinal cord in fishes and amphibians. Recently Dendy and Nicholls have shown that this ependymal structure, to which they have given the name of subcommissural organ, occurs in all vertebrates, including man. It is quite apparent in the human foetal brain, but is soon reduced to a vestige. The function and significance of the structure are unknown.

Constitution of the Mid- and Hind-Brain.—We have traced the development of the neural tube in a forward direction, and have reached the point where the mid-brain passes into the fore-brain. On the roof the point of transition is marked by the posterior commissure; below the floor the notochord ends (Fig. 65, p. 68). We have reached the end of the neural tube proper; the part in front—the fore-brain—appears to have arisen in connection with two great organs of sense—the nose and eye. We find that the neural tube, when it enters the region of the head, becomes greatly altered in its constitution. This is due, not only to the development of special parts such as the pons, the cerebellum, corpora quadrigemina and special nerve tracts which unite the cerebral and spinal centres, but especially to the fact that

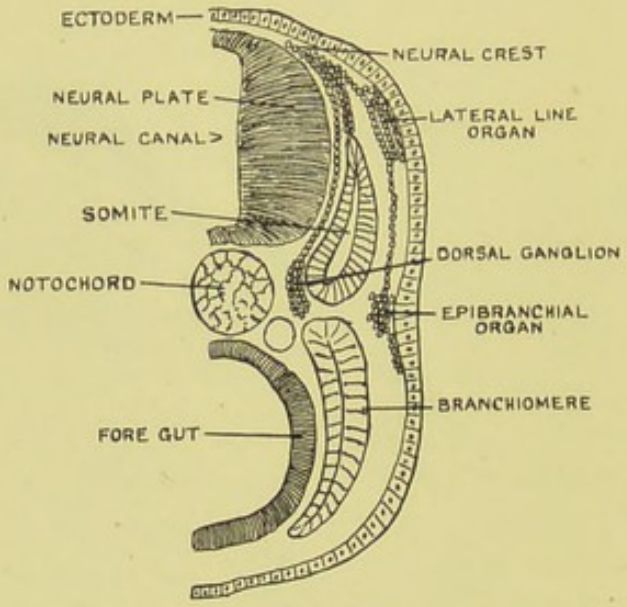


FIG. 79.—Diagrammatic Section across the posterior region of the Head of Ammoecetes—the immature form of the Lamprey—to show a Branchiomere and the ganglia derived from the Neural Crest of the Hind-Brain. (After Froriep.)

the structure of the head is more complex than that of the body. In the head region another element appears—a **ventral** mesoblastic somite or branchiomere—in addition to the **dorsal** mesoblastic somite seen in the trunk region (Fig. 79). The branchiomeres give rise to the gill arches, which are so apparent in the human embryo at the end of the first month. In the mid- and fore-brain special centres and nerves are developed in connection with the gill arches. In the spinal cord there were two columns of motor nerves in the basal lamina, one for the somatic or voluntary muscles of the body, another for the visceral musculature—the splanchnic—but here a third or intermediate column is added—the motor cells for the muscles connected with the gills. The branchial—or lateral somatic nerves are represented in the mid- and hind-brain by the motor or ventral root of the Vth nerve, by the motor part of the VIIth, by the parts of the IXth, Xth, XIth, which

supply striated muscles. The presence of branchial arches in the head region gives rise to a more complex arrangement of the nerve ganglia. In the trunk region the neural crest gave origin to posterior root ganglia, the ganglia of the sympathetic chain (prevertebral), and other ganglia stationed in front of the spine. In the regions of the mid- and hind-brain the neural crest also is developed, but besides giving rise to an inner ganglion (see Fig. 79) representing the posterior root ganglion and sympathetic ganglia found in the region of the trunk, it also gives origin to a lateral mass of nerve cells, from which the sensory fibres to the gills are produced. Associated with this lateral mass are also cellular formations representing two rows of sense organs[1] —an upper, the organs of the lateral line ; a lower, the epibranchial sense organs. In man only vestiges of these sense organs appear. The ultimate fate of the epibranchial rudiments is not known for certain, but it is probable that some of their cells are included in the ganglia at the trunks of the IXth and Xth nerves.

Nerves of the Segments of the Mid- and Hind-Brain.—We have already seen that the cephalic part of the neural tube shows distinct traces of segmentation in the human embryo of the 3rd week (see Fig. 65, p. 68). Two of these segments are in the mid-brain, five in the hind-brain. It is supposed that at one time each of these was connected with a head segment by its own nerves. The third segment—the first of the hind-brain series—shows the nearest approach to the primitive complement of nerves. The somatic motor fibres of this segment are represented by the VIth nerve (to the external rectus) ; the lateral somatic motor or branchial, by the motor fibres of the VIIth or facial ; the splanchnic efferent or motor by the secretory fibres of the chorda-tympani of the VIIth ; the afferent or splanchnic sensory by the gustatory fibres of the VIIth (chorda tympani and great superficial petrosal) ; the somatic sensory fibres by the VIIIth or auditory nerve. The cochlear and vestibular ganglia represent a posterior root ganglion ; the submaxillary ganglion—a vagrant sympathetic ganglion. Thus the 3rd neural segment has become associated with the hyoid (2nd visceral) arch, the eye and the ear.

In the other segments there have been great changes and reductions. As regards the nerve of the first segment, only its somatic motor nerve—the IIIrd nerve—remains ; its posterior root and ganglion are represented by the ophthalmic division of the Vth nerve. The ciliary ganglion represents the sympathetic ganglion of this segment ; the fibres from the IIIrd to this ganglion, the efferent or motor splanchnic fibres. The nerves of the second segment are represented by the IVth or trochlear nerve (somatic motor), the nerves to the muscles of mastication (lateral somatic or branchial root), the somatic sensory by the maxillary and mandibular divisions of the Vth nerve. The sensory

[1] The formation here named lateral line "organ" is better termed the dorso-lateral placode, and the epibranchial "organ" epibranchial placode.

root of the Vth nerve has spread its dominion until it now forms connections with all the segments of the mid- and hind-brains, and even reaches the upper part of the spinal cord. There are no sensory somatic fibres in the nerves of the 4th, 5th, 6th and 7th segments with the exception of the auricular branch of the vagus. The IXth or glossopharyngeal is the nerve of the 4th segment and contains lateral somatic, efferent and afferent splanchnic fibres. The vagus and bulbar roots of the spinal accessory represent the splanchnic efferent and afferent nerves of the 5th, 6th and 7th segments—the most important segments in the neural tube, for they contain the nerve centres which dominate the heart, the lungs and the greater part of the alimentary canal. The somatic motor roots of the 5th, 6th and 7th segments are represented by the fasciculi of origin of the XIIth nerve—the motor nerve of the tongue. It will be thus seen that embryology and comparative anatomy supply a clue to the manner in which the cranial nerves are arranged. The basis of that arrangement is strictly a physiological one, but the specialization in certain segments, which has occurred in the course of evolution, has destroyed the original simplicity of their arrangement. Further mention of the cranial nerves will be made in dealing with the nose, eye, ear, face and visceral arches. Those seeking for fuller details of the early development of the cranial nerves in the human embryo should consult Professor Streeter's various monographs, especially one in the *American Journal of Anatomy*, 1908, vol. 8, p. 285.

In the human embryo vestiges of posterior roots and ganglia may appear with the hinder hypoglossal fasciculi; we may infer that at one time the occipital segments had nerves with anterior and posterior somatic roots. Streeter also observed that the spinal rootlets of the XIth nerve have vestigeal ganglia (visceral sensory) on them when first formed (*Amer. Journ. Anat.* 1904, vol. 4, p. 83).

CHAPTER VIII.

THE FORE-BRAIN.

The Origin of the Cerebrum.—It is in connection with the fore-brain that the most distinctive and most complex of all human structures arises—the cerebrum. If we confine our attention purely to the developmental changes which occur in the fore-brain of the human embryo, we shall understand very imperfectly the origin and nature of

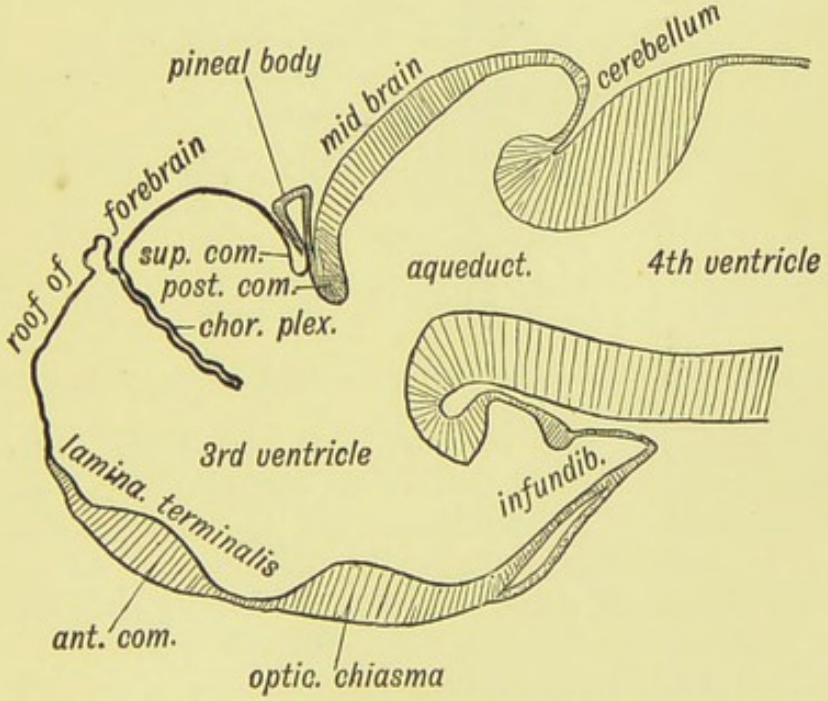


FIG. 80.—Longitudinal Section of the Brain of a Larval Fish, to show the primary form and relations of the fore-brain. (Kupffer.) Note especially that the whole roof is formed by a choroidal velum.

the human brain. It is true that on developmental evidence alone we may infer that the fore-brain, although situated at the anterior extremity of the neural tube, does not represent a prolongation of all the elements of the tube, but only of its alar or dorsal laminae, which we know to be sensory in their nature. We may infer that the fore-brain belongs to the sensory part of the nervous system—not to its motor or basal

lamina. To obtain a proper appreciation of the fore-brain, however, one must study this structure in the lowest of vertebrates—the Lamprey. In Fig. 81 the brain of this primitive fish is represented. The fore-brain is made up of two parts—a posterior—the **thalamencephalon** or **diencephalon,** with which the retinae and optic tracts are connected, and an anterior or **telencephalon**, in which the olfactory nerves terminate. The two parts of the fore-brain have thus arisen in connection with the sense of sight and the sense of smell ; secondary nerve masses have arisen in these two parts of the fore-brain—the optic thalamus in the posterior, and the corpus striatum in the anterior ; but the optic thalamus receives not only nerve tracts connected with the sense of sight, but others connected with touch and hearing, and thus becomes a higher centre for the control of lower centres. The corpus striatum—the secondary mass in the anterior or olfactory part

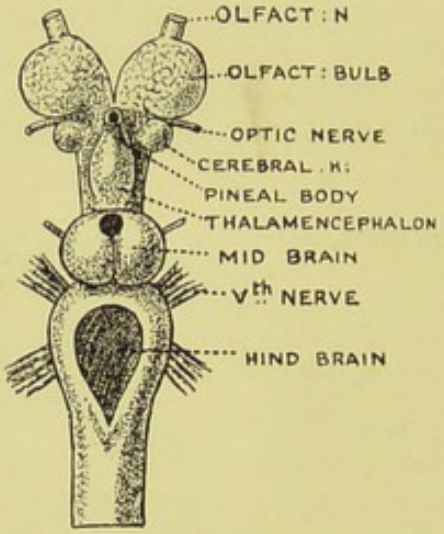


FIG. 81.—The Brain of the Lamprey from above. (After R. H. Burne.)

—the telencephalon—also receives tracts from the gustatory, and other lower centres besides those from the olfactory tracts. In the brain of the lamprey the mid-brain and the two parts of the fore-brain form a " federation of centres." [1] In mammals the telencephalon becomes the dominant part ; the cerebral hemispheres arise from it. Thus our cerebral hemispheres have arisen in connection with parts which have become insignificant—the olfactory nerve centres. The telencephalon has received and formed communications with all parts of the central nervous system, and become the central exchange of all sensory impulses and also the seat of consciousness.

The Fore-brain of the Human Embryo.—In the 3rd week of development there is a marked resemblance between the human fore-brain and that of a fish (compare Figs. 80 and 82). In some

[1] The phrase is Professor Elliot Smith's, whose researches on the evolution of the brain form the basis of the account given here.

respects the fish's brain is the more instructive. In the fish the roof of the 3rd ventricle—the name given to the central canal of the thalamencephalon—contains no nerve tissue ; it is membranous, and forms a choroid plexus. The pineal body arises from the posterior part of the roof, immediately in front of the posterior commissure (Fig. 80). The representatives of those parts are seen in the roof of the 3rd ventricle of the human embryo at the end of the first month (Fig. 82). On the narrow floor of the 3rd ventricle are seen the infundibular part of the pituitary body and the optic chiasma—or the plate in which the chiasma will be formed. In both the fish and the human embryo the anterior wall of the 3rd ventricle is formed by a plate of neural tissue—the lamina terminalis. The fore-brain of the human embryo (Fig. 82)

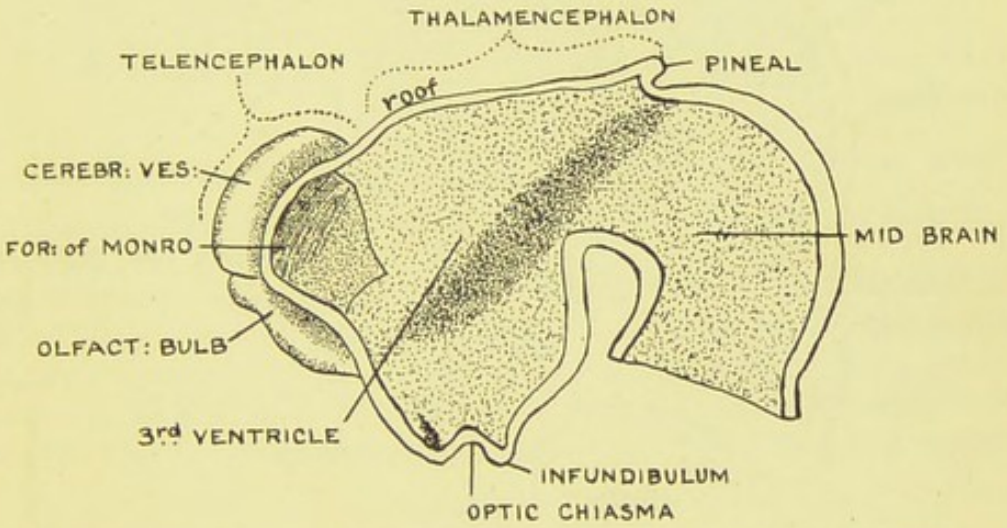


FIG. 82.—The Fore-Brain of a Human Embryo at the end of the first month of Development. (After His.)

shows very well the primary division into thalamencephalon (sight brain) and telencephalon (smell brain). At this stage the foramen of Monro is widely open, so that the 3rd ventricle (the cavity of the thalamencephalon) communicates freely with the lateral ventricles—the cavities of the telencephalon.

Parts developed in the Lateral Wall of the 3rd Ventricle.—In Fig. 83 is given a diagrammatic representation of the condition of the fore-brain towards the end of the 2nd month of development. On the lateral wall of the third ventricle the optic thalamus is developing. Its nerve masses come to receive nerve tracts, not only connected with sight, but also with hearing, touch, heat, cold, pain, etc. Other tracts will be formed to connect the optic thalamus with higher cortical centres, which will be developed subsequently in the expanding cerebral vesicles. Below the optic thalamus on the lateral wall of the 3rd ventricle is formed another neural mass—the hypothalamus (Fig. 83), from which the tuber cinereum and neighbouring nerve masses are differentiated. The corpus striatum has also appeared on the mesial

wall of the telencephalon—its caudate nucleus appearing in the 3rd ventricle through the foramen of Monro (Fig. 83).

The **Pituitary Body,** which is formed in connection with the floor of the 3rd ventricle, is present in all vertebrates. It belongs to the same series of organs as the thyroid, supra-renal, carotid and coccygeal bodies—glands which by their secretions, exercise an influence on the

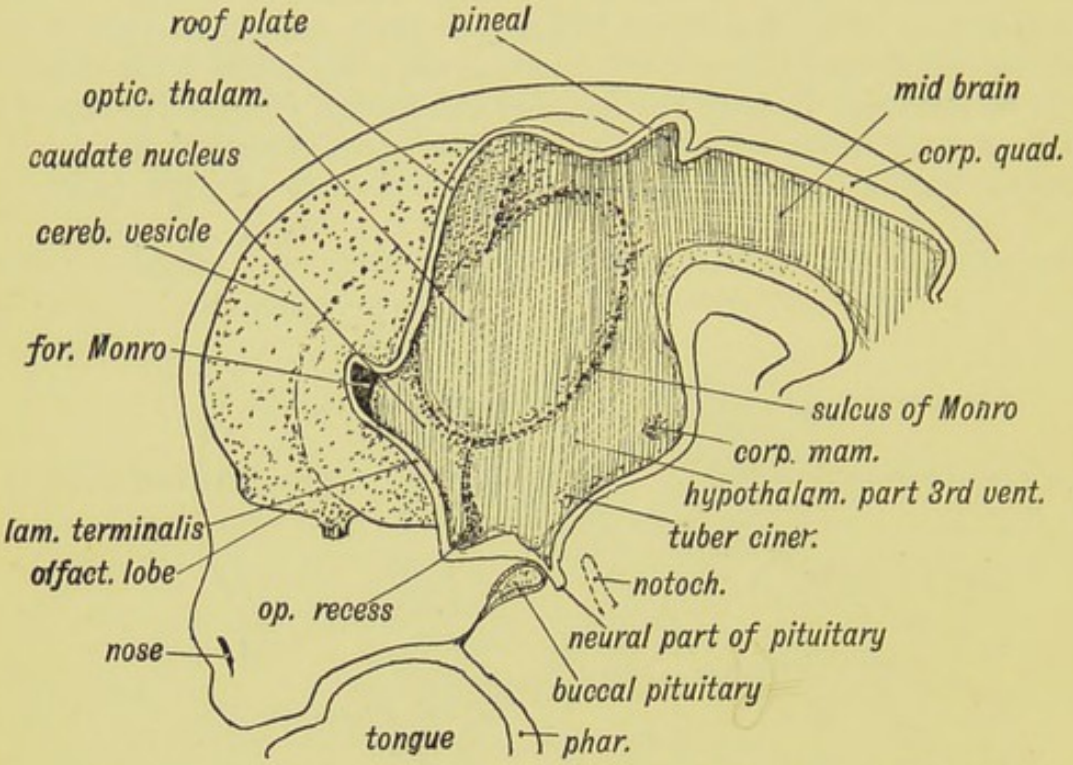


FIG. 83.—A Schematic Figure to show the parts derived from the Walls of the Fore-Brain. (After His.)

growth and nutrition of the tissues. Many theories have been framed to account for the position and formation of the pituitary in the floor of the 3rd ventricle, a favourite one being that it has been formed round the opening or mouth of the central canal of the nervous system when that canal was alimentary in nature. It seems more probable, judging from recent observations of Cushing, that the pituitary is so placed, because it discharges a secretion into the 3rd ventricle, which circulates in the cerebro-spinal fluid.[1] The pituitary gland arises from two elements :

(1) An epiblastic hollow bud from the stomodaeum.

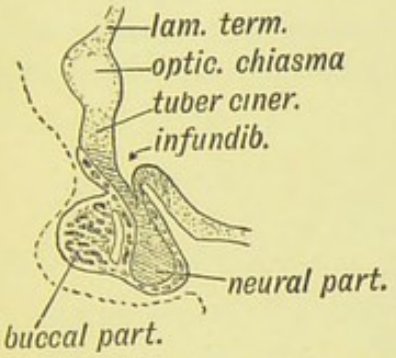
(2) A neuroblastic bud from the floor plate of the 3rd ventricle (fore-brain).

The union of the two processes takes place at the anterior extremity of the notochord in the first month of development. The epiblast of the stomodaeum and the floor of the neural tube are in contact from the

[1] For development and nature see P. T Herring, *Journ. Experiment. Physiol.* 1908, vol. 1, pp. 121, 161, 261, 281.

very beginning; subsequently the mesoblast grows in between the fore-brain and the epiblast of the stomodaeum, but the parts which form the pituitary adhere. The posterior or neuroblastic bud becomes solid; its structure is that of neuroglia into which many vessels have grown carrying mesoblastic tissue with them.

The anterior or stomodaeal bud embraces the posterior. While its posterior wall remains quiescent, its anterior throws out solid pro-



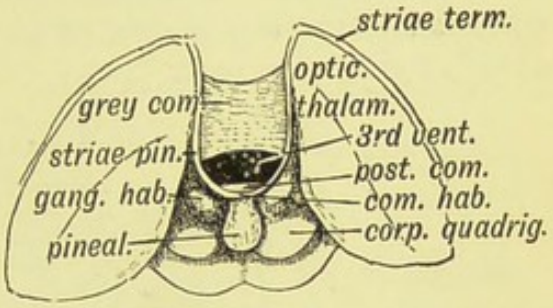


FIG. 84.—Section of the Pituitary Body of a Human Embryo in the 4th month. (Edinger.)

FIG. 85.—Showing the position of the Pineal Body and its commissure and ganglion.

cesses between which a network of vessels lies. This forms the glandular part of the pituitary—reticulated rows of cells surrounding blood channels—similar in structure to the medullary part of the supra-renals, carotid bodies and parathyroids. The segments of the head as well as those of the body were probably furnished with segmental or excretory

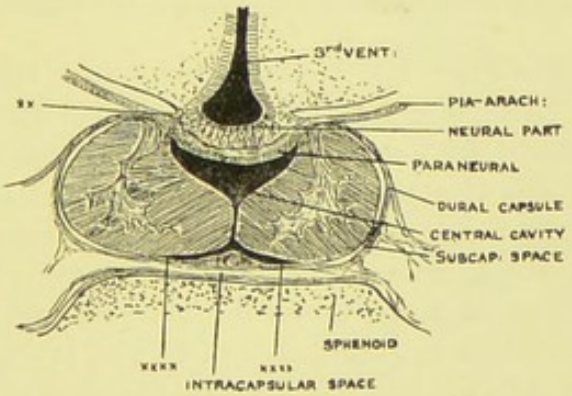


FIG. 86.—Transverse or Coronal Section of the pituitary body of a Human Foetus in the 3rd month of development.

organs in the ancestral stock of the vertebrates; the pituitary may be a derivative of one or more of these organs. The trabeculae cranii form round the pituitary. When the basi- and pre-sphenoids are developed in the trabeculae, the position of the stalk of the stomodaeal process is seen in the later months of foetal life between these two bones and forms the *canalis cranio-pharyngeus* (see Fig. 83). The point of origin of the stomodaeal bud corresponds to the posterior border of the septum of the nose (J. E. S. Frazer). Part of the stalk remains in the

mucous membrane of the naso-pharynx, and forms the naso-pharyngeal pituitary—a small body not larger than a grain of wheat. In Fig. 84 a sagittal section of the pituitary is shown with the central cavity dividing the anterior part of the buccal vesicle from the posterior (pars intermedia of Herring), which is applied closely to the infundibulum. The condition of the gland in the 3rd month of development is shown in Fig. 86 by a transverse or coronal section. The pars intermedia (paraneural part) is seen to be applied to the floor of the 3rd ventricle ; the central cavity of the buccal element, which afterwards becomes filled with colloid matter, is seen to be invaded by the lateral lobes of the anterior glandular part.

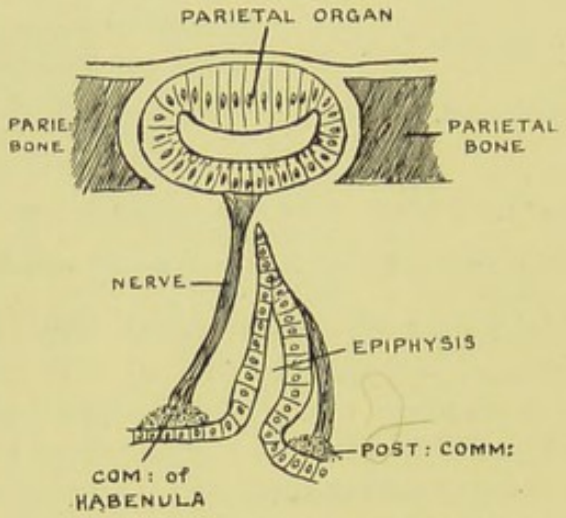


FIG. 87.—The Pineal Gland and Sense Organ in a Lizard. (Gaupp.)

Pineal Body [1] (see Figs. 83, 85, 87) grows as a bilateral hollow bud from the roof of the hinder part of the fore-brain during the 6th week, but in all vertebrates the final development involves only the part arising from the left side (Cameron). In fossil reptiles and in some forms still living it forms a median eye which perforates, and appears on, the dorsum of the head, between the parietal bones. It differs from the lateral eyes which grow from the third ventricle as the optic vesicles in this, that it produces the lens as well as the retina and optic stalk. The retina is inverted—*i.e.* the apices of the rods and cones point towards the vitreous chamber. The ganglion of the habenula, situated on the dorsal and inner aspect of the optic thalamus, appears to represent its terminal ganglion, but it must also be remembered that this ganglion receives the striae pinealis which arise from part of the rhinencephalon. The two ganglia become connected across the roof plate by a commissure (the superior or habenular commissure) (Figs. 83, 87). As will be seen from Fig. 87, the Pineal body is really made up of two parts—

[1] Recent papers on development and nature of the pineal body are : A. Dendy *Phil. Trans.* 1910, Ser. B, vol. 201, p. 227 ; J. Warren, *Amer. Journ. Anat.* 1911, vol. 11, p. 317.

a sense organ—the so-called parietal "eye" and a glandular structure—the epiphysis. In mammals, as in man, only the glandular part is formed. It produces a number of diverticula which are filled up by a proliferation of the cells forming the walls of the diverticula. It lies in the velum interpositum, which is forced down on it by the growth backwards of the cerebral hemispheres. Recent observations indicate that the pineal, like the pituitary, is a gland supplying an internal secretion.

The **lamina terminalis** (Figs. 80, 82, 83) is the plate which forms the anterior or terminal wall of the fore-brain, and unites the olfactory

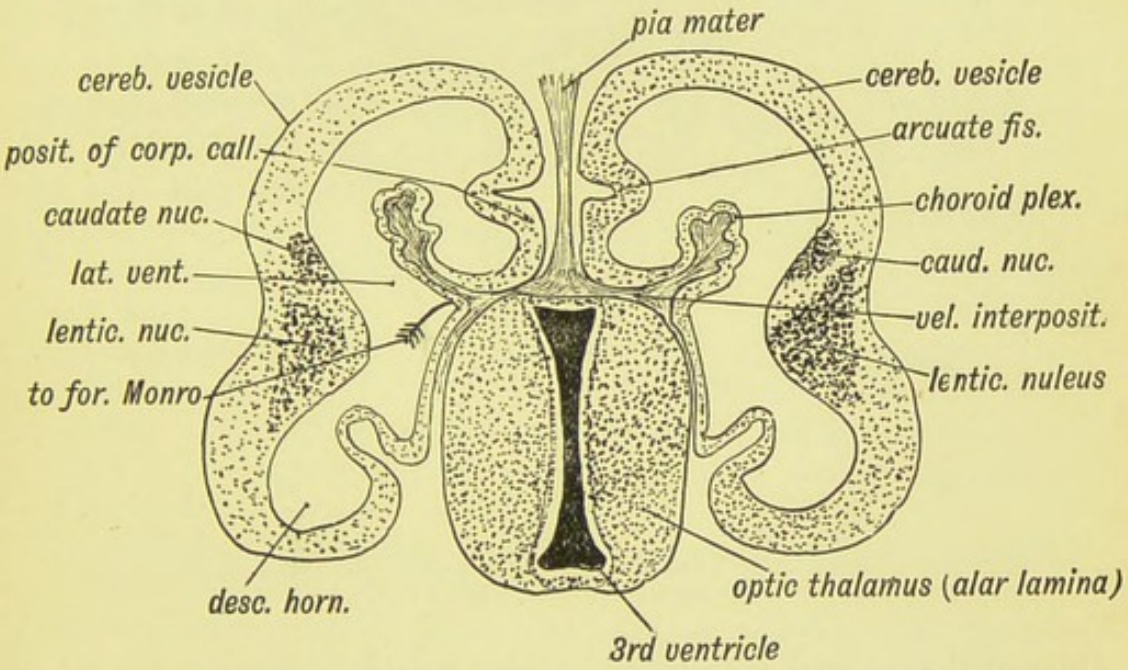


FIG. 88.—Transverse Section of the Brain of a Human Foetus at the commencement of the 3rd month to show the Cerebral Vesicles overlapping the Thalamencephalon (schematic).

part (telencephalon) of one side with the other. Its upper end is continuous with the roof plate of the fore-brain, its lower end with the floor of the 3rd ventricle (Fig. 83). In the lamina terminalis, roof and floor plates are developed all the commissures which connect the two halves of the brain—the anterior commissure, hippocampal commissure, corpus callosum and optic chiasma. The development of the lamina terminalis will be described later, but the lamina cinerea, between the corpus callosum above and the optic chiasma below retains with little alteration its early simple structure (Figs. 95, 96). The inter-peduncular space, which forms the floor of the 3rd ventricle, also retains in the adult to a considerable extent the simple embryonic form. In it are developed the corpora albicantia and posterior perforated space.

The **Optic Thalami** are formed in the lateral walls of the fore-brain (thalamencephalon) and in the adult occupy the whole extent of this wall. At first they are completely exposed on the outer aspect of the brain (see Fig. 73), but after the cerebral vesicles grow out from the

telencephalon, these are prolonged backwards and downwards over the optic thalami and thus bury them (Figs. 88 and 97, p. 108). As may be seen from Fig. 89, the optic thalami, with the internal capsule, appear to be the enlarged upward continuations of the tegmentum and crusta of the crura cerebri or mid-brain, but in reality the optic thalamus is probably a continuation of the alar laminae only, into which the

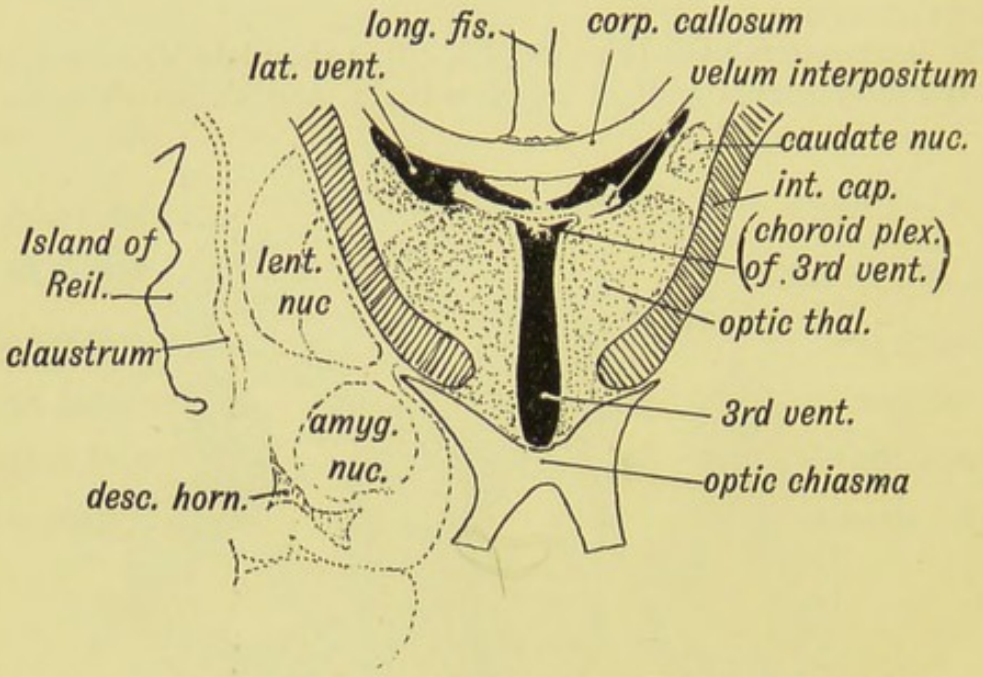


FIG. 89.—Diagrammatic Section across the 3rd Ventricle of the Adult to show the Structures formed in its Walls.

fibres of the internal capsule are subsequently introduced. The corpus striatum, which is separated by the development of the internal capsule into caudate and the lenticular parts, is altogether a different structure. While the optic-thalamus arises in connection with the thalamencephalon or "sight-brain" the corpus striatum arises in the telencephalon or "smell-brain." The one is primarily associated with sensory impulses from the nose, the other from the eye, but they also come to receive nerve tracts arising from all sensory nerves and nuclei. Both become connected with the cortex or neopallium which arises in the telencephalon. These connections are formed by tracts in the internal capsule. The apposition of the corpus striatum to the optic thalamus is a secondary development. The sulcus of Monro (Fig. 83), which runs from the opening of the aqueduct of Sylvius to the foramen of Monro, on the lateral wall of the 3rd ventricle, was believed by His to mark off the alar from the basal lamina of the thalamencephalon. A section across the 3rd ventricle and optic thalami, at the end of the second month is shown diagrammatically in Fig. 88. The internal capsule has not yet appeared. The cerebral vesicles already overlap and bury the optic thalami.

Roof Plate of the Fore-Brain.—The roof plate of the fore-brain, like that of the hind-brain, becomes modified to form the epithelial covering of a secretory membrane or velum. At each side the roof plate is attached to the optic thalamus; behind it is continuous with the roof of the mid-brain; in front it is continuous with the lamina terminalis (Figs. 80, 83).

The Cerebral Hemispheres.[1]—In the 3rd week very soon after the medullary plates have closed, a hollow bud, which almost immediately divides into a right and left half, grows out from the telencephalon. These two **vesicles,** which are united by the lamina terminalis and anterior part of the roof plate of the thalamencephalon, form the cerebral hemispheres. The lateral wall of each vesicle, which posteriorly is continuous with the lateral wall of the thalamencephalon, becomes thickened, and forms the corpus striatum (Fig. 90). The **lateral ventricles** with their horns represent the cavity of the primitive telencephalon; the foramina of Monro represent the original communication of the cavities of the telencephalon with the remainder of the central canal of the neural tube. The anterior horn of the lateral ventricle represents the anterior extremity of the cavity of the telencephalon—the point at which the olfactory lobe is produced; the descending horn represents the real posterior extremity of the vesicle; the posterior horn is a later diverticulum formed in connection with the growth of the occipital lobe.

The primitive simple relationship of the cerebral vesicle, which holds for low vertebrates (see Figs. 81 and 82) and for the first two months of foetal life, becomes obscured in the third by the vesicles growing over the optic thalami and burying them (Fig. 90). The junction of the optic thalamus with the lateral wall of the cerebral vesicle—in which the corpus striatum is formed—becomes greatly thickened, and a part of the vesicle—the choroidal lamina—actually fuses with the upper and outer aspects of the optic thalamus (Figs. 88, 89, 90). Hence the optic thalamus comes to form part of the floor of the body of the lateral ventricle and enters into the roof and inner wall of the descending horn.

In Fig. 90 a freely diagrammatic representation is given of the development of the cerebral vesicle in the human embryo about the middle of the 3rd month. The roof of the vesicle is cut away, exposing its floor which is occupied by the corpus striatum. The close relationship of this body to the olfactory bulb will be observed.

The anterior extremity is continuous with the olfactory tubercle, a part of the rhinencephalon behind the olfactory peduncle. Hence in

[1] G. Elliot Smith, "Arris and Gale Lectures," *Lancet*, 1910, Jan. 1st, 15th, 20th; *Anat. Anz.* 1908, vol. 33, p. 513 (Cortex of Lepidosiren); *Ibid.* 1910, vol. 36, p. 486 (Calcarine Fissures); *Ibid.* 1907, vol. 30, p. 574 (Asymmetry of Occipital Poles); *Ibid.* 1903, vol. 24, p. 216 (Transitory Fissures); *Journ. Anat. and Physiol.* 1907, vol. 41, p. 237 (Topography of Cortex); *Ibid.* 1907, vol. 41, p. 198 (Occipital Cortex).

the adult brain, the anterior end of the corpus striatum appears at the base of the brain in the anterior perforated space, a lamina of grey matter forming part of the rhinencephalon (Fig. 93A, p. 102). Behind the corpus striatum is continuous with the optic thalamus, the part of the ventricular wall which joins them becoming greatly thickened. The posterior extremity of the cerebral vesicle, in which the tail of the caudate nucleus is situated (Fig. 90), develops downwards, behind and

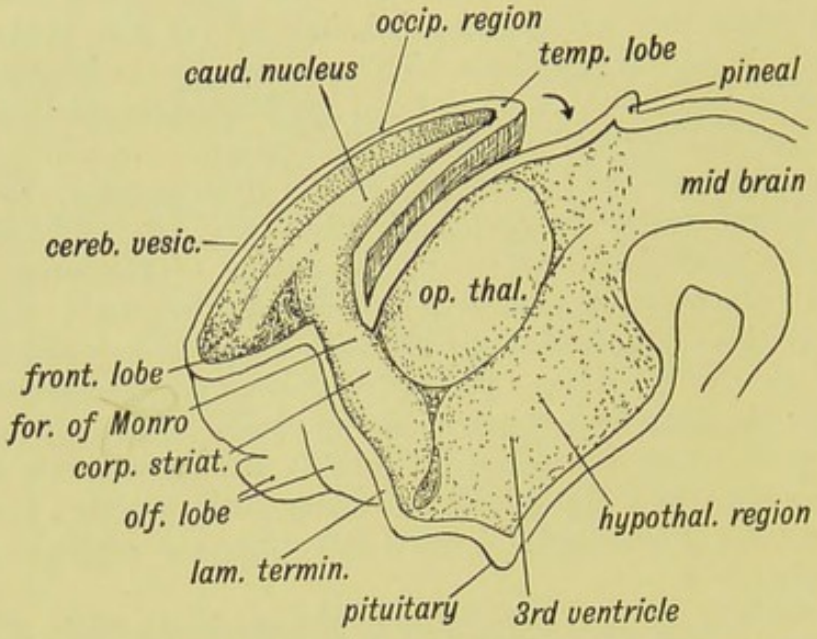


FIG. 90.—Showing the Development of the Corpus Striatum in the floor and outer wall of the Cerebral Vesicle.

below the optic thalamus, forming the descending horn of the lateral ventricle. Hence the occurrence of the tail of the caudate nucleus on the *roof* of the descending horn. The corpus striatum is imperfectly separated, during the 4th and 5th months of foetal life, into two parts, the caudate and lenticular nuclei, by the downgrowth, from the cerebral cortex of the fibres which form the internal capsule, crusta, and pyramidal tracts.

The Velum Interpositum.—It is during the growth backwards of the cerebral hemispheres over the thalamencephalon that the basis of that complex structure—the velum interpositum—is formed. The basis of this structure is really that area of the pia mater—the mesoblastic and vascular capsule of the brain—which is enclosed between the thalamencephalon and expanding cerebral vesicles (Fig. 90). The essential parts of the velum are its lateral edges, which project within the lateral ventricles and its lower surface lying over the third ventricle —parts which are covered by the inner lining of the neural tube—the ependyma. These parts form the choroidal villi—or plexuses— —covered by the ependymal epithelium, which secrete the cerebrospinal fluid.

We have seen that in the anterior part of the roof plate of the 4th ventricle the cerebellum is developed, while its posterior half becomes the inferior medullary velum—a secretory membrane (Fig. 76, p. 82). The roof plate of the third ventricle, from the foramina of Monro backwards to the stalk of the pineal body, becomes modified in a similar

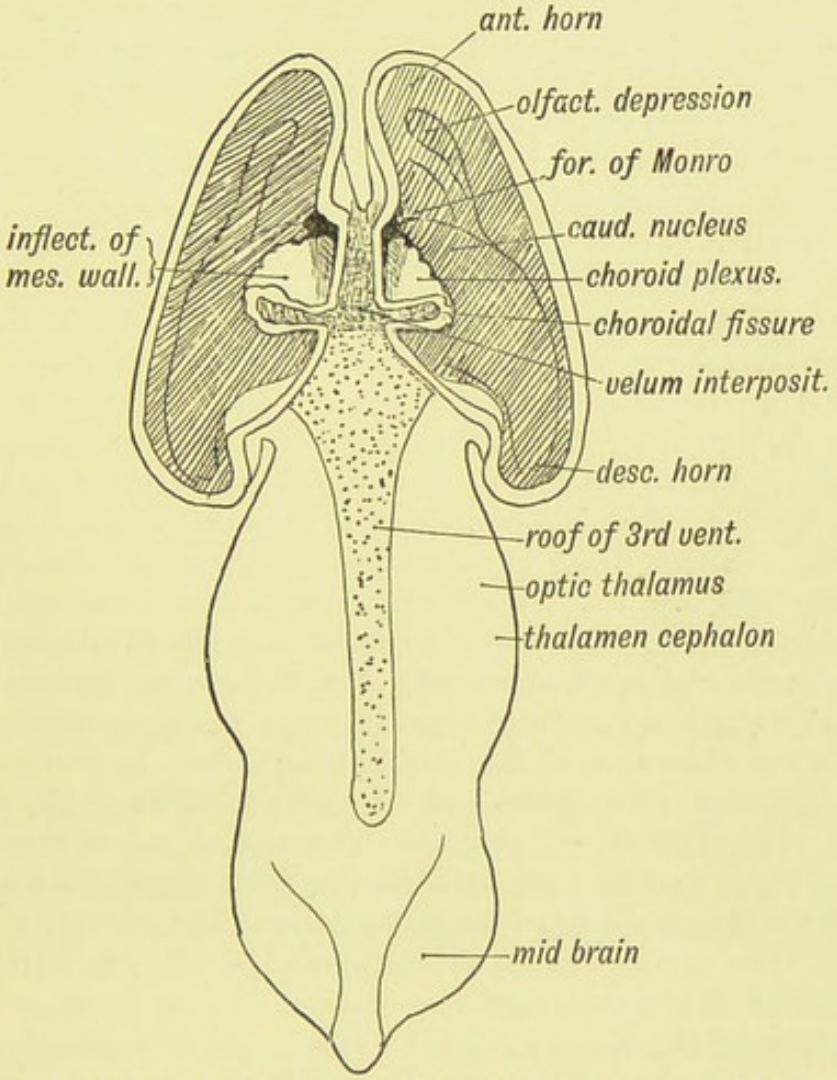


FIG. 91.—A dorsal view of the Fore- and Mid-brain at the 5th week of development to show the formation of the Velum Interpositum. The Cerebral Vesicles are laid open and the inflection of the roof of the Fore-brain shown on the ingrowing Velum. The Roof Plate of the 3rd Ventricle is also exposed. (Modified from His.)

manner (Fig. 80). It merely forms the ependymal covering of the lower surface of the velum interpositum, thus clothing the choroid plexus on the roof of the 3rd ventricle (Figs. 88, 89). The anterior part of the roof plate is produced into the cerebral vesicles over the foramina of Monro, and covers the apex of the velum interpositum (Fig. 91). The mesial wall of each cerebral vesicle from the foramen of Monro back to the posterior extremity of the vesicle (Fig. 91), which becomes the tip of the descending horn, is also inflected and forms a secretory ependyma, covering the velum interpositum and choroid plexus within the lateral ventricles. This inflection takes place at the

junction of the optic thalamus with the wall of the cerebral vesicle, and the part of the vesicle folded in is probably a prolongation of the roof plate of the fore-brain (Fig. 91). Into this inflection of the embryonic neural wall spreads the mesoblast, carrying vessels with it. The velum interpositum is thus composed of a basis of mesoblast and its intraventricular parts have a covering of the ependyma of the neural wall.

The ependymal covering of the entire velum is derived from :

(1) The roof plate of the 3rd ventricle (lower surface) ;

(2) The roof plate of the foramen of Monro ;

(3) An inflection of the mesial wall of the cerebral vesicle.

The choroid plexus, which merely fringes the velum in the adult, completely fills the cavities of the embryonic lateral ventricles, which for the first five months are relatively very large and the containing walls thin. The velum and choroid plexus must play an important part in the development of the cerebral vesicle in the early period of growth. The spread of the vesicles backwards and downwards over the optic thalami (Fig. 97, p. 108) obscures the original simple relationship of the velum to the brain ; but, when withdrawn from the transverse fissure, the velum is seen to rest on the optic thalami and project within the ventricle from the foramen of Monro to the tip of the descending horn, and that stretch marks the line at which the choroidal inflection took place. The striae terminalis, in the groove between the optic thalamus and caudate nucleus (Fig. 85), marks the line at which the mesial wall of the cerebral vesicle was primarily attached.

The fibrous substance of the velum interpositum is continuous with the pial covering of the brain, and also with the edge of the tentorium cerebelli. The corpus callosum and cerebral vesicles, as they develop, grow backwards and enclose, between the optic thalami below and the pillars of the fornix above, the fibrous basis of the velum interpositum (Fig. 88). The veins of Galen are developed in the velum and join the straight sinus in the tentorium.

Evolution of the Neopallium.[1]—The cerebral hemispheres, as we know them in the lowest vertebrates, are for the reception and interpretation of impulses from the olfactory end organs. Connections are established between the olfactory brain and the motor centres in the cord and in the hind- and mid-brain ; olfactory impressions can thus lead to action. Further, it is advantageous that there should be a nervous mechanism for the blending of impressions from the nose with impulses derived from sight, hearing and touch, so that the stimuli streaming in from the various senses may be combined and their reactions co-ordinated. In that stem of vertebrates which became mammalian the supreme co-ordinating mechanism was evolved in that part of the neural system connected with smell—the telencephalon.

In Fig. 92 is represented a diagrammatic section across the anterior part of the cerebral vesicle of one of the lower vertebrate types—such

[1] See Elliot Smith's " Arris and Gale Lectures," *Lancet*, 1910, Jan. 1st, 15th, 22nd.

a one as we may suppose preceded the modern mammalian form of cerebral hemisphere. There is a cavity within it—the lateral ventricle. The inner or mesial wall is formed of two parts : (1) the hippocampus or hippocampal formation—true cerebral cortex or mantle ; (2) below the hippocampus, the paraterminal body—a nuclear mass connected with the hippocampal formation by nerve tracts. The hippocampal formation receives fibres from the inner root of the olfactory tract. The lateral

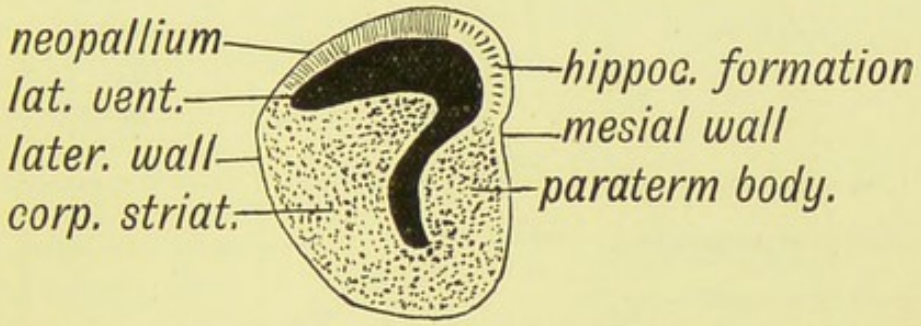


FIG. 92.—Section across the Left Hemisphere of the brain of a primitive vertebrate type anterior to the Lamina Terminalis, to show the small extent of the Neopallium and the relatively great development of the Corpus Striatum and Rhinencephalon. (After Elliot Smith.)

or outer wall of the primitive hemisphere is made up of two parts—the corpus striatum—a nuclear mass connected with the pyriform lobe—an area of mantle or cortex superficial to the corpus striatum. The pyriform lobe receives fibres from the outer root of the olfactory tract. These four parts—hippocampus, paraterminal body, pyriform lobe, corpus striatum—are connected with smell, and form the primitive mantle (archipallium) of the brain. In the roof of the ventricle an expansion of the mantle appears between the hippocampal formation on the inner side and the pyriform lobe on the outer side (Fig. 92) ; to this expansion Elliot Smith, whose account is followed here, gave the name of neopallium. It is this new mantle which becomes the basis for the higher combination of the sensory impressions coming in from all the organs of sense. It becomes the seat of consciousness and memory, and in man assumes enormous proportions, hence the great and rapid expansion of the cerebral vesicles in the human foetus.

Projection Fibres to the Neopallium.—A transverse section of a mammalian brain of a primitive type—made further back and in a more advanced stage of development than that represented in Fig. 92 —is shown in Fig. 93. The section illustrates the manner in which projection fibres arise from two of the sensory nuclei in the optic thalamus—those connected with the nerves of sight and of hearing—and spread outwards into the neopallium—each set streaming into the area which lies nearest to it. In this way the mantle of the telencephalon becomes a higher sensorium for the reception, blending and storing of all sensory impressions.

Localization of Function in the Neopallium.—In Fig. 93A the brain of a primitive mammal is represented on its lateral aspect. The major part is composed of the smell-brain or rhinencephalon—which

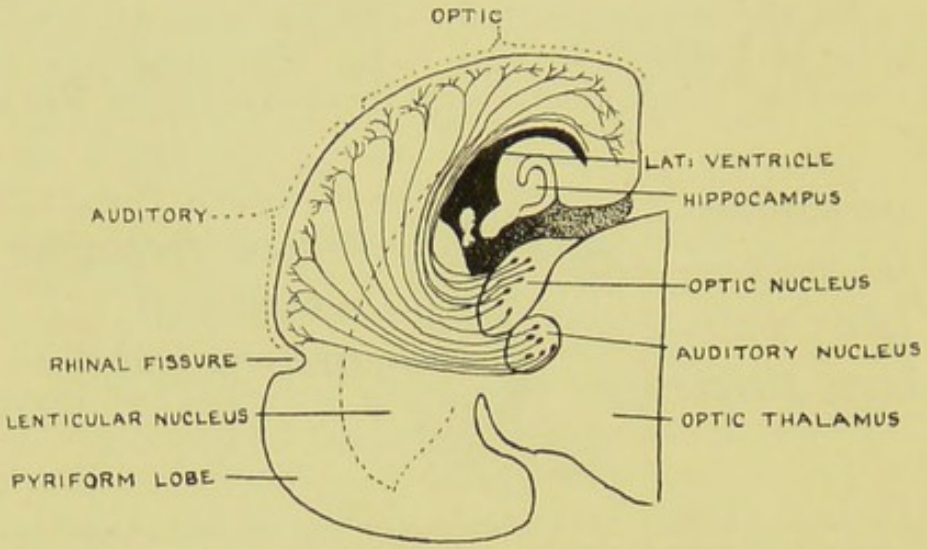


FIG. 93.—Coronal section of the right half of the Cerebral Vesicle of a primitive type of mammal showing the termination of projection fibres arising in the optic thalamus, in the neopallium. (Elliot Smith.)

embraces the olfactory bulb and tract, the olfactory tubercle, the pyriform lobe and the hippocampal formation, which is seen only on the mesial surface of the hemisphere. The rhinal fissure marks the junction of the neopallium with the older parts of the mantle on the outer or lateral aspect of the hemisphere (Fig. 93A). The areas adjacent

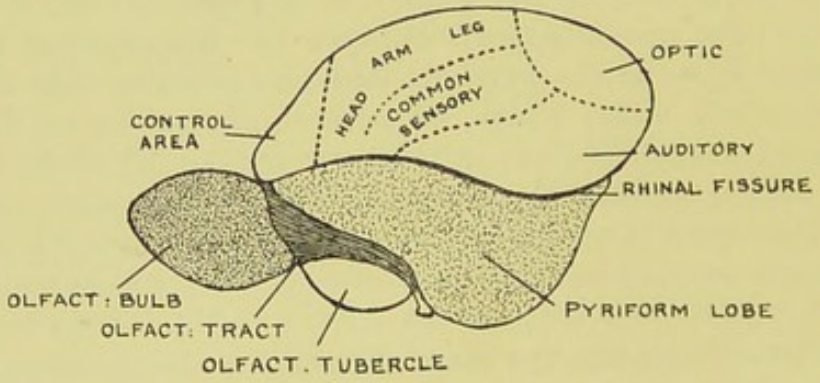


FIG. 93A.—Lateral aspect of the Cerebrum of a primitive mammal to show the Rhinal Fissure which separates the Neopallium above, from the older parts of the mantle below, represented by the Pyriform Lobe. The areas of the Neopallium in which the projection tracts from the optic thalami terminate are also shown. (Elliot Smith.)

to the various nuclei of the optic thalamus receive projection fibres from these nuclei. Thus it comes about that the lower and most posterior part of the neopallium, which forms the basis of the temporal lobe, receives fibres from the auditory centre; in the upper posterior part the fibres from the optic nuclei end; this area becomes the main

part of the occipital lobe. Anterior to these two areas terminate the projection fibres connected with the sensory nuclei of the Vth nerve and with the nuclei of common sensation—receiving impulses from the leg, trunk, arm and head. Hence the surface areas of the body are represented in the neopallium. Naturally it is in connection with this area—the area of common sensation—that the cortical fibres which control the lower motor nuclei arise. Anterior to the motor areas—occupying the region of the frontal pole—is an area connected with the control of the higher centres. These are the primary sensory areas of the neopallium. In the course of evolution, secondary or association zones have appeared round the primary areas, separating them widely and giving rise to the great mass of the human cerebrum.

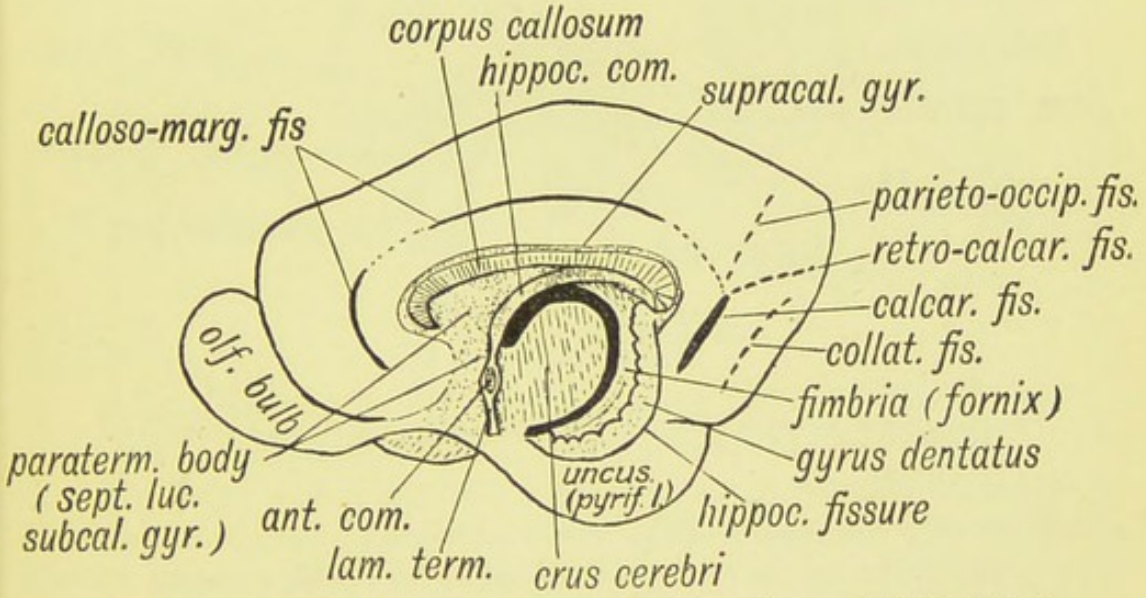


FIG. 94.—The Anterior, Hippocampal and Callosal Commissures, with the primary fissures on the Mesial Aspect of a typical Mammalian Cerebrum. (Elliot Smith.)

Development of Cerebral Commissures.—In order to secure a co-ordinated action of the whole brain, it is necessary not only that the cerebral centres of each hemisphere should be linked up by association and projection fibres, but that the centres of one hemisphere should be united by transverse or commissural tracts with the corresponding centres of the other hemisphere. The lamina terminalis (see Figs. 80, 83, 95) affords a natural bridge for the formation and passage of the commissures. In the most primitive vertebrates, in all of which the cerebral hemispheres are chiefly olfactory in nature, the anterior commissure is already present. The next to appear is a dorsal or hippocampal commissure which unites the hippocampal areas on the mesial surfaces of the cerebrum (Fig. 94). The last and greatest to be formed is the corpus callosum; it appears in the true mammals—not in the monotremes and marsupials. Its development is commensurate with the size of the neopallium; hence it is largest in man.

The cerebral hemispheres are thus connected by fibres which cross in the lamina terminalis, and form three commissures. (1) The **anterior** or **ventral commissure**, which connects the corpora striata, and afterwards parts of the temporal lobes; (2) the **dorsal** or **hippocampal** commissure also formed in the lamina terminalis; in man this commissure becomes the fornix; (3) the **corpus callosum**, which unites the neopallium of one side with that of the other. It is formed in the lamina terminalis above the dorsal or hippocampal commissure (Figs. 94, 95). The

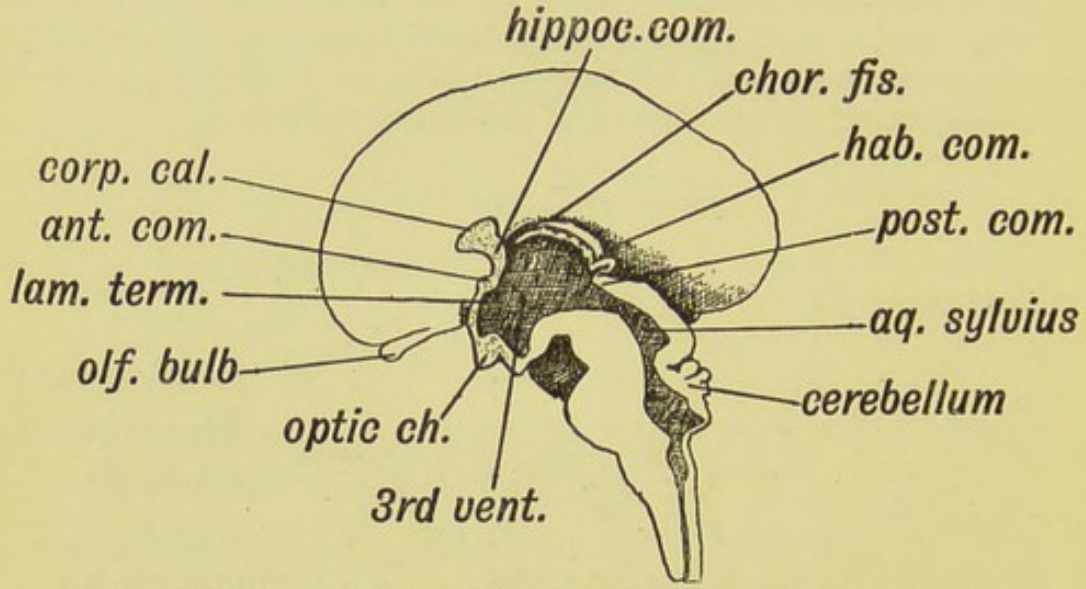


FIG. 95.—Mesial Aspect of the brain of a Human Foetus (4 months), showing the Lamina Terminalis and positions at which Commissures are formed. (After Goldstein.)

middle or grey commissure (Fig. 85) is merely an adhesion between the ependymal coverings of the optic thalami; the **optic chiasma** (p. 91), the **habenular** or superior commissures (p. 94) need only be again mentioned. The **posterior commissure** is formed in the roof plate at the junction of the mid- and fore-brains (Figs. 80, 95).

(1) **The Anterior Commissure** (Fig. 95) is developed in the lamina terminalis—the primitive anterior wall of the fore-brain. The commissure crosses in the lamina terminalis below and rather anterior to the foramen of Monro.

(2) **Hippocampal Commissure.**—Four parts are recognized in the fornix of the human brain (Fig. 96): (1) the body, adherent to the under surface of the corpus callosum; (2) the posterior pillars, which are continuous with (3) the fimbriae and fibres of the alveus, covering the ventricular aspect of the hippocampus; (4) the anterior pillars which end in the corpora mammilaria and optic thalami. The fornix contains two systems of fibres: (1) those which cross in the body and connect the hippocampus of one side with that of the other, and form the true dorsal or hippocampal commissure, (2) fibres which connect together the various parts of the rhinencephalon of the same side, and with the corpora mammilaria and optic thalami.

To understand the development of this system it is necessary to obtain a clear conception of the relationships of the lamina terminalis to the various parts which have been distinguished in the rhinencephalon (Figs. 94, 95, 96). On each side the lamina terminalis is continuous with the **paraterminal body**—that part of the rhinencephalon which joins the hippocampal formation behind and the peduncle of the olfactory lobe in front (Fig. 94, p. 103). The paraterminal body becomes the

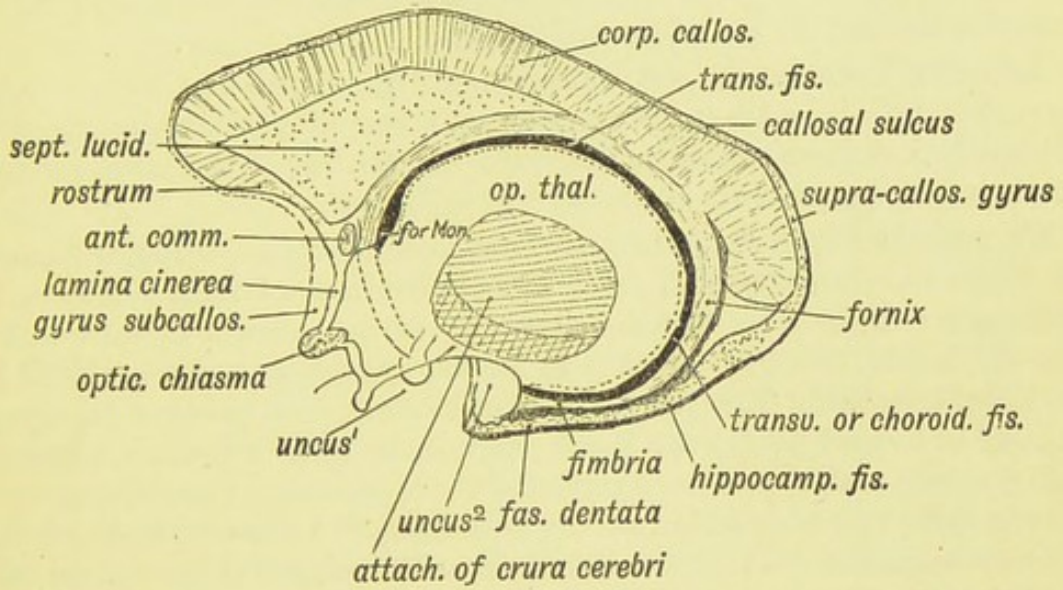


FIG. 96.—Diagram to show the structures formed in the Lamina Terminalis and Primitive Callosal Gyrus. (After Elliot Smith.)

subcallosal gyrus and septum lucidum in the mature brain (Fig. 96). The hippocampal formation, which includes the hippocampus and fascia dentata, bounds the choroidal fissure above (Fig. 96). Fibres developed in the hippocampal formation cross to the opposite side in the lamina terminalis above the anterior or ventral commissure, thus forming the **dorsal commissure** (Fig. 95). It becomes included in the body of the fornix. The posterior pillar is developed in the hippocampal cortex, which forms the lip of the choroidal fissure (Fig. 94). The anterior pillar lies in the paraterminal body and lamina terminalis.

(3) **Corpus Callosum.**—The corpus callosum is the commissure of the **neopallium**, and hence in man, in whom the neopallium forms by far the greatest part of the cerebrum, this commissure attains an enormous development. The commissural fibres begin to form towards the end of the third month, crossing in the lamina terminalis with the fibres of the hippocampal commissure, but situated on their upper or dorsal aspect (Figs. 94, 95). As the corpus callosum rapidly increases within the lamina terminalis, it presses backwards on the hippocampal formation, and forwards on the paraterminal body. The hippocampal commissure is stretched, and forms the body and anterior pillars of the fornix. The hippocampal formation becomes (1) the supra-callosal gyrus, the hippocampus and fascia dentata (Fig. 94). The velum

interpositum is beneath it as the corpus callosum grows backwards. The paraterminal body is stretched to form the septum lucidum and subcallosal gyrus (Fig. 94). Thus by the development of the corpus callosum those two parts of the rhinencephalon—the paraterminal body and hippocampal formation—originally in close union, become widely separated. The supra-callosal and subcallosal gyri are vestiges of their former union. The corpus callosum may not be developed—a rare occurrence; it is remarkable that this condition cannot be detected during the life of the individual.[1]

Lamina Terminalis.—By comparing Figs. 94, 95 and 96 it will be seen that out of the lamina terminalis are formed (1) the lamina cinerea, 2) the bed of the anterior commissure, (3) the bed of the hippocampal commissure, (4) the bed of the corpus callosum.

Choroidal Fissure.—The shape and extent of the choroidal fissure, at which the choroidal villi are inflected within the lateral ventricle, is profoundly altered by the development of the corpus callosum. In the 4th month (see Fig. 95) it is short and approximately horizontal in position, stretching from the foramen of Monro to the uncus. Its upper margin is formed by (1) the lamina terminalis in front, which becomes greatly elongated by the development of the hippocampal commissure and corpus callosum, and behind by the hippocampal formation in which the posterior pillar of the fornix and fimbria are developed (Figs. 94 and 96).

Temporary Fissures.—At one time it was believed that the mantle of the developing brain was thrown into fissures during the 4th and 5th months, which subsequently disappeared. Hochstetter found that they were absent when the foetal brain was hardened *in situ* immediately after death; this observation has been confirmed by Mall, Goldstein and others. Hence what were described as temporary fissures are now regarded as post-mortem products.

Formation of Fissures.—Until the 5th month the surface of the cerebral vesicle is comparatively smooth. Up till then the three strata of the cerebral vesicle, the ependymal layer within, the cortical or nerve-cell layer on the surface and the medullary or nerve-fibre layer between, have increased at an equal rate. In the 6th and 7th months certain areas of the cortex increase rapidly, the increase affecting the superficial area to a very much greater extent than the deep, and affecting the cortex much more than the medulla, with the result that the surface of the cerebrum becomes raised into certain definite eminences or gyri, separated by depressions or fissures. The chief fissures are already well differentiated in the foetus of the 7th month; during the last two months of intra-uterine development the secondary and tertiary sulci appear. The process of fissuration and convolution-formation are thus practically finished at birth. In the spinal cord

[1] See recent cases described by Elliot Smith and by Cameron, *J. Anat. and Physiol.* 1907, vol. 41, pp. 234, 293.

the tracts of nerve fibres are formed outside the masses of grey matter ; in the cerebral vesicle the tracts are formed beneath the grey matter—between the grey matter and the ependyma. The neuroblasts in the cortex have reached nearly their full number by the 7th month ; after then it is their dendrites and collateral fibres that continue to develop (His).

Development of the Cortex.—The mantle of the brain is differentiated into a thin outer grey layer or cortex, containing the nerve cells, and an inner deep stratum—the medulla—of great thickness and made up of nerve fibres and tracts associated with the nerve cells of the cortex. The cortex is the substratum of consciousness, memory and mind. We naturally expect the great mental development which takes place in the earlier years of life to be accompanied by a corresponding change in the microscopic structure of the cortex. There is such a change, but it is difficult to estimate for two reasons : (1) every area of cortex has its own peculiar structure and thickness ; Elliot Smith [1] has distinguished 28 areas in the cortex, each having its own peculiar structure ; (2) Dr Joseph Bolton [2] observed that in some cases a newly born child may show a more mature development than a child of 3 months, there being as much variation in structure of cortex as in degree of ability. The latter observer noted that the cortex began to laminate or divide into three strata of nerve cells at the beginning of the 6th month, when the fissures and convolutions are in process of formation. He also made the important observation that the outer or pyramidal stratum was the latest in growth, and that the great development of this layer is the characteristic of the human cortex.

The Principal Fissures (see Figs. 94, 104).—The principal fissures of the brain are : (1) those connected with the rhinencephalon—the hippocampal fissure and the incisura temporalis (ectorhinal fissure) (Fig. 104) ; (2) those connected with the isolation of the Island of Reil —the fissure of Sylvius, the superior, inferior and anterior limiting fissures ; (3) those in the occipital cortex connected with the sense of sight—the calcarine, retro-calcarine, lunate sulcus (Affenspalte), parieto-occipital and collateral, (4) the calloso-marginal of uncertain import, (5) the fissure of Rolando, which is formed between motor and sensory areas of the cortex, (6) the orbital, (7) the sulcus rectus, (8) the intra-parietal, (9) the 1st temporal or parallel, which partially demarcates the auditory cortex. In the 7th month the fissures on the human brain have a remarkable correspondence to those on the cerebrum of an ape (Figs. 99, 101).

Significance of Convolutions.—There is some circumstance which limits the thickness of the cortex. If the cortical cells increase in number, accommodation is obtained, not by increasing the thickness

[1] Prof. Elliot Smith, *Journ. of Anat. and Physiol.* 1907, vol. 41, p. 237.

[2] Dr. Joseph S. Bolton, *Brain*, 1910, vol 32, p. 26.

of the cortex, but by enlarging the superficial area of the cerebrum. The cortex is correlated in its extent with the bulk of the body and with the area of the integumentary covering. Hence large animals such as whales and elephants have much convoluted brains. The rich convolutions of man's brain may be in some degree related to the nude and sensitive skin of his body (Elliot Smith). The most satisfactory explanation of the number and arrangement of the convolutions of the human brain is to be found in a study of the evolution of its various functional areas. The cortex was originally composed of primary sensory areas—connected with sight, touch, hearing, smell, etc. When secondary and higher zones were produced in connection with the primary areas, the surface of the brain was necessarily thrown into folds and fissures to provide the increase of surface required. Hence we find that the principal fissures are distinctly related to certain cortical areas. Elliot Smith distinguishes three kinds of fissures: (1) those

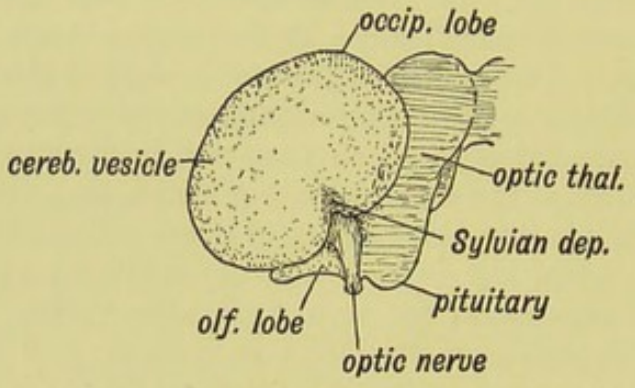


FIG. 97.—Lateral Aspect of the Cerebral Hemisphere at the beginning of the 3rd month.

like the calcarine and central fissures which separate one cortical area from another (*limiting* fissures or sulci); (2) those like the lunate, where the line of cortical demarcation lies, not at the bottom of the fissure, as in the last, but at the brink of the fissure. These are named **operculate**, because the convolution or operculum, which causes the fissure or depression, arises at the junction of two areas; (3) a developing area may fold inwards, thus giving rise to a depression in the centre of an area, like the retro-calcarine in the midst of the visuo-sensory area. The hippocampal fissure and Sylvian fossa are peculiar in their formation. Two fissures—the retro-calcarine and the collateral—actually cause an unfolding of the whole thickness of the mantle, and give rise to two elevations in the posterior and descending horns of the lateral ventricle.

Formation of the Island of Reil and Fissure of Sylvius.—When the lateral wall of the cerebral vesicle is examined at the 5th month (Fig. 98) an area of cortex is seen to be rapidly becoming submerged by the overgrowth of the surrounding cortex. The submerged area is the Island of Reil; it covers that part of the wall of the cerebral

vesicle which is thickened by the corpus striatum (Fig. 89). The submerged area becomes triangular in shape, the apex being directed backwards ; it is bounded by three **limiting sulci**—an anterior, superior and inferior. The rising lips of cortex, which bound the limiting sulci, form the temporal, fronto-parietal, and orbital opercula, and ultimately meet over the submerged area (Fig. 100). The fissure of Sylvius separates the opercula. It will be readily grasped that the development of the corpus striatum prevents the expansion of the insular part of the vesicle, whereas the thin-walled mantle, out of which the other lobes of the brain are developed, expands readily and overwhelms the thickened area. The corpus striatum begins to form during the 2nd month, hence as early as that date the insular depression is visible on the lateral wall of the hemisphere. This mechanical explanation of the origin of the fissure of Sylvius is probably only partially true ; the relatively great growth of the cortex which forms the opercula is due in

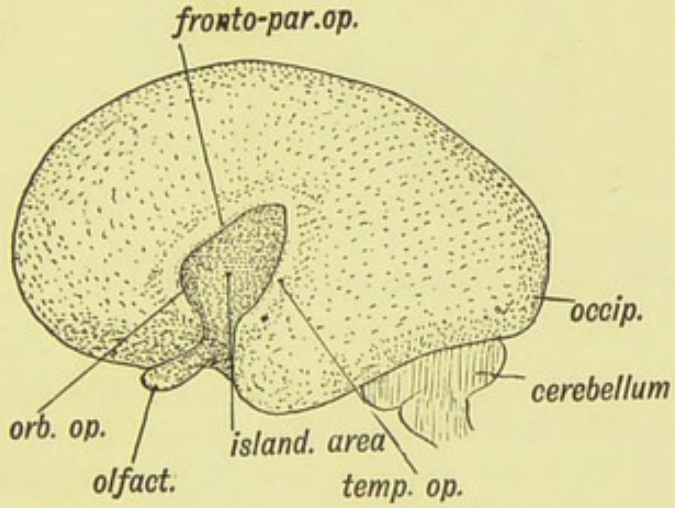


FIG. 98.—The same Aspect during the 5th month.

the main to its great functional importance. By comparing Figs. 97 and 99 it will be realized that the formation of the Sylvian fossa is connected with the expansion and downward growth of the temporal lobe. The growth of the temporal lobe and the differentiation of the occipital pole (see Fig. 98) give the impression that there has been an actual rotation downwards of the cerebral vesicle on the Island of Reil.

The lower end of the stem of the Sylvian fissure also indents the rhinencephalon, separating the uncinate gyrus from the anterior parts of the rhinencephalon (Fig. 103).

The student is already familiar with the fact that the Island of Reil forms a cortical cap to the corpus striatum. The structures between the islandic cortex and the foramen of Monro represent a section of the thickened wall of the cerebral vesicle (Fig. 89). Convolutions appear on it at the 7th month, when the rest of the cortex also becomes convoluted. Further, the larger the area of cerebral cortex in any

primate, the larger is the Island of Reil ; the more convoluted the cortex, the more convoluted the Island. Flechsig has shown that the cortex of the Island is joined to all the cortical areas of the mantle by bands of association fibres. Hence the Island must be regarded as playing a highly important part in co-ordinating the functions of the brain.

The Opercula.—Three opercula grow up and cover the Island of Reil (see Figs. 99 and 100) : (1) the temporal, (2) the fronto-parietal,

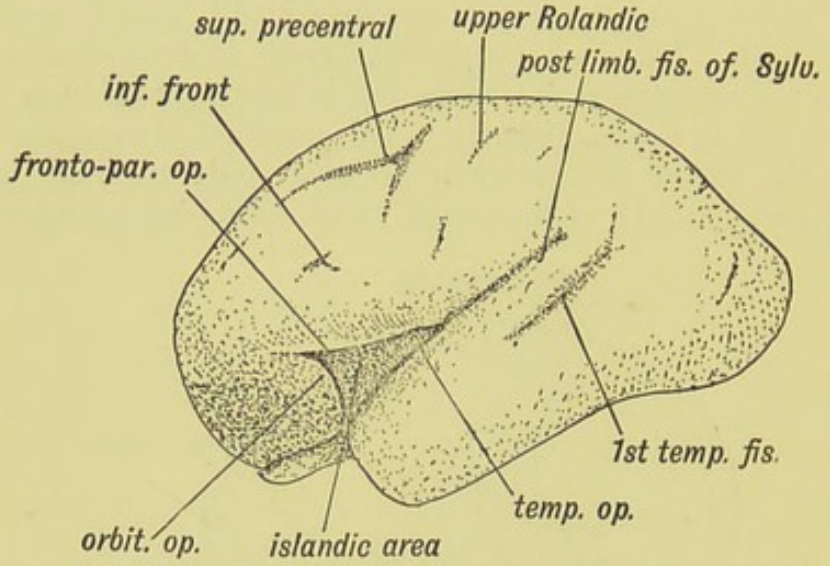


FIG. 99.—The same Aspect during the 7th month.

(3) the orbital. Cunningham, whose researches into this region of the brain have become classical, found that during the later months (7-9) of foetal life an opercular part, known as the **pars triangularis** (Fig. 100, *B*) appeared in quite 50 % of brains and was more frequently present on the left side than on the right, probably owing to the dominant centre for speech being situated on the left side. The pars triangularis is the anterior part of the upper or dorsal operculum (labelled fronto-parietal in Figs. 98, 99), the horizontal limb of the fissure of Sylvius being the anterior continuation of the upper limiting sulcus of the Island of Reil (Elliot Smith). The pars triangularis is cut off from the dorsal operculum by the formation of the ascending limb of the fissure of Sylvius (Fig. 100, *B*). The temporal operculum rises first (5th month), the others a month later. The opercula which bound the posterior horizontal limb of the fissure of Sylvius are the first to come in contact. By the end of the first year after birth all three opercula meet over the Island and completely hide it. At birth there is still a part of the Island exposed behind the orbital operculum and in lower human races this is frequently the condition throughout life. The anterior opercula (pars triangularis and pars orbitalis) become part of the centre of speech and represent later additions to the human brain. If the pars triangularis be not separated from the dorsal

operculum, which is commonly the condition on the right hemisphere, then the anterior limb of the fissure of Sylvius is not subdivided into anterior horizontal and ascending parts (Fig. 100, *A* and *B*). The posterior limb of the fissure of Sylvius is a **limiting** fissure ; it separates the audito-sensory area, situated in the first temporal gyrus—especially in the annectant convolutions of this gyrus buried in the posterior part of the Sylvian fissure, from the sensory-motor areas above the fissure.

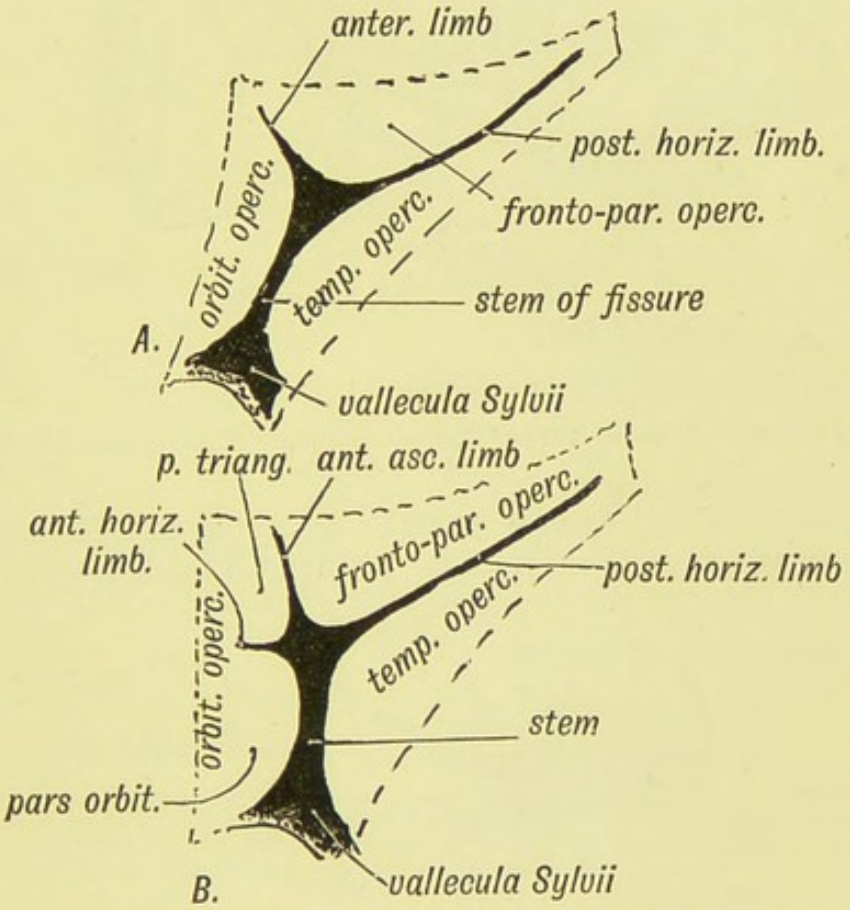


FIG. 100.—Diagram of the Opercula and Fissure of Sylvius.
In *A* the orbital operculum is undivided ; in *B* it is subdivided. (After Cunningham.)

Comparative Anatomy of the Opercula and Island.—The Island of Reil and its opercula are only well developed in the higher primates. In the typical mammalian brain the upper limiting sulcus of the Island of Reil is represented by the supra-Sylvian fissure (Fig. 103), the inferior limiting sulcus by the pseudo-Sylvian fissure, the anterior limiting by the fronto-orbital fissure (Elliot Smith). There are no opercula—the cortex corresponding to the Island of Reil forms part of the surface of the brain. Figs. 101 and 102, *A*, *B*, represent stages in the evolution of the Island and opercula in the primates. In Fig. 101 the condition in dog-like apes is represented. Only the upper and lower limiting sulci of the Island are hid by opercula, the anterior limiting sulcus (fronto-orbital) being still freely exposed. The Island, which is small, is continuous anteriorly with the frontal lobe. In anthropoids

(the gorilla, chimpanzee, orang and gibbon) the Island is larger; the upper and lower limiting sulci are buried; an imperfect anterior limiting

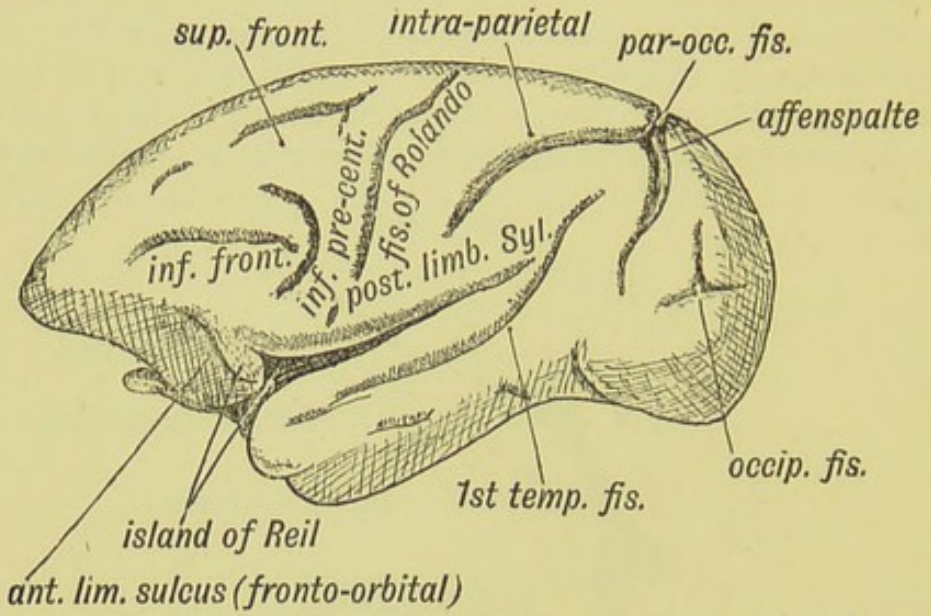


FIG. 101.—The Island of Reil and Fissures on the lateral Aspect of the Brain of a dog-like Ape.

sulcus (fronto-orbital fissure) partially separates the Island from the orbital surface of the frontal lobe. In man all three limiting sulci are

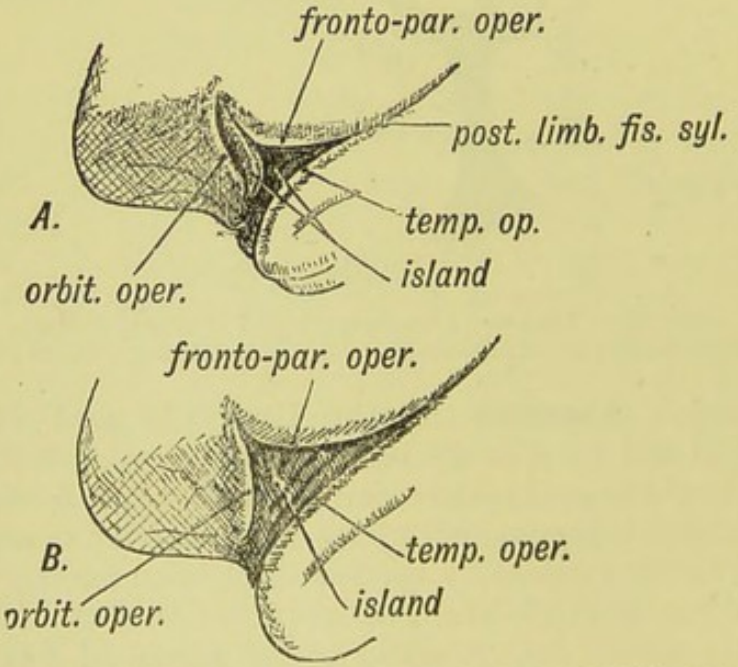


FIG. 102, *A*.—The more common condition of the Island of Reil in Anthropoids. *B*.—The complete isolation of the Island of Reil, the condition seen constantly in the Human Brain and occasionally in the Anthropoid.

covered by opercula and completely isolate the Island, and occasionally this is the condition (Fig. 102, *B*) in the higher anthropoids, but it is in man only that the orbital operculum grows up and meets with the

other opercula. This can be the more easily understood when it is remembered that the orbital part of the 3rd frontal convolution is connected with speech.

Hippocampal and Ectorhinal Fissures.—The hippocampal fissure (Figs. 94, 96) is found in all mammalian brains (Elliot Smith). The inrolling of the hippocampal cortex and formation of the hippocampal fissure, in which the cortex lies, is closely connected with the development and outgrowth of the fascia dentata (Fig. 96). The incisura temporalis (Figs. 103 and 165), all that remains of the ectorhinal

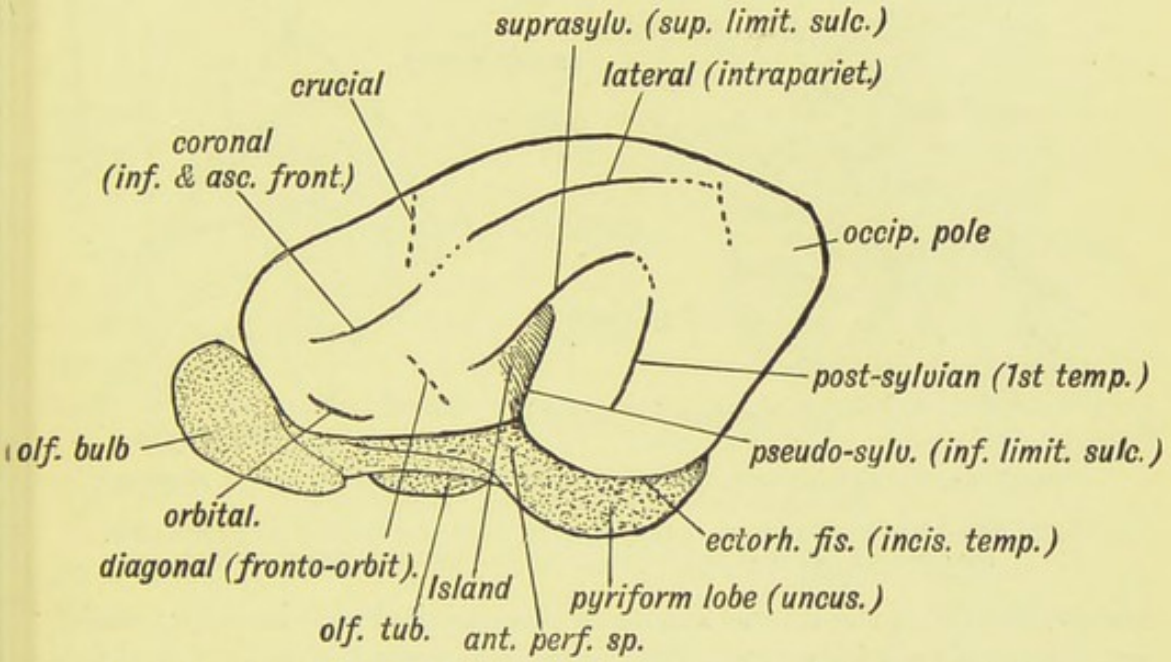


FIG. 103.—The Fissures on the Lateral Aspect of a typical Mammalian Brain. (Elliot Smith.) The Fissures to which these correspond in the Human Brain are indicated within brackets. The parts of the Rhinencephalon are stippled; the cortex corresponding to the Island of Reil, shaded.

fissure of the typical mammalian brain, separates the uncus—part of the rhinencephalon—from the cortex or neopallium of the temporal lobe. The ectorhinal, or rhinal fissure, as it is usually named, is thus a limiting fissure between olfactory and temporal cortex.

The Calloso-Marginal Fissure.—This fissure on the mesial aspect of the brain arises from the fusion of the genual and intercalary fissures of the typical mammalian brain (Fig. 94). Its origin is probably the result of a pressure due to the growth of the cortex surrounding the corpus callosum, for if that structure be absent, the usual form of this fissure is completely altered. It separates one set of cortical areas from another (Elliot Smith).

The Calcarine and Correlated Fissures.[1]—In the typical mammalian brain the calcarine fissure forms part of the same arcuate system as the genual and intercalary (Fig. 94). The part of the cerebral

[1] See Elliot Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 198.

wall in which it is formed projects within the posterior horn of the lateral ventricle (Fig. 192, *B*, p. 201). The cortex on the lower or posterior lip of the fissure shows the stria of Gennari which characterizes the cortex in which the optic radiations end. The calcarine fissure is thus a limiting fissure formed between striate and non-striate cortex. The **retro-calcarine fissure** or depression, which continues the calcarine sulcus backwards to the occipital pole, is formed by the growth and involution of the striate cortex (Fig. 105). In the ape's brain the

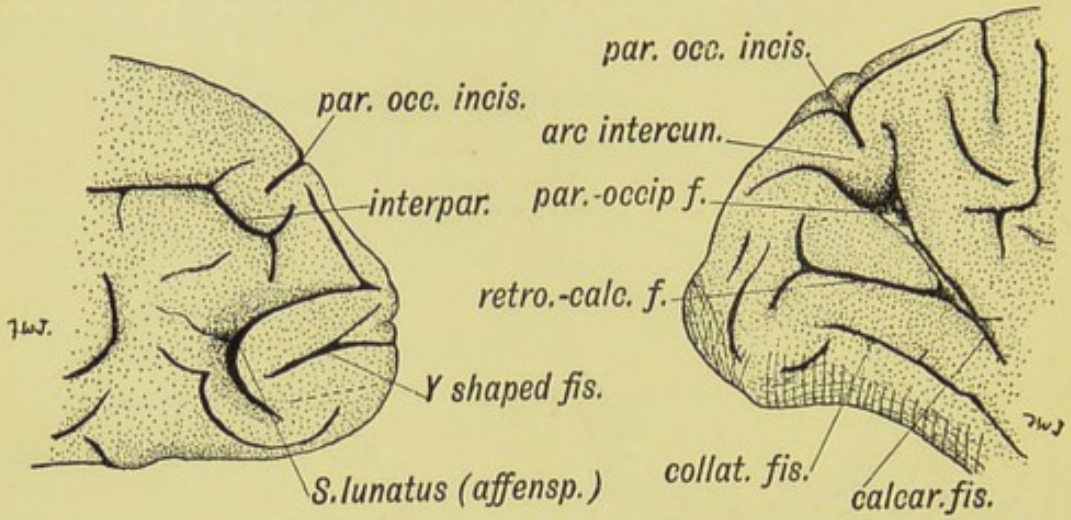


FIG. 104.—The Lateral Aspect of the Occipital Lobe of a Human Brain, showing the Sulcus Lunatus (Affenspalte). (Elliot Smith.)

FIG. 105.—The Mesial Aspect of the Occipital Lobe of a Human Brain, showing the complex nature of the Parieto-Occipital Fissure. (Elliot Smith.)

striate cortex on the lateral aspect of the occipital pole increases rapidly and rises up as a lip or operculum over the cortex of the parietal lobe. The depression in front of the operculum is known as the **simian fissure** (Affenspalte) or **sulcus lunatus** (Fig. 101). In the human brain the great increase of the parietal cortex, a seat of association centres, has pushed the sulcus lunatus almost to the occipital pole (Fig. 104), or it may, especially in the more civilized races, be completely obliterated. Further the Y-shaped occipital sulcus (external calcarine) on the lateral aspect of the occipital pole (Figs. 101, 104) may join the retro-calcarine sulcus. More recently Elliot Smith has distinguished not only the striate area, in which the optic radiations end, but two surrounding areas, an outer zone—the peristriate, and an intermediate—between the outer zone and the striate area. Certain sulci have arisen in connection with the evolution of these two association or visuo-psychic areas. The **collateral fissure** below the calcarine (Fig. 105) probably results from a mechanical pressure exercised by the growth of the striate area. The **parieto-occipital** fossa or depression on the mesial aspect of the brain results from the inflection of an area of cortex between the calcarine areas of growth behind, and the area of association centres on the mesial aspect of the parietal lobe in front (Fig. 105). The production of the parieto-occipital fossa, with its complex of buried

convolutions and sulci, is also related to the growth backwards of the corpus callosum. In human brains where this structure is absent the buried convolutions and sulci are superficial.

Orbital Fissure.—This fissure is present in most mammalian brains, but its significance is still doubtful.

Fissure of Rolando, or **Central Fissure**, appears during the sixth month as an upper and lower linear depression, which join together in the course of development (Fig. 99). The fissure forms between the motor areas of cortex in front of it, and the sensory areas behind it, and is therefore a limiting fissure. The upper part does not quite correspond to the crucial sulcus of the brain of the cat and dog, for in them that sulcus forms the *anterior* limit of the motor areas (Elliot Smith) (Fig. 103); the lower part may represent part of the coronal fissure. The fissure of Rolando reaches its fullest development in man; it is found only in the higher primates (apes and anthropoids).

Sulcus Rectus.—The sulcus rectus, or straight fissure, appears before that of Rolando, and is found in primate brains in which the Rolandic fissure is absent (Figs. 101, 103). It forms in the adult brain (1) part of the inferior frontal fissure, (2) the lower part of the precental fissure (ascending frontal). It lies between two areas of frontal cortex which are of different structure, and corresponds to the coronal fissure of the cat's brain (Fig. 103).

Intra-parietal Fissure.—The intra-parietal fissure appears between three areas of growth: (1) the cortex of the interior parietal lobule below, chiefly consisting of association areas related to the visual and auditory and perhaps also to the areas of common sensation; (2) the occipital cortex posteriorly; (3) the cortex behind the upper end of the fissure of Rolando above and in front (Fig. 99). It corresponds to the lateral fissure of the cat's brain (Fig. 103). The ascending, horizontal and occipital limbs of this fissure arise independently in connection with separate areas. They may or may not become conjoined. All the parts of the fissure are limiting in nature.

Parallel or First Temporal Fissure.—The first temporal fissure separates the first temporal gyrus, in which the auditory centres are situated, from the neighbouring cortex (Figs. 101, 103). As the first temporal gyrus rises to form the inferior operculum of the island of Reil, part of it, in the form of a number of gyri which connect it with the island, are buried in the fissure of Sylvius. In these gyri Campbell has located the terminations of the auditory tracts, the superficial part of the first temporal convolution forming association areas for the auditory centre (Fig. 210, *A*). The first temporal fissure corresponds to the post-Sylvian fissure of the typical mammalian brain (Fig. 103).

Secondary Sulci and Gyri.—During the eighth and ninth months the remaining sulci and convolutions of the brain are formed. For the greater part these are peculiar to the human brain.

Membranes and Arteries of the Brain.[1]—The dura mater is differentiated from the mesoblastic capsule of the brain, forming the inner lamina of the membranous basis in which the cartilage and membrane bones are developed. Hence it forms the inner lining or periosteum of these bones. As the cerebral vesicles expand, septa of the primitive dura mater are enclosed between the two hemispheres (falx cerebri). A fold is also pushed backwards under the expanding occipital lobes and forms the tentorium cerebelli. It is not until the third month that a subdural space is formed, separating the dura mater from the pia-arachnoid, the proper capsule of the brain. The internal carotid arteries supply the brain. Each divides into an anterior division which becomes the anterior cerebral, and a posterior division out of which the basilar is formed. The middle and posterior cerebral arteries appear later, and are secondary branches (Bertha de Vriese). The vertebral arteries are formed from the segmental arteries of the spinal cord. (For further details see Mall, *Amer. Journ. of Anatomy*, 1904, vol. 4, No. 1.)

[1] Bertha de Vriese, *Archiv. de Biol.* 1904, vol. 21, p. 357 (Morphology of Cerebral Arteries); F. P. Mall, *Amer. Journ. Anat.* 1904, vol. 4, p. 1 (Development of Cranial Venous Sinuses); O. Grosser, *Verhand. Anat. Gesellsch.* 1907, p. 179.

CHAPTER IX.

THE CRANIUM.

Natural Divisions of the Skull.—The human skull is the product of many long epochs, during which it has undergone great changes, but we have every reason for supposing that its general functions have remained much the same since the vertebrate form of animal was evolved. In the first place it has to form a brain-case—a neuro-cranium. Man's brain has reached a degree of development which rendered great changes necessary in this part of the skull. In the second place, the skull has to shelter and protect the special organs of sense—the ear (temporal bone), the eyes (orbits), the olfactory area (nasal region), and taste (bucco-pharyngeal region). In the third place, the skull forms an essential part of the structures concerned in mastication; the facial part of the skull is in reality a scaffolding for the palate and teeth. In the main the facial part of the skull is visceral or splanchnic in function, and hence is sometimes spoken of as the splanchno-cranium. The outstanding characters of the human skull are the great size of the neuro-cranium and the small size of the splanchno-cranium.

Certain Phases in the Evolution of the Skull.—The skull has also been closely related to the function of respiration. In fishes the visceral skeleton of the skull forms the arches which carry the gills. We have seen that the representatives of these arches make a temporary appearance in the head of the human embryo. When a pulmonary replaced a branchial system a nasal airway was separated from the mouth by the formation of a primitive palate, such a palate as is seen in amphibians, reptiles and birds. With the evolution of chewing teeth in the mammalian stock the complete palate was formed, thus allowing the mammalian young to suck, and the adult to chew and breathe freely at the same time. We see all of these stages manifested in the development of the human skull.

Growth of the Cranial Cavity.—The neuro-cranium is framed by the disposition of its bones and sutures, so as to allow a free and easy expansion of the brain. By a mechanism we do not fully understand

the bones entering into the formation of the cranial cavity grow as demand is made on them by the brain ; at least, this is so in early life. When the cranial bones begin to form in the latter part of the second month, the brain (cerebral vesicles) is only half an inch long—from frontal to occipital pole ; in the adult the length is fourteen times as much and its volume fifteen hundred times larger. As the cerebral vesicles expand the developing bones alter in shape. By the 7th

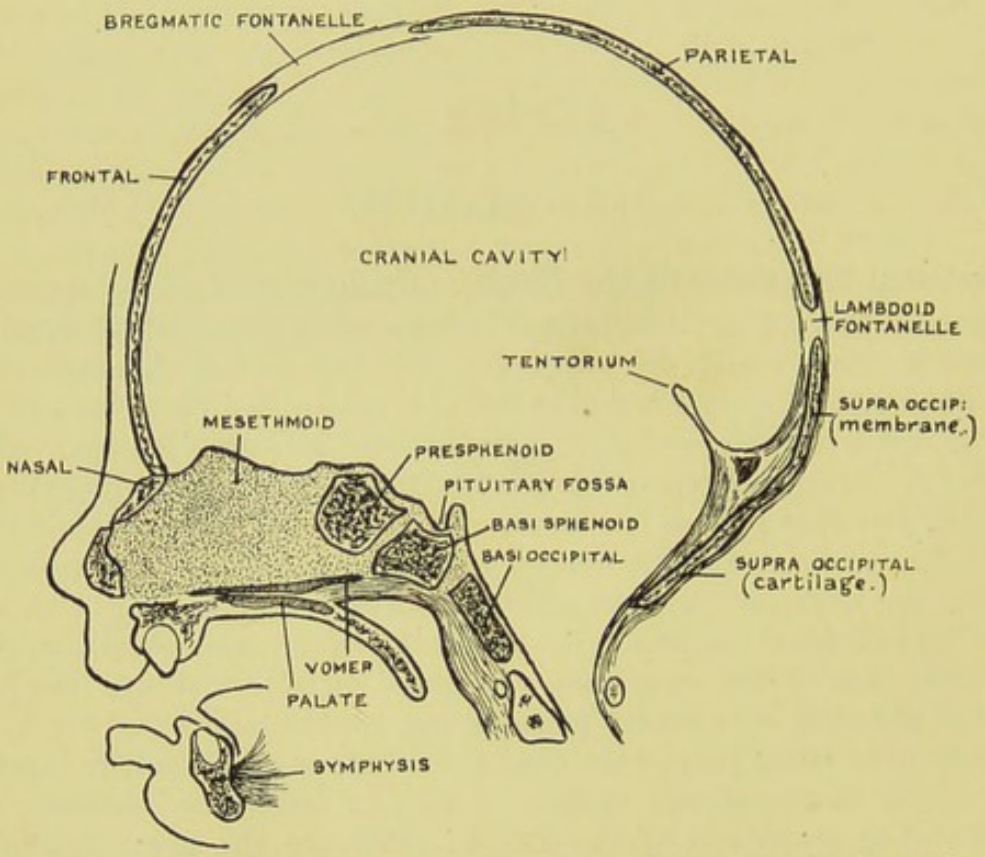


FIG. 106.—Median Sagittal Section of the Skull of a Foetus of the ninth month.

month of foetal life the relative proportions become approximately fixed. During the first four years of life brain and cranial growth go on rapidly. At birth the brain has attained from 20 to 22 per cent. of its size ; by the 4th year over 80 per cent. of the volume is already present. There is a steady increase until the 18th or 20th year, when the maximum is obtained (about 1500 cubic centimetres in Englishmen) ; after then there is a decline in the capacity of the cranium. The changes in the cranial walls are secondary to those in the brain.

From Fig. 106 it will be apparent that the walls of the cranium are made up of two very different parts—basilar and capsular. The basilar part is thick and developed in a cartilaginous basis. Growth proceeds as in a long bone ; the lines between the basi-occipital and basi-sphenoid, the basi- and pre-sphenoid, and between the pre-sphenoid and ethmoid are growing or epiphyseal lines. The growth of the base of the skull is determined as much by the needs of the

splanchno-cranium as by those of the neuro-cranium. The capsular part—occipital, parietal, frontal and temporal bones—on the other hand, respond easily to the expansion of the brain. They grow at their edges; the sutures are growing lines. Growth at the coronal and lambdoid sutures adds to the calvarial length; growth at the sagittal and squamous sutures increases the calvarial breadth. At the same time there is also a constant deposition or growth on the outer table and an absorption on the inner. In this manner the bones are modelled, and growth of cranial cavity and brain are co-ordinated. Only those bones which enter into the formation of the cranial cavity and help to form the brain chamber are dealt with in this chapter. These bones are the frontal, parietal, occipital, temporal, ethmoid and sphenoid.

Is the Skull made up of Segments?—We have just seen that the body is made up of 33 or more segments. Is the skull made up of a series of segments? The theory supported by Owen and many others that the cranium is really composed of four modified vertebrae is now no longer tenable. On the other hand the arrangement of the nerves and muscles, the evidence of development and comparative anatomy, indicate that it is composed of a number of segments, probably nine in number. The four posterior, which form the occipital region of the skull, are recognizable at an early stage of development, but at no period in the development of the embryo have the anterior five segments been seen to be demarcated.

The Primitive Membranous Skull.—The brain is developed in the same manner as the spinal cord from the medullary plates of the neural groove. In the same manner the mesoblast grows under and over the cephalic part of the neural canal, and forms for it a **menenchymal** or membranous covering. The covering of mesoblast thus formed is the primitive basis of the skull in the embryo.

Membrane and Cartilage Bones.—It is not possible to understand the manner in which the bones of the human cranial cavity are developed without some reference to comparative anatomy. Only the base of the human skull is developed in cartilage, the rest is developed in membrane. How has such a condition arisen? The brain of amphioxus, if it can be said to possess one, is wrapped in a membranous covering. In fishes with cartilaginous skeletons this embryonic mesoblastic capsule becomes chondrified—plates of cartilage develop in it. As in the spinal column, the process of chondrification begins at the base and spreads slowly round to the crown or dorsum of the head. The cartilaginous cranium is an advance on the membranous stage. In many fishes a further most important element is added. The **dermal** bony plates, to which the placoid scales are fixed, are applied to the cartilage over the sides and dorsum of the skull. Thus to the cartilaginous element of the skull is added a third element—bone formed in membrane. Now, in the mammalian skull, and especially in that of

man, the cerebral vesicles grow so quickly that long before the process of chondrification has had time to spread in the membranous capsule from the base to the crown, the dermal bones have formed, and thus supplant the cartilage on the calvarium. Hence, in the human skull, while the process of chondrification occurs in the base, and afterwards undergoes ossification, the whole calvarium and sides of the skull are formed by bones which, historically, are **dermal bones,** and hence are formed directly in membrane. The dermal bones of the human skull are : (1) the frontal, (2) the parietal, (3) the inter-parietal part of the

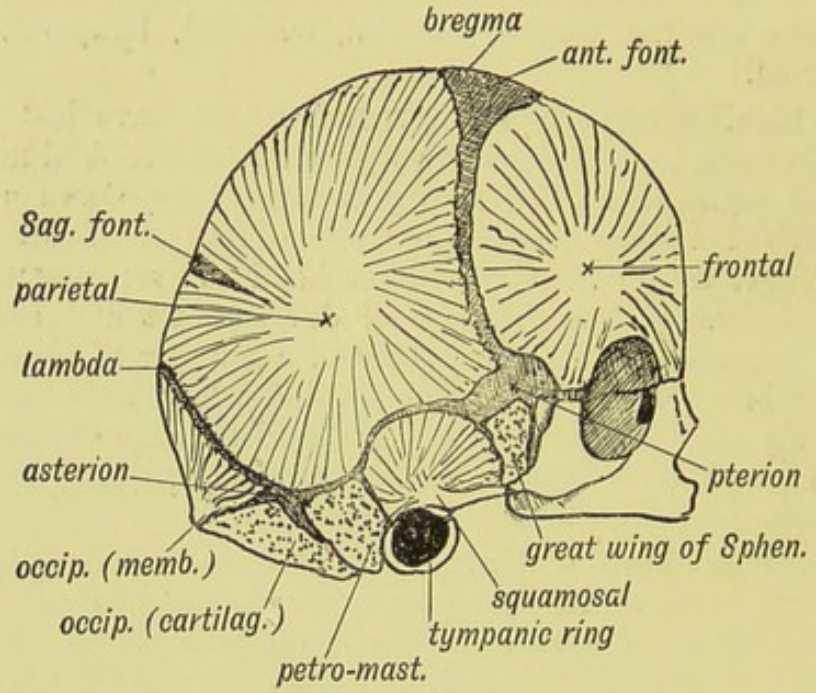


FIG. 107.—The Centres of Ossification for the Dermal Bones of the Skull. The bones which are formed in cartilage are stippled.

occipital (the part above the superior curved lines), (4) the squamous part of the temporal.

Thus the calvarial part of the skull passes directly from the membranous to the bony stage, while the base of the skull, like the spinal column, passes through three stages : (1) membranous, (2) cartilaginous, (3) bony. It will be thus seen that the base of the skull, developed in cartilage, is the most ancient part, while the dermal bones, which form the calvarium, represent a later addition.

Development of the Roof (membranous or dermal part) of the Skull.—In the 8th week of foetal life—the foetus being then about 30 mm. ($1\frac{1}{4}$ in.) long—there appear on each side of the membranous cranial capsule four centres of ossification :

(1) For the frontal bone, at a point which becomes afterwards the frontal eminence (Fig. 107).

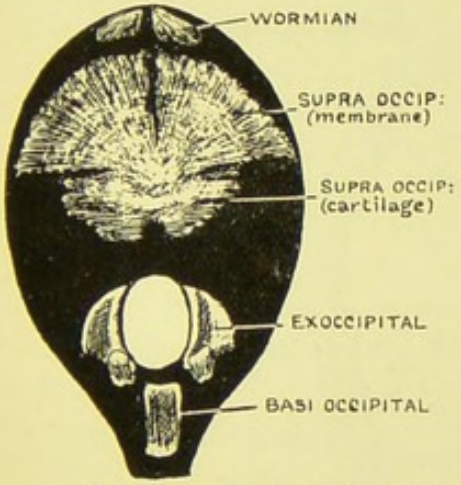
(2) For the parietal, at the position of the parietal eminence ; this

centre is double or even triple in nature, but the separate points are placed closely and soon fuse together;

(3) For the squamosal, at the base of the zygoma (Fig. 107);

(4) For the membranous part of supra-occipital (part above superior curved line). Maggi and Hepburn[1] have shown that there may be four centres (two on each side) in the membranous supra-occipital (Fig. 109).

The two or four occipital centres fuse early into one at the position of the external occipital protuberance, but occasionally these centres



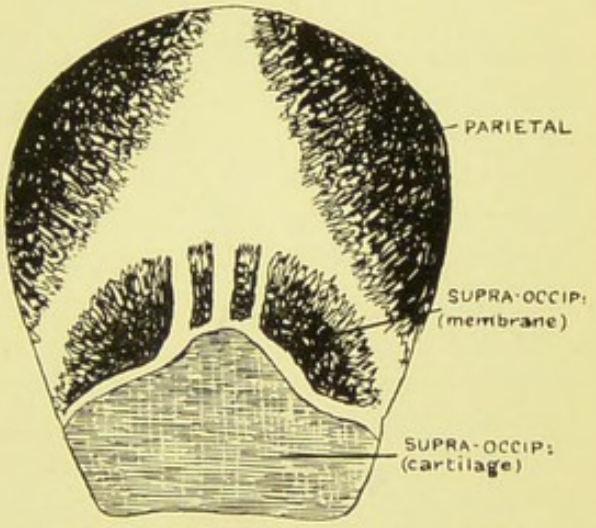


FIG. 108.—The Occipital Bone at the 4th month, showing pre-interparietal Wormian Bones. (After Sappey.)

FIG. 109.—The Supra-occipital from a Foetus of 3 months, showing four Centres of Ossification for the Membranous Supra-occipital. (After Maggi.)

may form two, three or four separate bones. The two frontal ossifications fuse about the end of the first year; the **metopic** suture, which separates them, disappearing then. This suture occasionally persists. One or both parietals may be divided by a suture or by a complex of sutures.[2] The centres of ossification in these cases have not fused. The parietal bones fuse together, at the sagittal suture, late in life, commonly between the 35th and 45th year, when the growth of the skull has entered a retrograde phase. The squamosal partly covers the petro-mastoid cartilaginous element and fuses with it in the first year, the temporal bone being thus formed. These bones, as they are laid down, accurately follow the contour of the brain. That organ forms a relatively small sphere when ossification commences. Hence the convexities or **eminences** at the regions of earliest formation.

The Manner in which these Bones are Developed.—In Fig. 110 a vertical section of the skull of a foetus 4½ months old is represented. The coverings of the brain are seen to be then (1) scalp, (2) a

[1] Professor Hepburn, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 88.

[2] Professor Patten, *Zeitschrift für Morph. und Anthrop.* 1912, vol. 14, p. 527; Professor Berry, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 77.

stout white fibrous capsule, (3) a fine membrane lining it—the inner layer of the dura mater, (4) the arachnoid covering the brain (not shown in figure). Ossifying fibres which form the parietal are seen developing within the capsule and radiating out from the centre of ossification. The ossific fibres, as they spread outwards from a common centre, unite by branches, thus forming an irregular network with osteoblasts and growing vessels within its meshes. Lower down are seen the ossifying fibres of the squamosal. The base of the skull is formed of cartilage which is covered, or ensheathed, by a perichondrium

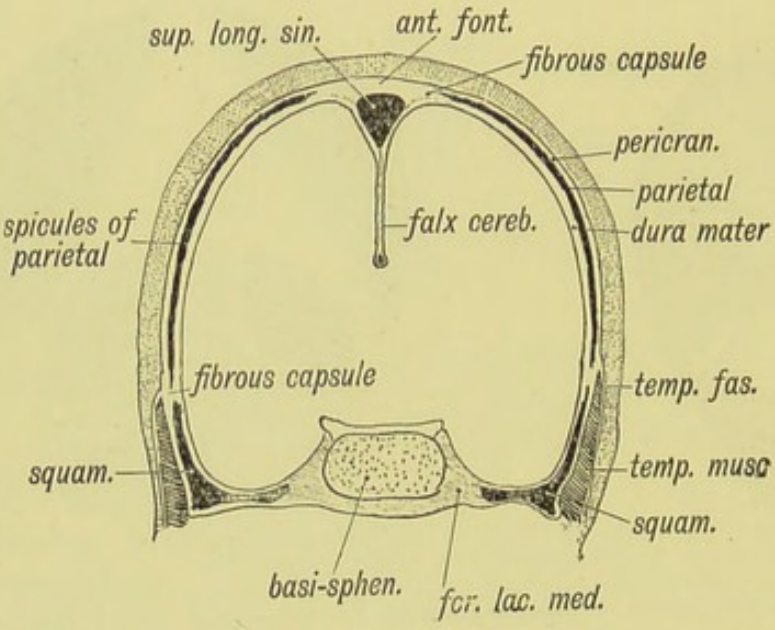


FIG. 110.—A Coronal Section of the Skull of a Foetus, 4½ months old.

continuous with the membranous capsule. In the cartilage appear the centres of ossification for the sphenoid.

As the bony fibres of the parietal spread out, they divide the primitive cranial capsule into an outer layer—the **pericranium**—and an inner—the **periosteal** layer of the dura mater. At the periphery of the bone and in the sutures the continuity of these two layers persists. The growth of the fibroblasts and osteoblasts in the sutural lines between the bones keeps time with the growing brain which expands the capsule, but there is, at each corner of the parietal bone, until the end of the first year, a part of the primitive cranial capsule left unossified. These unossified parts of the membranous capsule are the **fontanelles.**

The Fontanelles.—There are five fontanelles connected with each parietal bone, one at each of its rounded angles, and one, the **sagittal** (Fig. 107), which occurs between the radiating fibres of the parietal near the posterior end of the sagittal suture. The parietal foramen marks its position in the adult. In about 15 % of children this fontanelle is unclosed at birth ; a large parietal foramen may permanently mark its situation. The posterior inferior fontanelle, situated at the

asterion (Fig. 107), the anterior inferior at the **pterion,** and the posterior superior at the **lambda,** close before or about the time of birth. Separate ossifications, which become **Wormian** bones, are often developed in the primitive capsule of the skull at those three fontanelles and thus close them. The anterior superior fontanelle, at the **bregma,** cannot be distinctly felt during life after the first year (Warner), but it is not completely closed until the second year is nearly over. This fontanelle is lozenge-shaped, being bounded by four bones, viz. the two parietals and two frontals. The bregmatic or anterior superior and lambdoid or posterior superior fontanelles are median and common to both parietals.

The membrane-formed bones consist at first of a thin lamella of osseous fibres radiating out from the point at which ossification commenced. The osteoblasts beneath the pericranium on the outer surface of the lamella and the dura mater on the inner surface, deposit bone, and by the 5th year an outer and an inner table, with diploic tissue between, are developed. Into the diploë of the frontal bone protrude the growing buds of the two frontal sinuses. As the brain expands new bone is formed at the sutures to increase the capacity of the skull, but the operation of craniotomy to allow the expansion of a confined brain, by the formation of a new suture, is founded on the assumption that the arrest of brain-growth in microcephalic idiots is due to the closure of the sutures, whereas it is probably due to an inherent defect in the growth of the brain. We frequently see skulls where one or more sutures have been prematurely closed, but in such cases there has been compensatory growth at other sutures, giving rise to a peculiarity in cranial form. Growth of the cranial cavity could take place by a deposit of bone on the outer table and an absorption from the inner; for this manner of growth, sutures are unnecessary. The synostosis of the sutures does not necessarily prevent growth; synostosis of the skull bones occurs only when the brain has ceased to expand. If the brain of the infant is arrested in its growth, premature ossification of the sutures occurs, the condition of **microcephaly** resulting therefrom. In **hydrocephaly,** when the ventricles become enormously dilated, the membranous capsule of the cranium expands so quickly that the process of ossification cannot keep up with its rapid growth. Hence in hydrocephaly the fontanelles are enormous. The growing points of ossific fibres are detached and form Wormian bones. The cartilaginous part of the skull is scarcely affected in this disease. The membrane-formed part of the skull is liable to diseases which do not affect the cartilage-formed part. The dura mater is very adherent to the bones formed in cartilage.

Development of the Cartilaginous part of the Skull.[1]

(1) **The Occipital Bone.**—The occipital bone is developed from the

[1] F. and J. P. Tourneux, *Jour. d'Anat. et Physiol.* 1912, vol. 48, p. 57 (Base of Skull); see references under Bardeen, p. 46; Fawcett *Jour. Anat. and Physiol.* 1910, vol. 44, p. 303.

parachordal cartilages, two cartilaginous bars which partly surround the cranial part of the notochord and from their first appearance in man are fused in a basal plate (Robinson) (Fig. 47, p. 49). The parachordal cartilages represent a forward continuation of the vertebral axis ; they are formed by a chondrification of the mesenchymal sheath of the notochord ; the centre of chondrification in the basilar plate appears at the end of the first month, and is the first to be seen in the base of the skull. From each side of the basilar plate a wing is thrown out (Fig. 112) ; these meet over the hind-brain and form the exoccipitals

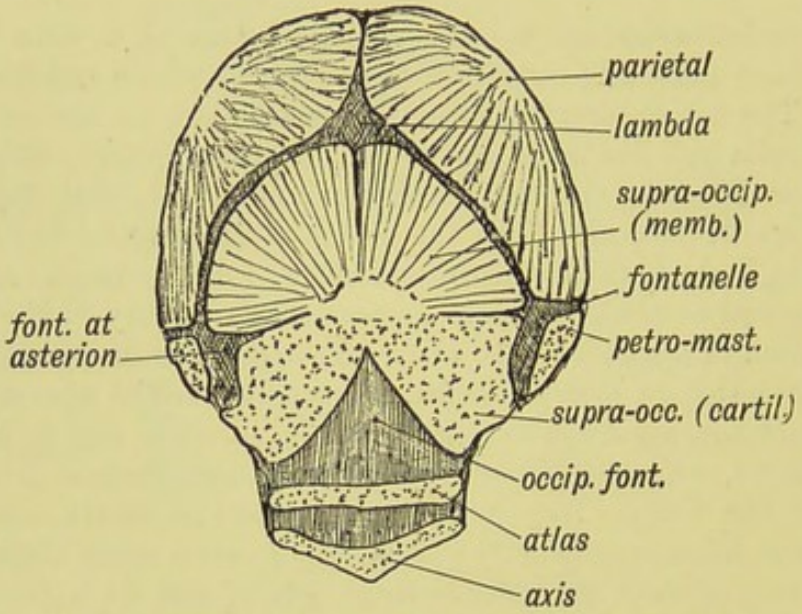


FIG. 111.—The Occipital Region, in a Foetus of 5 months.

and cartilaginous part of the supra-occipital, and thus enclose the foramen magnum. The plate of cartilage, from which these parts are developed, is known as the tectum. The tectum is also continuous with the mastoid cartilage of the petro-mastoid (see Fig. 115, *A* and *B*). In Fig. 111 the condition of the occipital region is shown in a 5th-month foetus. Four centres of ossification appear in the tectum, and quickly fuse to form the cartilaginous part of the supra-occipital. A suture between the membranous and cartilaginous parts is clearly visible—especially near the fontanelle at the asterion. The membranous and cartilaginous parts of the supra-occipital become completely fused soon after birth. It will be observed that the process of fusion between the lateral parts of the cartilaginous supra-occipital is not complete in the 5th month (Fig. 111). The occipital fontanelle projects upwards between them from the foramen magnum. This fontanelle is filled by a continuation of the posterior atlanto-occipital ligament, and becomes closed soon after birth. It is the most common site of a cerebral meningocele—a saccular protrusion of the membranes of the brain which contains cerebro-spinal fluid, and usually a part of the occipital

lobes distended by a dilatation of the posterior horns of the lateral ventricles.

Separate centres of ossification appear in the occipital cartilages to form (1) the basi-occipital, (2) the two exoccipitals, and (3) the supra-occipital.[1] The occipital consists of four pieces until the fourth year, when synostosis occurs. The occipital condyles are formed from the exoccipitals and basi-occipital, the exoccipital element constituting in the adult by far the larger part, but when the condyles first appear they are continuous at the anterior border of the foramen magnum,

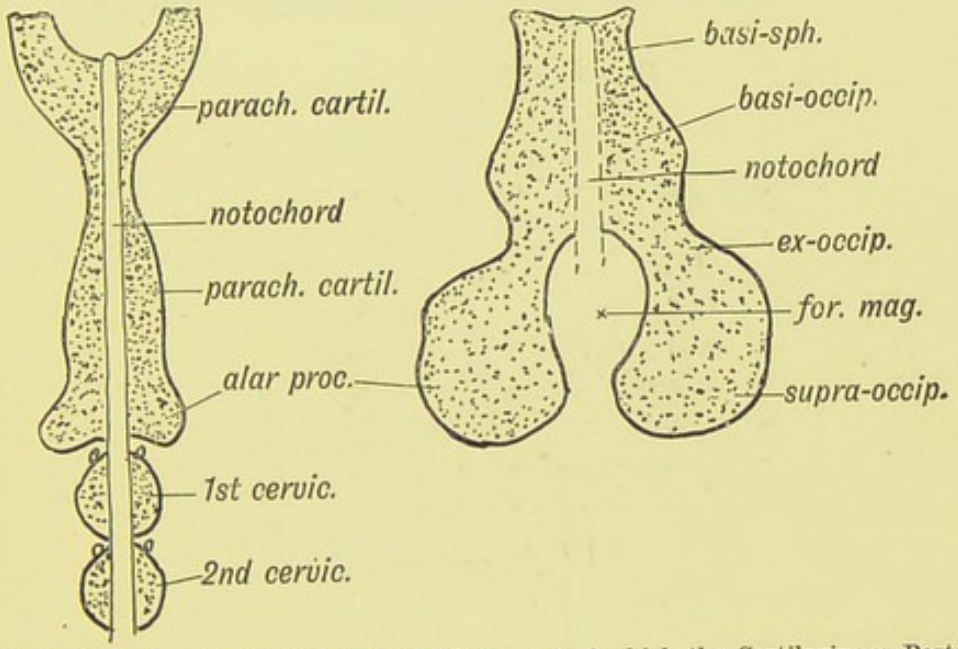


FIG. 112, *A*.—The Parachordal Cartilages out of which the Cartilaginous Parts of the Occipital Bone are formed.

B.—The expansion backwards of the Parachordal Cartilages to enclose the Foramen Magnum and form the Supra-occipital.

forming a single or median condyle as in reptiles, birds, and lower mammals. The anterior condylar foramen is formed between the two elements. The occipital protuberance is formed by both membranous and cartilaginous parts of the supra-occipital.

(2) **The Petro-mastoid** forms part of the base of the skull. We shall see that the petrous bone (p. 216) is primarily developed as an independent cartilaginous capsule round the inner ear, but at an early date (6th week) it fuses at certain points with the parachordal basis of the occipital bone, while an extension from the mastoid part of the capsule enters into the formation of the tectum (Fig. 115). Even as late as the thirtieth year remnants of the tectal cartilage may be found between the petro-mastoid and occipital bones, especially between the jugular process of the occipital and the mastoid. The fibro-cartilage in the foramen lacerum medium and Eustachian cartilage, which is continuous with it, are remnants of the periotic cartilaginous capsule.

[1] For a very complete account of the dates at which all centres of ossification appear in the skeleton see Mall, *Amer. Journ. of Anat.* 1905, vol. 5, p. 433.

(3) **Trabeculae Cranii** (Figs. 113, 114, and 115).—The notochord, with the parachordal cartilages developing above and on each side, terminates behind the pituitary fossa (Fig. 113). In all lower vertebrates the cartilaginous base of the skull in front of the notochord is formed by two irregular bars or plates of cartilage. Although in higher mammalian, as in human embryo, the process of chondrification has become complicated, yet there can be no doubt that the cartilaginous parts formed in the base of the human skull represent the simple and primitive trabeculae cranii shown diagrammatically in Fig. 113. In Fig. 114 are shown the parts which represent the primitive trabeculae. Their

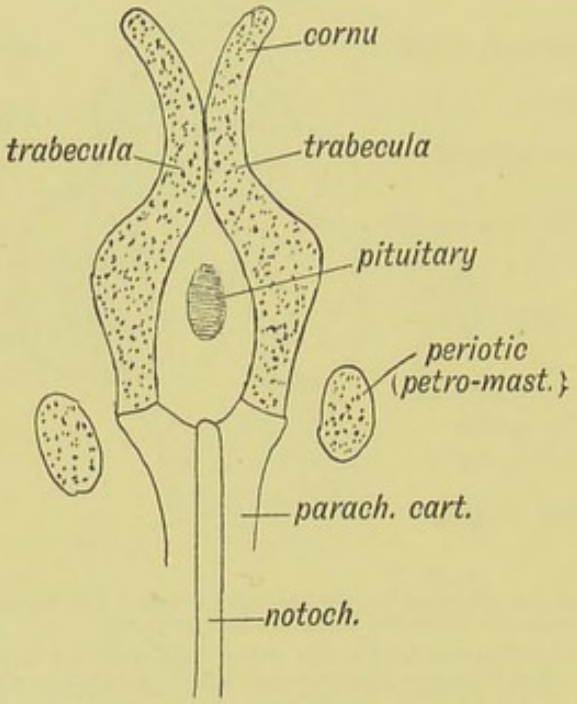


FIG. 113.—Diagram of the Trabeculae Cranii, Parachordal Cartilages, and Periotic Capsules.

posterior extremities fuse round the anterior termination of the notochord with the parachordal cartilages. The buccal part of the pituitary grows into the cranial cavity in front of the notochord and keeps the two cartilages apart ; but in front of the pituitary the two bars fuse in the middle line. The mesial fused parts of the trabeculae grow into the embryological basis of the nasal septum (Fig. 114). The posterior part of the median fused bars forms the cartilaginous basis of the pre-sphenoid and basi-sphenoid (Fig. 114). From the trabeculae four lateral processes or wings grow out on each side (Fig. 114). The **posterior,** which is small at first, represents the cartilaginous part of the great or temporal wings ; the **second** is originally large, and forms the small wings (orbito-sphenoids) ; the **third** and **fourth** outgrowths are closely joined,—they form the lateral masses of the ethmoid and alar cartilages of the nose. The nasal bones, the lachrymal and ascending nasal processes of the superior maxilla, develop in the membrane

over the lateral nasal wings of the trabeculae, in the same way as the vomer develops over the cartilage of the septum (see p. 147).

Development of the Sphenoid.—Recently Professor Fawcett (*Journ. Anat. and Physiol.* vol. 44, 1910) has examined the manner in which the cartilaginous basis of the sphenoid is formed in the human embryo. The mesoblastic or mesenchymatous basis of the sphenoid becomes chondrified during the second month. There is a double centre which forms the basi- and pre-sphenoids; each small wing chondrifies separately, while the great wing is formed in quite a complicated manner. There are two small centres of chondrification—

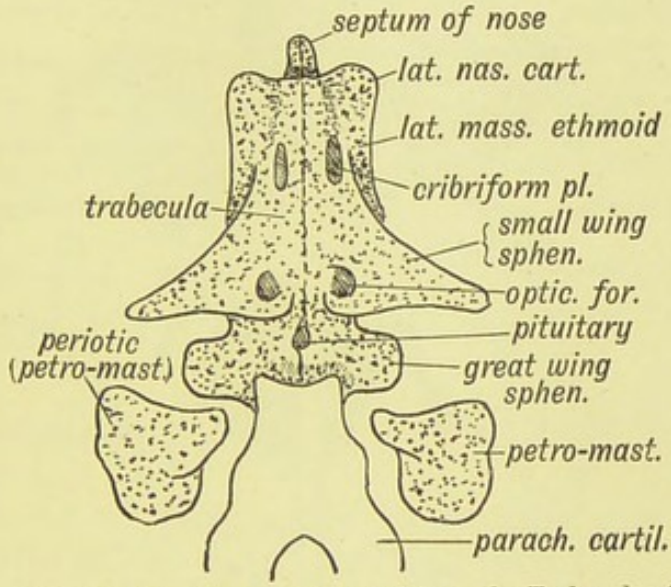


FIG. 114.—Diagram of the structures formed from the Trabeculae Cranii.

which together form that part of the great wing which is in relationship to the 2nd and 3rd divisions of the fifth nerve (see Fig. 115, *B*, processus alaris and ala temporalis). The part of the great wing which enters into the formation of the orbit and of the temporal fossa is developed from a separate mesenchymal mass, which undergoes a secondary chondrification (Fig. 115, *A*). There is also a separate centre for the dorsum sellae. During the latter part of the second month the point of the small wing extends into the temporal fossa on the side of the skull. A process (the parietal plate) of the periotic capsule extends towards it (Fig. 115, *B*). These two processes always meet, and form a cartilaginous plate in the temporal fossae of lower mammals (Gaupp). In the second month the cribriform plate is not yet formed; there is a gap between the mesial and lateral ethmoidal cartilages.

At birth the sphenoid bone consists of three parts, the great wings being separated from the rest of the bone. The sphenoidal turbinate bones, afterwards inflated by the development of the sphenoidal air sinuses, are then nodules of bone, surrounded by cartilage. They also are separate and form part of the lateral ethmoidal cartilaginous plates.

The internal pterygoid plates are also separate ossifications laid down in the membrane over a plate of cartilage, representing the palato-quadrate bar of lower vertebrates (see p. 150). Only its hamular process is formed in cartilage (Fawcett). The internal become adherent during the fourth month of foetal life to the external plates, which are developed as membranous outgrowths from the

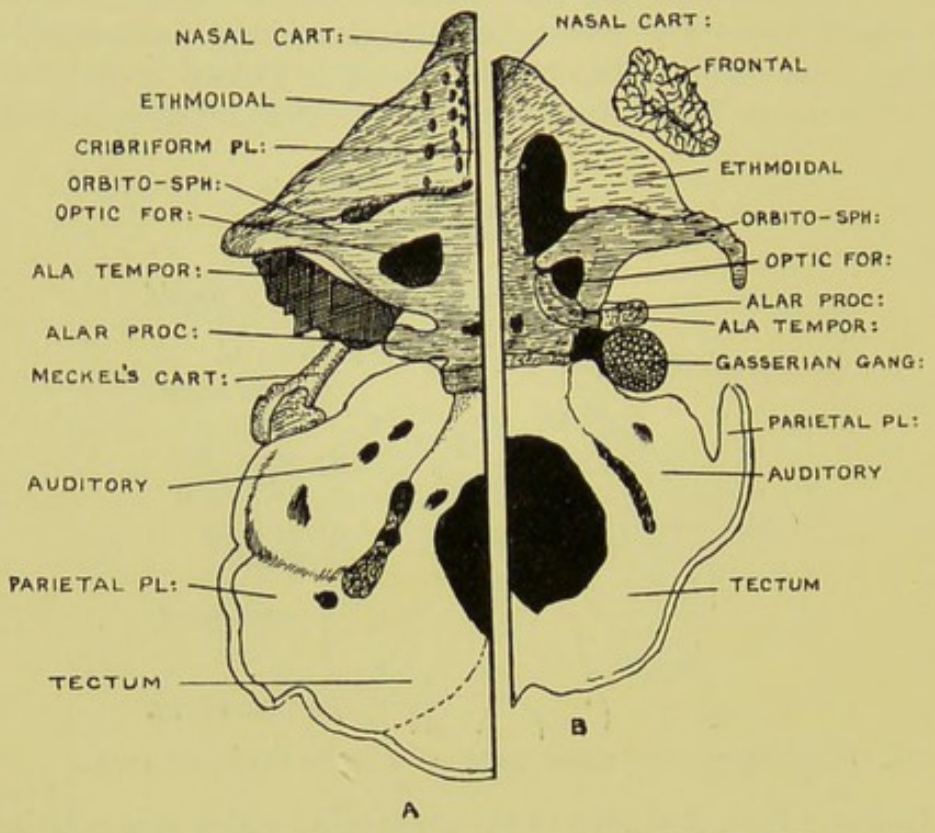


FIG. 115, *A*.—Left half of the Cartilaginous Basis of the Skull in a Foetus of three months. (After Kollmann.)

B.—Right half of the Cartilaginous Basis of the Skull in a Foetus of two months. (After Fawcett.)

ali-sphenoids or great wings. The pre-sphenoid unites with the basi-sphenoid in the 8th month ; the great wings unite with the basi-sphenoid soon after birth. The **lingula** which bounds the outer side of carotid groove (Fig. 116) is ossified from a centre which appears during the 4th month of foetal life. The orbito-sphenoids unite over the pre-sphenoid and cover its cranial aspect.[1]

The Pituitary Body is developed between the trabeculae cranii ; the pre-sphenoid is formed in front of it and the basi-sphenoid behind it. A canal may remain in the foetal or even adult bone to mark the point of ingress of the buccal part of the pituitary.[2] The wings of the vomer cover the opening of the pituitary canal on the pharyngeal aspect of the skull, if it be present. On the cerebral aspect it opens

[1] See reference, Mall, p. 125.

[2] H. Arai, *Anat. Hefte*, 1907, vol. 33, p. 411 (Cranio-pharyngeal Canal).

at the olivary eminence which also marks the union of the pre- and the basi-sphenoids. The writer has seen a child, in which the trabecular cartilages had remained apart, leaving a wide gap through which the pituitary projected within the septum of the nose. The pre-sphenoid and afterwards the basi-sphenoid are much altered by the growth of the sphenoidal sinuses which commence to expand rapidly about the 7th year. The great wings support the temporal poles of the brain, their size depending on the development of that part of the brain. They are much larger in man than in any other mammal, owing to

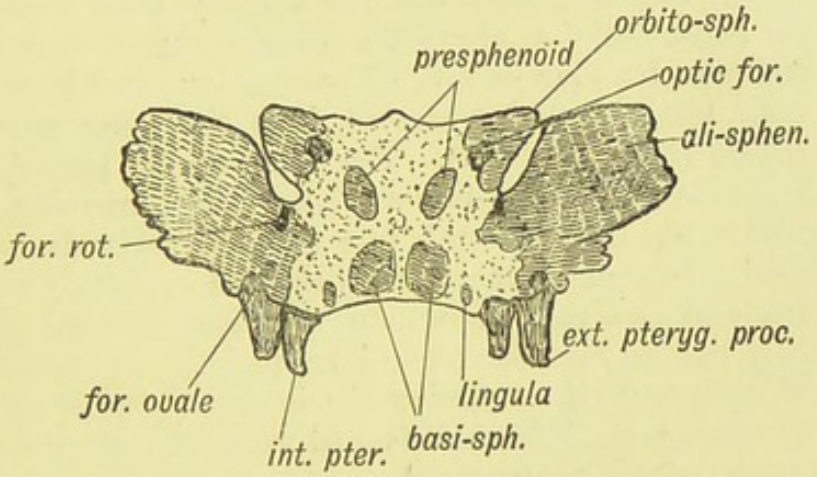


FIG. 116.—The Sphenoid in a Foetus of 4 months. The Centres of Ossification are deeply shaded. (After Sappey.)

the great size of the human temporal lobes. The small wings project within the vallecula Sylvii. In the early foetus the dorsum sellae is enormously developed, and fills the deep and sharp angle between the mid-brain and fore-brain (Fig. 73).

Formation of Foramina in Bone.—The foramina of the skull are formed in one of three ways (Sutton) :

(1) By the union of two bones ; examples of this form are the jugular foramen, sphenoidal fissure, Glaserian fissure, etc.

(2) By the union of two elements of one bone ; the anterior condyloid foramina, optic foramina, the foramen magnum, aqueductus Fallopii, etc.

(3) By the enclosure of a notch on the edge of a bone of which the foramen ovale is the best example. This foramen is at first a notch in the posterior border of the great wing of the sphenoid (Fig. 116) ; it remains in this condition in all mammals except man. In him the margins of the bone on each side grow out and fuse, and thus convert the notch into a foramen. Other examples are the foramen spinosum, the foramen rotundum, parietal foramen, mastoid, etc.

Wormian Bones.—In the six fontanelles which occur at the parietal angles separate ossific centres frequently appear and close them. The fontanelle ossifications form Wormian bones. They occur most frequently at the posterior angles of the parietal (Lambda and Asterion) ;

they are also common at the Pterion (epipteric Wormian) but rare at the Bregma. The Wormian at the last-mentioned point receives the name of os anti-epilepticum. Much confusion has been caused by naming a large Wormian, which may occur in the lambdoidal (posterior-superior) fontanelle, the inter-parietal bone. Wormian or sutural bones are particularly numerous in the skulls of infants who have been the subjects of hydrocephaly. It is possible that, during the rapid expansion of the skull, the tips of ossifying fibres have become detached, thus forming separate centres of ossification in the sutures and fontanelles.

The Inter-parietal Bone.—It has already been shown that the part of the supra-occipital above the superior curved lines is developed from membrane by four centres of ossification, and is at first, and almost until birth, nearly separated from the lower part developed from cartilage (Figs. 109, 111). The membranous part of the supra-occipital represents the inter-parietal bone. In marsupials, ruminants, and ungulates, the inter-parietals fuse with the parietals, and not with the occipital. In rodents they fuse with both occipitals and parietals. In primates and carnivora, as in man, they fuse with the occipital. It is extremely rare to find the whole inter-parietal separate in man, but a large Wormian, partly replacing the inter-parietal, is very frequent. Such a Wormian bone, if large, is named variously, os epactal, os Incae, os triquetrum, or pre-interparietal.

The Post-frontal does not occur in mammals as a separate bone; in them it has fused with the frontal, and forms that part of the bone which articulates with the great wing of the sphenoid and malar. A Wormian bone—the epipteric—which is occasionally developed in the fontanelle at the pterion, may be mistaken for it. Traces of a true post-frontal, partly separated from the frontal, rarely occur in man.

The Cephalic Index.—Anthropologists have employed the shape of the head as a character in classifying the races of mankind. The **cephalic index** is used to express the shape of the head. It states the proportion that the breadth bears to the length of the skull (Figs. 117, *A*, *B*). The length or **long diameter** of the skull is usually measured from the glabella to the most projecting point of the occiput—usually situated over the occipital poles of the brain; the breadth or widest diameter is measured between the widest points—usually some distance below the parietal eminences. If the length of a skull is 100 mm. and the breadth 75, the cephalic index of that skull is 75, *i.e.* the breadth is 75 % of the length. Human races, on an average, are either **Dolichocephalic** (long-headed), the breadth being 75 % or less of the length; **Brachycephalic,** in which the breadth is 80 % or more of length; or **Mesocephalic,** in which the breadth is between 75 % and 80 % of the length. Various methods are employed in estimating the height of the skull, but the best is that which takes the upper margin of the external auditory meatuses as representing the basal plane. The height is measured from this plane to the highest point in the sagittal suture,

when the skull is oriented so that the lower border of the orbit and the middle of the meatus are in one plane (see Duckworth, *Morphology and Anthropology*).

The English people have an average cephalic index of 75, the South Germans 83, but it must be remembered the individuals vary widely in every race. It will be seen that the topography of the brain, worked

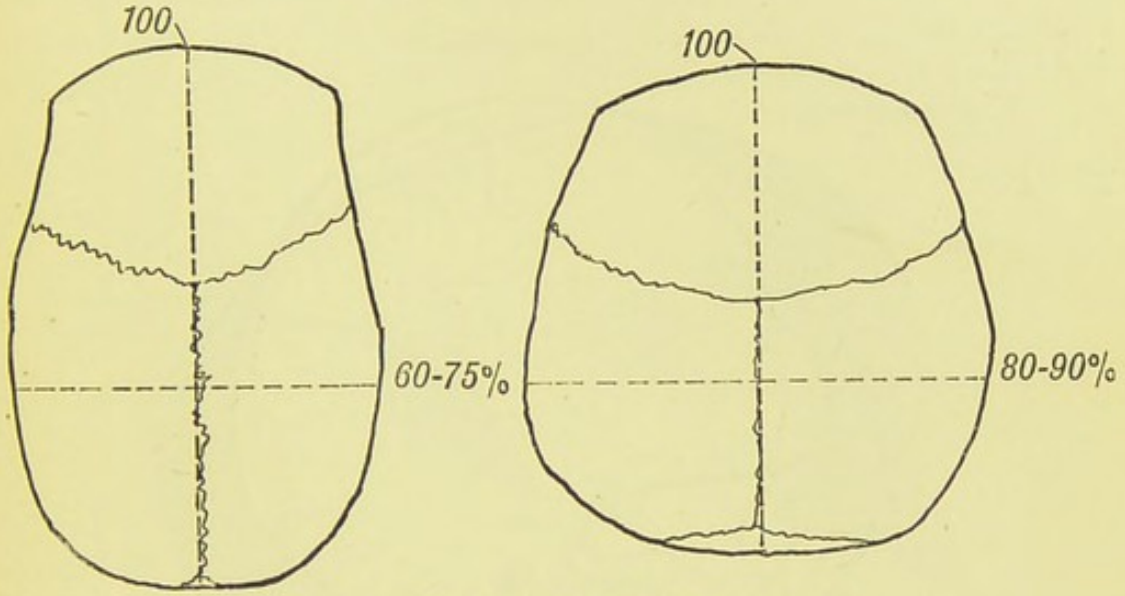


FIG. 117, *A*.—Diagram of a Long-head (Dolichocephalic).
B.—Diagram of a Short-head (Brachycephalic).

out by German surgeons, cannot be applied to the longer English heads without modification.

Factors which determine the Shape of Head.—The shape of the skull depends (1) on the size and shape of the brain; (2) on the size and strength of the muscles which arise from it—the muscles of mastication, or are inserted to it—the muscles of the neck. Brain growth is by far the most important factor, but we do not know the conditions which flatten the brain from side to side in dolichocephalic races, or shorten it from frontal pole to occipital pole in brachycephalic races. Muscular action can only exercise a minor effect. Recently Professor Arthur Thomson [1] has shown there is a correlationship between dolichocephaly and the size of the temporal muscles—which are relatively large in long-headed races—and the shape and mechanism of the mandible. It is to be remembered that (1) the muscles of mastication and of the neck undergo their greatest development between the 12th and 28th years; (2) before that time the brain has almost completely attained its adult size and shape; (3) all the evidence obtained from measurements in the living indicates that the changes in cranial form which take place then affect only its external contour, leaving the shape of the cranial cavity unaffected.

[1] Arthur Thomson, *Man's Cranial Form*, Oxford, 1903.

Abnormal Crania.[1]—It is possible that light will be thrown on the factors which determine head-form by the study of certain pathological conditions. In the disease known as Acromegaly, where there is always a great enlargement of the pituitary gland, the skull undergoes peculiar growth changes. The supra-orbital ridges become greatly developed, the face elongates, the temporal lines from which the temporal muscles arise, grow upwards on the side of the skull, thus increasing the area of the

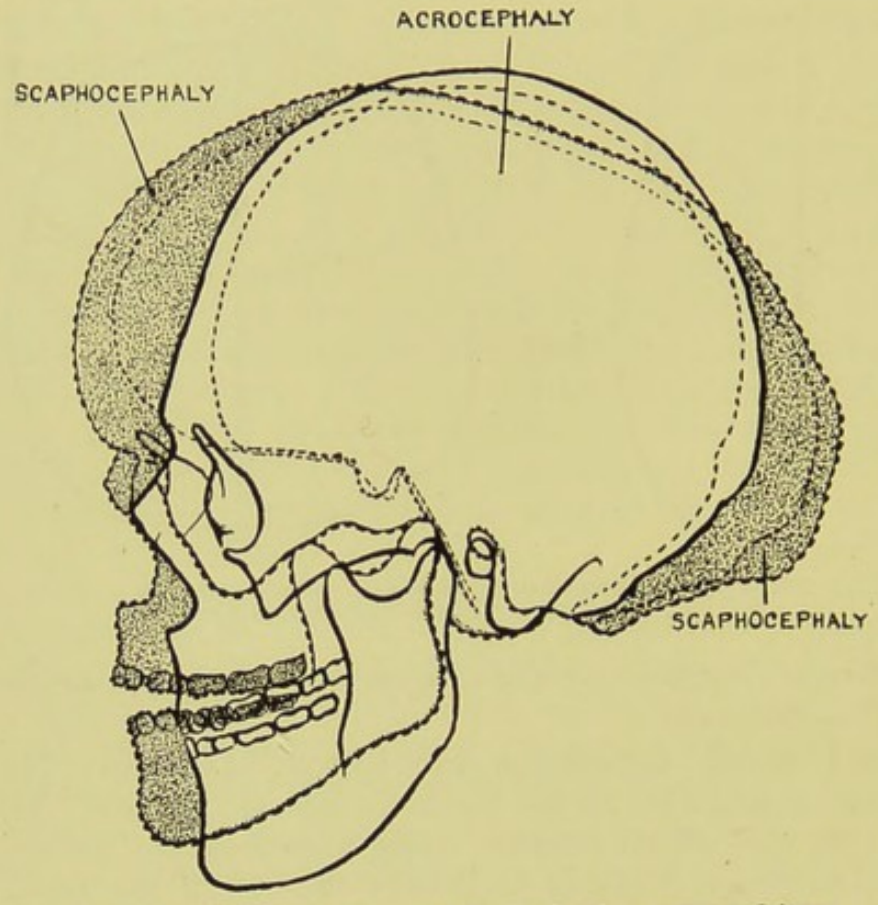


FIG. 118.—Outlines of Abnormal Skulls showing contrasted forms.

temporal muscles. At the same time the lines which mark the attachment of the muscles of the neck—the mastoid processes, superior curved lines and external occipital protuberance—also increase greatly in size. In achondroplasia and in rickets the skull assumes characteristic forms due to a disturbance in the growth of the base of the skull. To a certain degree the growth of the cranial bones is regulated by internal secretions. In Fig. 118 two common types of abnormal skull forms are shown. They are contrasted types; in one—Acrocephaly or steeple-skull—the base is abnormally short, owing to an arrest of growth at the junction of the pre-sphenoid and ethmoid. Compensation is obtained by an upward growth. In severe cases the optic nerves may be pressed on, and blindness thus caused. In the second type—Scaphocephaly,

[1] For skull in achondroplasia see Dr. Murk Jansen, *Achondroplasia*, Leyden, 1912; A. Keith, *Journ. Anat. and Physiol.* Jan. 1913.

or boat-shaped skull—the skull is very narrow from side to side, while the calvarial arc—from nasion to opisthion (posterior border of foramen magnum)—is greatly elongated. In scaphocephaly there is an arrest of growth—often a synostosis—along the sagittal suture. In acrocephaly the coronal suture is closed. In these two, and in allied conditions, there is a certain amount of evidence which points to a disturbance in the function of the glands of internal secretion.

The Facial Angle [1] is the angle at which the face projects from the axis of the skull (Figs. 119, 120). The skull consists in man, as in all

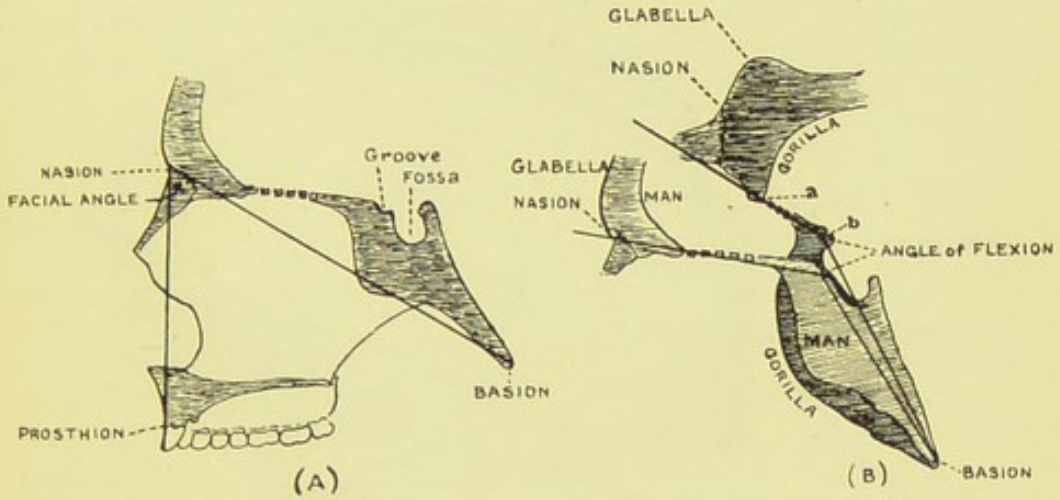


FIG. 119, *A*.—The Facial Angle as estimated by two lines drawn from the Nasion to the basion and to the prosthion (incisor alveolus).
B.—Method of estimating the degree of flexion and extension of the cranial axis. *a*, anterior border of cribriform plate; *b*, on olivary groove in front of olivary eminence. *a*, *b*, trabecular axis; *b*–basion=the chordal axis. The angle of flexion is contained by the two lines meeting at *b*.

mammals, of two parts—the facial part, which carries the teeth and is developed according to their size, and the **brain capsule,** which depends on the size of the brain. The smaller the brain and the larger the face, the more does the face project in front of the skull, and, therefore, the greater is the facial angle, and *vice versa*. It will thus be seen that the facial angle is to a certain degree an index of brain development. It is smallest in the most highly developed races of man; it is larger in the lower races, and larger still in the anthropoids; it increases in size with the advent of the permanent teeth and the necessary increase in the size of the face. It is, therefore, greater in the adult than in the newly born.

Flexion of the Cranial Axis.—In Figs. 119, *A*, and 120 the axis of the cranial base is represented by a line drawn from basion to nasion, but it is quite apparent that this line does not represent the axis accurately. The truth is that there are two functionally distinct parts in the cranial axis—a chordal or post-pituitary part and a trabecular or

[1] For a description of the various methods of estimating the facial angle see Duckworth's *Morphology and Anthropology*, 1904.

pre-pituitary part. In the higher primates—especially in man—the trabecular part is bent downwards—or flexed—on the chordal. The manner in which the degree or angle of flexion may be measured is shown in Fig. 119, *B*; it is a much opener angle in anthropoids than in man. The degree of flexion is most variable in man; in cases where the flexion is great the forehead is projecting and the face receding, the facial angle being apparently small. If there is a great degree of extension of the axis, then the forehead is receding, and the lower part of the face projecting or prognathous. Thus the facial angle is not a

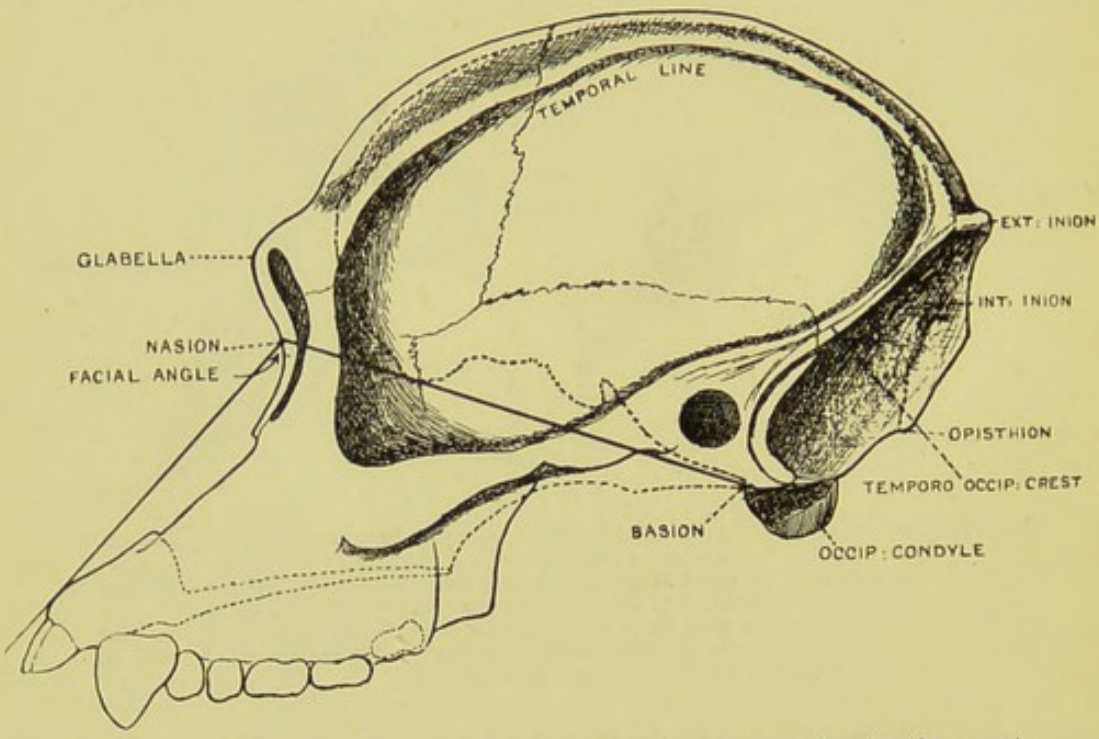


FIG. 120.—Profile of the Cranium of an Immature Chimpanzee showing the ascent of the Temporal Ridges, the formation of Occipital Crests and the lines of the Facial Angle.

safe guide to the degree of prognathism or face projection, because it may be exaggerated or masked by the extension or flexion of the cranial base.

The Para-occipital Process is sometimes present in man, and projects downwards from the jugular process of the occipital bone. The rectus capitis lateralis is inserted to it. The process represents the para-occipital process, which is so highly developed in four-footed mammals. The *para-mastoid* process projects from the temporal bone at the outer side of the para-occipital (Parsons).

Upgrowth of the Temporal and Occipital Ridges or Curved Lines.—In lower animals, such as the ape or dog, a great increase in the development of the temporal and nuchal muscles takes place with the eruption of the permanent teeth, the area of their origin from the skull being necessarily enlarged. The ridges of bone which mark the limit of attachment of these muscles, the temporal and occipital ridges, ascend

on the skull as waves of bone before the growing muscles. The ridges may meet, as in apes, along the sagittal and lambdoidal sutures and form crests, like that on a fireman's helmet. In Fig. 120 the position of the temporal lines in a juvenile chimpanzee is shown ; they are approaching the sagittal suture. They have extended backwards, and met with the occipital lines, which are ascending above the attachment of the growing muscles of the neck. The temporal and occipital lines are seen to be fused together to form a temporo-occipital crest. At the same time the temporal lines spread forwards on the frontal region, the frontal extension being accompanied by a marked growth of the supra-orbital ridges and of the zygomatic arches. Thus the skull is modified by the growth of the muscles of mastication and of the neck. In man these

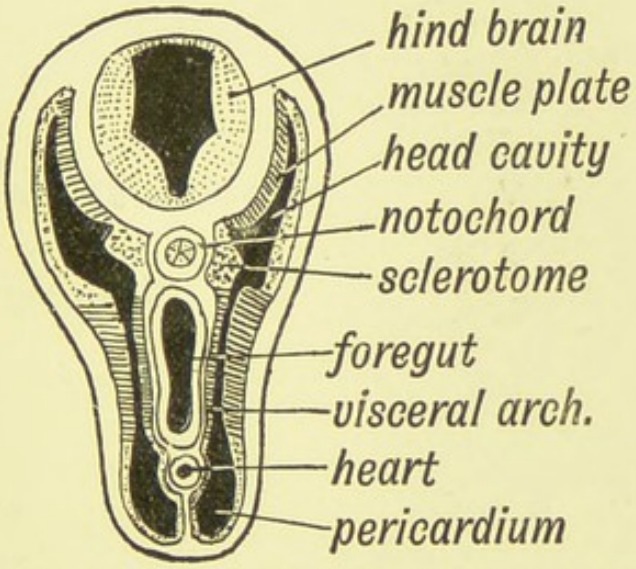


FIG. 121.—Scheme of a Segmental Head Cavity and of the various parts formed from it.

changes also take place, but to a less extent than in anthropoids. At birth the temporal lines are just above the lower border of the parietal bones. During the second year the mastoid part of the ridge for the attachment of the neck muscles grows downwards into a pyramidal process—the mastoid—which is peculiar to the human species. In Neanderthal man, the mastoid process is shaped as in anthropoids. (See Keith, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 251.)

Segmentation Theory of the Skull.[1]—It is inferred from investigations made on the developing heads of fishes and amphibians

[1] Some recent researches on the morphology and segmentation of the skull are : W. H. Gaskell, *Origin of Vertebrates*, London, 1910 ; E. S. Goodrich, *Proc. Zool. Soc. Lond.* 1910, Dec. 13th ; W. E. Agar, *Proc Roy. Soc. Edin.* 1907, Feb. 4th ; Schumacher, *Anat. Anz.* 1907, vol. 31, p. 145 ; Gaupp, *Verhand. Anat. Gesellsch.* 1907, p. 129 ; Grail, *ibid.* p. 29 ; F. H. Edgeworth, *Quart. Journ. Mic. Sc.* 1911, vol. 56, p. 167, *Journ. Anat. and Physiol.* 1902, vol. 37, p. 73 ; J. W. van Wijhe, *Petrus Camper.* 1906, vol. 4, p. 1 ; A. Meek, *Journ. of Anat. and Physiol.* 1911, vol. 45, p. 357 (Dev. Skull of Crocodile) ; W. Wright, *Lancet*, 1909, March 6th (Morphology and Variations of Skull).

that each primitive cephalic segment contained a cavity comparable to that seen in each body segment (p. 59), from the wall of which are developed (see Fig. 121): (1) a sclerotome, (2) muscle plate, (3) skin plate, (4) modified nephrotome, (5) a ventral part of the walls join in the formation of the coelom. A part of each segment, on the lateral aspect of the fore-gut, is modified to form a visceral arch (Fig. 121). The sclerotome of each segment forms (1) a cartilaginous sheath for the notochord, (2) a cartilaginous roof for the neural tube, (3) a process which runs into the segment. The number of segments in the mammalian head is by no means settled, but it is probably nine.

In Fig. 122 a diagrammatic representation is given of one of the many segmental theories of the skull. The parachordal cartilages

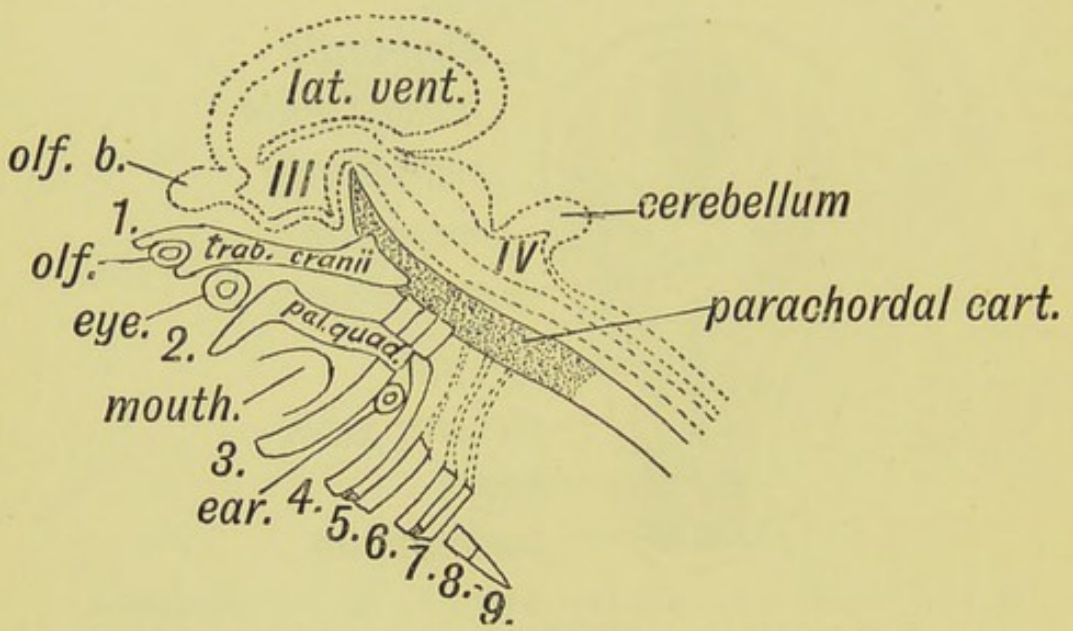


FIG. 122.—A schematic diagram of the segmental elements of the Skull. The numbers refer to the Cartilaginous Bars of the various Visceral Arches. The 4th and 5th are combined in the Hyoid Bone, the 6th and 7th in the Thyroid Cartilage, the 8th (and 9th ?) in the Arytenoid, Cricoid, and Tracheal Cartilages.

represent the unseparated centra of the nine segments. The primitive neural arches have been disturbed by (1) the enormous enlargement of the neural tube, but especially by the expansion of that tube in front of the notochord and parachordal cartilages to form the cerebrum and basal ganglia. In amphioxus the neural tube does not extend beyond the notochord. All that remains of the neural arches of the nine primitive segments are the occipital plates of cartilage. Of the cartilaginous processes of the nine segments the 1st form the trabeculae cranii (Huxley, Howes); with the forward protrusion of the neural tube these come to form part of the base of the skull; the 2nd form the palato-quadrate bars. Both of these processes are preoral. The 3rd forms the mandibular bar, the 4th the hyoid bar, the 5th, 6th, 7th, 8th form the cartilaginous bars in the 1st, 2nd, 3rd and 4th branchial arches. Thus the parachordal part of the skull is manifestly the oldest, and is known as

the **paleocranium**; whereas the trabecular part is more recent and known as the **neocranium**. Further details relating to the facial and pharyngeal parts of the head will be given in the following chapters.

Gaskell's Theory.[1]—Gaskell regards the trabecular or prechordal part of the vertebrate head as derivative of the prosoma, and the parachordal part from the mesosoma of an invertebrate form such as is now exemplified by the Kingcrab (Limulus). The prosoma carries 7 pairs of appendages which surround the mouth. The last of these represents the mandible, the first, the nasal processes; the intermediate appendages are combined in the maxillary processes. The mesosoma carries processes which serve for respiration and locomotion. In vertebrates these are modified to form branchial arches.

[1] See *Origin of Vertebrates*, London, 1910.

CHAPTER X.

DEVELOPMENT OF THE FACE.

Evolution of the Human Face.—In our survey of the neural part of the human cranium we have seen that its outstanding features are the result of a great cerebral development. When, however, we turn to the facial and pharyngeal parts of the skull and head, we find that the factors which have determined their shape are related to the functions of respiration and of mastication. It is unnecessary to again insist on the fact that the human embryo, in the latter part of the first month, shows a resemblance to a generalized type of fish; it possesses the basis of a branchial arch system (see Fig. 211, p. 222).

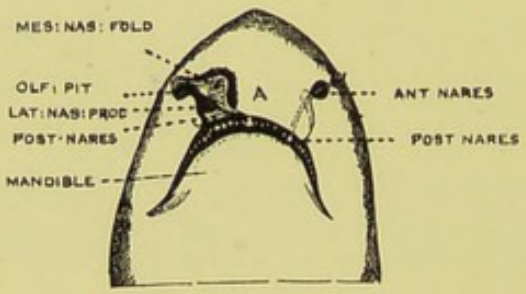


FIG. 123.—The Naso-Buccal Grooves of a Dog-Fish. On the right side the naso-buccal channel is exposed.

As in the fish, the olfactory organ is represented by a pair of pits or depressions, which at first have no communication with the mouth. In some forms of fish—certain rays and sharks (Fig. 123)—a channel is formed between each olfactory pit and the mouth. The functional meaning of such a channel is evident; the water imbibed is sampled by the nose before entering the mouth. When pulmonary breathing was introduced, as in Dipnoean fishes, the open naso-buccal channel became enclosed by the union of its bounding folds. In amphibians, reptiles and birds the naso-buccal channel becomes dilated to form a true respiratory nasal passage, and the parts bounding the passage unite on the roof of the mouth to form the **primitive palate.** In Fig. 124 the parts entering into the formation of the primitive palate are shown.

They are three in number: (1) a premaxillary and vomerine part developed between the nasal passages; (2) a right and left maxillary part, laid down on the lateral or outer aspect of each passage. In mammals a fourth element is added to the primitive or reptilian palate, and in this way the mammalian mouth is separated from the nasal respiratory passage, and can serve the purposes of mastication and suction. Thus in the evolution of the face there have been three

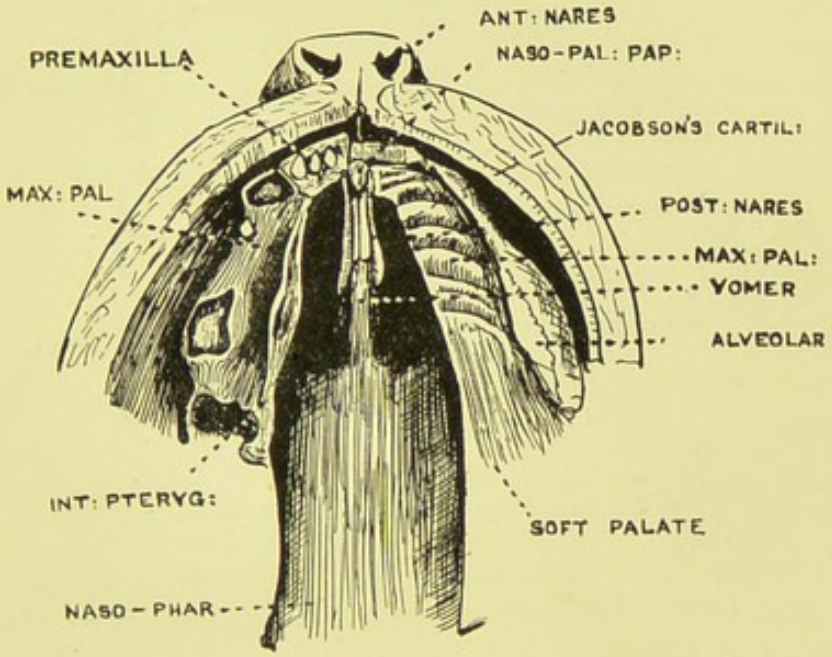


FIG. 124.—Roof of the Mouth of a Lion-Pup, showing the condition of Cleft Palate recalling in form the Palate of Reptiles. On the right side the bones are exposed by removal of the soft parts.

distinct stages: (1) a piscine, in which the nose and mouth were formed independently; (2) an amphibian stage, where the nasal respiratory passage opened on the roof of the mouth; (3) a mammalian stage, in which it opened in the naso-pharynx. In the development of the human embryo we see these three stages reproduced.[1]

Processes which form the Face.[2]—Towards the end of the third week of foetal life, five processes begin to spring from the base of the primitive cerebral capsule, which by the end of the second month have completely united together to form the facial part of the head. In Fig. 125, a diagrammatic representation is given of the condition of these five processes about the end of the first month. Of the five, one, the **nasal** or **fronto-nasal,** composed of symmetrical right and left halves is median, and projects beneath the fore-brain; the others are lateral, two on each side, the **mandibular** and **maxillary.** The cavity

[1] See Keith, "Malformations of the Head and Neck," *Brit. Med. Journ.* 1909, August.

[2] K. Peter, *Anat. Anz.* 1911, vol. 39, p. 41 (Development of Face).

which these five processes surround is the **stomodaeum** (Fig. 125), a space ultimately destined to form part of the nasal and buccal cavities.

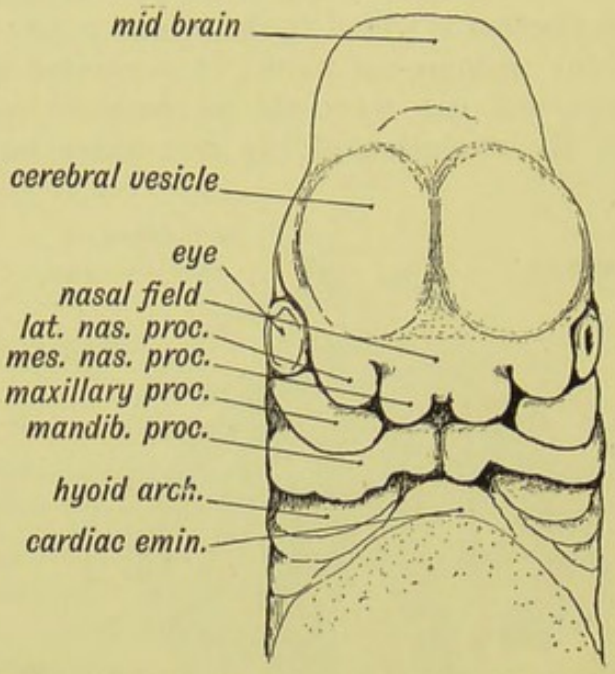


FIG. 125.—Showing the formation of the Face by the Nasal, Maxillary and Mandibular Processes in an Embryo of the 4th week. (After His.)

The representatives of these five elements are recognizable in certain fishes (see Fig. 123). The part of the adult face formed by each process is shown in Fig. 126.

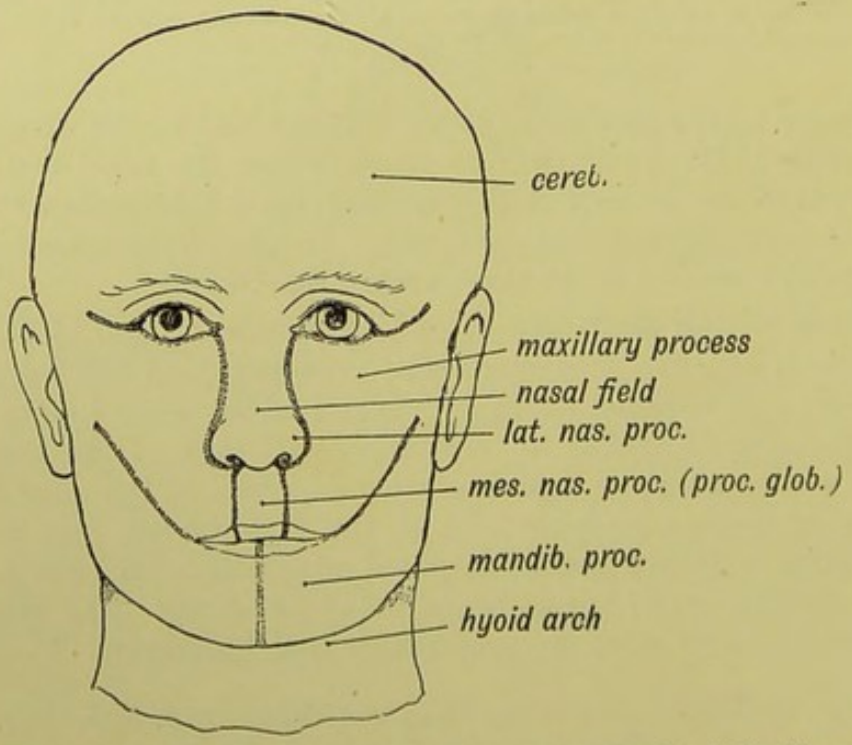
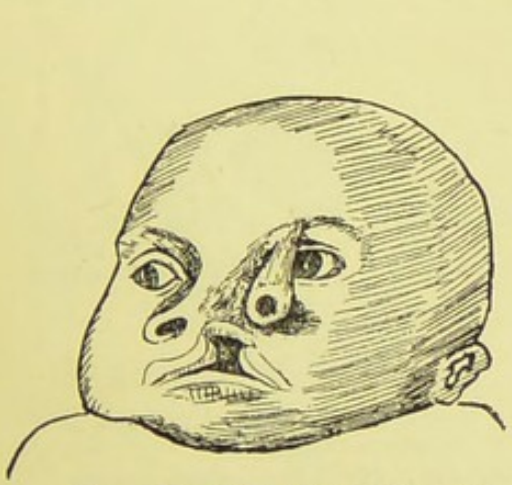


FIG. 126.—Showing the parts of the Face formed from the Nasal, Maxillary and Mandibular Processes.

Malformations of the Face.—These processes may fail to unite in the second month, and in this manner malformations of the face are produced. The most common anomaly is a partial failure of the nasal and maxillary processes to fuse, various degrees of **hare lip** and **cleft palate** being thus caused. In **hare lip,**[1] the cleft appears in the upper lip between the middle part formed by the middle nasal processes and the lateral parts formed by the maxillary processes (Fig. 126). In **cleft palate,** the failure of union occurs between the deep parts of the nasal and maxillary processes (Fig. 141). The lateral or the mesial parts of the nasal process may fail to fuse with the maxillary processes and thus appear on the face as polypoid or irregular projections (Figs. 127, 128). In such cases the right and left maxillary processes may unite and form the whole of the upper lip. **Macrostoma** is due to a partial



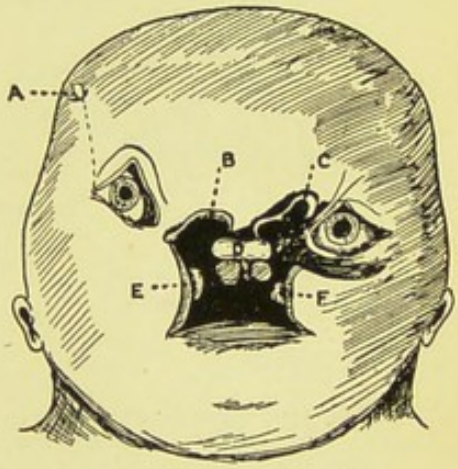


FIG. 127.—Face of a Child showing the left Lateral Nasal Process as a free Polypoid Body and the left Maxillary Process ununited with the Mesial Nasal (left Hare Lip). (After Kirchmayer.)

FIG. 128.—Face of Child in which the Nasal and Maxillary Processes are ununited. *A*, Polypoid Tubercle in line of Naso-Maxillary Cleft; *B*, Right Lateral Nasal Process; *C*, Left Lateral Nasal Process; *D*, Mesial Nasal Process; *E*, *F*, Maxillary Process. (London Hospital Medical College.)

failure of the mandibular to unite with the maxillary element. Any of these processes may be under- or over-developed; over-development of the nasal and under-development of the mandibular (micrognathia) are of common occurrence.

The **cleft in the lip** of the hare is exactly in the middle line, and is due to a separation of the right and left parts of the mesial nasal process. The condition of **median hare lip**, which is rare in man, is represented in Fig. 129; in this case there was a partial cleft of the palate, and the pituitary body formed a tumour-like mass within the septum of the nose. A median cleft in the lower lip is also rare, and is due to a failure in the union of the right and left mandibular processes of

[1] For an account of the development of the lips see: L. Bolk, *Anat. Hefte*, 1911, vol. 44, p. 227 (describes curious pits seen in abnormally developed lower lips); M. Ramm, *Anat. Hefte*, 1905, vol. 29, p. 55; W. L. H. Duckworth, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 349 (Lips of Primates).

the lower jaw (Fig. 130). Another remarkable condition is shown in Fig. 170, p. 182, where the nasal processes have united together to form a single proboscis-like structure projecting above the eyes, which are partly fused (cyclops). In this condition the palate and upper lip are formed by the union of the maxillary processes. The condition is not uncommon, and shows how adaptable the various embryological parts of the face are.

The Method of Fusion.—The manner in which embryological parts unite is similar in nature to the healing of wounds. Fig. 131 represents a coronal section of the head of a human embryo, in which the mesial

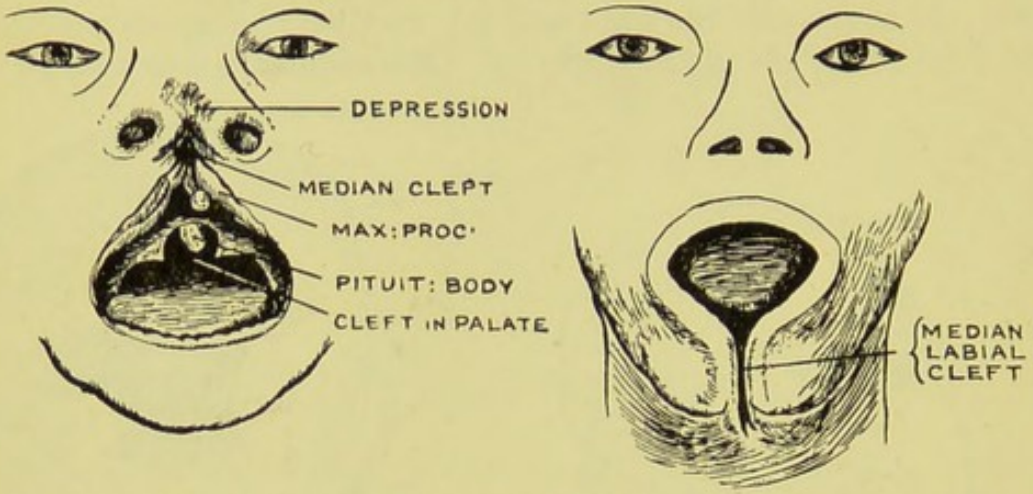


FIG. 129.—Median Hare Lip in a Child with Partial Cleft Palate and Ectopia of the Pituitary. (Mr. A. R. Tweedie's case.)

FIG. 130.—Median Cleft of the Lower Lip and Jaw. (Prof. MacCormick's case.)

nasal process containing the germinal epithelium of the upper incisor teeth is about to unite with the maxillary. The ectodermic coverings of the processes are in contact. Across the epithelial union thus formed the mesoblast tissue spreads, the two processes thus becoming intimately united. We know that the process of healing may be arrested by many pathological conditions; the process of embryological union may be also arrested, but the exact causes of the arrest we do not yet know. If union of the facial processes fails to take place, then subsequent growth tends to move the processes apart, and union becomes impossible. The cleft in the lip or palate increases in width as the foetus becomes older. The tongue lies between the maxillary plates (Fig. 132), a normal position during the 2nd month. It is extruded as the palate is formed.

The Nasal Processes.—The nasal process at a very early stage is seen to be divided into **two lateral** processes and **two mesial,** the latter having globular enlargements as tips (Fig. 125). They form the walls of the primitive olfactory chamber. It must be remembered that the lateral and mesial nasal processes are really vertical septa springing from the basis of the primitive capsule of the fore-brain, and

the parts seen on the face are the anterior extremities of these septa (see Fig. 133). The nasal processes, both mesial and lateral, contain a forward prolongation of the **trabeculae cranii** which may be regarded as the skeletal basis of the nasal processes (see p. 126).

What becomes of the Mesial Nasal Processes.—From the mesial nasal processes, which fuse together, and may enclose epithelial remnants between them, are formed the whole septum of the nose (Fig. 133), the premaxillary part of the upper jaw, and the middle third of the upper lip (Figs. 124, 128).

Structures formed in the Mesial Nasal Processes.—The mesial nasal processes fuse together; in their anterior inferior angles

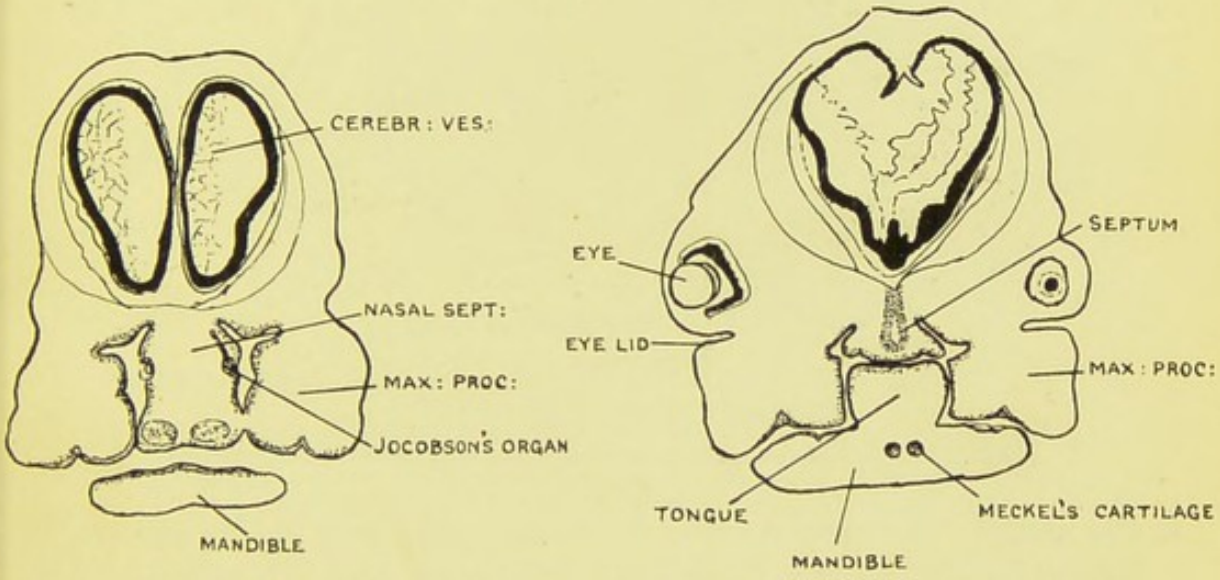


FIG. 131.—Coronal Section of the Head of a Human Embryo in the 6th week of development and 14 mm. long. (After J. L. Paulet, *Archiv. für Mik. Anat. und Entwickl.* 1911, vol. 76, p. 658.)

FIG. 132.—Similar Section of the same Embryo further back, showing the Tongue in the Palatal Cleft. (J. L. Paulet.)

are formed the premaxillae. The remainder forms the septum of the nose.

In the septum between the nasal cavities a laminar plate of cartilage is developed, which is continuous with, and forms part of, the trabeculae cranii (Fig. 115, p. 128). Part of this cartilage remains as the **septal cartilage** of the nose (Fig. 133). From the septal cartilage, just over the naso-palatine foramina, a small scroll-like or turbinate process is thrown off on each side to form a hood for an isolated piece of olfactory epithelium—the organ of Jacobson (Figs. 124, 131). They form the **cartilages of Jacobson.** The cartilages and organs are vestigial in man. In the mesial nasal processes are developed also the mesial or septal limbs of the **alar cartilages** of the nose (Fig. 133).

The **Vomer** is developed in the membrane (perichondrium) which covers the primitive septal cartilage (Fig. 140). A centre of ossification appears at the end of the 2nd month at each side of the cartilage;

these fuse together under the palatal margin of the cartilage. Thus the vomer forms at first a shallow trough in which the cartilage of the septum appears to be implanted (Fig. 134).

The **Vertical Plate of the Ethmoid** is formed by a direct ossification of the primitive cartilage of the septum. Ossification begins in the

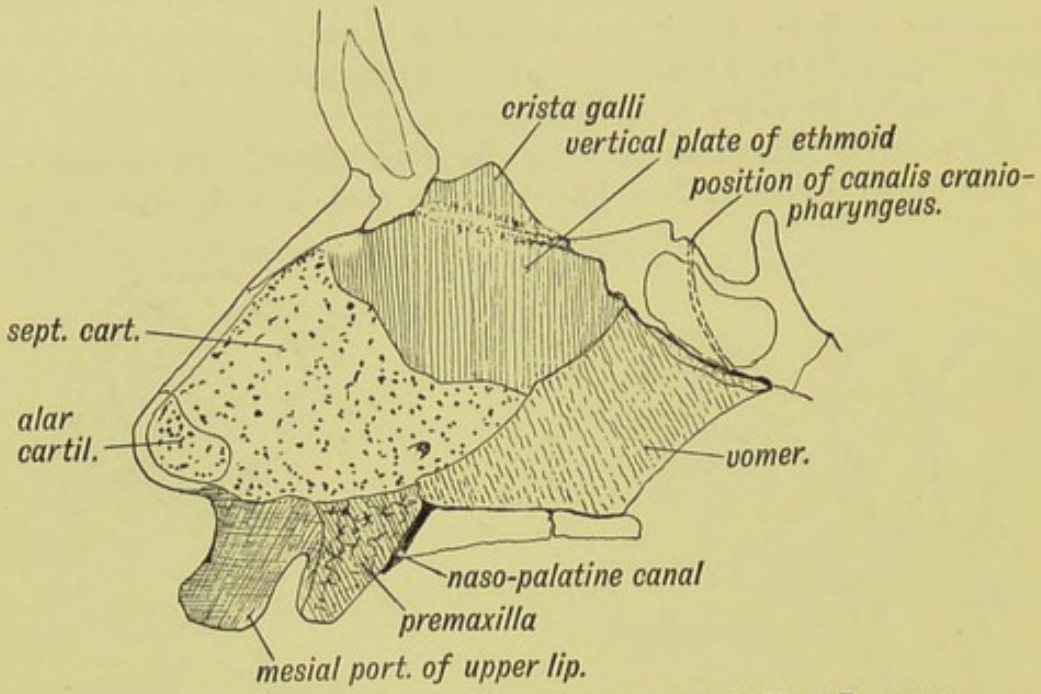


FIG. 133.—Showing the structures formed in the Mesial Nasal Processes.

4th month. The crista galli, the intra-cranial part of the septum, is formed in part by the ossification proceeding into the attachment of the falx cerebri.

Premaxillary Bones.—The two premaxillary bones form the sockets of the upper incisor teeth. In the human foetus at birth the

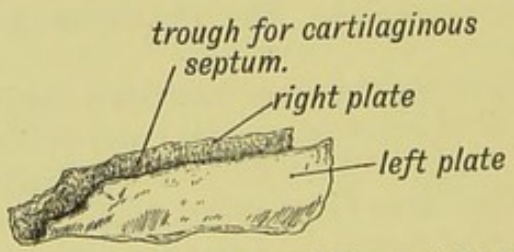
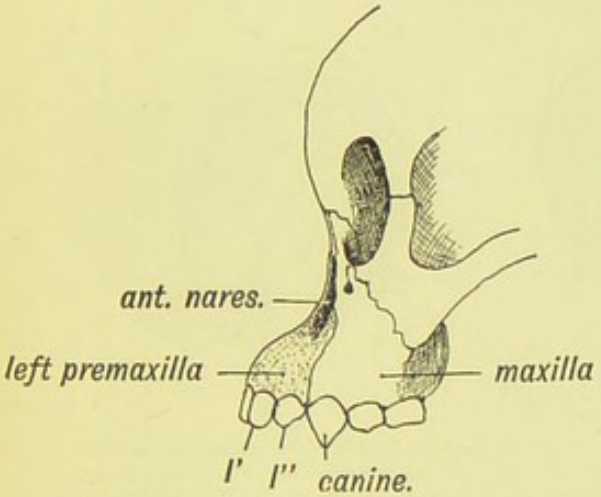


FIG. 134.—Showing the trough-shaped Vomer of the newly-born.

suture between the premaxilla and maxilla can be seen on the hard palate; it runs on each side from the naso-palatine foramen to the alveolus between the lateral incisor and canine (Fig. 136). As is illustrated in Fig. 136, the relationship of this suture to the tooth sockets is variable, but the relationship just mentioned is the usual one. On the facial aspect, the premaxilla fuses with the superior maxilla at the beginning of the 3rd month of foetal life, the maxillae

overlapping and almost completely excluding them from the face. The nasal spine is formed by the premaxillae.

In mammals generally the premaxillae are highly developed and form the snout part of the face. In the higher Primates the face becomes less elongated, less **prognathous,** or projecting, and the premaxillae less developed. In the orang, for instance, the premaxillae are distinctly seen on the face at birth (Fig. 135), but as the permanent canines begin to develop they fuse with the maxillae. The premaxilla



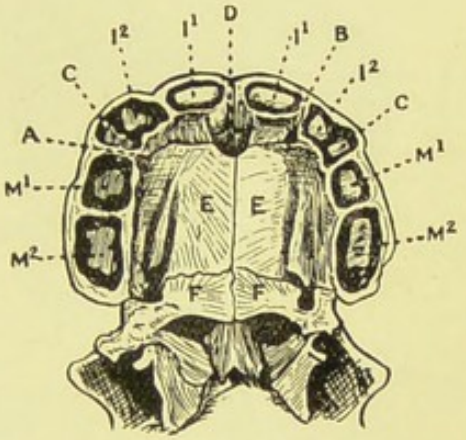


FIG. 135.—Showing the suture on the face between the premaxilla and maxilla in the skull of a young orang.

FIG. 136.—Palate at birth, showing varieties of the suture between maxilla and premaxilla. On the right side (*A*) the suture between the palatal processes of premaxilla and maxilla ends at the socket of the canine; on the left (*B*) between the mesial (I^1) and lateral (I^2) incisors; *D*, naso-palatine foramen, in which the anterior end of the vomer appears; *E*, *F*, palatal processes of the maxillary and palate bones.

is more reduced in man than in any other primate; in him it fuses with the maxilla in the 3rd month of foetal life; in them fusion does not occur until the eruption of the permanent teeth. The vestigial character of the premaxilla in man is due to the reduced size of his masticatory apparatus and the consequent retrogression in the development of the facial part of the skull.

Relationship of the Premaxilla to Cleft Palate.[1]—It is usual for the sockets of all four incisor teeth to be formed by the premaxilla. In many cases of cleft palate (see Fig. 138) only the two central incisors are situated on the premaxilla, the sockets of the lateral incisors being attached to the maxilla. Even in the normal palate (Fig. 136, *B*) this may be the case. Albrecht supposed that each premaxilla was made up of two bones—an outer and an inner—and that in cleft palate the fissure might lie between the elements of the premaxillary or to their outer side. We now know (1) that cleft palate is not due to a

[1] M. Inouye, *Anat. Hefte*, 1912, vol. 45, p. 481 (Premaxilla in Man), 1912, vol. 46, p. 1 (Dev. of Palate, Mammals); E. Gaupp, *Anat. Hefte*, 1911, vol. 42, p. 311 (Evol. of Palate); G. Schorr, *Anat. Hefte*, 1908. vol. 36, p. 69 (Dev. of Palate); E. Fawcett, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 400 (Ossific. of Palate).

failure of ossific centres to join, but to a non-union of two embryological masses—the mesial nasal and maxillary; (2) that the partial suture, which may divide the palatal part of the premaxilla, is due, not to two centres of ossification, but to the formation of the palatal part by two processes—one corresponding to the middle incisor socket, the other to the lateral incisor; (3) the germ or bud of the lateral incisor is formed at the point of union of the mesial nasal and maxillary processes.

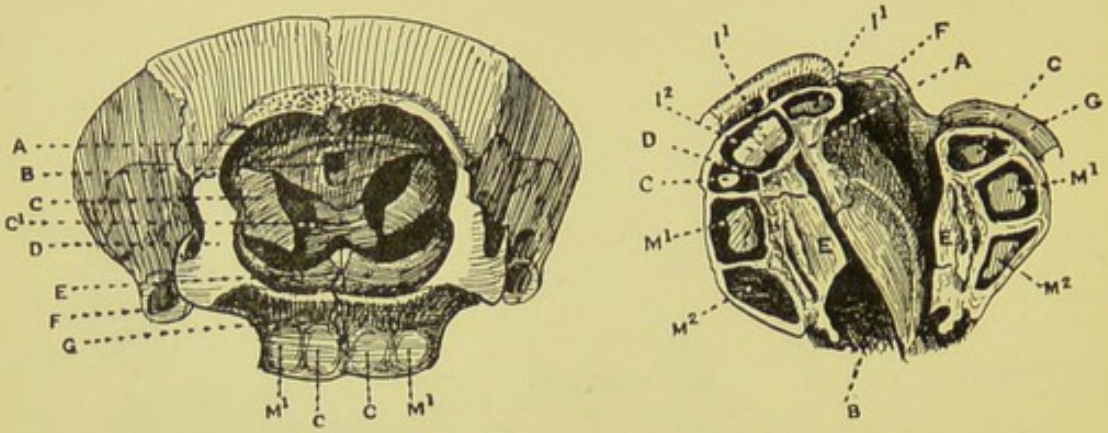


FIG. 137.—Facial part of the Skull of a Cyclops Foetus, in which the nasal processes formed a free proboscis, the eyes a median structure and the maxillary processes the palate. *A*, orbital plates of frontal; *B*, fused optic foramina; *C*, orbital plate of sphenoid; *C'*, basi-sphenoid; *E*, orbital plate of maxilla; *F*, ear; *G*, superior maxilla; *C*, canine; *M'*, first milk molar.

FIG 138.—Case of Cleft Palate, in which the maxillary and premaxillary processes have remained ununited on the left side. *A*, septal process of premaxilla; *B*, nasal septum; *C*, canine; *D*, palatal process of premaxilla; *E*, palatal process of maxilla. The left lateral incisor was absent.

If these processes fail to join, the bud of the lateral incisor, as the processes move apart during subsequent growth, may be carried away by the maxillary or premaxillary element, or, as I have seen, be left stranded in the cleft between the processes. If the lateral incisor remains attached to the maxillary process, then its socket is formed by that element; if by the premaxillary, then the cleft appears in the more usual situation, and the socket forms part of the premaxilla. Mr. Clement Lucas has shown that the lateral incisor is often small or even absent in families subject to cleft palate.

Naso-palatine Foramen.—The naso-palatine foramina are formed where the mesial nasal and two maxillary processes unite to form the **palate** (Fig. 142). In animals with well-developed premaxillae the two naso-palatine (anterior-palatine) foramina are large, and through each passes the naso-palatine duct, which allows a communication between the buccal and nasal cavities. The odour of the food within the mouth thus reaches the organ of Jacobson, which is situated on the septum, close to the nasal orifice of the duct. In man the upper ends of the ducts remain open; they terminate blindly below, behind the mesial incisor teeth, in the naso-palatine or incisive papilla (see Figs. 124 and 131).

Nasal Duct.—The lachrymal sac and nasal duct, through which tears pass from the eye to the inferior meatus of the nasal cavity, are formed between the lateral nasal and maxillary processes (Figs. 126 and 128). The epithelium of the skin (epiblast) enclosed between the processes, forms at first a solid cord (6th week); it afterwards (3rd month) becomes canaliculized to form the duct. In Fig. 128 the lateral nasal and maxillary processes have not fused; the eye is separated by two folds from the nasal cavity; the outer represents the semilunar

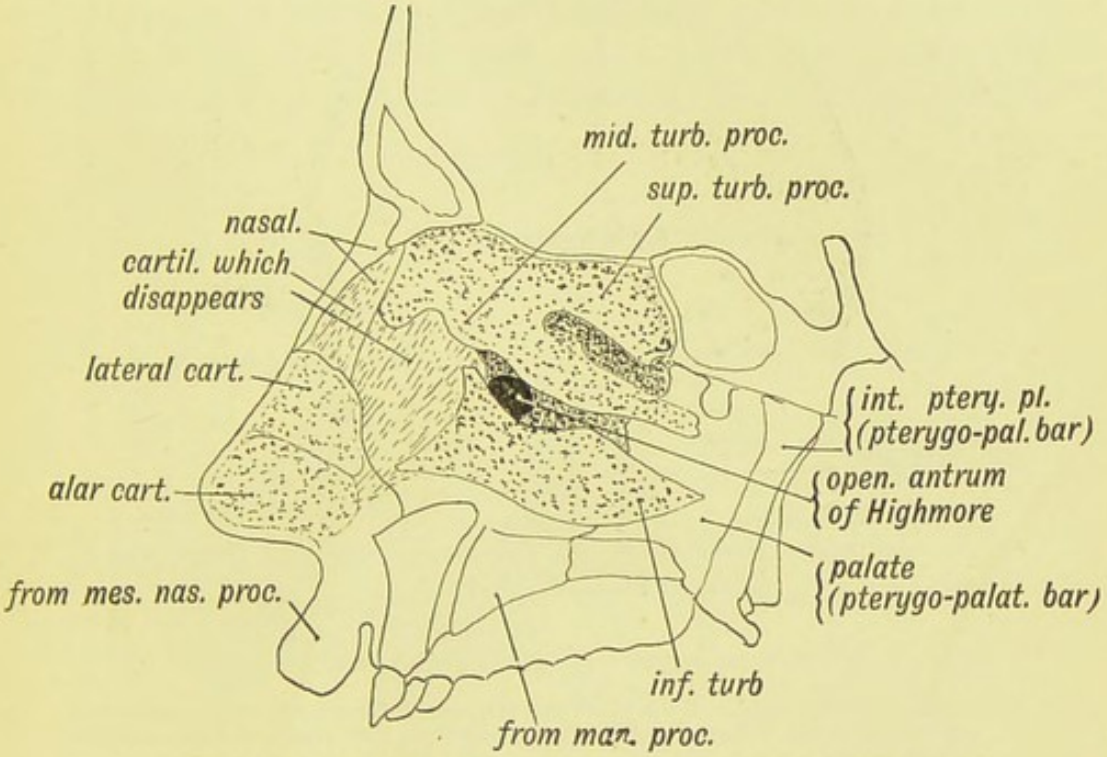


FIG. 139.—Showing the structures formed in the Lateral Nasal Processes.

fold, the inner a fold in which the lachrymal canaliculi and caruncula lachrymalis are formed.

Structures Formed in the Lateral Nasal Process.—In each lateral nasal process a laminar plate of cartilage is developed; it is continuous with, and forms part of, the trabeculae cranii (Fig. 115, p. 128). Its upper or attached margin is continuous with the septal cartilage of the mesial nasal process; it forms on each side the roof and lateral wall of the nasal cavities (Fig. 140).

What becomes of the Cartilage of the Lateral Nasal Process [1] (Fig. 139).—It forms on each side:

(1) The cribriform plate around the olfactory nerves as they issue from the olfactory bulb;

(2) The lateral mass of the ethmoid, at first merely a plate of cartilage; the superior and middle turbinate processes are developed from the plate (Fig. 140); ossific centres appear in the cartilage of the

[1] See Fawcett, *loc cit.* p. 123.

lateral mass and turbinate processes during the fourth month of foetal life ;

(3) The inferior turbinate bone (Fig. 140) (maxillo-turbinal). The body of the superior maxilla is developed on its outer side in the maxillary process (Fig. 140) ;

(4) The lateral and part of the alar cartilages of the nose ;

(5) In the membrane over the cartilage, between the ethmoid behind and the cartilages of the nares in front, are developed the lachrymal

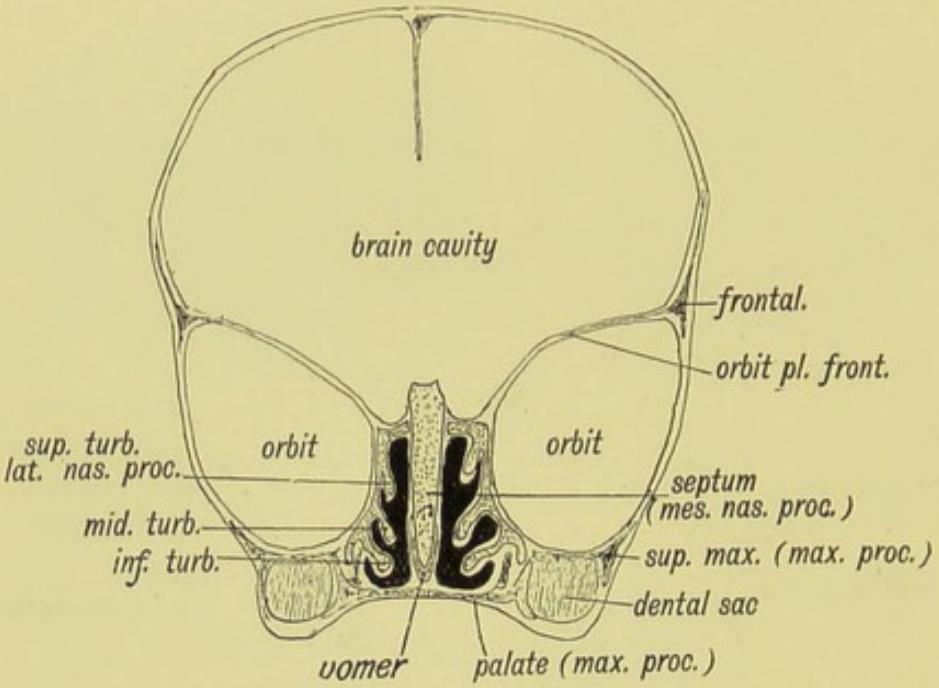


FIG. 140.—Coronal section of the Skull of a 7th month Human Foetus to show the cartilages of the Lateral and Mesial Nasal Processes and the bones formed round them.

and nasal bones, and the ascending process of the superior maxilla. The cartilage beneath these bones disappears after birth (Fig. 139). Ossification of the nasal bone appears at the beginning of the 3rd month ; the centre for the lachrymal appears late—at the beginning of the 4th month (Mall).

Arteries and Nerves of the Nasal Processes.—A knowledge of the development of the face assists one to unravel the complicated distribution of its arteries and nerves. Each process carries its own vessels and nerves.

1. Mesial Nasal Process. The chief artery and nerve of this process are the naso-palatine, but branches also come from the nasal nerve and its accompanying artery, the anterior ethmoidal.

2. Lateral Nasal Process. The nerves of the lateral nasal process are derived from Meckel's ganglion and from the descending palatine nerve. Vessels accompany these nerves from the descending palatine artery. The nasal nerve and anterior ethmoidal artery supply the process in front.

The Parts formed from each Maxillary Process.—The maxillary process springs from the base of the mandibular process at the end of the 3rd week of development, and sweeping forwards below the eye, separates that structure from the mouth (see Figs. 37, 38, 39 and 125). In front it comes in contact and fuses with the lateral nasal process, which it assists to form the outer wall of the nasal cavity, and, in the 6th week, with the globular process of the mesial nasal which forms the premaxillary part of the palate and the middle part of the upper lip. The part of the face formed by the maxillary process is shown in Fig. 126. The hard palate (with the exception of the premaxillary part) is formed by **a horizontal plate** which grows inwards

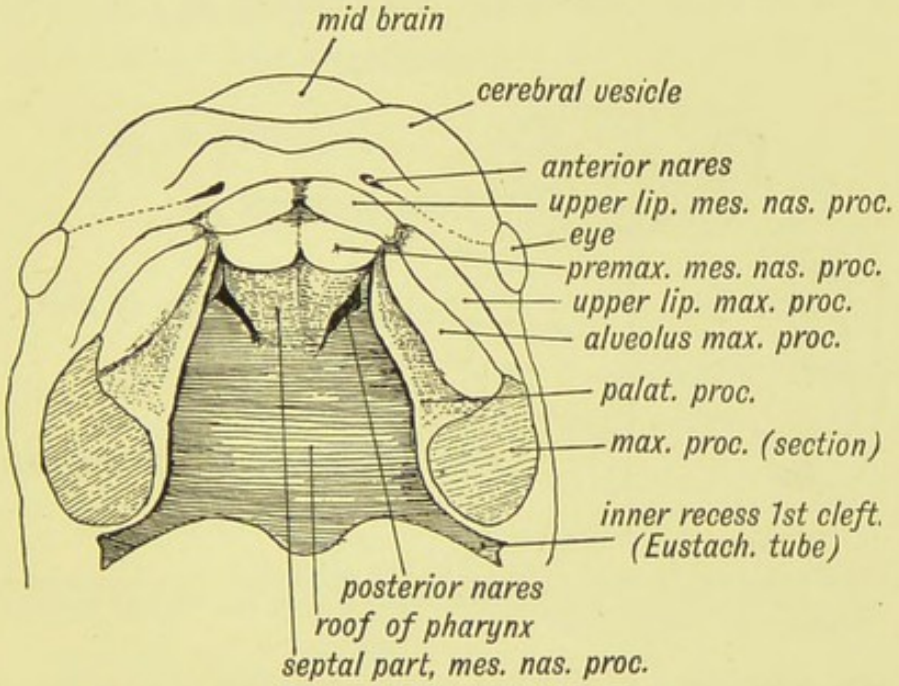


FIG. 141.—Showing the ingrowth of the Palatal Plates of the two Maxillary Processes early in the 2nd month. The openings erroneously indicated as "posterior nares," are the primitive choanae. (After Kollmann.)

from the maxillary process in the latter part of the 2nd month (Fig. 141) and fuses with the plate of the opposite side during the 3rd month. The palatal processes separate the buccal from the nasal cavities, forming the roof of the one and the floor of the other (Fig. 141). The horizontal plates meet first with the premaxillary part; behind that they come in contact with each other; the process of fusion spreads backwards, and by the end of the third month it is complete. The septum of the nose becomes differentiated at the same time. In the anterior part of the palate the lower border of the septum is included between the horizontal plates of the maxilla; but in the posterior part, the horizontal plates meet under and then fuse with the septum. The condition of **cleft palate** is due to a partial or sometimes a complete failure of the process of fusion. In Fig. 138 the cleft on the left side is complete, the nasal cavity being exposed from anterior to posterior

nares. On the right side the cleft is limited to a failure of union between the horizontal plates and the septum. The wide gap and bent septum are due to changes produced by growth in the later months of foetal life. An asymmetrical growth is a result of the failure in the union of the processes.

The Soft Palate.—While the hard palate is derived from the horizontal plates of the maxillary processes, the soft palate is derived from a fold which arises as a prolongation backwards of each horizontal plate into the pharynx.[1] Into the **palatal folds** spread derivatives of the superior constrictor to form the palato-pharyngeus, palato-glossus and azygos uvulae, and possibly also the levator palatae. The posterior pillars of the fauces are continuations of the palatal folds

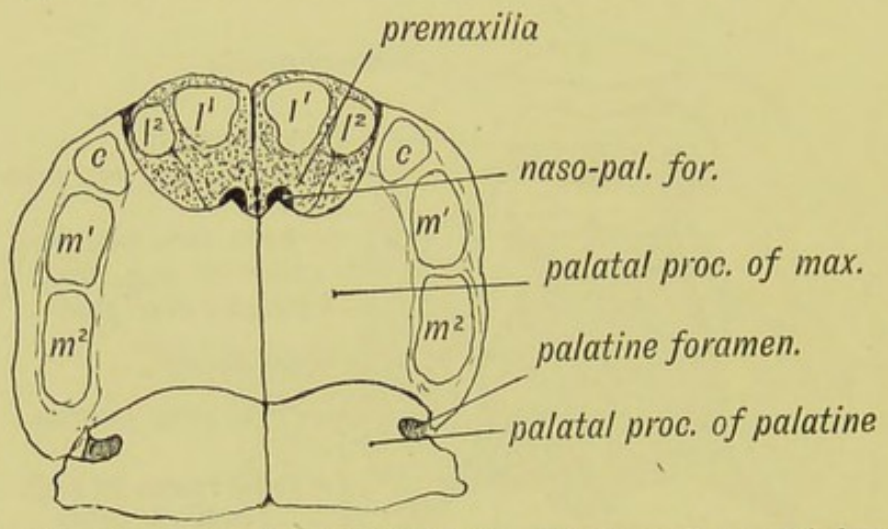


FIG. 142.—Showing the Hard Palate at birth. The premaxillary part is formed from the Mesial Nasal Processes; the remainder by the Palatal Plates of the Maxillary Processes.

within the pharynx. A divided uvula represents a failure of the final stage in the formation of the palate.

Bones formed in each Maxillary Process.[2]—The zygomatic process of the temporal, the malar, and the greater part of the superior maxillary are formed directly in the connective tissue within the process. They are membrane-formed or **dermal** bones. The centre for the maxilla appears at beginning of the 7th week in that part of the process which lies under the eye. Very soon, after the various processes of the face are fully united, an extension passes upwards over the lateral nasal cartilage towards the frontal bone (frontal process); the orbital, alveolar, and palatal processes are later extensions from the single centre of ossification (Mall, Fawcett).

Pterygo-palatine Bar.—In lower vertebrates the maxillary process is supported by a skeletal bar of cartilage known as the palato-

[1] See J. Ernest Frazer, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 190.

[2] E. Fawcett, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 378 (Ossification of Maxilla). See also Mall, p. 125 (Maxilla).

quadrate bar, because it stretches from the palate to the quadrate bone, situated at the base of the mandibular arch (Fig. 143). Although in the human embryo this cartilaginous bar is at no time clearly differentiated (Fawcett), there can be no doubt that two bones have arisen in connection with it—namely the palate and internal pterygoid (Fig. 144). The internal pterygoid plate—the first part of the sphenoid to ossify—is formed early in the 3rd month in membranous tissue which overlies the position of the middle part of the bar, while the vertical plate of the palate is developed in membrane over its more anterior part. Ossification extends to the horizontal plate at the end of the 2nd month within the horizontal plate of the maxillary process.

The mandibular process has also a cartilaginous bar developed within it known as **Meckel's cartilage** (Fig. 143). Thus each of the processes which grow out to form the face has a basis of cartilage, but while

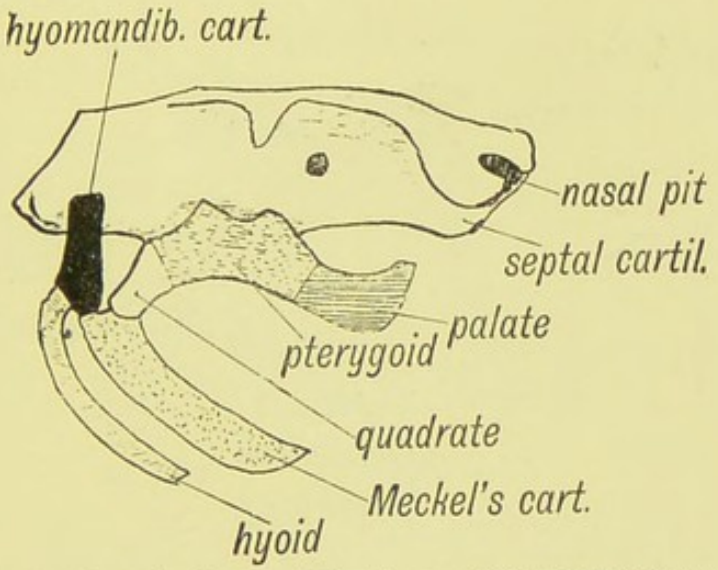


FIG. 143.—The Cartilages in the Nasal, Maxillary and Mandibular Processes of a Shark.

the cartilages within the nasal processes are continuous with the trabeculae which form the base of the skull, the cartilage within the maxillary process comes in contact by its posterior extremity with Meckel's cartilage. The quadrate bone, which is well seen as a separate element in birds and reptiles, forms a movable base on which the lower jaw articulates. This form of joint gives birds and reptiles an easy faculty of swallowing unmasticated food. It is not yet definitely settled what becomes of the quadrate element in mammals. Dr. Gadow has suggested that it becomes the tympanic ring and plate (Figs. 143 and 144). With the development of grinding and chewing teeth in the very early ancestry of mammals a more stable form of temporo-maxillary articulation was evolved, the mandible during the change coming gradually to articulate with the temporal bone, thus leaving the upper end of Meckel's cartilage and the quadrate free to be utilized as the malleus and incus by the organ of hearing. If this theory of

the quadrate bone is accepted—and it seems the true one—the tympanic ring and plate must be regarded as a new element—formed as a membranous ossification round the drum.

The simplest condition of the cartilages of the maxillary and mandibular processes is seen in certain fishes. In the common base of these two processes, there is developed a cartilage which binds the basal ends of the palato-quadrate bar and Meckel's cartilage to the skull. The cartilage of the hyoid arch is also bound to it, and hence it is known as the hyo-mandibular cartilage. In mammals, the auditory ossicles are formed out of this cartilage (Gadow). (Compare Figs. 143 and 144).

Nerves and Arteries of the Maxillary Process.—A knowledge of the manner in which the maxillary process is developed explains the distribution and course of its arteries and nerves. The second

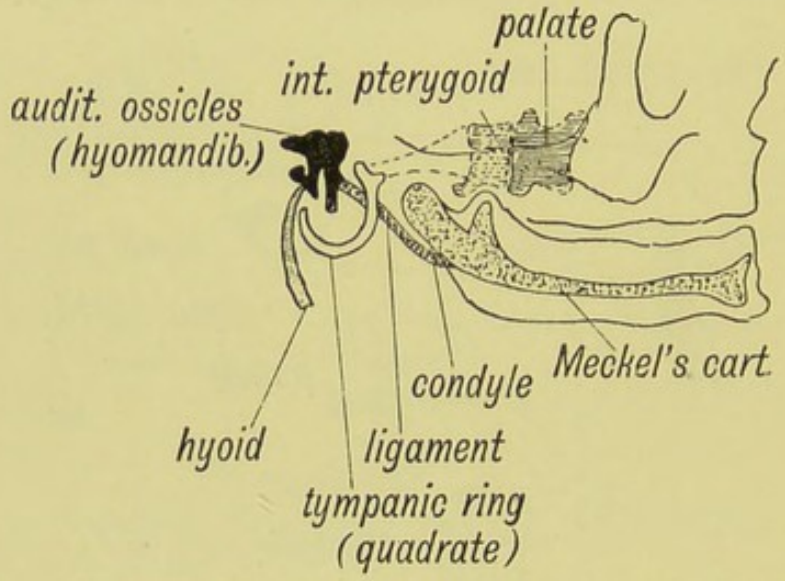


FIG. 144.—The parts formed from the Cartilages of the Maxillary and Mandibular Processes in the Human Skull. It is now recognized that the cartilaginous parts of the condylar and coronoid processes of the mandible arise independently of Meckel's cartilage (see Fig. 148). In this figure, too, Dr. Gadow's interpretation of the tympanic bone as the quadrate is followed, but, as will be seen from the text, that theory is not adopted now by the author.

division of the 5th, represented by the infra-orbital, descending palatine, pterygo-palatine, and Vidian nerves, forms its nerve supply. Its main artery is the internal maxillary.

Formation of Foramina and Canals in Bone.—The development of canals and foramina in the bones of the maxillary process illustrates the manner in which these are formed in the skull generally. Many foramina and canals occur between elements which unite in the course of development (see p. 129). The Vidian nerve lies between the internal pterygoid plate (a separate bone) and the external pterygoid, a plate which grows into the maxillary process as a prolongation of the great wing of the sphenoid. The pterygo-palatine canal is situated between the pterygoid and palatal parts of the pterygo-quadrate bar.

The descending palatine nerve lies between the palate bone and superior maxilla. These are canals formed between different elements. The infra-orbital nerve at first passes forwards in a groove on the orbital aspect of the superior maxilla, but in the later months of foetal life, upgrowths from the centre of ossification of the maxilla meet over the nerve and convert the groove into a canal.

The foramen rotundum and foramen ovale are at first notches on the edge of the great wing of the sphenoid, but in the course of foetal growth the notches are converted into foramina. Hence wherever a nerve foramen or canal is found one may conclude that it marks the junction of two elements, originally distinct, or is originally a groove or notch on the edge of the bone (Bland Sutton). The foramina for nerves in the malar bone appear to be exceptions to this rule. Only one centre appears for the ossification of this bone (7th week), and the

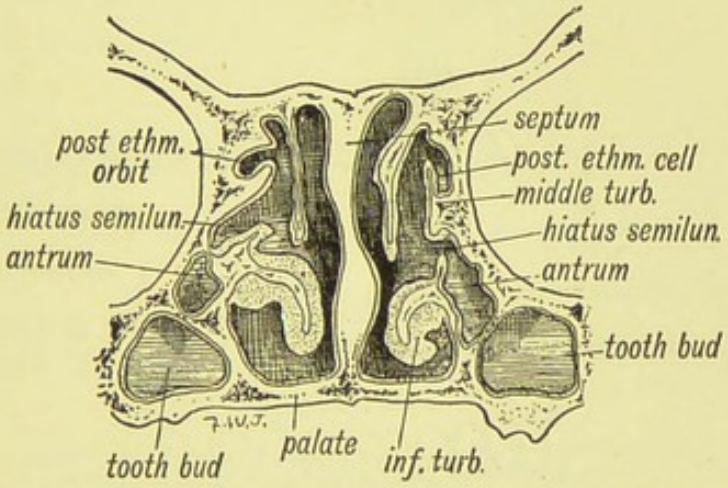


FIG. 145.—Section of the Nasal Cavities of a Newly-Born Child showing the development of the hiatus semilunaris and air sinuses.

nerves evidently become inducted during ossification of the membranous basis. Apparently the malar bone may be ossified from two centres which may fail to unite ; the bone is then divided by a suture passing from the orbit to the temporal fossa. A divided malar occurs rather more frequently in Japanese and Mongolian skulls, hence the name of **Os Japonicum.**

Palatal Rugae.—In all classes of mammals the mucous membrane on the hard palate is ridged transversely ; three or four of these transverse ridges are seen on each side of the palate of the newly born child ; they tend to disappear in the adult. Food is triturated between them and the rough papillae on the palatal aspect of the tongue. Their disappearance in man is probably due to the soft nature of his food.

The Antrum of Highmore.—It will be seen from Fig. 145 that the maxillary process is at first a thin plate, lying between the orbit and mouth, containing the canine and molar tooth buds. It rests on the outer aspect of the lateral nasal process, and to some extent assists

that process to form the outer wall of the nasal cavity (Fig. 140). About the third month of foetal life the mucous membrane in the middle meatus begins to bud outwards, presses before it and bursts through the lateral nasal plate of cartilage and begins to distend the maxillary process. At birth the antrum is only a shallow recess on the outer wall of the middle meatus, above the germ of the first milk molar (Fig. 145). It continues to grow until the 25th year, and is the only one of the air sinuses developed from the nasal cavity which is more than a rudiment at the time of birth. In the years of adolescence the antrum expands until it inflates the maxillary part of the malar. As it expands backwards the posterior border of the maxilla, which contains the buds of the permanent molar teeth, undergoes a rotation downwards, so that what was situated on the posterior border comes to be situated on the alveolar border (Fig. 146). If the processes of

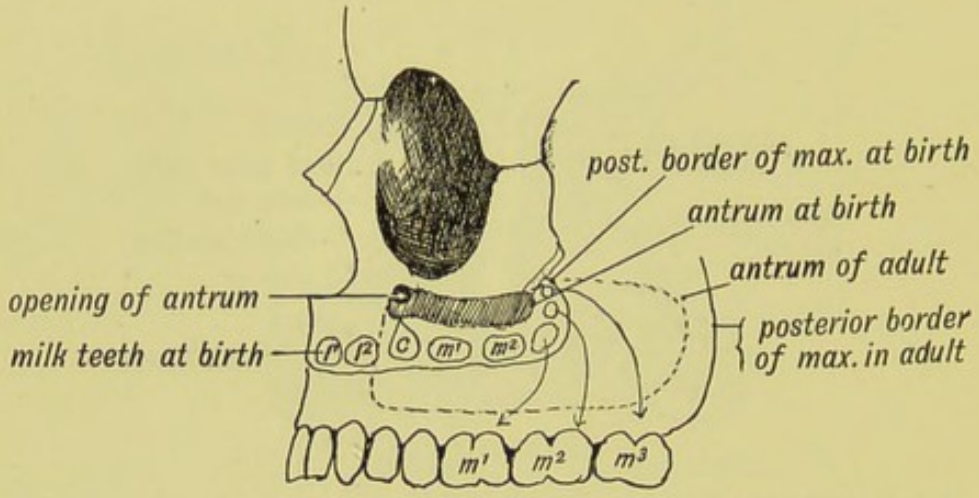


FIG. 146.—Showing the manner in which the development of the Maxillary Antrum affects the size of the palate and position of the molar teeth.

growth and rotation are arrested, the last molar (wisdom) tooth is left on the posterior border of the maxilla, where it may give rise to pain and suppuration. The maxillary antrum is peculiarly large in man and in the anthropoid apes. It is small in monkeys, a greatly expanded inferior meatus taking its place.[1]

Mandibular Processes and Arch.—The two mandibular processes unite in the middle line and form the mandibular or first visceral arch. The arch forms the lower or hinder boundary of the stomodaeum (Fig. 147). The right and left processes are in contact in the 3rd week of development, but the process of fusion, which may be arrested (Fig. 130), is not complete until the middle of the second month.

[1] See Keith, *Proc. Anat. Soc. Great Brit. and Ir.* May, 1902, *Brit. Journ. Dent. Sc.* 1902, vol. 45, p. 529; J. Parsons Schaeffer, *Amer. Journ. Anat.* 1912, vol. 13, p. 1; J. Schaeffer, *Amer. Journ. Anat.* 1912, vol. 13, p. 1 (Formation of Nasal Duct), J. Schaeffer, *Amer. Journ. Anat* 1910, vol. 10, p. 313 (Formation of Antrum).

Parts formed from the Mandibular Arch.—Besides the lower jaw, there are formed from this arch the soft parts over and under the jaw, the lower lip, the muscles of mastication, the mylo-hyoid and anterior belly of the digastric, the tensor palati, and the tensor tympani. The anterior two-thirds of the tongue, the sublingual and submaxillary glands are formed from the floor of the primitive pharynx between the mandibular and the second or hyoid arch. These parts are supplied from the nerve of the mandibular arch, and are therefore probably derived, in part at least, from the substance of the arch. The whole arch and its derivatives are set apart primarily for the purpose of mastication. Only in mammals are the **lips** separated from the alveolar processes. In the human embryo the lower lip is demarcated from the

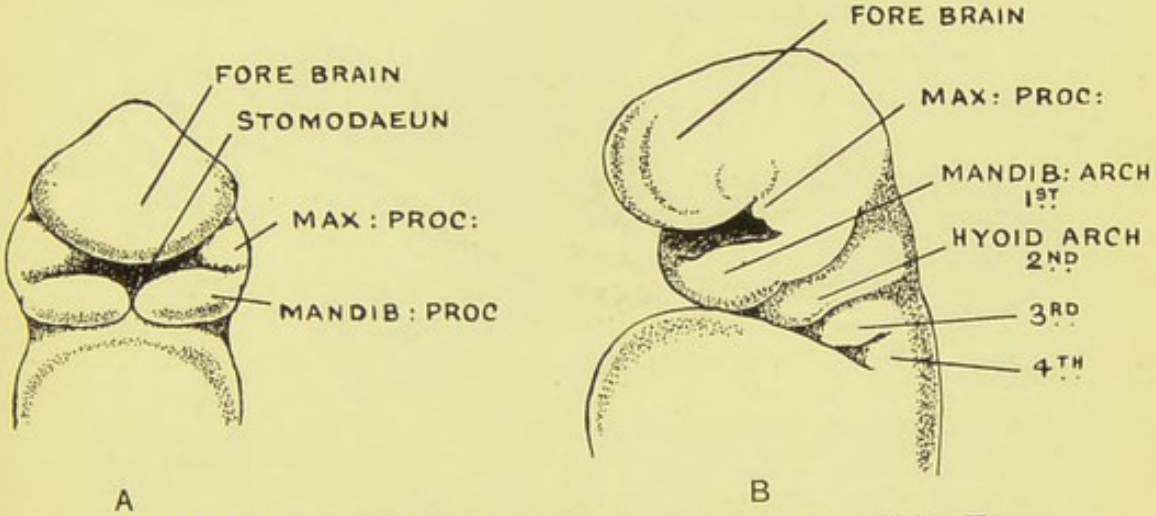


FIG. 147.—The Mandibular Arch and Stomodaeum (primitive mouth) in a Human Embryo of the 3rd week. (After Rabl.) *A*, from the front; *B*, from the side.

alveolus by the downgrowth of an epithelial groove (the labio-alveolar plate or groove) about the middle of the 2nd month.

The **Mandibular Arch** bounds the stomodaeum behind, and is the foremost of the visceral arches which encircle and form the walls of the primitive pharynx. **Meckel's cartilage** [1] forms its skeletal basis (Figs. 143, 144). The 3rd division of the 5th is its nerve, but its artery, the first aortic arch, has only a transient existence, although the inferior dental may represent part of it.

Development and Ossification of the Lower Jaw.[2]—In Fig. 148, which represents the condition of the human mandible at the beginning of the 4th month, the primitive cartilaginous skeleton of the mandibular arch can still be followed from the symphysis to the tympanum. Only one part of the cartilage takes a direct share in the

[1] E. Gaupp, *Anat. Anz.* 1911, vol. 39, pp. 97, 433, 609 (Morphology of Mandible).

[2] I have followed the account given by Dr. Alex. Low, *Journ. of Anat. and Physiol.* 1909, vol. 44, p. 83. See also Professor Fawcett's account in *Journ. Amer. Med. Assoc.* 1905, vol. 45, p. 695. For abnormal ossification of Meckel's cartilage see Keith, *Journ. Anat. and Physiol.* vol. 44, p. 151.

formation of the mandible—that part which lies near the symphysis and assists to form that section of the mandible which carries the incisor teeth (Low). The ventral extremities persist through foetal life as cartilaginous nodules; they may become ossified. The upper end of Meckel's cartilage forms the malleus; all the rest of the bar disappears, although the long internal lateral ligament occupies the site of part of the cartilage. In rare instances the cartilage may undergo complete and independent ossification. Thus the lower jaw, which shares with the clavicle the distinction of being the first bone in the body to ossify, is a membrane or dermal bone. Early in the 7th week a centre of ossification appears in each half, on the outer side of the Meckel's

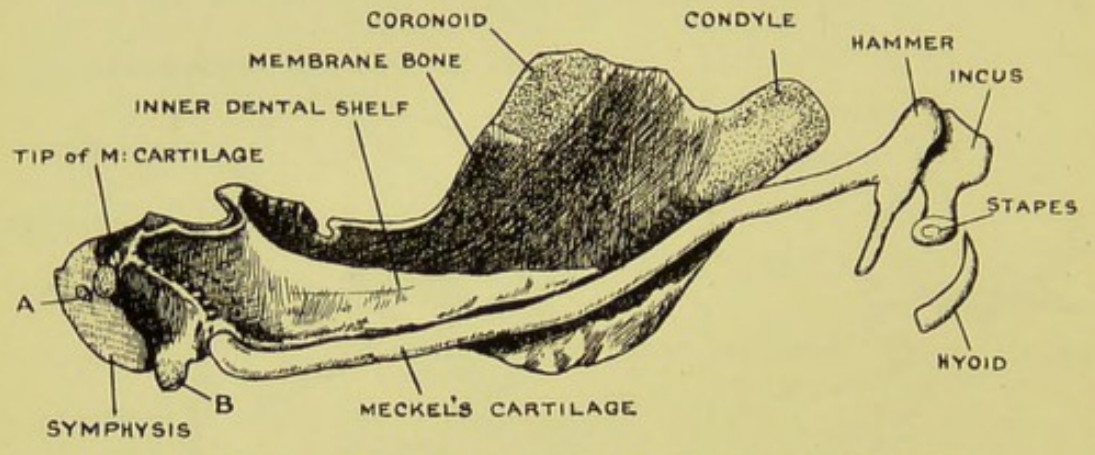


FIG. 148.—Meckel's Cartilage and Mandible of a Foetus in the 4th month of development, viewed on the inner or lingual aspect. (From a drawing and reconstruction by Dr. Alex. Low.) *A* and *B*, cartilaginous ossicles at symphysis; *C*, termination of Meckel's cartilage.

cartilage, and near the site of the future mental foramen. Each half of the lower jaw is ossified by the extension of a single centre. Processes grow up on either side of the inferior dental nerve which, with the tooth buds, comes to lie in a primitive alveolar trough. During the third month the ascending ramus begins to form. In the condylar and coronoid processes a formation of secondary cartilage occurs; thus the condyle and coronoid are ultimately laid down in cartilage. The two halves of the mandible unite at the symphysis during the second year; in some animals, such as the kangaroo, the symphysis remains open.

Evolution of the Mandible.—To interpret the appearances seen during the development of the human mandible we must suppose that Meckel's cartilage is the primitive skeleton of the mandible—a condition we know to occur in various forms of fishes (see Fig. 143). The malleus apparently formed the upper end of the skeleton of the jaw, the joint between the malleus and incus representing the mandibular joint. The second stage in the evolution of the jaw is the formation of membrane or dermal bone to strengthen the cartilaginous rod and form supports for the teeth. This stage is also seen in fishes. The

third and final stage is the formation of an ascending ramus and the evolution of a new joint between the condyle of the ascending ramus and the squamosal part of the temporal. This stage evidently occurred in the early ancestry of the mammals. In all other vertebrates—amphibians, reptiles and birds—the primitive joint persists.

Growth Changes in the Jaw.—The mandible undergoes great changes in the course of growth. As the permanent teeth erupt behind the milk set, increased alveolar space is required. This is obtained (see Fig. 149) by new bone being deposited along the posterior border

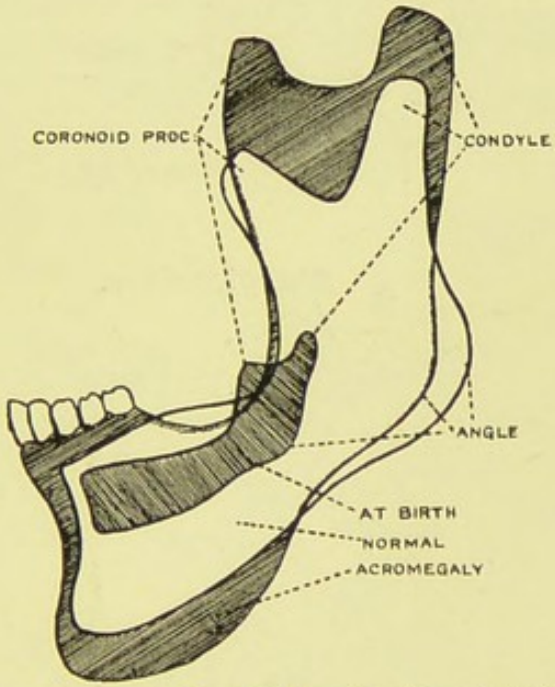


FIG. 149.—Mandibles of a Child at Birth, of a Normal Adult, of a Man, the subject of the disease of growth known as Acromegaly, superimposed to show the manner in which growth takes place.

of the ascending ramus, while absorption takes place at the anterior border. Growth in the vertical height is obtained by the deposition of new bone along the upper border of the ramus.

Growth of the upper jaw and of the antrum of Highmore, by pushing downwards the body of the lower jaw, leads to an elongation of the ascending ramus, and to its assuming a more vertical position to the body of the jaw (Fig. 149). In old age, when the teeth drop out and the alveolar margins are absorbed, the ascending ramus again becomes oblique, to allow the lower jaw to come in contact with the upper during mastication. The **mental eminence** is present at birth, and is a human characteristic.

As the teeth erupt, growth occurs both at the lower and alveolar borders, and also over the mental eminence or chin. These growth changes are well exemplified in the subjects of acromegaly (Fig. 149). In this disease growth of the jaw proceeds after adult years are reached. The deposition of new bone at the condylar process leads to the chin

and teeth being pushed forwards in front of the upper jaw and teeth. The chin and lower border also increase in size.

The Temporo-maxillary Articulation.—Two types of this joint are found in mammals, one (see Fig. 150, *A*), exemplified in the carnivora, in which only a hinge action is permitted, and hence the jaws act like scissor blades ; the second (see Fig. 150, *C*), in which a gliding movement is allowed, the teeth being thus able to act as grinders.

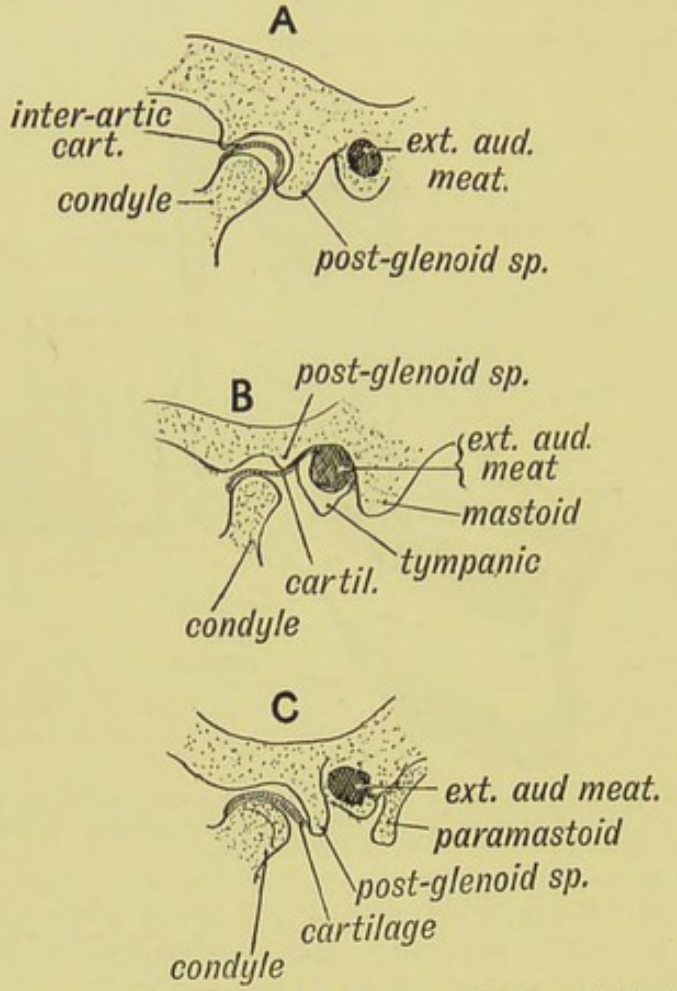


FIG. 150.—The chief types of the Temporo-Maxillary Articulation.
A. Carnivorous Type. *B*. Omnivorous Type. *C*. Herbivorous Type.

The second type occurs in all vegetable feeders. The human articulation combines the characters of both types (Fig. 150, *B*), the gliding action taking place between the interarticular cartilage and the skull, the hinge action between the cartilage and the condyle. In rodents the glenoid cavity is a narrow gutter in which the plate-like condyloid process glides backwards and forwards. The interarticular cartilage is developed in all the Mammalia except the monotremes, and one or two marsupials (Parsons).[1] At the end of the third month the cartilage appears as a condensation of fibrous tissue between the coronoid process and root of the zygoma. There is at that time no articular cavity ;

[1] "Joints of Mammals," *Journ. of Anat. and Physiol.* vol. 34.

the disc appears to arise from tissue caught between the condylar process and future glenoid cavity (Vinogradoff).

Development of the Tympanic Plate and Articular Eminence.—If the chin be depressed the condyle of the jaw moves on to

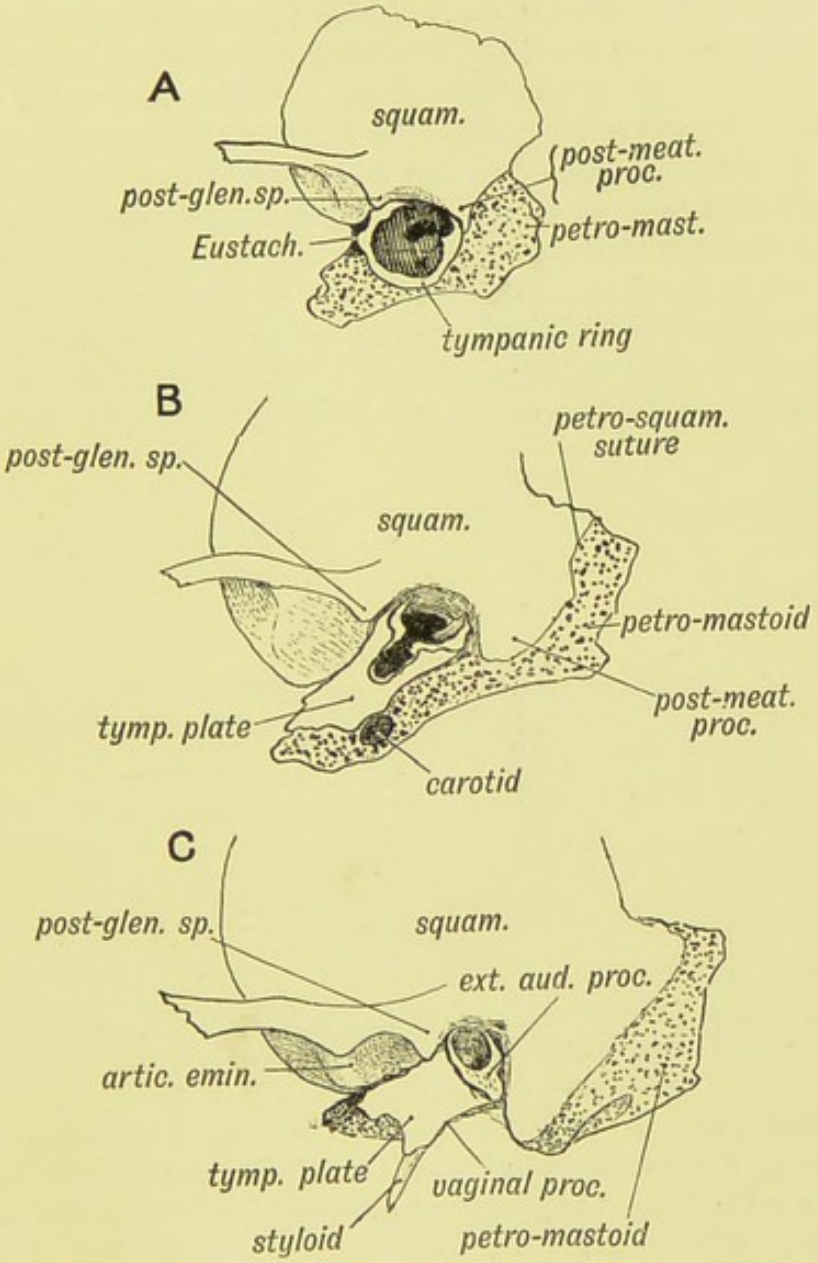


FIG. 151.—Showing the chief changes after birth in the form of the Temporo-Maxillary Articulation.
A. At Birth. *B*. At Two Years. *C*. In the Adult.

the articular eminence (Fig. 150, *B*); if over-depressed it springs over the eminence, and a dislocation is produced. This is impossible in the early years of life, for at birth there is no eminence and no glenoid cavity (see Fig. 151, *A*). At birth the **membrana tympani** lies exposed on the surface of the skull behind the condyle, supported in a fine osseous hoop, the **tympanic ring.** The ring is imperfect above, and there the

flaccid part of the membrane occurs. By the second year the ring has grown into a plate by sending out two processes, which, as they grow out, unite and leave a gap between (Fig. 151, *B*). This, as a rule, is soon filled up. By the 20th year the tympanic plate is three-quarters of an inch long, forming the bony floor of the external meatus and the posterior wall of the glenoid fossa, which in man is remarkably deep. It protects the meatus from the condyle, and must be regarded as an accessory part of the mandibular joint. Every year until the 20th the bony meatus gets longer, while the fibro-cartilaginous part becomes relatively shorter. In the adult the bony part forms two-thirds of the meatus. As the tympanic plate grows outwards, the membrana becomes less easily accessible to the surgeon (Fig. 151, *C*). The plate also grows inwards to form the floor of the bony part of the Eustachian tube and downwards to form the vaginal process, to which the upper end of the carotid sheath is attached (Fig. 151, *C*). Gadow regards the tympanic plate as the representative of the quadrate bone of birds and reptiles.

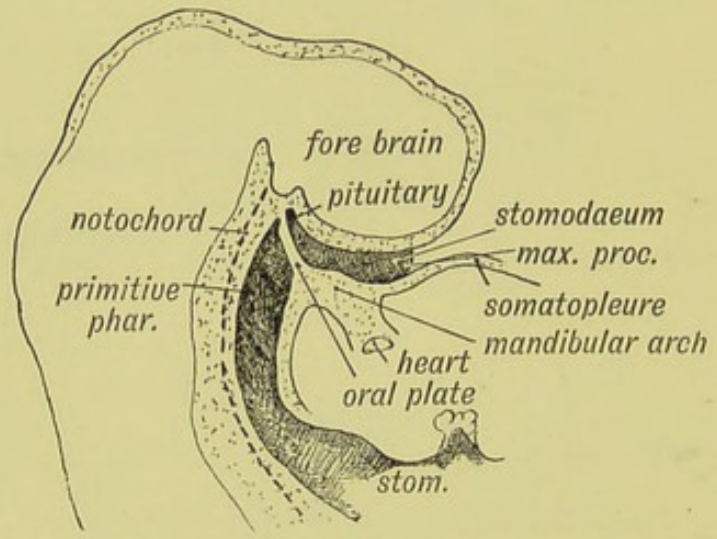


FIG. 152.—Sagittal Section showing the Stomodaeum and position of the Oral Plate in the 3rd week. (Schematic.)

The **stomodaeum** or primitive buccal cavity is the depression or narrow pocket formed between the fore-brain above and the mandibular arch below (Fig. 152). It is bounded laterally by the maxillary processes (Fig. 147) and lined by the covering epithelium of the skin —epiblast (ectoderm). It is blind at first, the floor or fundus being formed by the **oral plate,** which separates it from the primitive pharynx (Fig. 152, *A*). The premaxillary part of the mesial nasal and palatal plates of the maxillary processes divide it into an **upper part**—included in the nasal cavities—and a **lower,** which forms part of the permanent buccal cavity (see Fig. 153). In Fig. 128, these processes are not united ; the mouth and nasal cavities are in free communication. The tongue is developed in the floor of the pharynx and the tonsils in the pharyngeal wall, but the lips, teeth, and gums are formed in the walls of

the stomodaeum. In the 3rd week of foetal life the oral plate breaks down and the stomodaeum then communicates with the pharynx.

The Origin of the Pituitary Body.[1]—The lining epithelium (epiblast) of the stomodaeum becomes pouched out against the floor

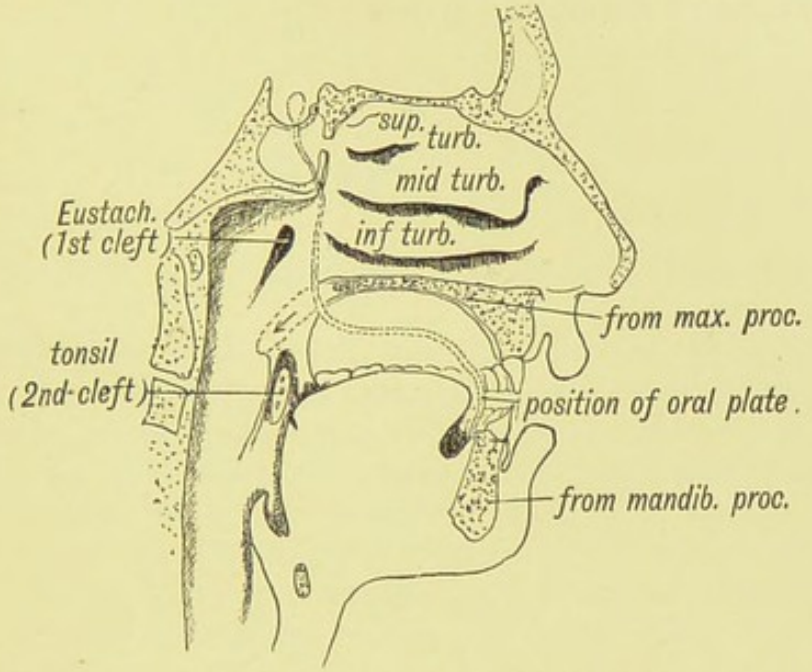


FIG. 153.—Showing the parts of the Buccal and Nasal Cavities formed from the Stomodaeum. The relative position of the Oral Plate is indicated.

of the fore-brain and forms the buccal element of the pituitary (see p. 92). A process from the floor of the hinder part of the fore-brain (thalamencephalon) meets it and forms the neural part of the pituitary. The buccal evagination is sometimes called Rathke's pocket. With the development of the base of the skull, the stalk of the buccal evagination disappears. A canal may occasionally be seen passing upwards between the basi- and pre-sphenoid, and opening at the olivary eminence, marking the position occupied by the pocket in the foetus (canalis cranio-pharyngeus, Fig. 133). Gaskell, who regards the neural or cerebro-spinal canal as the homologue of the invertebrate alimentary canal, homologizes the pituitary evagination of the buccal epiblast with the invertebrate mouth and gullet, and the pituitary body itself with the coxal glands of crustaceans. The pituitary body exercises a curious influence on the growth of certain parts, especially on the face and limbs. Disease of the pituitary body may lead to overgrowth of the limbs, as in giants, or of the face, as is seen in cases of acromegaly (see also p. 128).

In this chapter an account has been given of the various embryological elements which go to form the face. In the chapters dealing with the eye, nose, teeth and tongue further details will be described.

[1] J. P. Tourneux, *Jour. d'Anat. et Physiol.* 1912, vol. 48, p. 233 (Stalk of Pituitary).

The chief feature of the human face is its power of expression—due to the high differentiation of its subcutaneous musculature and to the elaborate nervous mechanism controlling that musculature. The muscles of expression, we shall see, arise in connection with the hyoid arch ; their wide distribution on the face occurred with the evolution of the pulmonary respiratory system.

CHAPTER XI.

THE TEETH AND APPARATUS OF MASTICATION.

In previous chapters dealing with the Cranium and Face, many of the changes in the apparatus of mastication have already been mentioned. At the end of the second year the alveolar parts of the palate and mandible are only sufficiently large to carry the milk dentition—which comprises 20 teeth altogether, 8 of these being incisors, 8 milk molars, and 4 canines. During the eruption of the permanent teeth, from the 5th to the 22nd year, space has to be found for the 12 permanent molar teeth, the place of the milk teeth being occupied by the permanent incisors, canine and premolar teeth. Hence the rapid growth of jaws, the enlargement and strengthening of the face, the development of supra-ciliary ridges and the upgrowth of the temporal line, which are seen to take place as the permanent teeth come into position. At the same time growth changes affect the muscles of mastication.

Evolution of Teeth.—The teeth are products of the skin. Both the cutis or dermis and the epithelium or epidermis enter into their formation. A tooth is a papilla of the dermis which has undergone a peculiar form of ossification (dentine) ; it is coated by an extremely hard substance—enamel—which is formed by the epidermis. Between the placoid scales which cover the skin of the shark and the complicated molar tooth of an elephant, there is a connecting series of intermediate forms. The primitive teeth have a conical or peg-like form, but with the evolution of mastication in the primitive mammalian stock the conical teeth became differentiated into various and complicated forms —the molar teeth departing very markedly from the primitive simple type. The recognition of the true nature of teeth was delayed by the fact that, during the development, the dental papilla and its epidermal covering are submerged beneath the lining membrane of the mouth.

The Structure of a Tooth.—A tooth may be considered as made up of five parts (see Fig. 154) :

(1) The **pulp,** situated within (2) a capsule of **dentine ;** the exposed part or crown of the dentine is coated by—(3) the **enamel ;** the

embedded part or root by a layer of bone—(4) the **crusta petrosa.** The root is secured within its socket by (5) the **peridental membrane**, which acts as a periosteum to both the crusta petrosa and bony wall of the tooth socket. An account of the development of a tooth has to deal with the origin of each of these five parts.

(1) **Origin of the Enamel.**—The enamel is formed by the epiblast of the stomodaeum. In the 7th week the epiblast within the labial

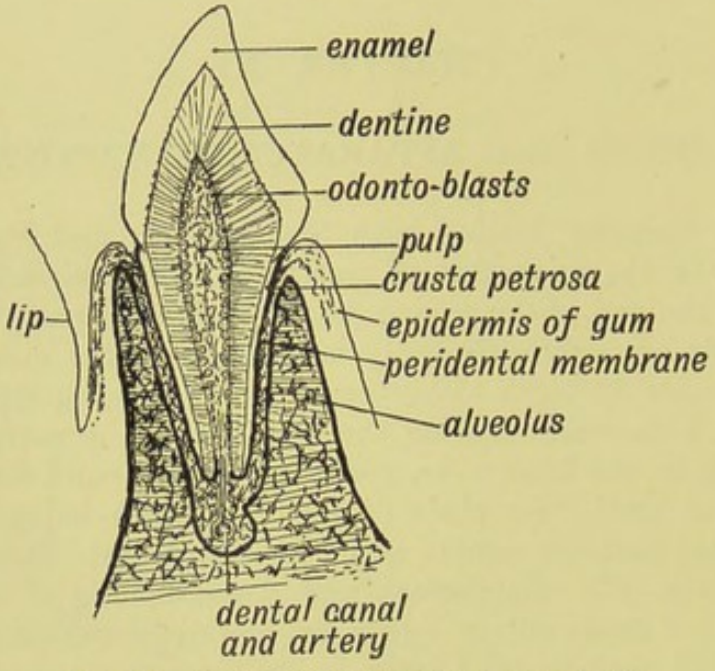


FIG. 154.—Showing the parts of an Incisor Tooth.

margin grows downwards so that a narrow semicircular invagination of epithelium is formed within the mandibular arch below, and within the premaxillary and maxillary parts of the primitive palate above. To the plate of epiblast thus infolded the name of **dental shelf** is given ; its position is marked superficially by an epithelial crest—the dental ridge (Fig. 156). As may be seen in a section of the foetal lower jaw (Fig. 155) the dental shelf is continuous at its origin with the epithelial downgrowth which separates the lip from the alveolus. From the ingrowing or deep margin of the dental shelf ten epithelial buds arise during the 3rd month, both in the upper and lower jaw. Each of these twenty **enamel buds** or **organs** produces the enamel to cover the crown of a milk tooth. Each bud grows downwards and inwards from the surface and comes against a condensed formation in the mesoblast of the jaw—the **dental papilla.**[1] On the papilla the enamel bud becomes partly invaginated, the papilla coming to lie within the invagination (Fig. 155). During the 4th month the epithelium covering the papilla becomes a layer of columnar enamel-producing cells or **ameloblasts.** The basal part of the ameloblasts are converted gradually into enamel,

[1] A. Masur, *Anat. Hefte*, 1907, vol. 35 p. 263 (Dev. of Dental Pulp).

or to put it somewhat differently, they form and deposit enamel in their bases and thus produce a coating for the dental papilla. Each ameloblast is gradually converted into an enamel fibre, but their more superficial parts are never so converted, but persist as the **cuticular membrane** which covers the enamel at birth and is soon afterwards worn off. The enamel of the milk teeth is completely formed before birth ; and that of the first permanent molar is already partly deposited. From the 5th month onwards the dental shelf—between the tooth germs and the surface of the alveolar margin—undergoes a gradual disruption and absorption. Isolated masses of the shelf may persist

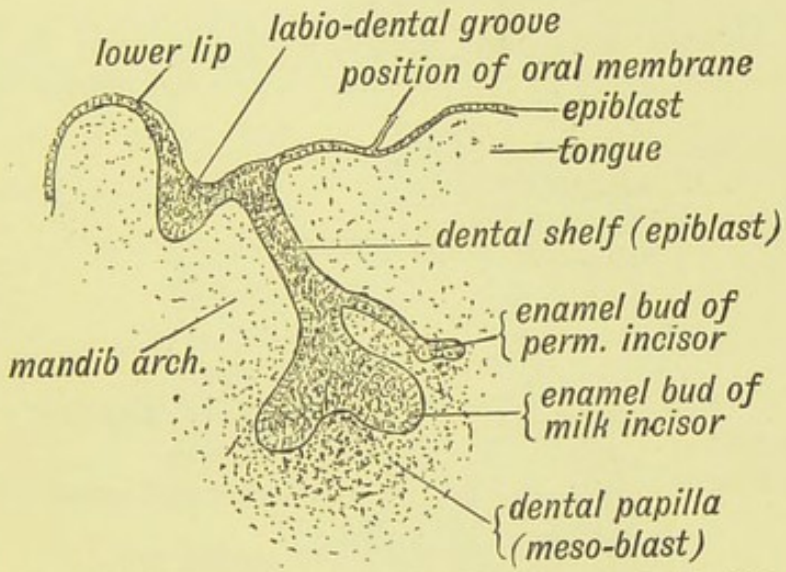


FIG. 155.—Section through the Lip and Mandible of a Foetus in the third month, showing the down-growth of the Dental Shelf.

within the gums and in certain cases give rise to masses of dental tissue—odontomes.

(2) **Origin of the Dentine.**—The dental papilla, formed from the mesoblast, corresponds to a depressed skin (dermal) papilla, the enamel cells representing its covering of epithelium. The dental papilla determines the shape of the tooth. In its superficial layers it contains numerous cells, **odonto-blasts,** with branched processes radiating towards the enamel epithelium. By the agency of the odonto-blasts a substance is deposited which becomes calcified into dentine or ivory. It is deposited in the matrix round the processes of the odonto-blasts. The cavities in which the processes are enclosed form the tubules of the dentine. In rodents especially, but also in all mammals, although only to a slight extent in civilized races of mankind, the odonto-blasts react to wear, add new layers of dentine to the wall of the pulp cavity, and thus prevent the pulp from being exposed. The dentine is deposited first in the crown of the tooth beneath the enamel ; the neck is laid down next, and then the root, the last point of all to be formed being the narrow canal at the apex of the root by which the dental vessels

and nerves reach the pulp cavity. The dental crowns reach their full size at the time of their formation. Teeth thus differ from all other structures of the body in undergoing no growth subsequent to the period of their development.

(3) **The Pulp.**—The pulp is the remnant of the dental papilla enclosed by the dentine. It is made up of a matrix of branching cells and is said to have no lymphatics. Thus, like the tissue of the umbilical cord and vitreous humour of the eye, it retains the embryonic form of the mesoblast (Berry Hart). It contains the ramifications of the artery, vein and nerve of the tooth. Fine processes of the nerves pass into the dental tubules (Mummery).

(4) **The Dental Sac.**—The foetal tooth, as may be seen from Fig. 156, lies embedded in the alveolus within the dental sac. When

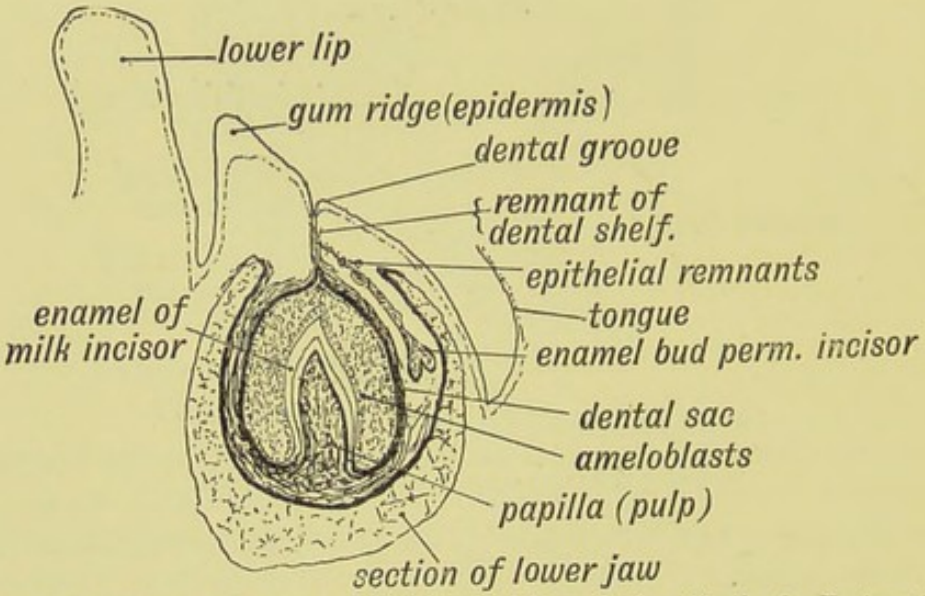


FIG. 156.—Showing the stage of development in an Incisor Tooth of a Foetus of six months.

the enamel bud is invaginated by the dental papilla, the **invaginated** layer forms the enamel, while the **invaginating** or parietal layer becomes surrounded by a dense layer of mesoblast and forms the dental sac. Between the enamel (invaginated) and parietal (invaginating) layers, filling the cavity of the sac, lies a mass of jelly-like epithelium corresponding to the corneous epithelium of the skin. As the crown of the tooth grows it rises within the sac of the enamel germ, and causes the absorption of the gelatinous material.

(5) **The Peridental Membrane.**—The peridental membrane (Fig. 154) is formed by that part of the dental sac which surrounds the fang of the tooth. The part of the dental sac which surrounds the crown is destroyed by the eruption of the tooth (Fig. 156).

(6) **The Crusta Petrosa.**—The peridental membrane is of the nature of periosteum, and contains osteoblasts which deposit the crusta

petrosa (bone) on that part of the dentine which forms the fang and also on the inner wall of the alveolus. The centres of ossification in the upper and lower jaw spread round the labial and lingual aspects of the dental sacs, thus enclosing them in a bony gutter or trough. Subsequently septa are developed between the dental sacs, and thus the developing teeth come to be situated in bony crypts. The roof of the crypt is never completed; a hole or window persists through which the neck of the dental sac emerges to become continuous with the mucous membrane covering the alveolus. The crowns of the teeth erupt at the point of union between the dental sac and alveolar membrane.

Origin of the Permanent Teeth.—From the dental shelf, besides the buds for the milk teeth, there grow inwards, during the latter part

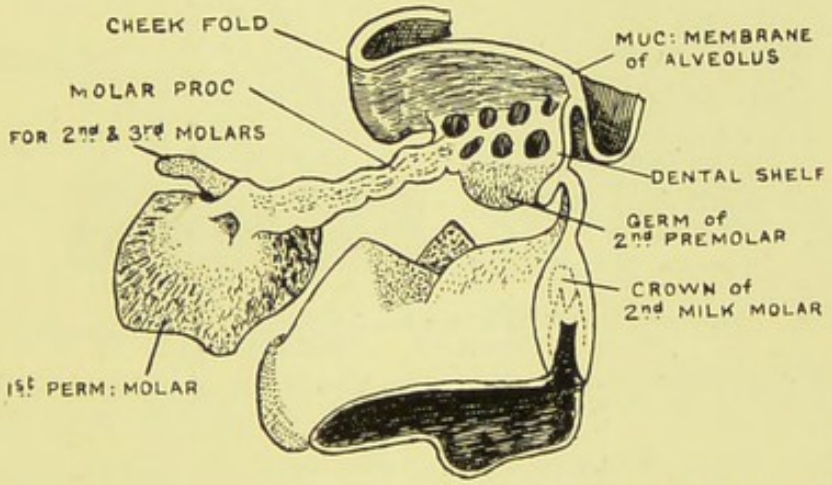


FIG. 157.—Mucous Membrane covering the posterior part of the Alveolus of a newly born Child with the Dental Shelf still attached to it. Proceeding backwards from the end of the dental shelf is seen the "molar process," which gives rise to the three permanent molar teeth. The crown of the second milk molar and the germ of the second premolar are also shown. (After Roese.)

of the 3rd month of development, so as to lie on the lingual aspect of the milk buds, processes of epiblast which form the enamel of the ten teeth which replace the milk teeth (Figs. 155 and 156). The three permanent molars of each side arise from a process which prolongs the dental shelf backwards behind the part from which the enamel buds of the milk teeth arise (Fig. 157). The first molar is the earliest of all the permanent teeth to undergo development. The permanent teeth are formed in exactly the same manner as the milk set. They develop on the lingual aspect of the roots of the milk teeth (Fig. 156), and if the milk teeth be roughly extracted the permanent bud may also be torn out. Being developed deeper in the alveolus than the milk teeth, the neck of the dental sac is more elongated, and has been named the **gubernaculum dentis** under the belief that it serves to guide the teeth during eruption. The opening by which the gubernaculum emerges from the crypts of the permanent incisors and canines are seen

on the lingual side of the alveolus near the sockets of the corresponding milk teeth. In the case of the premolars, the openings lie within the crypts of the milk molars (Carter).

Dentigerous and other Cysts of the Jaw.[1]—Cysts with epithelial walls, containing fluid, teeth or other dermal contents, occasionally develop in the jaw. They are formed from epithelial remnants of the dental shelf, which normally breaks up and disappears completely, or from detached parts of the enamel buds (see Figs. 155, 156 and 157).

Number of Dentitions.—In many lower vertebrate forms, such as sharks, the dental shelf gives off constantly a series of buds, so that as soon as one tooth is lost another springs up in its place from behind (Fig. 158). In mammals generally, as in man, the dental shelf gives

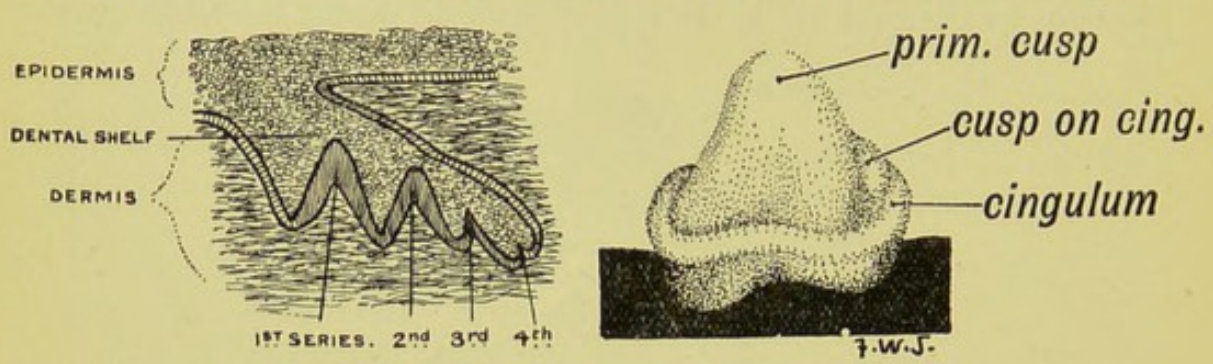


FIG. 158.—Diagrammatic Section across Dental Shelf of a Shark showing a Succession of Dentitions. (After Vialleton.)

FIG. 159.—Premolar Tooth of a Carnivorous Mammal to show the Primitive Cone, Cingulum and Secondary Cusps springing from the Cingulum. (Marett Tims.)

off only two series of buds—one for the milk set and another for the permanent set. In marsupials it gives off only one series, so that the first set of teeth is never replaced by a second. Thus in the most primitive vertebrates there is a succession of teeth, owing to the fecundity of the dental shelf. In man there are only the primary and secondary broods, but it is possible that occasionally representatives of a 3rd brood may be produced, for there are cases on record where a permanent tooth has been replaced by another late in life.

Morphology of Human Teeth.[2]—The crowns of all the human teeth seem to be modifications of the same type, all being evolved from the simple conical tooth found in fishes and reptiles (Figs. 159, 160). The conical peg-like tooth is to be regarded as the most primitive type, and in man vestigial teeth of this type occasionally occur. A modified example of the type is seen in the premolars of carnivorous mammals (Fig. 159). Here the base of the peg-shape crown is surrounded by a ring of enamel—the **cingulum.** From the conical tooth was evolved the **tritubercular** type, one in which the crown carries three tubercles

[1] P. Adloff, *Anat. Anz.* 1912, vol. 40, p. 177 (Abortive Dental Buds).

[2] A. C. F. Eternod, *Verhand. Anat. Gesellsch.* 1911, p. 144 (Bicuspid Theory of Teeth); C. S. Tomes, *Manual of Dental Anatomy.*

or cusps, two on the labial side of the crown and one on the lingual margin (Fig. 160, *A*). Secondary cusps arise from the cingulum (Marett Tims), and by the fusion of these with the original cone the two outer cusps are produced, while the inner cusp arises within the cingulum. The canine retains the conical form of crown; the prominence or heel on the lingual aspect of the crown represents the inner cusp; occasionally this cusp is well developed on the human canine (Farmer). The cutting edge of the incisors represents the two outer cusps; when newly cut, the incisor crowns show five serrations or cuspules. In the premolars or bicuspids the outer cusp, as may be seen in many of the lower primates, is really double.

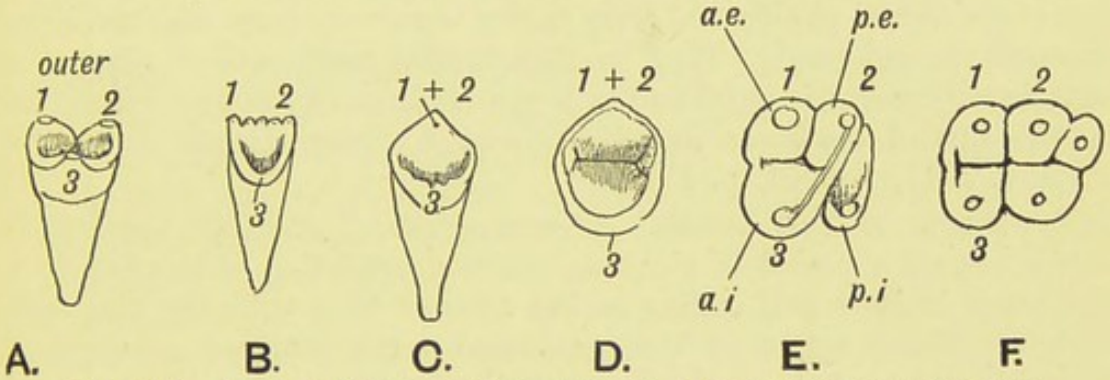


FIG. 160.—*A*. The Tritubercular Type of Tooth. The corresponding cusps are shown in the crowns of an Incisor (*B*), Canine (*C*), Bicuspid (*D*), Upper Molar (*E*), and a Lower Molar (*F*).

In the upper molar teeth, to the three primary cusps which form a cup, a fourth has been added (see Fig. 160, *E*). The two outer or buccal cusps are distinguished as the A.E. cusp (antero-external), the P.E. cusp (postero-external); the two inner as the A.I. (antero-internal) and P.I. (postero-internal). In the upper molars the cusps are situated alternately and the P.E. and A.I. cusps are united by an oblique enamel ridge, which represents the posterior margin of the crown of the primitive tritubercular tooth (Fig. 160, *E*). In the upper molar teeth of civilized races, especially in their wisdom teeth, the 4th or posterior internal cusp is often absent, the primitive tritubercular tooth thus reappearing. In the lower molars two cusps have been added to the three primary ones, making 5 in all. The fifth cusp is situated at the posterior border of the crown; the others are arranged in opposite pairs. The fifth cusp has become lost in the 2nd and 3rd lower molars of civilized races. Harrison found in Sphenodon, a primitive type of lizard, that **concrescence** or fusion of the simple peg-like teeth takes place in the posterior part of the jaw; it is possible that the molar teeth of mammals may have originated thus (Marett Tims). **Gemmination** may occur in human incisors; the incisor bud divides so that two crowns are produced on one root.[1]

[1] J. T. Wilson and J. P. Hill, *Quart. Journ. Mic. Sc.* 1907, vol. 51, p. 137 (Tooth Formation in Monotremes); W. Ramsay Smith, *Journ. Anat. and Physiol.* 1907, vol. 42, pp. 126, 226 (Morphology of Teeth of Australian Natives).

The Roots.—The upper molar teeth have three roots, two outer and one inner, but in the wisdom teeth, especially of civilized races, the roots are usually fused. The lower molars have two roots, but each root appears to be essentially double in nature. In lower primates the upper bicusps have three roots, but in man these are usually fused so as to form one or sometimes two roots. The lower bicuspids have usually one root, but as in lower apes, they may have two. The roots are the last parts to be formed. When the roots of the molar teeth come to be developed, the base of the dental papilla is differentiated into three parts—round each of which a root is formed. In that peculiar ancient and extinct race of men—known as the Neanderthal race—the dental papilla and pulp cavity were very large and the roots were short and wide. Thus in **Neanderthal teeth**—the condition is occasionally seen in a modern tooth—the pulp cavity almost descended to the tips of the roots (see Keith and Knowles, *Journ. Anat. and Physiol.* 1911, vol. 46, p. 12).

Eruption of the Teeth.[1]—The eruption of the milk teeth commonly covers a period of eighteen months, beginning in the 6th with the lower incisors and ending in the 24th or 30th with the 2nd milk molars. The eruption of the permanent teeth occupies a period of about eighteen years, beginning with the 1st permanent molar in the 6th year and ending about the 24th with the 3rd molar. The milk molars are replaced by the permanent premolars. In civilized races the third molars or wisdom teeth frequently remain imbedded in the alveolus and may give rise to an abscess. The upper wisdom tooth is developed in the posterior border of the superior maxilla, which bounds the spheno-maxillary fissure in front. The growth backwards of the maxillary antrum converts part of the posterior border of the superior maxilla into the alveolar border, thus bringing the wisdom teeth into position (see p. 153 and Fig. 146). The inferior wisdom teeth are developed in the alveolus on the inner aspect of the ascending ramus.

A fourth molar sometimes appears behind the third. The original primate stock is supposed to have had three incisors and four premolars on each side, yet a supernumerary incisor or premolar is a rare abnormality. The upper lateral incisor may be very small or even absent, there being a distinct tendency towards the disappearance of this tooth in civilized races. If the teeth are too large for the jaw, a not uncommon condition in civilized races, they appear in irregular positions.

Mechanism of Eruption.—As regards the mechanism which causes teeth to erupt there is still a considerable degree of uncertainty. One naturally infers that the growth of the root will tend to force the crown upwards and the tissues over the crown to atrophy. The process of eruption is a much more complex one than the mere formation of a root. It is well known that a rootless tooth may cut the gum, while

[1] G. Fischer, *Anat. Hefte*, 1909, vol. 38, p. 617 (Eruption of Permanent Teeth).

in another case the root may form and yet the tooth remain embedded in the jaw. Eruption is a definite growth movement—allied in nature to the mechanism which leads to the extrusion of a foreign body by the tissues. During the eruption of a tooth there is not only an absorption of the overlying tissues of the gum—probably due to pressure—but there is also the positive growth of the peridental tissue at the base of the tooth-sac which, as it presses the tooth towards the surface, moulds the surrounding wall of the dental crypt into a suitable alveolar socket. Thus the formation of the socket or alveolus appears to be part of the mechanism of eruption. Mr. J. T. Carter regards the gubernaculum dentis as playing an effective part in tooth eruption (see *Brit. Dent. Journ.* 1904, Feb.).

Effect of Civilization.—Mention has been made of the fact that the eruption of the last molars in highly civilized peoples may be long delayed or arrested; in a small proportion of individuals these teeth may be quite absent. When the teeth and jaws of ancient European races are compared with those of their successors, certain changes are very evident. These are (1) the crowns of the teeth in the ancient races are much worn; (2) the palate is well formed, and large enough to carry the teeth without crowding or irregularity; (3) the wisdom teeth are in position, but usually show a reduction in size and development; (4) diseased and carious teeth are uncommon; (5) the edges of the incisor teeth come into apposition in biting. In modern Europeans the degree of wear or erosion is slight; the palate is often vaulted, contracted and the teeth crowded and misplaced; the wisdom teeth are often unerupted or absent; diseased teeth are extremely common; the edges of the lower incisors ascend behind the crowns of the upper (scissors bite). The cause or causes of these remarkable changes are ill-understood, but it is probable that some or all are due to a change in diet.

Muscles of Mastication.[1]—The four muscles of mastication—the temporal, masseter, external and internal pterygoids arise in the mandibular arch. A single muscular mass is apparent at the end of the first month; during the second month it is differentiated into its several parts—the internal pterygoid being the first to separate from the common mass. The masseter and external pterygoids are derived from the primitive temporal muscle. The external pterygoid is a late addition; even in man it is often imperfectly separated from the temporal. The muscles of mastication differ from the ordinary striated muscles of the body in being derived from the musculature of a visceral arch. Their motor nerve—the motor root of the Vth—represents the splanchnic nerve of the second segment of the head (see p. 87). The somatic motor nerve of the segment is the 4th or trochlear nerve; the somatic musculature of this segment is represented by the superior

[1] Nature of; see reference under Edgeworth, p. 135.

oblique. The sensory nerves of the teeth—the 2nd and 3rd divisions of the Vth nerve—represent the skin or somatic sensory fibres of the second or mandibular segment of the head. It will be thus seen that the apparatus of mastication has been evolved in connection with the second cephalic segment—the neuromere of this segment being the second of the mid-brain.

CHAPTER XII.

THE NASAL CAVITIES AND OLFACTORY STRUCTURES.

Evolution of the Nasal Cavities.—Although the sense of smell is a minor one in the economy of the human body, it is very evident that in the root-stock from which mammals have been evolved the olfactory organ must have held a foremost place amongst the sensory

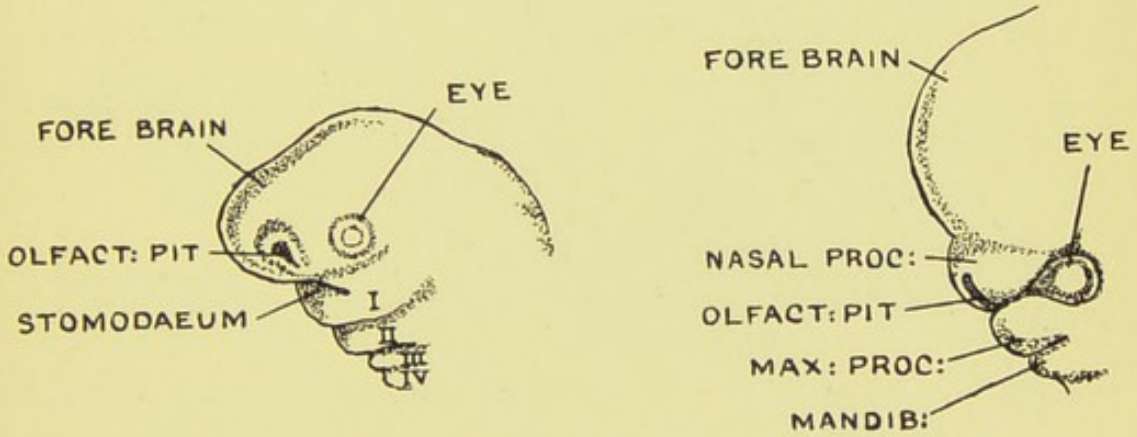


FIG. 161, *A*.—The Olfactory Pit and Face of an Embryo in the 4th week of development. (After Broman.)

FIG. 161, *B*.—The Olfactory Pit and Facial Processes in an Embryo in the 6th week of development. (After Hochstetter.)

structures. We have seen that the great superstructure of the brain rests on the primary ganglia connected with the olfactory nerves. When now we examine the changes connected with the development of the nose and nasal cavities in the human embryo, we shall see, behind the complicated processes at work, a recapitulation of conditions which are to be seen in animals occupying a very low position in the vertebrate kingdom. At the end of the 3rd week the olfactory membrane appears as two plaques of ectoderm in contact with the under surface of the fore-brain (Fig. 161, *A*); in the 4th week the plaques or plates become two pits—right and left, the usual condition in fishes; in the 5th week each pit becomes connected with the primitive mouth or stomodaeum by a groove—a condition seen in the dog-fish; in the 5th

and 6th weeks the pit is deepened and turned downwards by its edges rising up into folds or processes ; the processes unite, and a nasal cavity similar to that of the air-breathing or dipnoan fishes is established. In the 6th and 7th weeks the cavity of the pit is rapidly enlarged ; free communication with the mouth is established ; the nasal cavity has then become, as in amphibians, the functional vestibule of the respiratory system. In the 3rd month the palate is complete, and the stage peculiar to mammals thus established.

In tracing the development of structures subservient to the sense of smell, the following elements have to be dealt with :

(1) The olfactory sense epithelium and olfactory nerves ;
(2) The parts of the brain concerned with the sense of smell ;
(3) The capsule which contains the olfactory epithelium ;
(4) The respiratory tract of the nasal cavities.

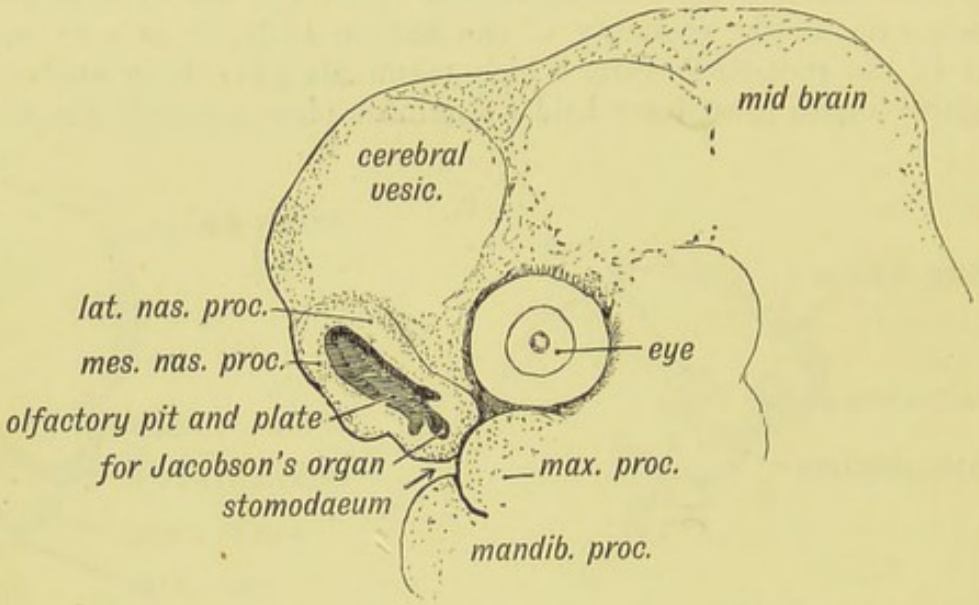


FIG. 162.—The Olfactory Pit and Nasal Processes in a Human Embryo about one month old. (After Kollmann.)

(1) **Origin of the Olfactory Sense Epithelium.**[1]—At the end of the 3rd week, a small area of the epiblastic cells lying under the fore-brain becomes demarcated on each side, to form the **olfactory plates.** Around these two plates the lateral and mesial nasal processes grow up (Fig. 162), the plates becoming at the same time invaginated to form the **olfactory pits.** With the growth of the nasal processes the olfactory pits are thrust into the roof of the stomodaeum (Fig. 161), and ultimately form the epithelial lining of the nasal cavities, with the exception of the inferior meatus, which is derived from the stomodaeum. A small island is detached from each plate to form the basis of Jacobson's organ (Fig. 162). The sense epithelia in the olfactory area send

[1] For development of Nasal Cavities see J. E. Frazer, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 416 ; K. Peter, *Ergebnisse der Anat.* 1911, vol. 20, p. 43.

out nerve processes which form arborescences round the neural cells of the outgrowing olfactory lobe (Fig. 163). The olfactory nerves are thus formed. At first the olfactory plates are directly in contact with the brain, but later on they are separated by the formation of the cerebral capsule and cribriform plates.

In the foetus the olfactory or sense epithelium is widely distributed, as is the case in mammals with a keen sense of smell. It descends almost to the lower border of the middle turbinate on the outer or lateral wall, and to the junction of the upper two-thirds with the lower third on the mesial or septal wall. In the adult the distribution

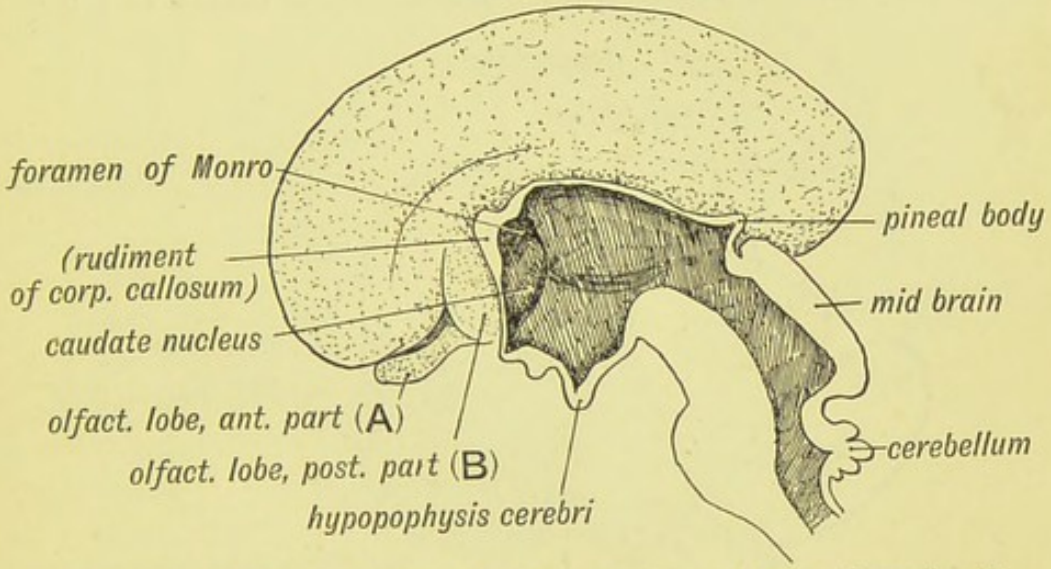


FIG. 163.—*A*. The Mesial Aspect of the Brain of a Human Foetus, 3½ months old, showing the Olfactory Lobe. *B* represents the paraterminal part of the rhinencephalon.

is much restricted—occupying areas only about one finger breadth in extent below the cribriform plate.

(2) **The Olfactory Lobe.**—As the olfactory pits are being thrust into the roof of the stomodaeum during the 5th week, the anterior part of the floor of the fore-brain grows out on each side as a hollow protrusion to form the olfactory lobes (Fig. 90, p. 98). At the end of the 3rd month the olfactory lobe has assumed the form shown in Fig. 163, *A*). Its cavity is at first continuous with that of the cerebral vesicle, but this connection is lost in the 3rd month ; it becomes solid, and forms the olfactory bulb and tract (Fig. 165). The tip of the anterior horn of the lateral ventricle marks the point at which the cavity of the olfactory lobe communicated with the cerebral vesicle.

The Rhinencephalon.—The Rhinencephalon is made up of those parts of the cerebrum which are primarily connected with smell. These parts are best seen in a typical mammalian brain such as is shown in Fig. 164. They are, following the classification of Elliot Smith : (1) the olfactory bulb and peduncle or tract, both of which are developed from

the olfactory lobe ; (2) the olfactory tubercle, represented in the human brain by a small area behind the trigone ; (3) the paraterminal body (Figs. 163, 164) which is represented in the human brain by the gyrus subcallosus and septum lucidum ; (4) the hippocampal formation represented in the human brain by the supra-callosal gyrus, gyrus dentatus, hippocampus and fornix (Fig. 165) ; (5) the pyriform lobe (the uncus of the human brain) ; (6) the anterior perforated space. In man these parts are reduced in size owing to (1) his less acute sense of smell ; (2) the great development of the corpus callosum and mantle of the brain. The rhinencephalon represents the oldest part of the brain, and its grey matter differs from the rest of the cortex in structure.

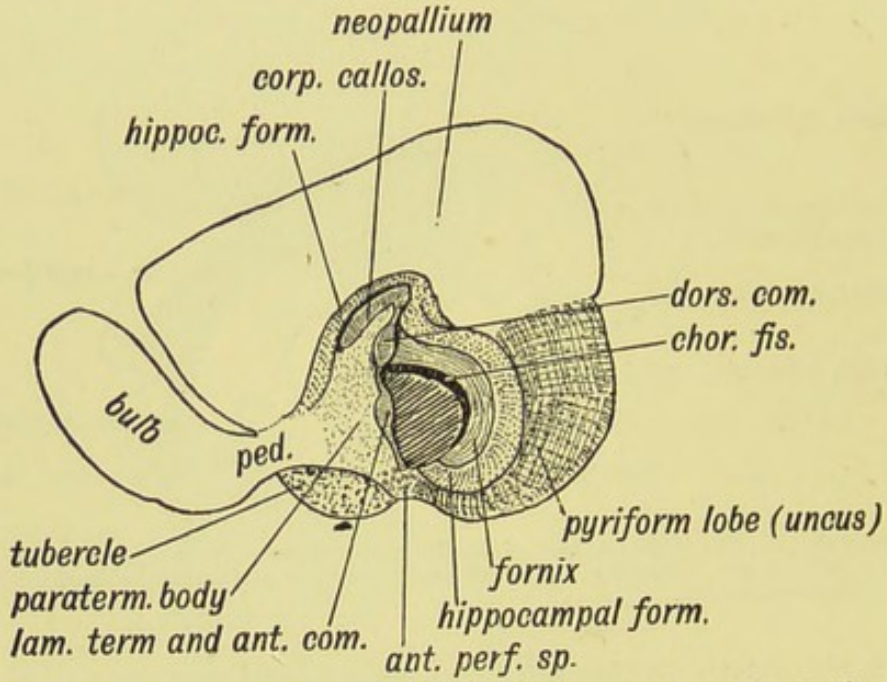


FIG. 164.—The Mesial Aspect of a typical Mammalian Cerebrum showing the parts of the Rhinencephalon. (Elliot Smith.)

The mesial root passes by the fornix and supra-callosal striae to the fascia dentata which forms the margin of the cerebral cortex or pallium (Fig. 165). The fascia dentata thus represents the **sensory** olfactory cortex ; the hippocampus—or hippocampal cortex, buried within the hippocampal fissure—represents the olfactory **association** area. The paraterminal body is a ganglionic mass correlated with the hippocampal cortex. The dorsal or hippocampal commissure (Fig. 164) unites the hippocampal formations of the two sides, and is thus an olfactory commissure. The lateral root of the olfactory tract ends chiefly in the pyriform lobe or uncus, and the olfactory tubercle (Fig. 164), which is situated behind the trigone in the anterior perforated space. The pyriform lobe in the human brain is represented by the uncus of the temporal lobe ; the incisura temporalis represents the rhinal fissure (see Fig. 165 and Fig. 103, p. 113). In Fig. 165 the stippled area has been extended beyond the limits of the uncus or pyriform lobe.

The Nasal Cavities.—The nasal cavities are formed by: (1) the ingrowth and enlargements of the nasal pits, which are lined by olfactory epithelium; (2) by the outgrowth of the nasal and maxillary processes. When these processes unite in the 6th week, the primitive nasal cavity thus enclosed rapidly expands, and an opening is formed in its fundus or floor, the primitive choanae, situated in the roof of the mouth (Fig. 141). The choanae are separated by the primitive nasal septum,

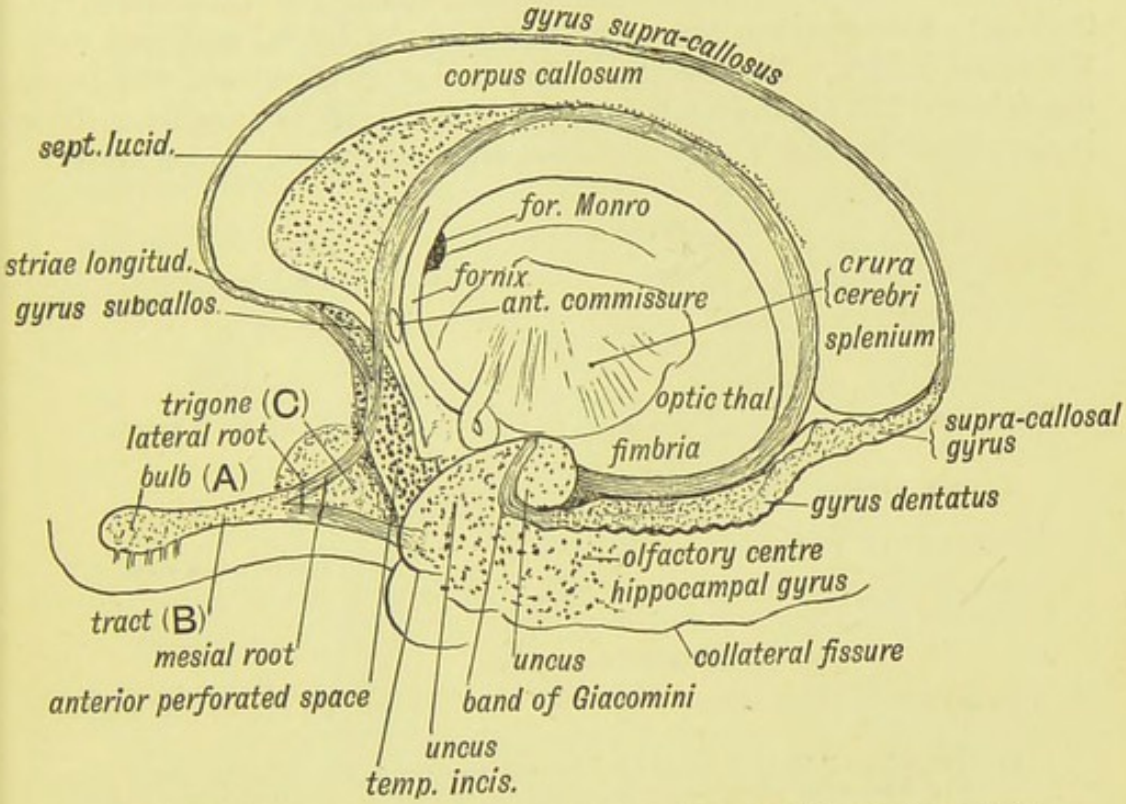


FIG. 165.—The parts of the Rhinencephalon in the Human Brain. Professor Elliot Smith proposes to apply the name "paradentate" to the gyrus designated "hippocampal" in the figure and substitute "pyriform lobe" in place of the term "uncus."

and are well in front of the pituitary outgrowth—Rathke's pocket (Fig. 166). In the latter part of the 2nd month and the earlier half of the 3rd the primitive nasal septum grows downwards and backwards until the mouth of Rathke's pocket is caught on its posterior border (J. E. S. Frazer, Fig. 166). In this manner the secondary nasal septum is formed, and the nasal cavities greatly deepened. At the same time the floor of the nasal cavities is prolonged backwards by the formation of the secondary palate, and the secondary choanae are established within the region of the naso-pharynx before the end of the 3rd month (see Fig. 166). The process of chondrification spreads into the walls of the nasal cavities from the region of the trabeculae during the period at which the secondary palate is being formed. In this way the cartilage of the septum and lateral mass of the ethmoid are laid down. The last part to chondrify is the cribriform plate. The part of the nasal

cavity beneath the level of the inferior turbinate processes is formed from the primitive buccal cavity.

Development of Turbinates and Air Sinuses.[1]—Before cartilage has actually been formed in the walls of the primitive nasal cavities, linear outgrowths of the lining epithelium are observed to occur in the lateral wall and roof. These outgrowths give rise to the meatuses of the nose—the inferior under the maxillo-turbinal appearing first, about the 8th week, the superior last, about the 12th week. The turbinate processes are thus carved out of the lateral wall and roof of the nasal cavity. The usual number is five in mammals, but in man the 4th and 5th are only temporary. The inferior or maxillo-turbinate is developed on the lateral wall, but the middle and upper appear on

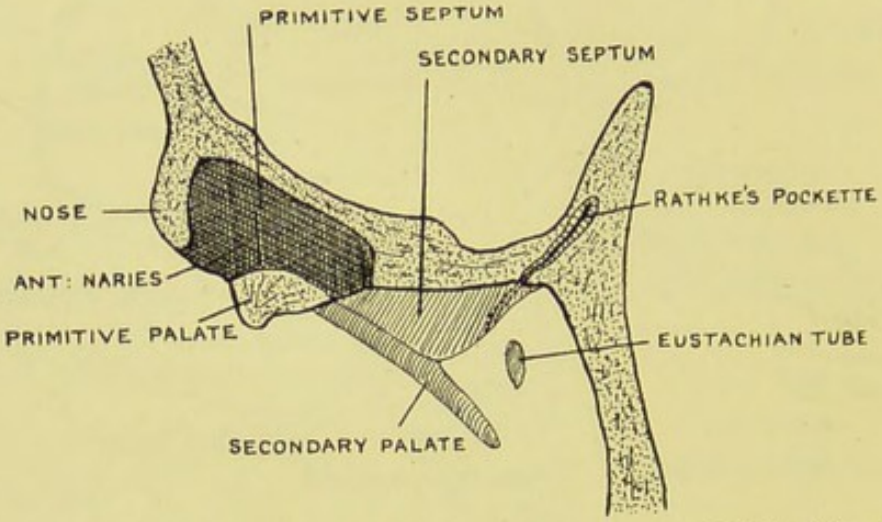


FIG. 166.—The Primitive Nasal Cavities and Choanae at the end of the 6th week. The formation of the secondary septum and palate are indicated. (After J. E. S. Frazer.)

the roof and septal wall, their lateral position being attained in the course of development. The sphenoidal turbinate also belongs to the ethmoidal series, but becomes applied to the body of the presphenoid. The turbinates and meatuses are developed in connection with respiration. They increase, it is true, the olfactory area, but their chief use is apparently to filter and warm the inspired air.

The manner in which the nasal mucous membrane pushes its way from the middle meatus into the maxillary process to form the **antrum of Highmore** has been already described (p. 153). The other air sinuses —the frontal, lachrymo-ethmoidal, anterior, middle and posterior ethmoidal, and sphenoidal sinuses—six in all, arise in the same way as the antrum, but begin, with the exception of the last named, to enlarge at a much later date. Although they begin to bud out about the time of birth, they assume their active growth in the earlier years of puberty, and reach their full size before the 30th year.

[1] See references, p. 154.

At birth, the lateral mass of the ethmoid is a thin plate, carrying the superior and middle turbinate processes, which almost fill the nasal cavity (Fig. 140). The entire ethmoid is narrow, and hence the proximity of the eyes in children. Beneath the middle turbinate is a thumbnail-like impression—the **hiatus semilunaris**, formed during the 3rd month (Figs. 145, 167). The antrum buds out near its posterior

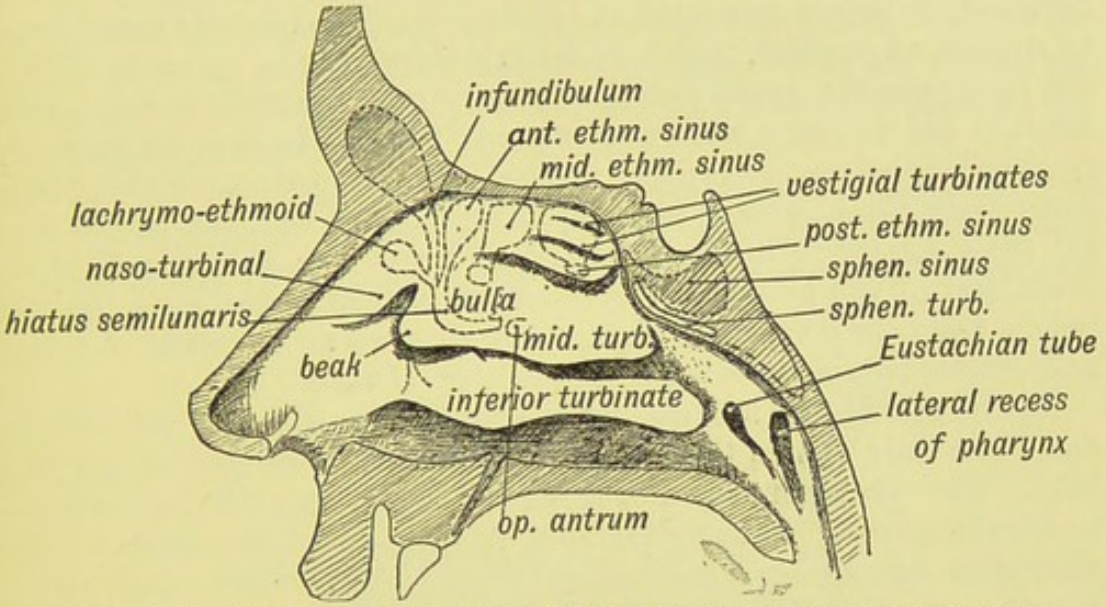


FIG. 167.—A Diagram of the Lateral Wall of the Nasal Cavity, showing the position of the Air Sinuses. The parts beneath the turbinate processes are indicated by stippled lines.

end, and the point at which the bud starts becomes its opening (Fig. 145). The uncinate process of the lateral mass of the ethmoid forms the prominent lower margin of the hiatus. A second opening may be present below the level of the uncinate process, or this may be the only one present.

From the upper end of the hiatus a bud of mucous membrane grows upwards to form the **frontal sinus,** gradually works through the ethmoid, and pushes its way into the frontal bone, separating the outer from the inner lamellae. The bud is formed in the first year, but is nascent until the fifth. A second frontal bud may arise in the middle meatus above the first, and may partially or completely supplant the primary frontal outgrowth. As a rule, by the 25th year the sinus reaches outwards over the inner two-thirds of the orbital roof, and is an inch or more both in height and depth at its mesial part. It is smaller in women than in men, but it may be, and often is, arrested at an early stage of development, or it may be absent altogether. The size of the glabellar prominence is no index to its development.

The stalk of the frontal bud forms the infundibulum, which is narrow, half an inch long, and difficult of catheterization from the nose. Into it open (or sometimes into the hiatus) the **lachrymo-ethmoidal** and **anterior ethmoidal cells** which surround the infundibulum. They are

developed as outgrowths from the infundibulum (Fig. 167). Occasionally the antrum of Highmore, as is frequently the case in the gorilla, sends a process to form part of the frontal sinus, and hence there may be a communication between the sinus and the antrum.

The development of the frontal sinuses and supra-orbital ridges leads to a marked change in the face at puberty. By the formation of the frontal sinuses the basal area of the skull, to which the face is attached, is largely increased in extent. Such an increase is necessary to support the palate, which grows rapidly in size at puberty. Up to the fifth year the upper jaw has to carry only ten milk teeth; in the adult it has to carry sixteen permanent teeth. To support these the face and palate grow rapidly in size. The formation of the frontal sinus gives the necessary increase in the area of the base of the skull for their support. It should be remembered that the growth of the brain and of the cranial cavity is comparatively slight after the fifth year. Only the gorilla and chimpanzee show an arrangement of frontal and ethmoidal sinuses comparable to that of man.

Above the hiatus lies the **bulla ethmoidalis,** which is inflated by, and commonly carries the opening of, the middle ethmoidal cell (Fig. 167). The posterior ethmoidal sinus opens beneath the superior turbinate process, and is developed from the superior meatus. The **ethmoidal sinuses** are produced in the cartilage of the ethmoidal or lateral nasal plate (Fig. 145). They inflate the ossifying cartilaginous plate until it becomes a cellular mass, thus increasing the breadth of the intra-orbital septum. The **sphenoidal sinus** (Fig. 167) is formed during the 3rd month by the mucous membrane growing into and expanding the sphenoidal turbinate bone, which is a small, slightly ossified cartilage lying beneath the presphenoid at birth, and forming the uppermost (sixth) of the nasal turbinate processes. Latterly the sinus grows into and expands the presphenoid and part of the basisphenoid, the sphenoidal turbinate remaining as its anterior wall (Fig. 167). The sphenoidal turbinate is a detached part of the ethmoidal cartilage.

It will thus be seen that all the nasal air sinuses are produced primarily by a budding outwards of the nasal mucous membrane into the cartilaginous basis of the lateral nasal processes. Disease may readily spread to these sinuses from the nasal cavities. By means of the sinuses the area of the face is increased to support the adult palate bearing the permanent teeth. Most of them open on the respiratory tract of the nasal cavity. They are ventilated with every breath. They act also as resonance chambers.

Vestigial Turbinates.—There is frequently to be seen in the adult one, or even two, secondary meatuses above the superior; these are constantly present in the chimpanzee and in mammals with a keen sense of smell. In the human foetus of four months six turbinates are usually present, besides secondary processes in the meatuses beneath

them. The uppermost of these, the sixth, becomes the sphenoidal turbinate; the fifth disappears; the third and fourth may remain separate or become united; the first and second form the inferior or maxillo-turbinal and middle turbinate processes. The agger nasi (naso-turbinal, Fig. 167), in front of the attachment of the middle turbinate process, is a vestige of the naso-turbinal, a process well developed in most carnivora and animals with a strong scent. The uncinate process, which forms the lower border of the hiatus semilunaris, is continuous at its base with the naso-turbinal. Through the hiatus semilunaris acting as a gutter, the antrum may become a cesspool for a suppurating frontal sinus.

Organ of Jacobson.[1]—Mention has already been made of the organ of Jacobson—situated on the nasal septum above the naso-palatine canals. During development (Fig. 162) a part of the olfactory

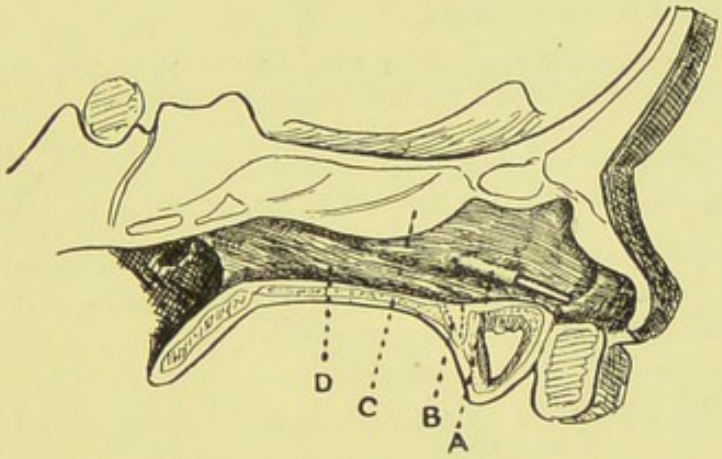


FIG. 168.—Nasal Septum of a Child at Birth, showing a rod inserted in the pocket of Jacobson's organ (*A*). *B*, closed naso-palatine canal; *C*, pre-sphenoid; *D*, vomer.

plate becomes detached, and is afterwards invaginated in a pocket in the septum and guarded by a scroll of cartilage. It reaches its maximum development in the human foetus at the 5th month, and afterwards becomes a mere vestige—often unrecognizable. It sometimes persists and forms a very evident structure on the septum. A pocket can usually be seen on the septum at birth (Fig. 168).

Nasal Duct.[2]—Although in no way connected with the sense of smell, the nasal duct is closely related to the nasal cavities. It is formed between the lateral nasal and maxillary processes (Figs. 161, 162). It is laid down as a solid epithelial cord along the naso-maxillary groove at the end of the second month. It becomes canaliculized during the 3rd month (see Schaeffer, *Amer. Journ. Anat.* 1912, vol. 12, p. 1). Three bones bound it: the superior maxilla on the outer side, formed in the maxillary process; the inferior turbinate, formed in the cartilage of

[1] E. Zuckerkandl, *Ergebnisse der Anat.* 1908, vol. 18, p. 801.

[2] See references, p. 154.

the lateral nasal process, and the lachrymal, formed over the lateral nasal cartilage, bound it on the inner side. The formation of the palate

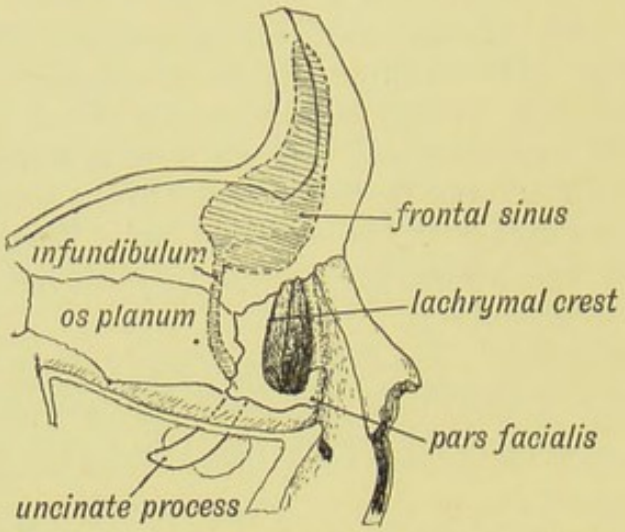


FIG. 169.—Showing on the Inner Wall of the Orbit (1) the Position of the Infundibulum, (2) the Pars Facialis Lachrymalis.

cuts the duct off from the mouth. The hamulus of the lachrymal varies much in size, and is the vestige of a larger process, which in lower

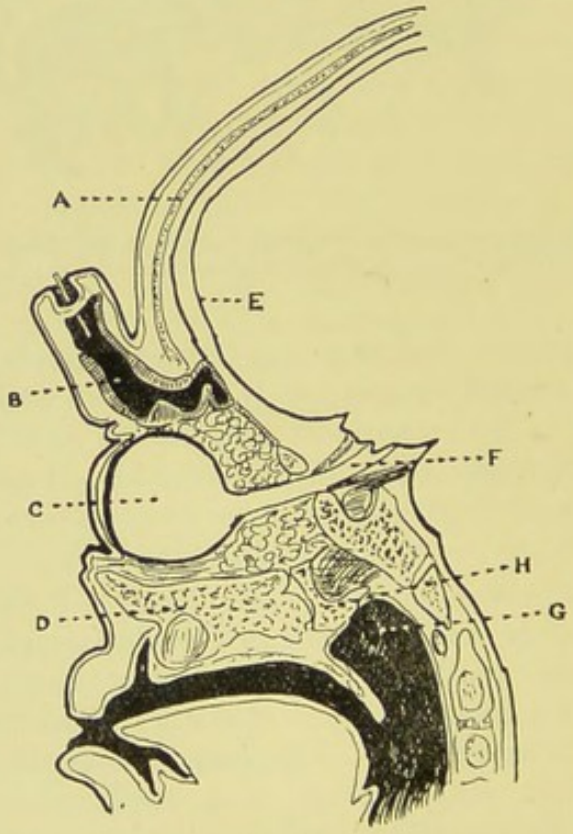


FIG. 170.—Median Sagittal Section of the Head and Face in a Case of Cyclops. *A*, frontal bone; *B*, single median nasal cavity contained in a proboscis formed by the nasal processes; *C*, median or fused eye; *D*, palate formed by the maxillary processes only; *E*, median cerebral vesicle; *F*, single optic nerve; *G*, Eustachian tube; *H*, palate bone.

primates enters into the formation of the inferior margin of the orbit. This **pars facialis** sometimes occurs in man (Fig. 169). The relation of the infundibulum to the lachrymal bone is shown in Fig. 169 ; it is seen to lie entirely in the lateral mass of the ethmoid behind the lachrymal. Occasionally the frontal and superior maxillary bones may articulate in an interval between the lachrymal in front and lateral mass of the ethmoid behind.

Malformations of the Nose.—In Figs. 127 and 137 two malformations of the nose are represented. In Fig. 127 the rare condition is shown in which one olfactory pit and its corresponding processes form a polypoid body ; in Fig. 170 the condition of cyclops, where both nasal cavities are enclosed in a proboscis is represented. The eyes are also fused. The condition of the facial skeleton in such a case is represented in Fig. 137. In such cases there has been an arrest of growth of the cephalic end of the embryonic plate, with a fusion of the olfactory bulbs and also of the optic vesicles. The two olfactory plates and pits are united in a single median structure. In this condition we seem to have represented a pure developmental abnormality—not a reversion to some past stage in evolution.

Two other malformations require mention. During the 3rd, 4th and 5th months of foetal life an epithelial plug is formed within the anterior nares—where the cutaneous and nasal epithelial coverings meet. In rare cases the plug becomes organized, and forms a dense septum within the nares. A similar obstruction, often containing bone, may be formed near the posterior nares. The posterior narial septum may arise from a persistence of the floor of the primitive nasal cavities.

CHAPTER XIII.

DEVELOPMENT OF THE STRUCTURES CONCERNED IN THE SENSE OF SIGHT.

The Nature of the Eye.—It is in vain that we appeal to comparative anatomy for light on the various stages in the evolution of the eye ; the eye of the vertebrata is already fully formed in the earliest form known. Our knowledge of its origin and nature rests on an embryological foundation ; during the first month of human development we see the eye compounded from three sources : (1) the retina and optic nerve arise as an outgrowth of the neural tube ; (2) the lens arises from the ectoderm or body covering ; (3) the tunics and mechanism of accommodation from the mesoblast or mesenchyme. The union of these three tissues to form the most marvellous contrivance of the human body is a product of countless ages of evolution. A comparison with the olfactory organ, described in the last chapter, assists us in understanding the peculiar nature of the eye. The olfactory plates are neural in nature ; their sensory cells give rise to the fibres of the olfactory nerves. The olfactory plates are situated near the open anterior end (neuropore) of the neural tube ; one can easily understand how they might shift towards the neural tube, merge with it, and become enfolded with the part which forms the olfactory bulb. It is very possible that the retinal plates arose as separate structures and afterwards became merged with the neural laminae. During an early part of the 3rd week the two retinal plates are depressions on the sides of that part of the medullary folds which are enclosed to form the forebrain (Fig. 171). The epithelium which lines the optic evaginations, clearly parts of the original surface covering of the embryo, does not become ependymal cells but, like the olfactory plates, gives rise to those highly modified sensory cells—rods and cones. Besides the rods and cones the optic evagination gives rise to nerve and other cells, in this respect resembling a typical part of the neural tube. If we compare the eye and nose, we must regard the retina as a compound of olfactory bulb and olfactory plate. It is thus clear that the olfactory and optic nerves are of a totally different nature to the other cranial

nerves. We must seek the origin of the retina as a superficial sense organ, which has become so modified in the course of evolution that its primitive simple nature is hard to detect.

The **structures concerned in the sense of sight** are :

(1) The Eyeball and the Optic Nerve ;

(2) The Eyelids and Lachrymal Apparatus ;

(3) The Orbit, and the Muscles, Nerves and Vessels contained in it ;

(4) The Nerve Centres and Tracts.

The Eyeball.—The condition of the eye in the third week of foetal

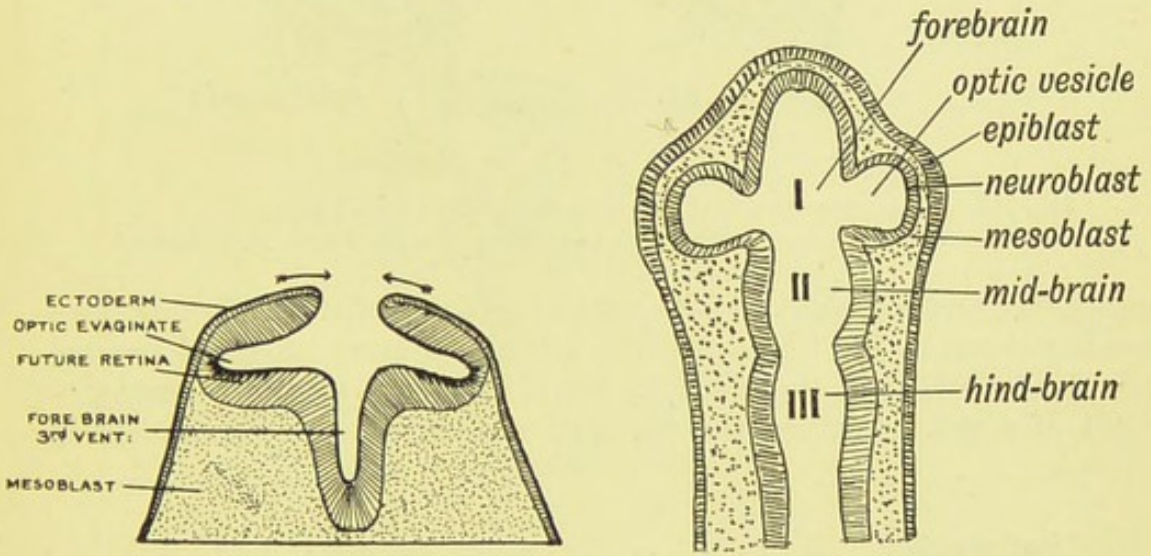


FIG. 171.—Diagrammatic Section across Fore-brain of a Human Embryo in early part of 3rd week to show the Optic Evaginations. (After Professor Bryce.)

FIG. 172.—Diagram of the Elements which form the Eyeball.

life is shown diagrammatically in Figs. 171, 172. The three elements which unite to form the eyeball are as yet separate. They are :

(1) **Epiblast,** which forms (*a*) the epithelium of the cornea, (*b*) the lens, and probably (*c*) the capsule of the lens.

(2) **Neuroblast,** which forms (*a*) the optic nerves, (*b*) sensitive retina, (*c*) pars ciliaris retinae, (*d*) uvea, (*e*) pigmentary layer of retina, (*f*) the hyaloid membrane.

(3) **Mesoblast,** which forms (*a*) outer tunic (sclerotic and fibrous cornea) ; (*b*) middle tunic (choroid, ciliary-choroid and iris) ; (*c*) the vitreous humour.

1. **Structures derived from the Epiblast.**[1] (*a*) **The Lens.**—The lens is developed by a saccular invagination of the epiblast situated over the optic vesicle at the beginning of the 4th week (Fig. 173). About a week later it becomes a closed sac by the severance of its connection with the epiblast, its wall being formed by a single layer of epithelial cells. The cavity of the lenticular vesicle is gradually obliterated by

[1] E. Kallius, *Ergebnisse der Anat.* 1904, vol. 14, p. 234 ; 1906 vol. 16, p. 746 ; 1907, vol. 17, p. 463 (Development of Eye).

the cells of the posterior wall becoming elongated (Fig. 174) until they reach the anterior wall (7th and 8th weeks). Each elongated cell is transformed into a lens fibre.

The cells of the anterior wall retain their primitive form (Fig. 174). New lens fibres are added by the cells at the margin (equator) becoming

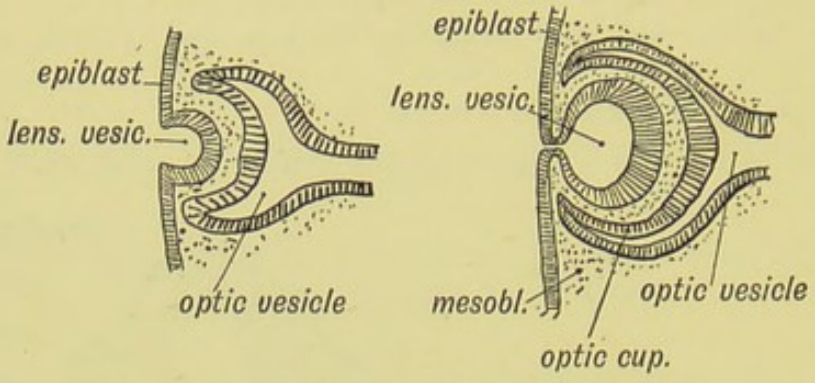


FIG. 173, *A*.—Invagination of the Epiblast to form the Lens Vesicle.
B.—The manner in which the Lens Vesicle is severed from the Epiblast.

multiplied and elongated. The central fibres, which are formed first, are the shortest, the fibres of every additional layer produced become longer than those of the previous layer, hence the concentric arrangement of fibres. Further, the fibres of each layer are so graduated in

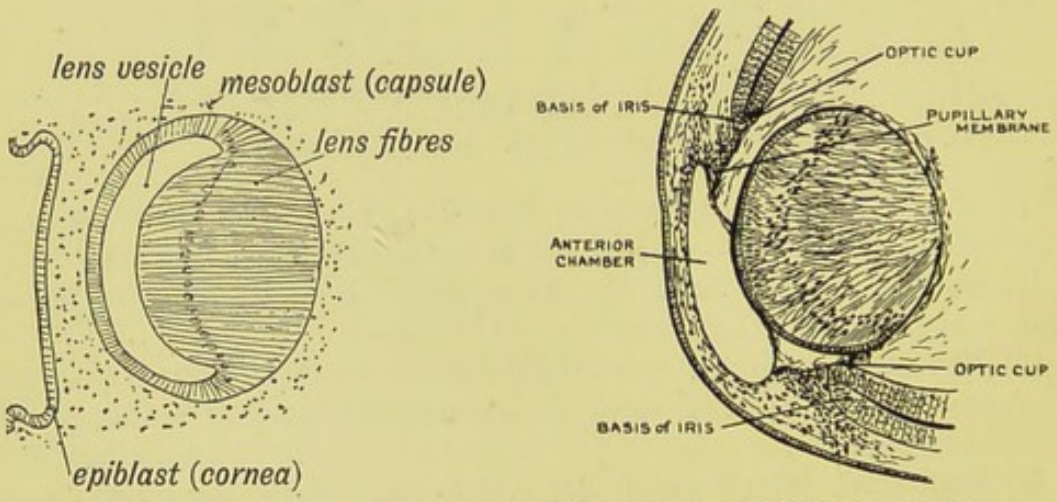


FIG. 174.—The Formation of the Lens Fibres from the Epithelium on the Posterior Wall of the Vesicle.

FIG. 175.—Diagrammatic Section of the Anterior Part of the Eyeball to show the state of the Anterior Chamber and Iris in the 5th month. (After Broman.)

length that, when produced, they meet along certain lines which radiate from the anterior and posterior poles of the lens. The lens is relatively large at birth, being two-thirds of its final size ; growth continues until puberty, and even then has not ceased, for Priestley Smith found that there is an appreciable addition to its weight with each decade of life. It will thus be seen that the lens is an area of modified epidermis and

in manner of development closely resembles the sense organs in the skin of fishes and amphibians. Like the epidermis, it shows a tendency in the aged to be transformed into keratin. The oldest cells (the central or nuclear fibres) alter first; hence the central position of the cataract which occurs so frequently in old people.

(*b*) **The cornea.**—The epithelial covering of the cornea is continuous with the epidermis. It becomes transparent. The mesoblast which grows in between the lens vesicle and epiblast forms the connective-

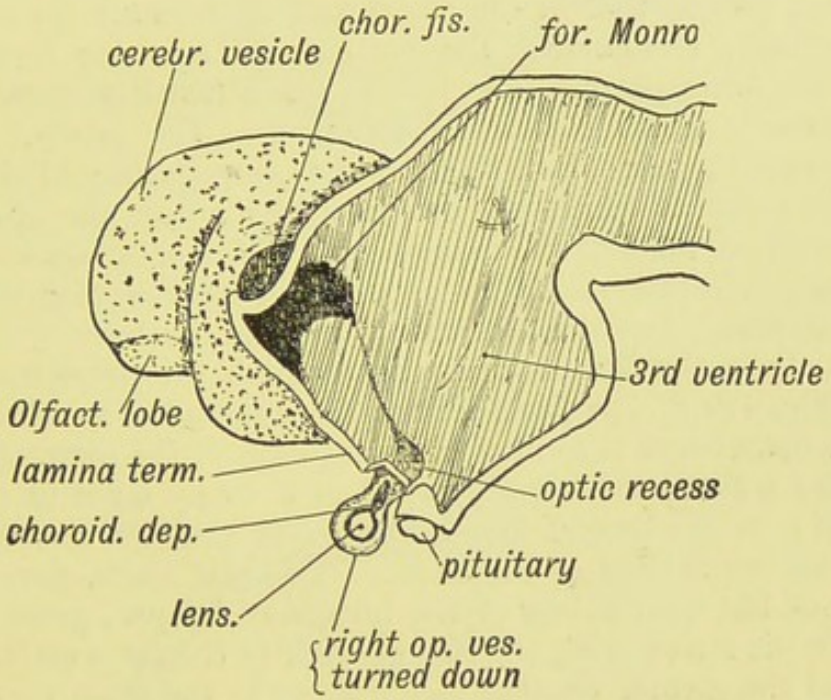


FIG. 176.—Diagram showing the condition of the Optic Stalk and Vesicle at the commencement of the 2nd month. (After His.)

tissue basis of the cornea and also the vascular capsule of the lens (Fig. 174).

(*c*) The capsule of the lens is a cuticular membrane formed by the lenticular cells. Outside the proper capsule a vascular tunic is formed from the mesoblast (Fig. 175).

2. **Structures formed from the Optic Vesicles (neuroblastic element).—The optic nerve** is formed out of the stalk of the optic vesicle. The vesicle is well developed soon after the commencement of the third week (see Figs. 171, 172); even before the medullary plates have quite met to enclose the cavity of the fore-brain the optic vesicles have commenced as evaginations of those plates. They form a great lateral diverticulum on each side of the fore-brain—a cavity which becomes the third ventricle in the adult. The condition of the optic nerves at the commencement of the second month is shown diagrammatically in Fig. 176. The stalk or neck remains constricted while the vesicle enlarges.

Invagination of the optic vesicle.—Almost as soon as it begins to grow out the optic vesicle becomes invaginated, one half being pushed within the other. It is invaginated by the lens-bud in the same manner as a schoolboy's fist indents a punctured india-rubber ball. The invaginated vesicle is known as the **optic cup.** Fine fibres unite the neuroblastic cells which line the optic cup with the deep aspect of the lenticular vesicle (Cirincione). The invagination of the vesicle, which takes place in an oblique manner—the pressure being applied from below and behind—leads to the closure not only of the cavity of the vesicle, but also to that of the distal half of the stalk (optic nerve). The mesoblast, surrounding the lens, grows into the invagination amongst the fibres passing from lens to retina (lenticulo-retinal fibres) and afterwards forms the vitreous humour. The artery, which is folded in with the mesoblast, becomes the central artery of the retina. Hence the point at which the central artery enters the optic nerve marks the upper limit of the invagination of the optic stalk. By the fourth week the optic vesicle no longer communicates with the cavity of the fore-brain, but the recessus opticus in the floor of the third ventricle, above the chiasma, remains to mark the point at which it entered (Fig. 176). The parts formed from the optic vesicles are :

(*a*) **The optic nerve** is formed from the stalk of the optic cup. The wall of the stalk is at first composed of a single layer of columnar epithelium ; in the second month these cells produce a sponge-work of fibres on the surface of the stalk. The optic fibres, developed as processes of the neuroblasts of the invaginated layer, grow into the brain from the retina along the sponge-work of the optic stalk.[1] Thus are formed the greater number of the fibres in the optic nerve. The optic fibres also form the chiasma in the floor of the third ventricle and the optic tracts on the wall of the fore-brain (Fig. 190). It will thus be seen that the optic nerves and vesicles are of the same origin as the cerebral vesicle—both representing parts of the wall of the fore-brain.

(*b*) **The pigmentary layer of the retina** is formed from the ensheathing or outer layer of the optic cup (Fig. 177). At first the wall of the optic vesicle is composed of a single layer of epithelium ; the outer or pigmentary layer of the retina retains this embryonic form.

(*c*) **The uvea** is the layer of pigmented epithelium which covers the posterior surface of the iris. It is formed out of both outer and inner layers of the optic cup, and represents the rim of the cup (Figs. 175, 177).

(*d*) **The pars ciliaris retinae** is formed out of that part of the inner or invaginated layer of the optic cup which lies in the shadow of the iris and is therefore inaccessible to light rays. It also retains the primitive columnar or partly transitional form of the epithelium (Fig. 178). The ora serrata marks the junction of the pars ciliaris retinae and sensitive retina.

[1] See Cameron, *Journ. Anat. and Physiol.* 1905, vol. 39.

Ciliary Processes.[1]—At the commencement of the third month, the pars ciliaris retinae becomes plicated or puckered into 60 or 70 small folds; mesoblast of the middle tunic (choroid) grows into the puckers and forms the ciliary processes. It should be observed that the lens

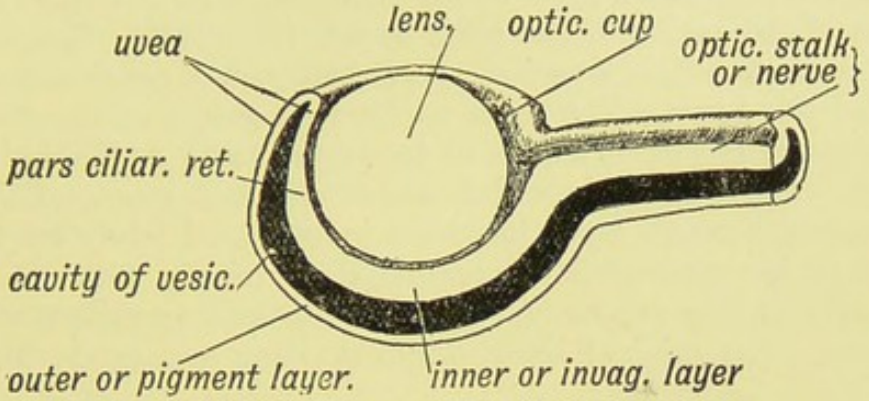


FIG. 177.—Diagrammatic Section of the Optic Cup and Lens.

lies within the optic cup and the ciliary processes are formed round the equator or circumference of the lens. The retinal epithelium which covers the ciliary processes is secretory in nature. It forms the aqueous humour, thus recalling the ependyma, which covers the choroid plexuses

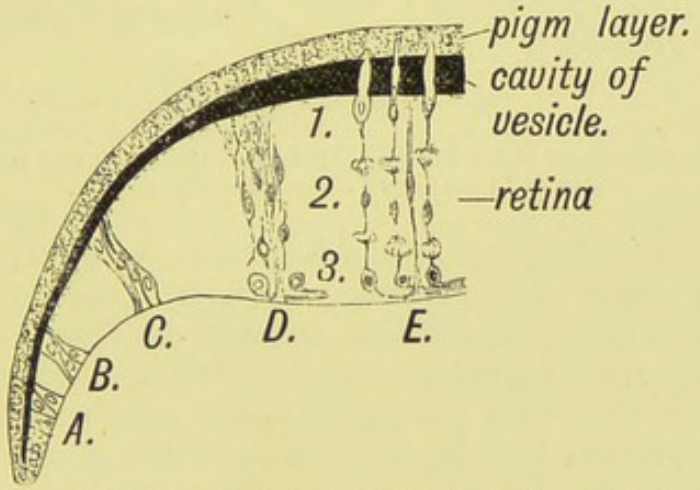


FIG. 178.—Diagrammatic Section across Optic Cup to show the manner in which the Cells of the Inner Layer of the Optic Cup are differentiated to form the Retina. (After Fürst.)

A, *B*, *C*, *D*, *E*, show stages in the development of the Retina from the simple layer of Cells.

1. The outer stratum of Sense Cells (rods and cones).
2. The middle stratum connecting (bipolar) Nerve Cells.
3. The inner stratum of Ganglionic Cells and Fibres.

The cavity of the Optic Vesicle, which is closed by the invagination of the retinal layer within the cup and obliterated by the outgrowth of the rods and cones, is represented by a wide black zone in the diagram.

of the ventricles of the brain. It is strange that from the same layer as gives origin to nerve cells there should also arise supporting (neuroglial) and secretory cells.

[1] M. von Lenhossék, *Verhand. Anat. Gesellsch.* 1911, p. 81 (Dev. of Ciliary Body).

(*e*) **The sensitive retina** is formed out of the inner or invaginated layer of the optic cup (Fig. 178). At first the inner wall is composed of a single layer of epithelium. The pars ciliaris retinae retains this form. What is called the **outer** aspect of the primitive retina is directed towards the pigmented layer but is separated from that layer by what remains of the cavity of the optic vesicle (Fig. 177). That cavity, it will be remembered, is a prolongation of the neural canal or ventricular cavity of the brain. The **inner** or vitreous aspect of the retina, corresponding to the outer aspect of the neural tube, is directed towards the lens. The manner in which the complicated strata of the retina arise from the single layer has been investigated lately by Professor Fürst, and is represented diagrammatically in Fig. 178. Differentiation starts at the centre of the optic cup and spreads towards the periphery. The original layer, while dividing and producing broods

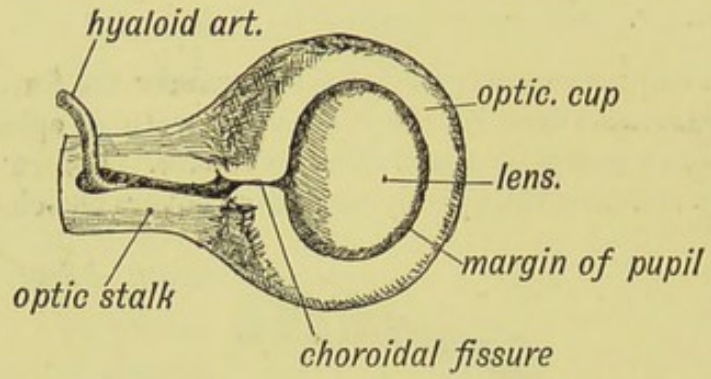


FIG. 179.—The Optic Stalk and Cup, viewed on the lower and lateral aspect, showing the Closure of the Choroidal Fissure.

of cells, still retains its position, the daughter cells being pushed towards the vitreous aspect of the retina. On each surface of the retina is developed a cuticular or **limiting membrane.** Some of the original epithelial cells are elongated between the limiting membranes and form the fibres of Müller. On passing from the margin of the cup to its centre all stages will be seen between the single layer and the multistratified condition. Ultimately three strata can be recognized in the retina. Beneath the outer limiting membrane the original cells remain as the retinal sense epithelium ; processes from these cells break through the outer limiting membrane to form the rods and cones ; the middle stratum forms bipolar cells ; beneath the inner limiting membrane ganglionic cells are formed. The middle stratum by its processes links together the sense epithelium and the ganglionic cells, and thus stands in the same relationship to the sense epithelium and ganglionic cells as a posterior root ganglion does to the touch corpuscles of the skin and the cuneate and gracile nuclei of the medulla. In many ways the development of the retina recalls the development of the spinal cord. Both form part of the neural tube.

The Choroidal Fissure.—Occasionally congenital fissures are seen in

the lower segment of the iris (coloboma iridis) or choroid (coloboma choroidea) (Fig. 180). A white line, due to absence of pigment, may be seen in the corresponding segment of the retina when the interior of the eye is examined. These are due to imperfect closure of the choroidal fissure. The choroidal fissure is the result of the peculiar mode in which the optic vesicle is cupped or invaginated. The lens grows into it from the malar or lower lateral aspect. The lens is lodged in the anterior part of the depression; the posterior part becomes the choroidal fissure (Fig. 179). The margins of the fissure unite, all traces of it normally disappearing in the 7th week. Its union recalls the closure of the fissures in the upper lip. Coloboma and harelip are lesions of a similar nature. With the closure of the choroidal fissure the optic cup is completed. Its brim or margin becomes the site of the pupil.

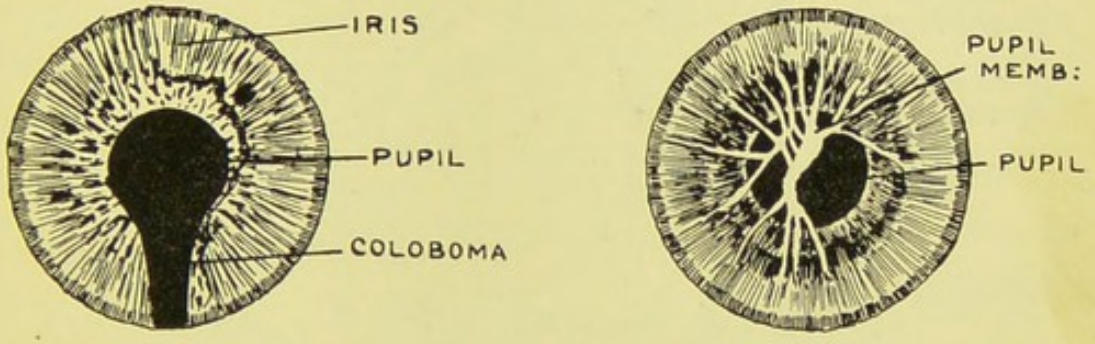


FIG. 180.—Coloboma or Cleft of Iris. (After Seggel.)
FIG. 181.—Remains of Pupillary Membrane. (After Prof. Hippel in Schwalbe's *Missbildungen des Menschen*.)

Binocular Vision.—At first the optic vesicles are directed laterally in the human embryo, and in mammals generally the eyes are so directed, each eye having its own field of vision. In the Primates the eyes swing forwards during the second month; binocular vision is thus made possible. With binocular vision and the combination of images appear in the highest primates:

(1) A fovea centralis and macula lutea (L. Johnston);

(2) A partial crossing of the optic fibres at the chiasma;

(3) Certain alterations in the attachments of the oblique muscles of the eyeball.

The primitive cavity of the Optic Vesicle (Fig. 177) is of some clinical importance. It is obliterated by the invagination of the vesicle; the rods and cones formed in the inner or invaginated layer grow out across the cavity into the outer or ensheathing pigmented layer of the retina (Fig. 178). From accident or disease the retina may be detached, thus causing blindness; the separation takes place between the pigmented epithelium, which remains *in situ*, and the rods and cones, which fall inwards with the nerve layer. Fluid then collects in the site of the primitive cavity of the optic vesicle. The optic part of the medullary plate in amphibian embryos has been transplanted and

produced a retina in its new site. Some experimenters found that the ectoderm over the optic graft gave rise to a lens.[1]

3. **Parts of the Eyeball formed from the Mesoblast.**—After the optic vesicle has been invaginated against the lens, a continuation of the same layer of mesoblast, which surrounds and forms the coverings of the brain, envelopes the optic cup and spreads inwards

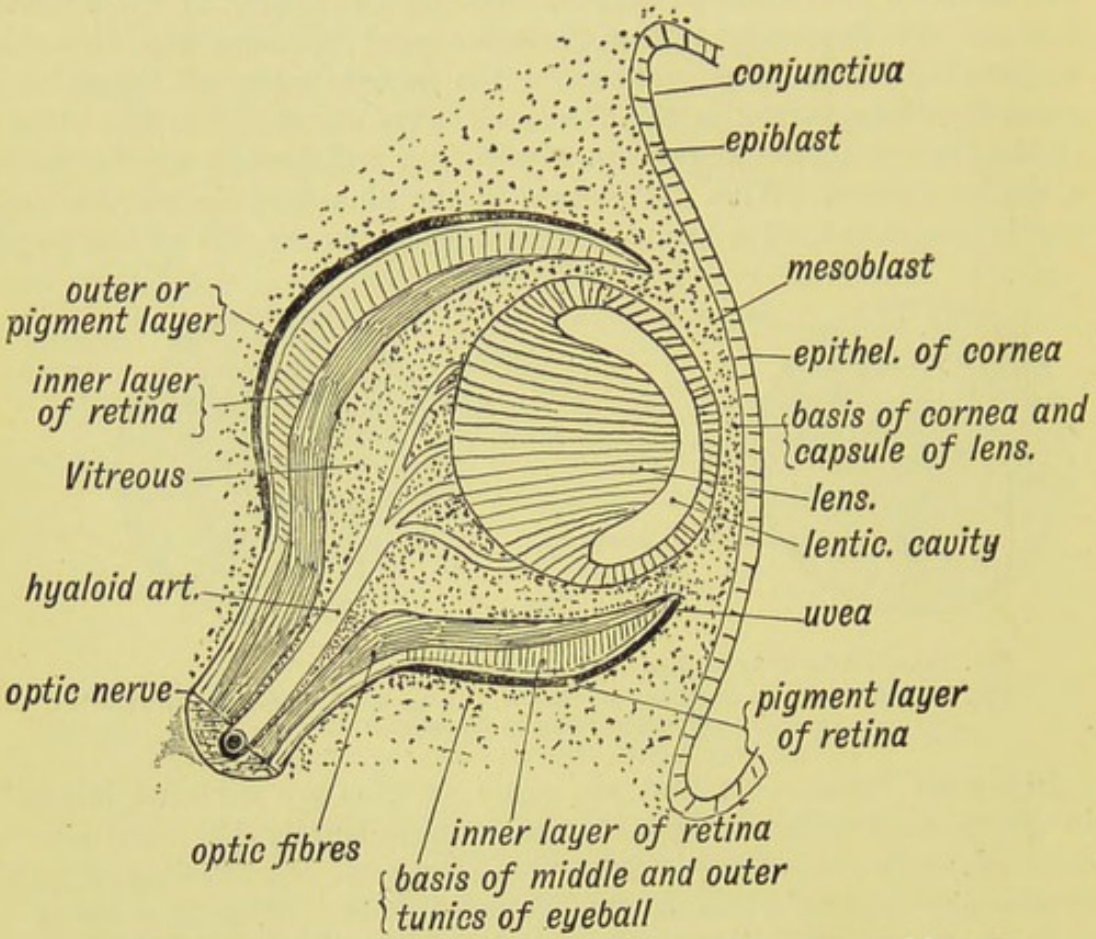


FIG. 182.—Diagrammatic Section of the Eye showing the parts formed from the Mesoblast. (After His' Model of the eye of a 3rd month human embryo.)

between the lens and retina. Thus the lens is surrounded and the cup filled by the mesoblast (Fig. 182).

The structures formed from the mesoblast are :

(1) **The vascular tunic of the lens.**—It is developed out of mesoblast which surrounds the lens. At first this capsule is continuous in front with the basis of the cornea ; behind, it is continuous with the mesoblast of the vitreous humour (Fig. 182). The hyaloid artery terminates in the vascular tunic. Beneath this tunic lies the proper capsule of the lens, which is formed from the epithelium of that body.

(2) **The vitreous humour.**—This is formed out of the mesoblast which fills the optic cup behind the lens. On the other hand, Kolliker was of

[1] Most of these instructive experiments have been carried out by American investigators. For a recent list of researches see Spemann, *Zool. Jahrbuch*, 1912, vol. 32. Heft 1. Lewis, *Amer. Journ. Anat.* 1907, vol. 7, p. 259.

opinion that the mesoblastic cells were absorbed and that the vitreous was wholly produced from the lenticulo-retinal fibrillar network. The closure of the choroidal fissure cuts the vitreous humour off from the mesoblast which covers the outer layer of the optic cup and becomes transformed into the tunics of the eyeball. The vitreous humour—like Wharton's jelly of the umbilical cord—represents an early form of embryonic tissue. It consists of cells embedded in a jelly-like matrix. All the connective tissues of the body are originally of this type, and remain as such until the fifth month (Berry Hart).

(3) **The hyaloid artery.**—This is the vessel which supplies the mesoblast of the optic cup ; it terminates in the vascular capsule of the lens (Fig. 182). In the 7th month foetus a trace of the artery can still be seen passing through the vitreous humour from the optic disc to the lens. With the gradual obliteration of the artery, the mesoblastic capsule of the lens becomes thin and clears up. A foetus born in the seventh month is blind, because the mesoblastic capsule of the lens has not quite disappeared. The anterior part of the capsule—filling the pupil—is the **membrana pupillaris.** A trace of the membrane may occasionally be seen crossing the pupil (Fig. 181). The part of the hyaloid artery within the optic nerve persists as the central artery of the retina. The canal of the artery within the vitreous humour, from the optic disc to the lens, remains as the **hyaloid canal**—a lymph path. The hyaloid artery may persist and cause partial or complete blindness. It disappears some days after birth in cats and rabbits.

(4) **The aqueous chamber** is a cleft or space formed in the mesoblast which lies between the epiblast of the cornea and the lens (compare Figs. 182 and 175). Part of this mesoblast becomes the anterior capsule of the lens ; part becomes the connective-tissue basis of the cornea. The aqueous chamber is simply an enlarged lymph space formed between these two parts. Up to the time of birth, the anterior chamber of the aqueous is very shallow (Fig. 183), the lens lying near the cornea. Even so late as the 6th month (see Fig. 175) the posterior part of the aqueous chamber—the part which lies between the iris in front and the lens behind—is not opened up.

(5) **The choroid, ciliary processes and iris.**—These form the middle or vascular tunic of the eye, and are developed out of the mesoblast which covers the optic cup. They form a vascular and pigmented covering through which the optic cup is nourished, and correspond to the combined pia mater and arachnoid membranes of the brain. The ciliary muscle is formed in this tunic. The iris is late in its development. The uvea on its deep surface is formed from the brim of the posterior surface, while the main substance—an anterior prolongation of the middle or choroidal coat—arises from the cleavage of the mesoblast which lies between the cornea and the lens. In the 4th month the sphincter, and then the dilator muscles, are produced—their origin being peculiar. The muscle fibres arise from the epithelial cells of the

uveal part of the optic cup (Szili). The iris is fully formed in the 7th month and can then react to light.

(6) **The sclerotic.**—This is the outer covering or tunic of mesoblast. It is continuous in front with the cornea ; behind, with the sheath of the optic nerve and dura mater. In some vertebrates, but not in mammals, plates of bone are developed in the anterior half of the sclerotic, recalling the deposition of dermal bones in the primitive capsule of the brain.

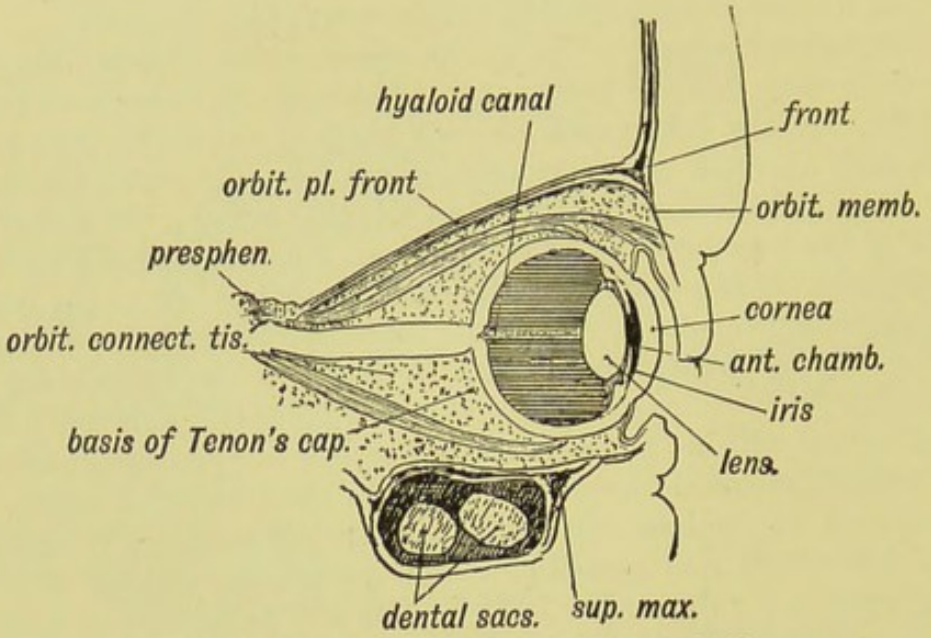


FIG. 183.—Section of the Eye and Orbit at birth.

The tapetum lucidum is absent in the human and primate eye. It gives the metallic lustre seen on the retinal surface of the eye of the ox, and is formed by a layer of fine fibres which are developed on the retinal surface of the choroid.

(7) **The capsule of Tenon,** the bursa or connective-tissue socket of the eyeball, is developed in the mesoblast surrounding the eyeball. A lymph space separates it from the sclerotic, which is but slightly marked until after birth. The **choanoid muscle** (retractor bulbi, orbital or Müller's muscle) which surrounds the sclerotic part of the eyeball as a muscular hood in mammals and vertebrates generally, has become greatly reduced in man and the higher primates. Remains of the retractor bulbi—a striated muscle—have been recently described by Dr. Whitnall in the human orbit (*Journ. Anat. and Physiol.* 1911, vol. 46, p. 36). The non-striated muscle forms two parts ; the **orbital part** bridges the spheno-maxillary fissure ; the palpebral part forms the non-striated musculature found in the insertions of the levator palpebrae (Groyer). Probably some fibrous remnants help to form the capsule of Tenon. The non-striated muscle is supplied by sympathetic nerves. Its function is obscure, but is probably designed to regulate the pressure and circulation of the venous blood of the orbit.

Growth of the Eyeball.—The eyeball is relatively large at birth, its diameter (17-18 mm.) being three-fourths of the adult diameter (24 mm.). In rate and precocity of growth it is comparable to the brain. The maculo-lutea and fovea centralis are said to have reached their full size at birth. A child born at the end of the 7th month is sensitive to light and darkness; appreciation of form comes towards the end of the 1st year, while colours are not recognized until the 2nd or 3rd years—or in some cases the colour sense is not developed. The colours at the opposite ends of the spectrum (red-violet) are the first to be recognized (Edridge Green).

Formation of the Orbit (Fig. 184).—The orbit is formed (1) above by the capsule of the fore-brain in which the frontal bone is developed; (2) externally and below by the maxillary process (Fig. 126, p. 140). In the maxillary process the malar bone and superior maxilla (except the ascending nasal process) are developed (Fig. 184). (3) The inner

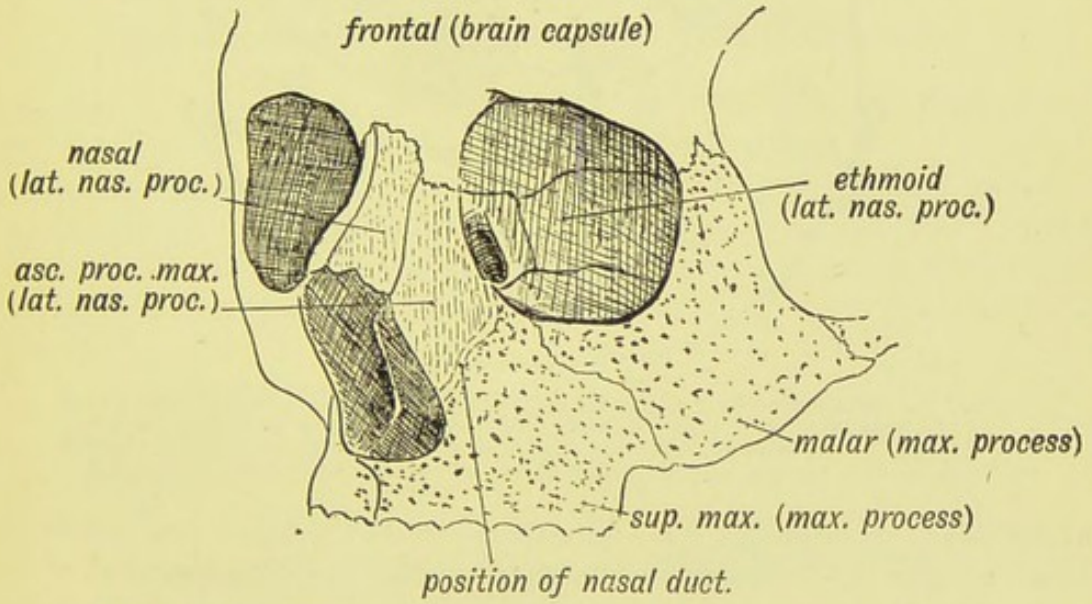


FIG. 184.—The Origin of the Bones entering into Formation of the Orbit.

wall is formed by the lateral nasal process, in which the nasals, lachrymals and lateral mass of the ethmoid, are formed. The optic nerve enters the orbit between the orbito- and pre-sphenoids—derivatives of the trabeculae cranii—both of which help to form the orbit. The orbital surface of the great wing is formed at a later period in a membranous basis (see Fawcett, p. 127). The **orbital plate** of the malar cuts the orbit off from the temporal fossa; it is developed in higher primates only. The nasal duct is formed between the maxillary and nasal processes (Figs. 126 and 185). In lower primates and mammals generally the hamular process of the lachrymal appears on the margin of the orbit; the **pars facialis lachrymalis** is sometimes seen in the human skull (Fig. 169, p. 182).

The eyelids are formed in the earlier weeks of the 3rd month by folds

of epiblast which commence above and below the superficial part of the eyeball. Mesoblast grows into the folds and forms the tarsal plates. The upper eyelid is formed from the capsule of the fore-brain, the lower from the maxillary process. About the middle of the 3rd month the edges of the lids meet, adhere, and remain adherent until the end of the sixth month. In rabbits, mice, kittens and puppies the lids are still closed at birth. The upper eyelid is developed in two parts—outer

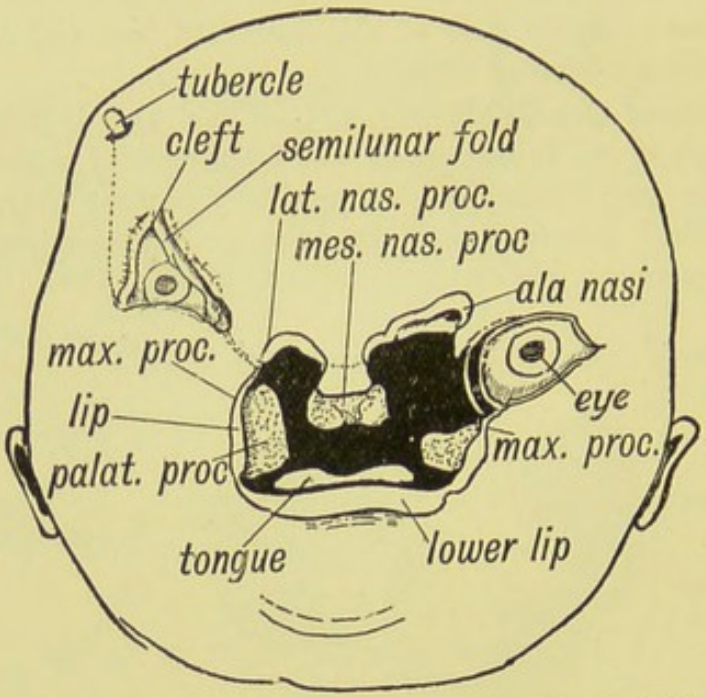


FIG. 185.—Malformed Face of a newly born Child in which the Double Formation of the Eyelid is seen. The Lateral Nasal and Maxillary processes have not fused. Two folds separate the Eye from the Nasal Cavity. The inner fold represents the Caruncula Lachrymalis and the outer the Plica Semilunaris.

and inner; occasionally a notch remains on the margin, and marks the point at which the two parts unite (Fig. 185). The upper end of the plica semilunaris is attached in the embryo at the position of the notch. The epiblast on the deep surface of the folds retains a columnar shape, and forms the palpebral conjunctiva. It is continuous with the epiblast of the cornea. From the epiblast between the adherent edges of the lids, buds grow during the 4th and 5th months, and form the eyelashes, Meibomian and other glands, in the same manner as hairs and sweat glands are developed. The Meibomian glands represent modified sebaceous glands, but the hair or cilia from which they primarily arose have vanished. The curious epicanthic fold is shown in Fig. 186. It is represented in all races during foetal life.

The plica semilunaris (Fig. 187), a fold of conjunctiva in the inner canthus of the eye, is a vestige of the third eyelid (membrana nictitans) which is fully developed in birds and reptiles. In the snake's eye Mayou found that this membrane formed what is commonly called the anterior lamina of the cornea; it is the epithelium of this membrane

which desquamates and renders the animal temporarily blind. The plica semilunaris is relatively large in the human foetus, reaching its maximum development in the 5th month. It is well seen in the cat, partially crossing the cornea as the lids are shut. The lachrymal

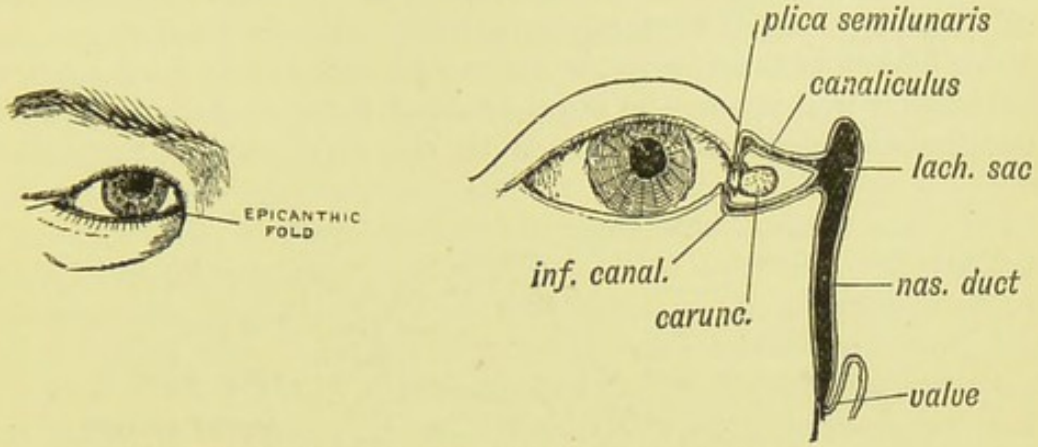


FIG. 186.—Epicanthic or Mongolian fold. (After Meckel.)
FIG. 187.—Diagram of the Plica Semilunaris and Lachrymal Canaliculi.

papillae in man rub in the grooves at the outer and inner margins of the fold.

The Lachrymal Gland [1] arises at the beginning of the 3rd month as a number of epiblastic buds which spring from the fornix of the conjunctiva beneath the upper lid, and grow into the tissue of the outer and upper segment of the orbit (Fig. 188). The outer buds form the

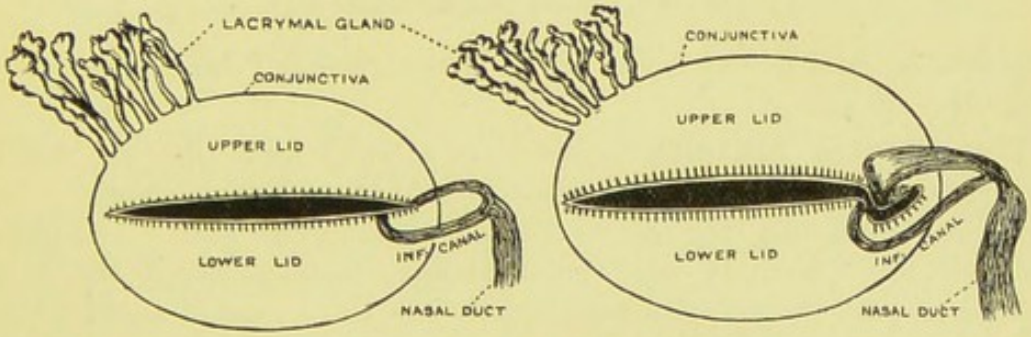


FIG. 188, *A*.—Showing the Termination of the Lower Lachrymal Canaliculus some distance from the Mesial End of the Lower Eyelid, in a foetus 2 months old. The tubular outgrowths of the lachrymal gland are also shown.

B.—The Mesial Extremity of the Lower Eyelid cut off to form the Caruncula. The lachrymal outgrowths are more complex in structure. From a foetus in 4th month of development. (After Ask.)

orbital part of the gland; the more internal buds form the palpebral part. Smaller lachrymal glands may occasionally be found at the outer angle of the eye, which is the position occupied by the lachrymal glands of birds and reptiles (Wiedersheim). The lachrymal canaliculi

[1] Development of lachrymal gland, F. Ask, *Anat. Hefte*, 1910, vol. 40, p. 489, 1908, vol. 36, p. 189.

and sac and nasal duct are formed out of solid epithelial cords enclosed between the maxillary and lateral nasal processes (see p. 147). The canaliculi are formed during the 3rd month as sprouts from the upper end of the solid rod of epithelium representing the nasal duct. While the bud of the upper canaliculus opens at the inner end of the upper lid (Fig. 188, *A*), the inferior canaliculus extends some way along the lower lid before it comes to the surface (Ask). It may form a secondary communication nearer the inner angle of the eye, thus giving rise to a congenital lachrymal fistula. With the formation of the lachrymal

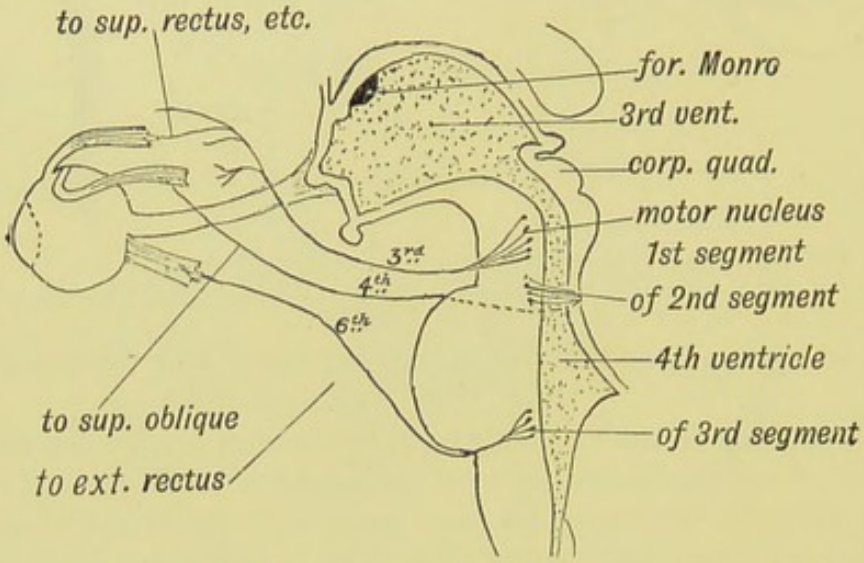


FIG. 189.—Diagram of the Motor Nerves of the Muscles of the Eye derived from the 1st, 2nd, and 3rd Cephalic Segments.

canaliculus, part of the lower eyelid is cut off and forms the caruncula (Fig. 188, *A* and *B*).

The Orbital Muscles.[1]—We have already seen that the head is composed of nine segments, at least four of these being occipital; also, that each segment gives rise to a muscle plate (Fig. 121). The muscle plate of the maxillary or premandibular—usually called the first—segment forms the muscles supplied by the third cranial nerve—which is the motor nerve of that segment. The mesencephalon (crura cerebri) contains the corresponding segment of the neural tube. The ciliary muscle and sphincter of the iris also belong to this segment, and are supplied by the 3rd nerve (Fig. 189). The muscle plate of the mandibular, usually named the second head segment, produces the superior oblique. In the course of evolution the superior oblique of the right side has shifted to the left and the left to the right (Gaskell), hence the decussation of the 4th nerves (the motor nerves of this segment) on the anterior part of the roof of the hind-brain—the valve of Vieussens. The muscle plate of the hyoid or third cephalic segment gives rise to

[1] For an account of the development of orbital vessels see F. Dedekind, *Anat. Hefte*, 1909, vol. 38, p. 1.

the external rectus ; the 6th nerve is the nerve for the somatic musculature of the segment, the seventh supplying the splanchnic muscles.

The sensory nerves of these three segments are fused together in the three divisions of the 5th nerve. The ciliary ganglion is the splanchnic (sympathetic) ganglion of the premandibular segment. The nerves for the choanoid (Müller's) muscle, the non-striated muscle of the upper eyelid, and the dilator fibres of the iris, issue from the upper three dorsal segments of the spinal cord, and reach the eye by the cervical sympathetic chain and cavernous plexus. The nerve fibres for the orbicularis palpebrarum pass out with the facial, but they are said to arise from, or have connection with, cells in the first segment of the neural canal (oculomotor nucleus). The ophthalmic division of the fifth represents the sensory somatic nerve of the same segment to which the third nerve belongs ; hence the reflection of pain along this nerve (frontal headache) in disorders of accommodation, the muscle of accommodation being the ciliary, and its nerve, the oculomotor, both also derivatives of the first segment.

Development of the Nerve Centres concerned with Sight.—Five parts of the brain are concerned with vision. They are :

(1) The optic tracts.

(2) The basal centres surrounding the termination of the aqueduct of Sylvius in the 3rd ventricle.

(3) The optic radiations.

(4) The occipital lobes—in part at least.

(5) The angular gyrus.

(1) **The optic tracts** are made up of fibres developed from the ganglionic cells of the retina and also in part of efferent fibres developed from cells of the basal ganglia in which the optic tracts are seen to terminate. The fibres grow in by the optic stalk, decussate in the floor of the third ventricle between the origins of the optic vesicles, and thus form the chiasma. The optic fibres grow backwards on the surface of thalamencephalon (see Fig. 190) and on the optic thalamus to reach the nerve centres which afterwards form the pulvinar, geniculate bodies and the superior corpora quadrigemina. In these centres the optic fibres end. From some of the cells of these ganglia the efferent fibres of the optic tracts are developed. It is said that 80 per cent. of the fibres from the central area of the retina terminate in the external geniculate bodies, and it is from these that the fibres of the optic radiation, which terminate in the striate or sensory area of the occipital lobes, take their origin.

(2) **The basal ganglia.—The corpora quadrigemina.**—Almost in every structure the human embryonic condition resembles the adult condition of lower vertebrates. A good example is seen in the corpora quadrigemina. The human foetus at the commencement of the third month (Fig. 190) shows the corpora quadrigemina represented by a prominent thickening in the roof of the cavity of the mid-brain, which forms subsequently the aqueduct of Sylvius. The thickening is divided

into lateral halves by a median sulcus, each half being nearly as large as the cerebral vesicle of that period. In Fig. 191 is shown the condition in an adult lizard ; there is one body on each side—the **optic lobes** or corpora bigemina. As the human foetus grows older, each lateral lobe becomes divided into an upper and lower part by the formation of a transverse groove, the upper and lower pairs of the corpora quadrigema being thus formed. The upper pair are connected with sight. In the mole they are vestigial, but in compensation the inferior corpora are

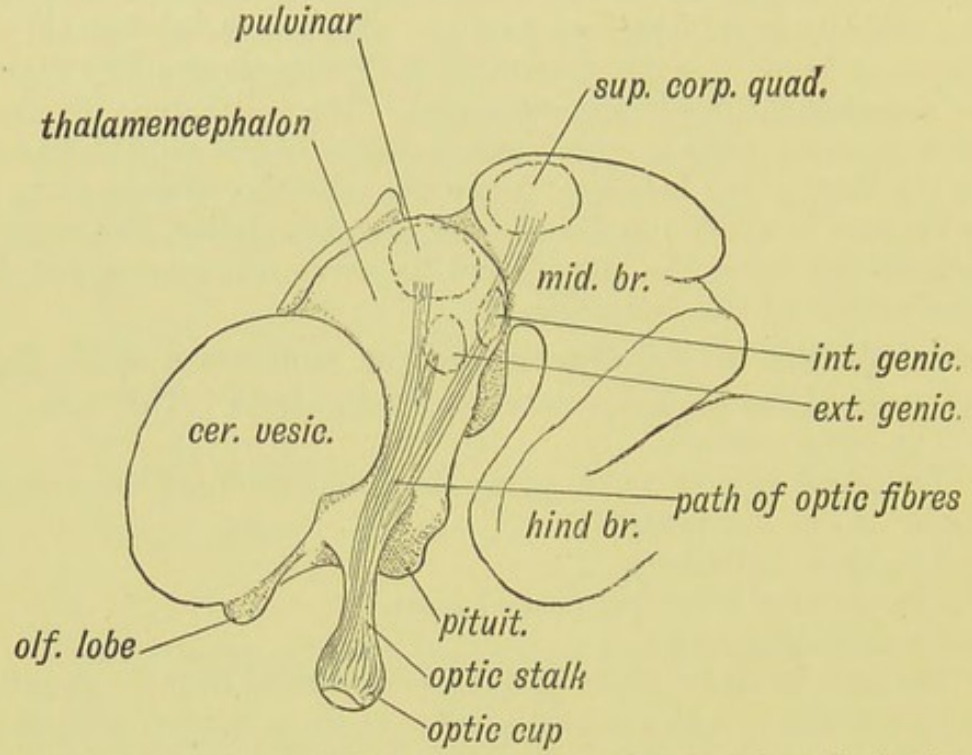


FIG. 190.—Diagram of the Foetal Brain at the end of the 2nd month, showing the position in which the Optic Tracts are developed.

well developed as they are connected with the sense of hearing, which is very acute in that animal.

The **internal geniculate body** also belongs to the mid-brain (mesencephalon) ; the pulvinar and external geniculate body, in which the upper division of the optic tract ends, are developed on the wall of the 3rd ventricle (thalamencephalon). The mid-brain is the part primarily connected with sight ; in the floor of its cavity—the aqueduct of Sylvius—are situated the motor nuclei for the muscles of the eye ; on its roof—the terminal centres for the optic tract. As the vertebrate scale of animals is ascended, the termination of the optic tracts is found to be transferred more and more to the centres on the thalamencephalon. The projection of the optic fibres to the occipital cortex from the nucleus of the pulvinar is shown in Fig. 93, p. 102.

(3) **The optic radiations** connect the basal optic centres just named with the mesial surface of the occipital lobes. The fibres join the posterior part of the internal capsule, and pass under and round the

posterior horn of the lateral ventricle to end in the cortex of the calcarine fissure and neighbourhood. The cortex in which the optic radiations terminate is divided by a narrow white stratum—the **line of Gennari**—into a superficial and deep layer.

(4) **The occipital lobe and calcarine fissure.**—A mesial view of the 5th month foetal brain is shown in Fig. 192. The occipital lobe is

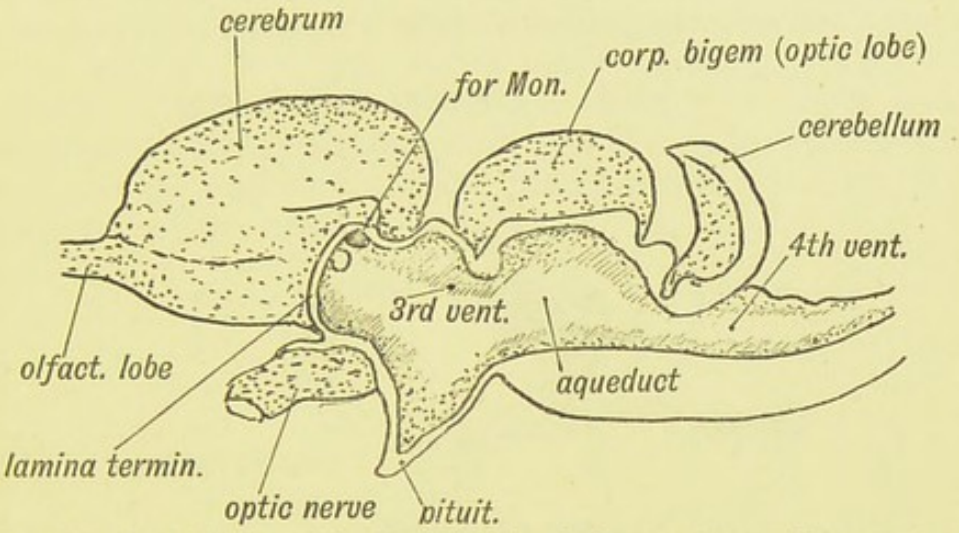


FIG. 191.—Mesial Section of the Brain of a Lizard, showing the resemblance to the Human Foetal Brain (Fig. 190) especially in the development of the Corpora Bigemina.

already well formed ; its inner aspect shows the calcarine and parieto-occipital fissures. A section across the occipital lobe is shown in Fig. 192 ; the posterior horn is large ; the calcarine fissure indents its inner

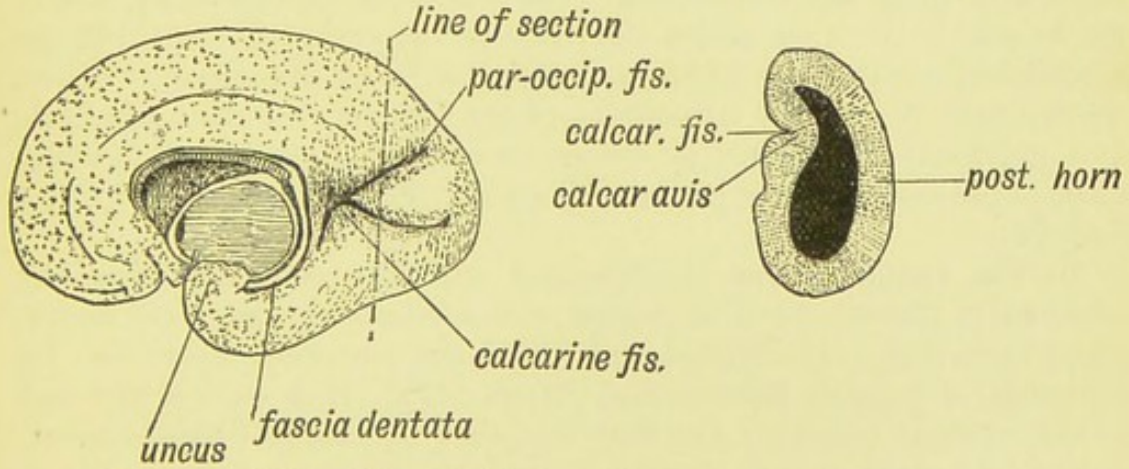


FIG. 192, *A*.—View of the Mesial Surface of the Brain in the 5th month.
B.—Section of the Occipital Lobe at the position marked in Fig. 112.

wall, giving rise to the **calcar avis** or hippocampus minor, a feature which is seen in the brains of nearly all mammals (Elliot Smith).

The **calcarine** is one of the first fissures to be formed on the brain ; it appears early in the fifth month. This and the hippocampal fissure, which is connected with the sense of smell, are the two fissures most

commonly present in the mammalian brain. The posterior part of the calcarine fissure is a later formation, and is distinguished as the retro-calcarine (see Fig. 105, p. 114). The optic radiations end in the cortex of the retro-calcarine fissure.[1] In Fig. 193 the condition of the occipital lobe in the 4th week is shown. The cerebral vesicle has arisen as a hollow protrusion from the anterior superior end of the fore-brain (3rd ventricle). The lateral ventricle is as yet undifferentiated into horns, and only the rudiment of the occipital lobe is present. The

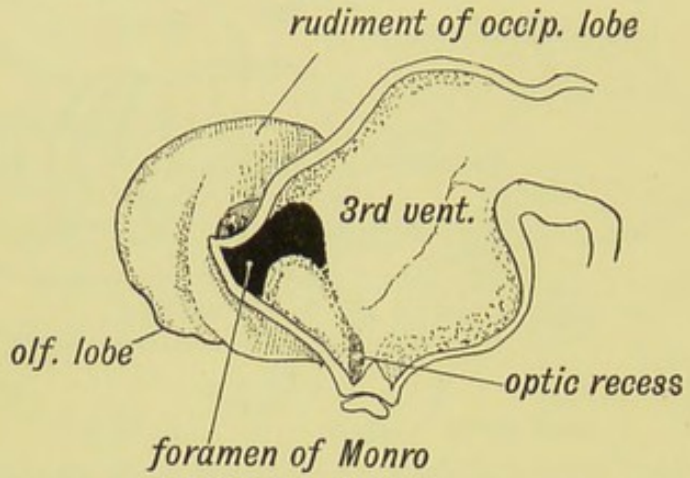


FIG. 193.—Mesial Section of the Brain at the 4th week, showing the rudiment of the Occipital Lobe. (After His.)

occipital lobe is produced by a backward growth of the cerebral vesicle, the posterior horn being produced as a diverticulum of the cavity of the vesicle. By the 5th month the occipital lobe has reached far enough back to overlap the cerebellum. The striate or visuo-sensory area of the human brain is not larger than that of the anthropoid ape, but the association or visuo-psychic area is infinitely more extensive. " Thus, we can take it that the superiority of the human over the ape's brain as a psychical organ must be the result mainly of the higher development of the association or peri-striate areas " (Elliot Smith, *Lancet*, 1910, Jan. 22).

(5) **The angular gyrus** is connected with the calcarine region by association fibres. In it is seated the word-seeing and word-understanding centre. It is developed round the posterior end of the 1st temporal or parallel fissure (Fig. 101, p. 112). It is part of the wall of the cerebral vesicle. The first temporal or parallel fissure appears during the sixth month and is one of the primary fissures. It is found in the brains of all primates except the lowest.

Summary.—It will thus be seen that three parts of the neural tube are specialized in connection with sight.

(1) The optic vesicle, an outgrowth from the fore-brain (thalamencephalon).

[1] For a description of the cortex of the visual areas see Elliot Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 237 See also references on p. 97.

(2) The occipital end of the cerebral vesicle, which receives fibres projected from the basal nuclei connected with the eyes.

(3) The walls of the 3rd ventricle (thalamencephalon) and mid-brain (mesencephalon), in which the basal optic ganglia are developed.

The tunics of the eye are extensions of the embryological coverings of the brain. The choroid coat and the vitreous humour spring from the same layer as forms the pia mater and arachnoid. The sclerotic is a prolongation of the primitive cerebral capsule, in which the skull bones are formed. The optic vesicle carries with it a prolongation of the arteries and veins of the fore-brain. Part of the optic vesicle is transformed to a secretory epithelium over the ciliary processes in the same way as the wall of the neural tube becomes a covering for the choroidal villi of the brain.

CHAPTER XIV.

THE ORGAN OF HEARING.

The Nature of the Labyrinth.—It often happens, when we seek to interpret the developmental changes which give rise to an organ or system of the human body, that a reference to the condition seen in certain groups of fishes—especially those belonging to the shark kind, selachians—gives us great assistance. That is true as regards the organ of hearing. In a shark or ray every part of the internal ear—the labyrinth with its semicircular canals—is already evolved with the exception of one part—the canal of the cochlea ; it is represented by a mere rudiment. The labyrinth of the shark is not an organ of hearing, for it is generally admitted that fishes are insensitive to sound-waves, but for the balancing or orientation of the body. Most men who have investigated the nature of the labyrinth of fishes agree that it represents a specialization of one of a series of superficial sense organs set on the sides of fishes—the organs of the lateral line—these also being connected with the functions of balancing and movement. Hence we find that the labyrinth begins as a pocket-like invagination of the ectodermal covering in the head region. The auditory or cochlear part of the labyrinth appeared when the land-forms of vertebrates were evolved. In vertebrates above fishes the rudiment of the cochlea begins to be differentiated and an apparatus for converting sound waves into mechanical waves in the labyrinth is evolved.[1] A vibrating drum was established in the site of the first of the pharyngeal or visceral clefts. We must also suppose that in the piscine type, which gave origin to the ancestry of the mammals, the mammalian form of mandible was already evolved, for it is from remains of the primitive cartilaginous skeleton of the lower jaw that the malleus and incus are differentiated in the human and mammalian embryo.

The Structures which form the Organ of Hearing.—In Fig. 194 is shown diagrammatically the derivation of the five elements

[1] G. L. Streeter, *Journ. Experiment. Zoology*, 1906, vol. 3, p. 543 ; 1907, vol. 4, p. 431 (Results of Experiment on Developing Internal Ear).

which unite together to make up the organ of hearing. The five elements are :

(1) The **otocyst**—an area of epiblast (epithelial covering of embryo) above the first visceral cleft which becomes invaginated in a saccular form, and forms the epithelial lining of the membranous labyrinth. Some of its lining cells become differentiated into sensory and auditory epithelium.

(2) A **ganglion** derived from the " neural crest " of the hind-brain (Fig. 194). The nerve cells form the cochlear and vestibular ganglia.

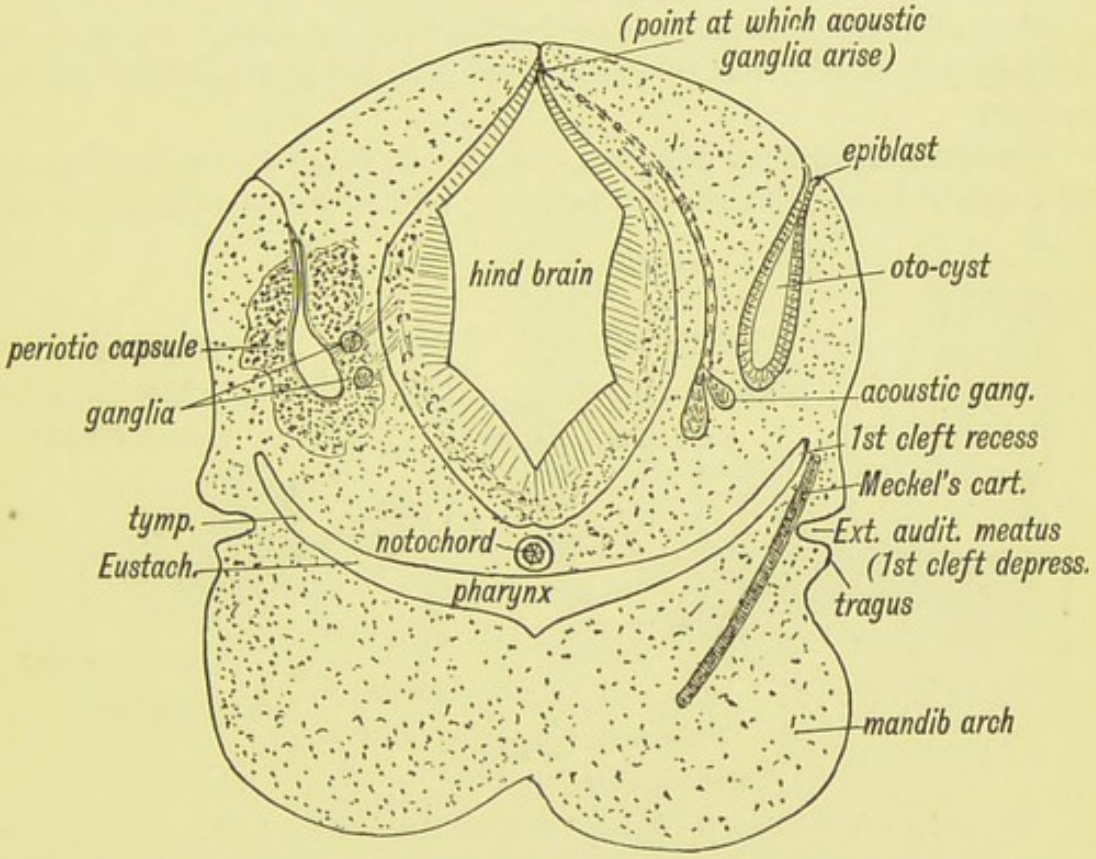


FIG. 194.—Diagrammatic Section through the Cephalic Region of an Embryo, showing the origin of the Auditory System.

Each cell sends out two processes, one to become connected with the epithelium of the otocyst, the other to end in groups of nerve cells in the floor of the 4th ventricle, their collective fibres forming the auditory nerve. The development of the auditory nerve thus resembles that of the posterior or sensory root of a spinal nerve.

(3) The otocyst (membranous labyrinth) becomes surrounded by a capsule of cartilage—the **periotic capsule.** This ossifies from several centres, and forms the bony labyrinth and petro-mastoid.

(4) **A part near the dorsal end of the first visceral cleft.**—In connection with the inner recesses of the first and second pharyngeal clefts the Eustachian tube, the tympanum and antrum of the mastoid are developed ; the external cleft depression forms the point of origin for

the external auditory meatus; while out of the tissue between these, representing in position a "cleft-membrane," is formed the membrana tympani.

(5) The **hyomandibular cartilage**, which served primarily to bind the cartilages of the maxillary process, mandibular and hyoid arches to the base of the skull, becomes the incus or, according to others, it is subdivided to form the malleus, incus and stapes.

In fishes the auditory apparatus is composed of the three elements named first. In amphibians, reptiles and birds a membrana tympani is developed, which is connected with the inner ear by an unjointed derivative of the hyomandibular cartilage, *the columella*. In mammals a tympanic cavity, external auditory meatus, and auditory ossicles appear.

External Auditory Meatus.—A section along the external meatus of a newly born child shows that it is divided by a constriction into

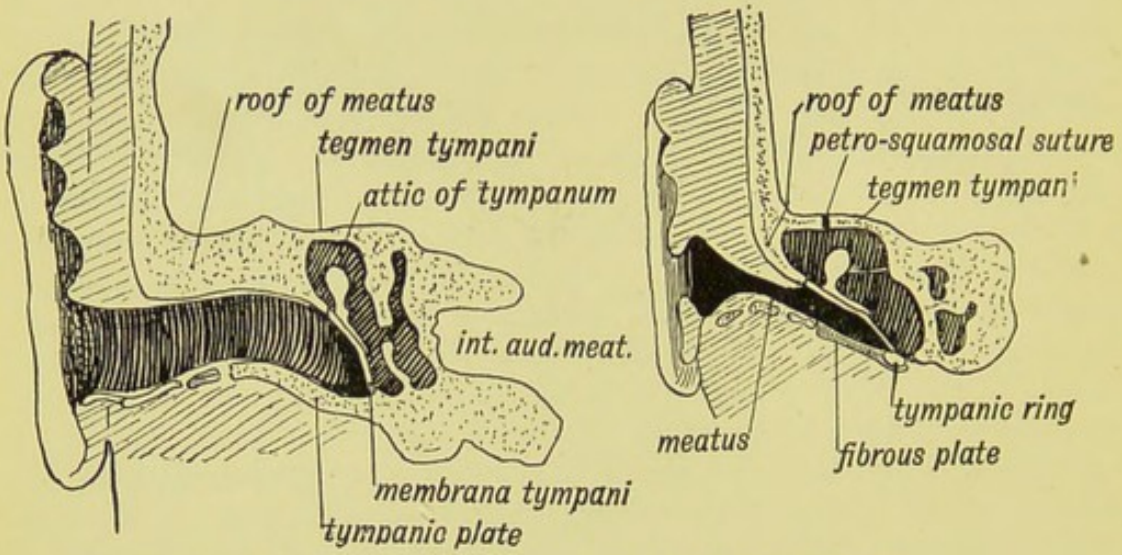


FIG. 195, *A*.—A Section of the External Auditory Meatus of the Adult.
B.—A Section of the External Auditory Meatus at Birth. (After Symington.)

outer and inner parts (Fig. 195, *B*). The outer part is derived directly from the first cleft depression; the inner part arises during the 2nd and 3rd months by a solid ingrowth of epithelium which, commencing from the fundus of the cleft depression, grows inwards until it comes in contact with the handle of the malleus, when it expands to form the fundus of the meatus (Fig. 201). During the 7th month the deeper part of the meatus and outer aspect of the drum are formed by a breaking down of the central, and therefore older, cells of this ingrowth. Cartilage surrounds the part of the meatus derived from the cleft; the floor of the deeper part is formed at birth by a fibrous plate continuous with the tympanic ring. In the adult the tympanic ring has grown outwards in the fibrous tissue, as we have already seen (p. 159), to form the tympanic plate and the inner two-thirds of the meatal floor. The squamous part of the temporal, which is developed in its roof, also

grows outwards, and forms a thick, horizontal plate in the inner two-thirds of the meatal roof (Fig. 195, *A* and *B*). Over the roof lies the third temporal convolution.

The meatus is supplied in front by the nerve of the mandibular arch (auriculo-temporal branch). Why the vagus should supply it with a branch (Arnold's nerve) is obscure. In fishes a branch of the vagus passes backwards beneath the skin on each side and supplies the sense organs of the lateral line. Many regard the auricular branch of the vagus as a vestige of such a branch.

In the newly born child the membrana tympani is so obliquely set that its outer surface is almost in contact with the meatal floor. With the development in length of the meatus, it becomes more vertical in

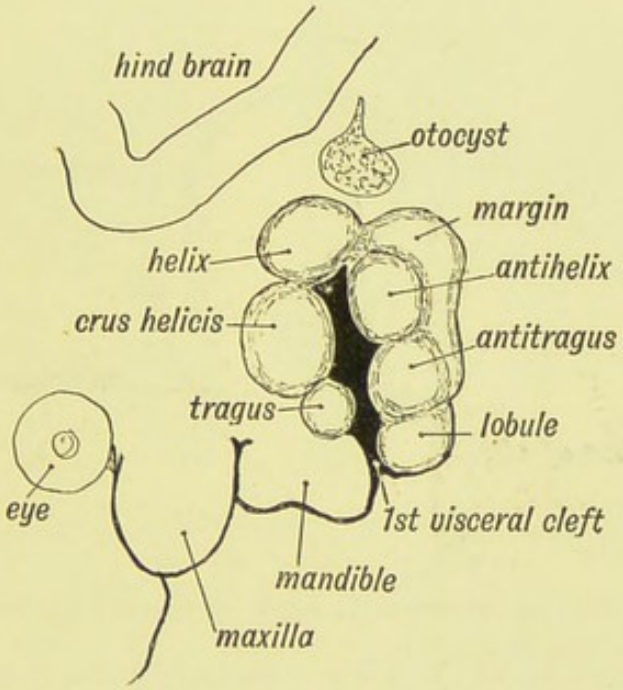


FIG. 196.—Showing the Tubercles which arise round the First Visceral Cleft to form the External Ear.

position. The deeper part of the meatus may fail to form, or the whole cleft may become closed. In such a case there is commonly a corresponding absence of development of the middle and internal ear.

The External Ear.—Six tubercles appear on the mandibular and hyoid arches round the 1st cleft depression and form the external ear (see Figs. 196 and 197). Three of these tubercles grow from the mandibular arch and form the tragus, crus of the helix, and helix; three from the hyoid to form the lobule, antitragus and antihelix. The posterior margin of the ear, or descending helix, with the lobule, arises as a mere thickening or elevation of the skin behind the tubercles on the hyoid arch. During the latter part of the 2nd month and first part of the 3rd, the auricula begins to assume its definite form. The tubercles of the helix and antihelix send out processes which cross the

upper part of the cleft and obliterate it, while the neighbouring tubercles fuse to form the definite parts of the ear. The posterior margin and lobule rise up at the same time as a free fold. The auricular tubercles may not fuse completely and thus leave fistulae between them. Such fistulae are commonly seen between the tragus and root of the helix, or between the antihelix and the helix. The mandibular part of the auricle is supplied, as one would expect from its origin, by the third division of the 5th, while the sensory fibres of the hyoid part come from the 2nd cervical by the great auricular and small occipital nerves.

Darwin's Tubercle.—The human ear appears to be derived from a form in which the margin was pointed at the posterior superior angle,

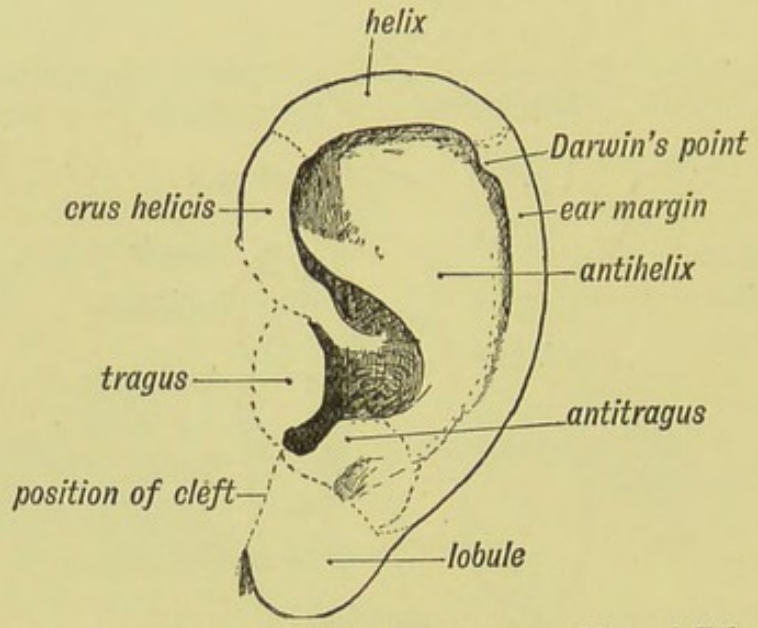


FIG. 197.—Showing the part of the Adult Ear formed by each Tubercle.

such as is seen in many of the lower forms of apes and mammals generally. With the retrogression of the posterior border or descending helix and increased development of the antihelix in the human ear, the posterior margin became infolded ; hence the tip appears as a tubercle on the inturned posterior margin or welt of the human ear (Fig. 197). The small and almost stationary external ears of the higher primates result from the free manner in which these animals can turn their heads in the direction of sounds.

Muscles of the External Ear.—These are derived from the platysma sheet and are supplied by the nerve of that sheet—the 7th or facial. The part of the platysma sheet which surrounds the external meatus and acts on the ear appears to have been the first of the facial muscles to be evolved. The ear muscles are not so reduced in man as in some other primates, such as the orang.

The Eustachian Tube.—The Eustachian tube has usually been regarded as a derivative of the first of the inner cleft recesses—a

diverticulum of the lining membrane of the primitive pharynx between the mandibular and hyoid arches (Fig. 198, *A*). Recently Mr. J. E. Frazer has made a thorough enquiry into its origin, and has found that its origin is more complicated than was supposed. In Fig. 198, *A*, the left half of the floor of the pharynx of a human embryo, nearly one month old, is represented. Between the 1st and 2nd and between the 2nd and 3rd arches the lining mucous membrane of the pharynx is seen to dip outwards; as yet there is no sign of Eustachian tube or of tympanum. In Fig. 198, *B*, the opposite half of the floor of a pharynx

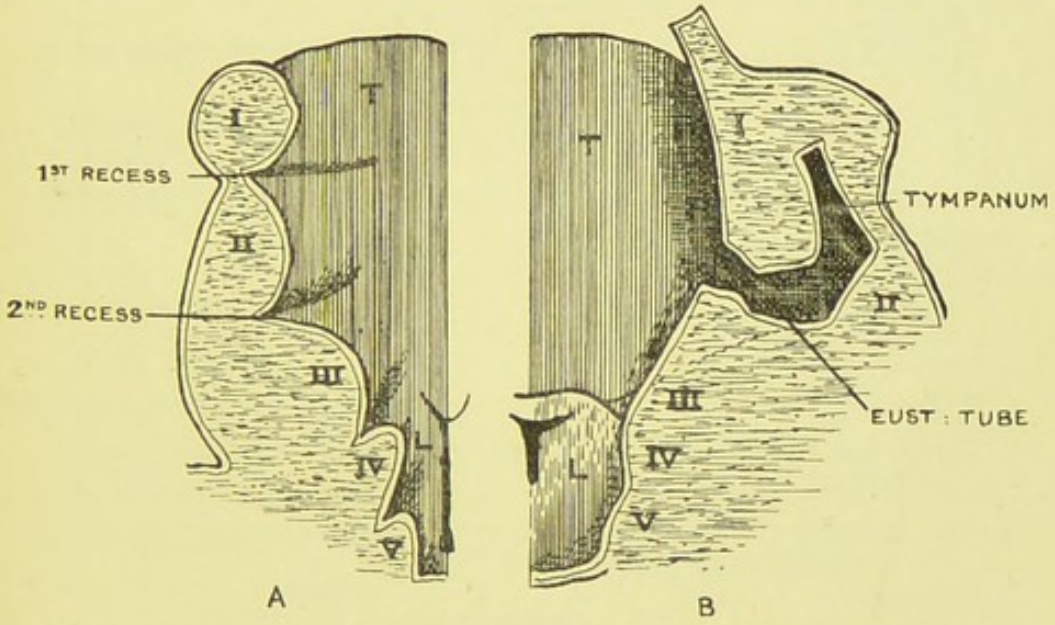


FIG. 198.—Figures illustrating the Development of the Eustachian Tube and Tympanum. (After J. E. Frazer.)

A.—The Floor of the Pharynx of a Human Embryo nearly one month old. The visceral arches are cut across and the inner cleft recesses indicated.

B.—The Floor of the Pharynx of a Human Foetus seven weeks old, showing the origin of the Eustachian Tube by an Evagination of the Pharynx opposite the 2nd or Hyoid Visceral Arch. *T*, rudiments of tongue on floor of pharynx; *L*, larynx.

of a human embryo towards the end of the 2nd month of development is shown; the basis of the Eustachian tube and tympanum is now apparent as a wide recess between the first and third arches, the part of the second arch on the outer side of the recess being now superficial in position. The oblique fold forming the roof and posterior wall of the Eustachian tube is derived from the roof of the primitive pharynx. The Eustachian tube retains through life the ciliated epithelial lining of the primitive pharynx. Its inner two-thirds is bounded behind by a triangular plate of cartilage, which is attached at its inner or pharyngeal end to the internal pterygoid plate, by its outer to the tympanic ring, both of which are probably derived from the palato-quadrate bar (Fig. 143, p. 151). The cartilage is developed in the 4th month of foetal life. The tympanic plate grows inwards and forms the floor of the outer third of the tube (Fig. 200), while the periotic capsule (petro-mastoid)

which is developed above and behind the 1st cleft, grows forwards and forms the roof of its outer third. The part of the petro-mastoid which grows over it is the **tegmen tympani**; it also forms the roof of the tympanum and of the antrum of the mastoid. The tensor tympani and tensor palati are developed on the mandibular side of the first

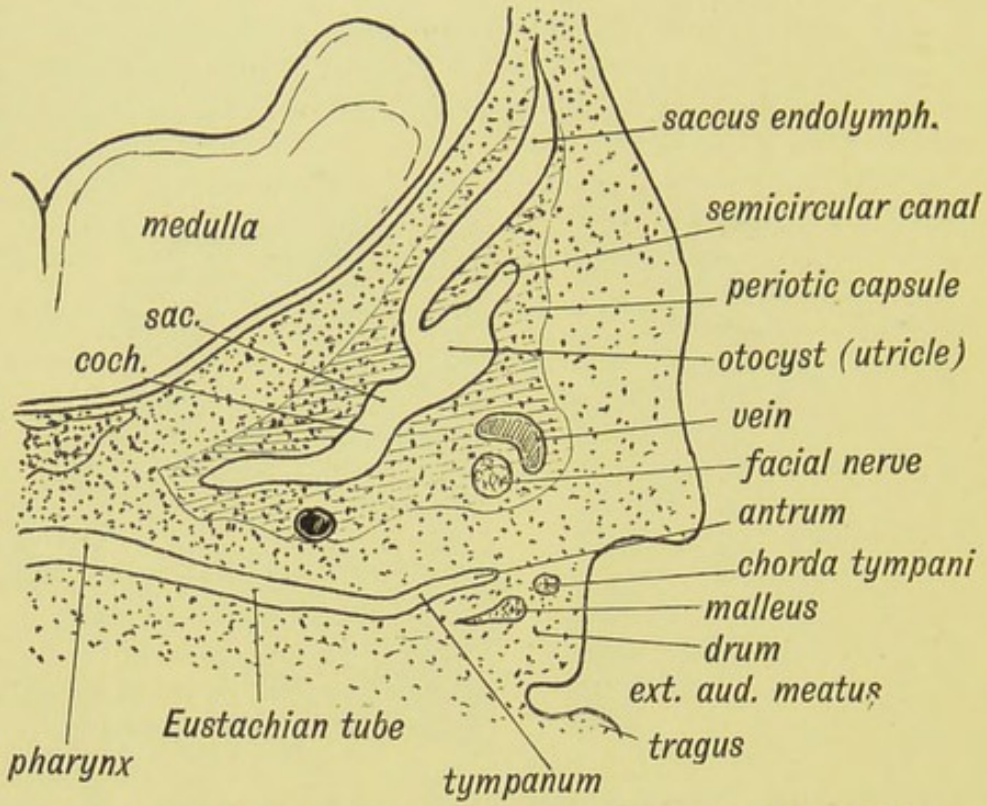


FIG. 199.—Showing the condition of the Auditory Organs in a 7th week Human Foetus. (After Siebenmann.)

cleft and are supplied from the nerve of the mandibular process through the otic ganglion.

The Tympanum.—As may be seen from Fig. 199, the tympanum can scarcely be said to exist at the sixth week of foetal life. The Eustachian recess ends in the jelly-like tissue containing the cartilaginous bases of the malleus and incus. It is directed outwards and backwards between the periotic capsule to its posterior and inner side, and the external cleft depression (meatus) and developing squamosal to its outer (Fig. 199). As the internal recess extends outwards and backwards, the gelatinous tissue is absorbed before the time of birth, so that, in the later months of development, the malleus and incus and developing stapes, with the chorda tympani, become surrounded by the hypoblastic lining of the inner cleft recess and appear to be situated within the cavity thus formed—the tympanum. The tympanic plate forms the floor of the tympanum, the membrana tympani and squamosal its outer wall, while the petro-mastoid forms its inner wall and roof (Fig. 200). That part of the tympanum which lies above the level of

the membrana tympani is named the **attic,** and contains the head of the malleus and body of the incus (Fig. 195).

In carnivora and some other mammals the floor of the tympanum, formed by the tympanic plate, is inflated into a bulla, the tympanic

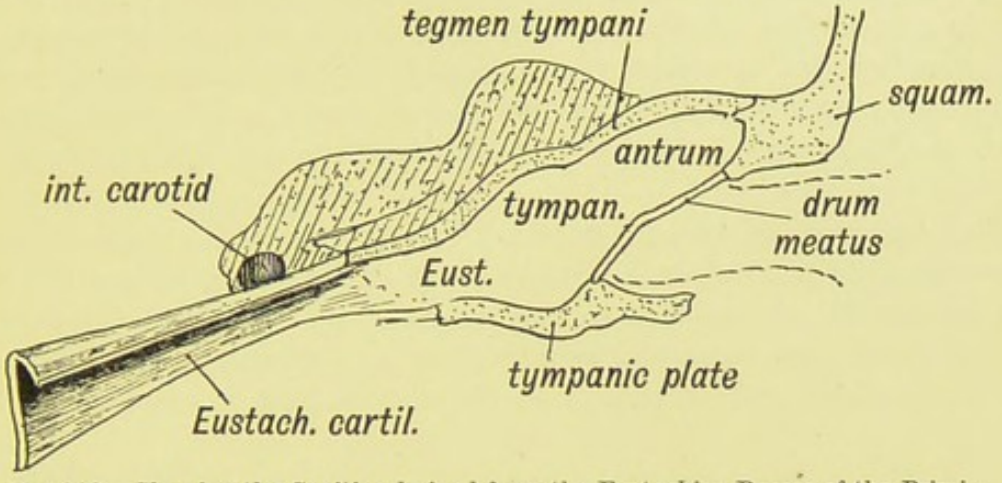


FIG. 200.—Showing the Cavities derived from the Eustachian Recess of the Primitive Pharynx.

bulla. Its meaning is unknown, but when a bulla is developed the antrum of the mastoid is small or absent.

Auditory Ossicles.—In the 3rd month the auditory ossicles become clearly differentiated in cartilage in the mesoblastic tissue between the meatal recess on their outer side and the Eustachian

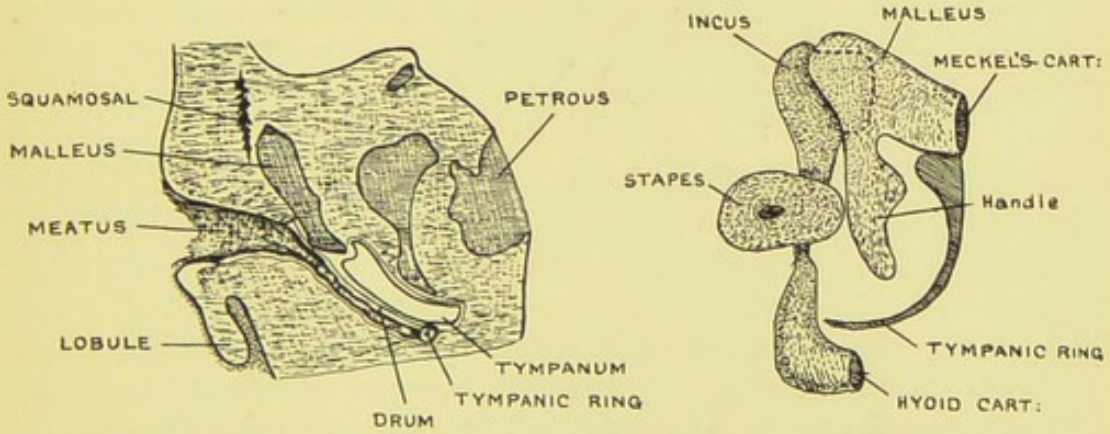


FIG. 201.—Section of the External Auditory Meatus, Drum and Tympanum of a Human Foetus in the 4th month of development. The meatal plug fills the deep part of the meatus and only the handle of the hammer is in the tympanic cavity. (After Broman.)

FIG. 202.—The Auditory Ossicles of the Left Side, seen on their Inner Aspect, during the 3rd month of development. (After Broman.)

recess on their inner. Concerning their development, the exact researches of Broman,[1] of Hammar, and of Jenkinson [2] give us a very

[1] See Broman's excellent *Normale und abnormale Entwicklung des Menschen,* Wiesbaden, 1911.

[2] J. W. Jenkinson, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 305; Hugo Frey, *Anat. Hefte,* 1911, vol. 44, p. 363.

full account. The malleus represents the upper or articular end of Meckel's cartilage (Fig. 202) ; the incus, developed beyond the articular end of Meckel's cartilage, represents the cranial articular base—the quadrate or hyomandibular element of lower vertebrates. The stapes is developed from the upper end of the hyoid arch (Fig. 202). Even in the 4th month of development the cavity of the tympanum has only reached the handle of the malleus (Fig. 201). The upper part of the drum (par flaccida) is not yet differentiated. The attic, antrum, head of the hammer, and body of the incus are still outside the cavity of the tympanum.

The Antrum of the Mastoid.—The antrum of the mastoid represents the extreme outer or posterior end of the chamber derived from the extension of the Eustachian recess (Figs. 199 and 200). It is formed during the 6th and 7th months by an expansion of the tympanic cavity upwards and backwards in the surrounding mucoid tissue. Its

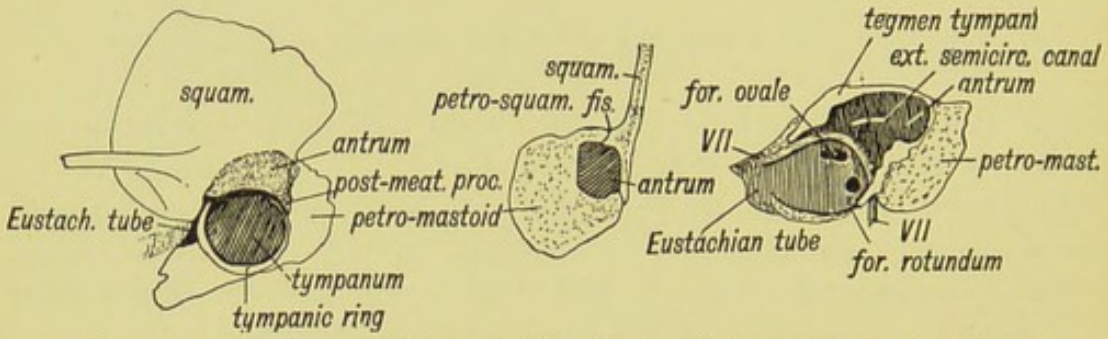


FIG. 203.—The Temporal Bone at birth, showing the formation of the Antrum between the Squamosal and Petro-mastoid.

FIG. 204.—A Transverse Section showing how the Walls of the Antrum are formed.

FIG. 205.—Showing the outer aspect of the Petro-mastoid at birth after the Squamosal is removed.

use is unknown, but it has frequently to be exposed by the surgeon to remove the effects of chronic middle-ear disease. At birth its outer wall is formed by the thin post-auditory part of the squamosal (Figs. 203 and 204). The squamosal forming its outer wall is then only 2 mm. thick, but every year until the 20th, or later, this plate increases nearly 1 mm. in thickness, so that by the 20th year the antrum is buried by a plate of bone about 20 mm. thick. There is a great individual variation, however, in the thickness of its outer wall. The antrum lies above and behind the level of the external auditory meatus ; the post-auditory spine and supra-meatal triangle formed by the post-auditory part of the squamosal lie over it and serve as surface guides to it. The antrum opens in front into the attic of the tympanum. The tegmen tympani (Fig. 204) forms its roof and the petro-mastoid its floor and inner wall. The aqueductus Fallopii runs down the inner wall of its mouth (Fig. 205), and in its inner wall is situate the external semicircular canal. The petro-squamous suture in its roof (Fig. 204) and the masto-squamous suture on its outer wall (Fig. 151, p. 159) become closed in

the second year, and thus the escape of pus from it is rendered more difficult. The rudiments of the mastoid cells are already present as evaginations or pits of the antral lining at birth (Arthur Cheatle).

The Primitive Jugular Vein.—In the petro-squamous suture a vein or sinus, frequently of considerable size, runs forwards from the lateral sinus, and commonly ends in a tributary of the middle meningeal vein. It receives as it runs along venules from the antrum and attic and may be the means of carrying infection from the middle ear to the lateral sinus or to the meningeal veins (Cheatle). The petro-squamous sinus represents the primitive jugular vein, and may open in man, as it does in mammals generally, at the post-glenoid foramen, situated at the outer end of the Glaserian fissure, near the base of the zygoma. In the early weeks of embryonic development, when the cerebral vesicles are yet small and situated in front of the auditory vesicle, the primitive jugular is the chief vein from the brain, but as the cerebrum grows backwards the internal jugular vein enlarges and takes its place, and thus the blood of the lateral sinus comes to pass out by the jugular foramen instead of by the petro-squamous sinus and temporal canal at the base of the zygoma (see also account on p. 286).

The Membrana Tympani.—As may be seen from Fig. 199, the membrana tympani is of very considerable thickness until the gelatinous tissue in the tympanum is absorbed. It has an inner covering of hypoblast and an outer of epiblast. In the mesoblastic tissue between the coverings lie parts of the malleus, incus and chorda tympani. As the gelatinous tissue round the fundus of the Eustachian recess is absorbed during the later months of foetal life, the tympanic lining membrane expands, and thus the handle of the malleus and chorda tympani come to appear as if they lie on the membrane, although really within it (Fig. 201). The mucous lining of the tympanum covers them. The membrane is supported by the tympanic ring, the age changes of which have already been dealt with (p. 159). The nerves and arteries of the first cleft supply the drum.

The Membranous Labyrinth.—The various parts of the membranous labyrinth of the internal ear are represented in Fig. 206. It consists of (1) the utricle; (2) three semicircular canals opening into the utricle; (3) the saccule; (4) a Y-shaped duct uniting the utricle and saccule—the ductus endolymphaticus. All of these parts constitute the vestibular or balancing part of the labyrinth. (5) The cochlear canal—the part connected with hearing. The labyrinth, although a complicated structure, has a very simple beginning. The cells of a certain area of epiblast, situated above and behind the first cleft (Figs. 194 and 196), become ultimately sensitive to sound waves and movements of the head. This area is invaginated during the third week, and forms a simple closed pyriform sac, the **otocyst,** which lies above the first visceral cleft in the mesoblastic tissue between the hind-

brain and the epiblast. The sac contains a fluid, the endolymph, and also otoliths are found in it later. The otocyst lies at first close to the side of the hind-brain with the ganglionic mass belonging to the 7th and 8th cranial nerves to its inner and anterior side. It receives a thin coat of mesoblast. The epithelial cells lining it, all of which are originally columnar, soon become flattened, except at the maculae acousticae,

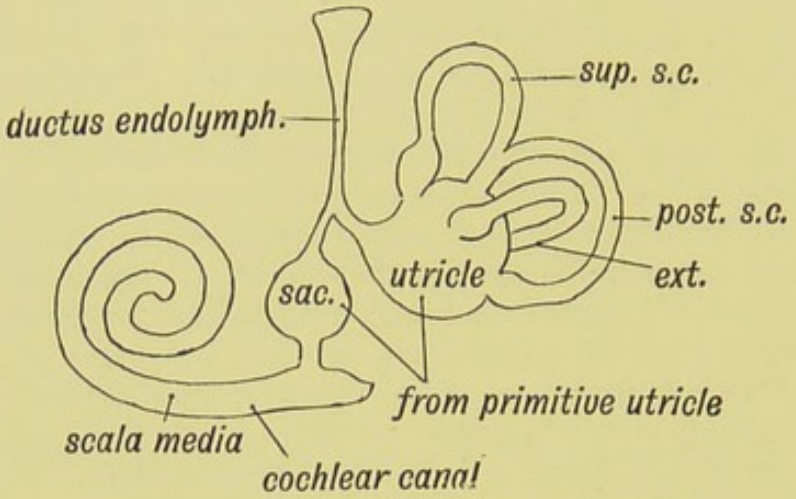


FIG. 206.—Diagram of the Membranous Labyrinth.

where they retain the columnar form and develop hair-like processes. These become connected with the hind-brain by the auditory nerve fibres of the cochlear and vestibular ganglia. The otocyst clearly represents a sense organ which was primarily situated in the skin and through its hair-like processes was sensitive to the position and movements of the body. Its auditory function arose at a later stage.

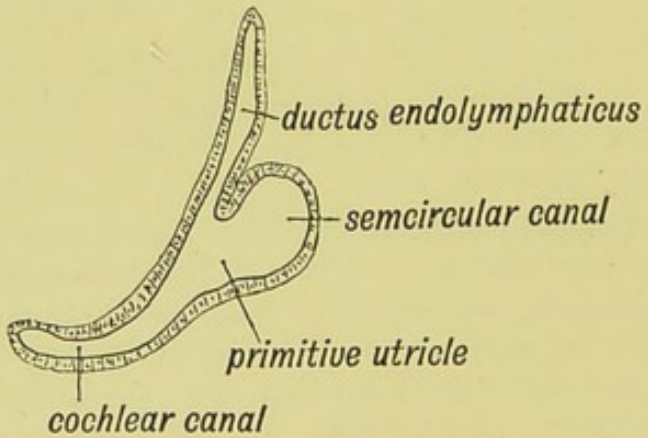


FIG. 207.—The Otocyst in an Embryo of five weeks ; it shows a demarcation into the various parts of the Membranous Labyrinth.

In the lower vertebrates, as in the earlier embryonic stages of the higher mammals, the otocyst is of a saccular form with a stalk above—the **ductus endolymphaticus** (Figs. 206 and 207). The simplest form of vertebrate otocyst is seen in the lamprey ; the superior and posterior semicircular canals are present, but, as in the mammalian embryo, the

primitive cyst is undivided into utricle, saccule and cochlear canal. The semicircular canals grow out from the cyst as flat, hollow plates, but only the circumferences of the plates persist, the centres disappearing.

The development and differentiation of the human otocyst has been closely studied by Prof. Streeter.[1] In Fig. 208 three stages depicted by him are represented. At the 4th week there are three parts : (1) the ductus endolymphaticus. at one time regarded as the stalk which connected the cyst with the surface of the head, but now known to be an outgrowth formed after the stalk is obliterated ; (2) the vestibular pouch or part ; (3) the cochlear pouch or rudiment. At the 6th week

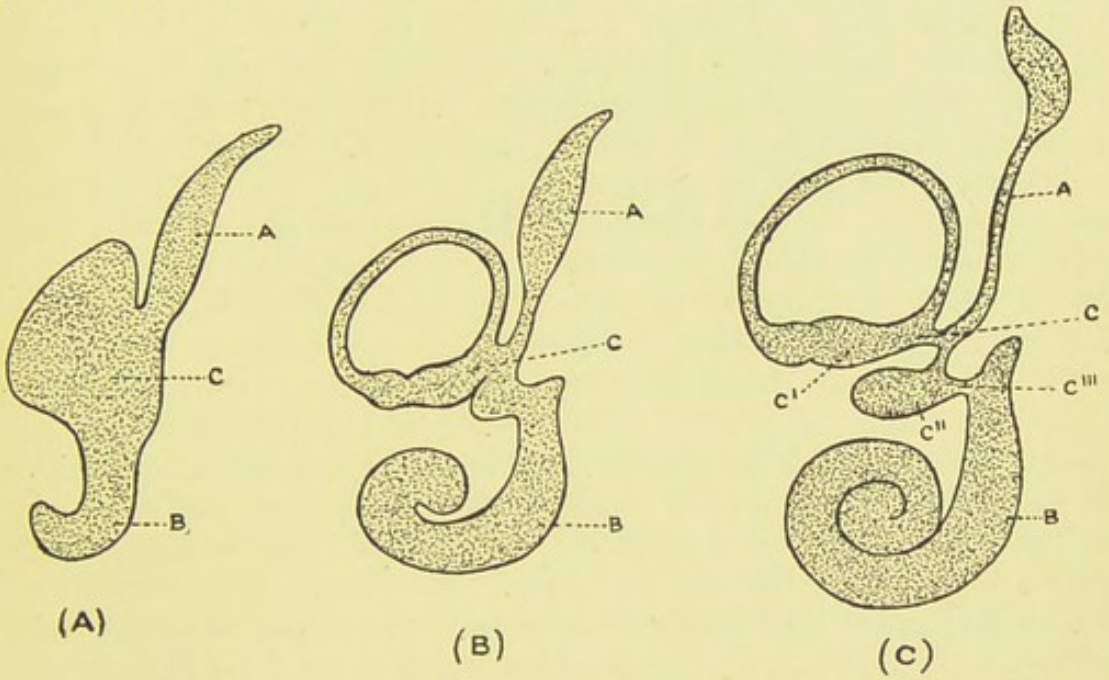


FIG. 208.—Three stages in the development of the Human Membranous Labyrinth. *A*, at the end of the 4th week ; *B*, at the end of the 6th week ; *C*, at the end of the 10th week. (Streeter.)

a higher stage of differentiation is reached ; all the parts of the adult labyrinth are indicated—the ductus and saccus endolymphaticus (both of uncertain import), the semicircular canals, with their ampullae ; the utricle and saccule. All of these are derived from the vestibular part of the otocyst. The cochlear rudiment has extended into a bent canal, and its communication with the saccule is constricted to form the canalis reuniens. In the 10th week all the various parts are present, almost in their adult form. The utricle and saccule are now separated and only communicate by means of the ductus endolymphaticus. The cochlear canal has assumed its spiral form.

The **primitive utricle** or vestibular pouch, which represents the main part of the otocyst, subdivides into the saccule and utricle (Fig. 206). The division occurs at the entrance of the endolymphatic canal, which thus comes to open into both saccule and utricle. The endolymphatic

[1] *American Journal of Anatomy*, 1907, vol. 6, p. 139 ; 1906, vol. 6, p. 203 (Development of Ganglia of vii, viii).

canal is enclosed in the petro-mastoid, its extremity appearing at the hiatus vestibuli, where it ends beneath the dura mater in a dilatation. The cochlear canal (scala media), the real auditory part of the labyrinth, although late in point of evolution, is not late in its developmental appearance. There is merely a rudiment of the cochlea in fishes and other amphibians. In reptiles, birds and monotremes it is a straight canal—the **Lagena.** Only in mammals is it arranged spirally. In it the organ of Corti is developed.

The Petro-mastoid. Origin.—The mesoblast surrounding the membranous labyrinth and dorsal aorta (internal carotid) above the first visceral cleft becomes cartilaginous at the end of the 2nd month of foetal life, forming the periotic capsule (Figs. 194 and 199). There are two centres of chondrification, one for the vestibular part—surrounding the vestibular division of the labyrinth, and one for the cochlear part—surrounding the cochlea. The cartilage of the cochlear part fuses with the parachordal or basilar cartilage; the vestibular part becomes continuous with the occipital plate (see p. 126). The tissue which immediately surrounds the membranous labyrinth does not undergo chondrification, but becomes converted into an open meshwork of cells, the intercellular spaces containing perilymph. The lymphatic space thus formed within the petro-mastoid, containing the saccule and utricle, is the vestibule. The scalae tympani and vestibuli of the cochlea are of similar origin. An oval space on the outer wall of the vestibule is not chondrified; it contains the footplate of the stapes and forms the foramen ovale. The foramen rotundum also remains unchondrified and separates the tympanum from the scala tympani (Fig. 205). The aqueductus cochleae is the outlet of the perilymphatic space. It passes from the scala vestibuli to the anterior wall of the jugular fossa.

Ossification of the Petro-mastoid.—About the end of the 4th month, four ossific centres appear in the periotic capsule; one, the **pterotic,** gives rise to the tegmen tympani which forms the roof of the antrum, tympanum, and Eustachian tube; the petro-squamous suture marks its outer edge; the hiatus Fallopii marks its junction with a second centre—the **opisthotic.** This centre forms the posterior half of the petrous bone. The **pro-otic** forms the anterior half; the mastoid part, which appears on the surface of the skull, is developed from the **epiotic** centre. While the greater part of the petro-mastoid is formed in a cartilaginous basis, the dense layers which form the immediate bony capsule of the labyrinth is laid down by the lining membrane of the perilymphatic space.

The Mastoid.—The mastoid part of the petro-mastoid is flat at birth; about the 2nd year the mastoid process appears as a slight knob, and it gradually grows downwards to form a cephalic lever for the sterno-mastoid, splenius and trachelo-mastoid muscles. The

period of its most active growth is marked by the eruption of the permanent teeth. In most mammals the mastoid grows out as a flat, wing-shaped process continuous with the occipital crest, and thus increases the basal area of the skull on which the neck muscles are inserted (Fig. 120, p. 134). The post-auditory process of the squamosal forms a considerable part of the mastoid process; it reaches to the apex and forms the anterior border (Fig. 151, *C*, p. 159). As the mastoid process grows the diploic spaces within it enlarge into air spaces. Those round the antrum come to open into it, but the more distal remain closed. These spaces occupy the whole of the mastoid part of the temporal, but they also extend forwards in the post-auditory process of the squamosal, and may spread backwards to the occipital. Three varieties of mastoids are recognized:

(1) Dense processes in which the air cells are minute or absent (infantile type of Cheatle);

(2) Containing numerous large spaces (pneumatic);

(3) An intermediate type with large cells round the antrum, and a few small ones near the surface. The third type is the commonest.

The Floccular or Subarcuate Fossa.—At birth there is a fossa situated on the posterior aspect of the petro-mastoid. It is filled with a process of the dura mater in the human embryo, but in all except the highest primates it contains the paraflocculus, a part of the cerebellum which is quite vestigial in man. The posterior semicircular canal surrounds the fossa. This is the condition in most mammals throughout life, but soon after birth the fossa becomes closed in man, merely a remnant being seen above and internal to the hiatus vestibuli in the bone of the adult.

The Acoustic Ganglia.—It has already been shown (Fig. 194) that the mass of nerve cells which come in contact with the otocyst arise from the neural crest of the hind-brain in the same manner as the ganglion of a posterior nerve root. The mass of nerve cells represents the ganglion of the nerve of the 2nd or hyoid arch (p. 87). It becomes divided into three parts: (1) the geniculate ganglion of the facial nerve, which is included in the petro-mastoid, but has no functional relationship to the labyrinth; it gives rise to the great superficial petrosal nerve, chorda tympani and pars intermedia (root part of ganglion) in the same manner as a ganglion of the posterior root produces the sensory fibres of a spinal nerve (Dixon); (2) the vestibular part—applied to the vestibular part of the labyrinth; (3) the cochlear part, which differentiates with the cochlear canal (scala media). The differentiation of the vestibular and cochlear ganglionic masses proceeds at the same rate as the development of the membranous labyrinth.[1]

In Fig. 208 four stages in the differentiation of the nerve equipment of the ear are reproduced. The figures are those of Professor Streeter

[1] Cameron and Milligan, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 111.

(*Amer. Journ. Anat.* 1907, vol. 6, p. 139), and represent stages in the first, second and third months of development. Towards the end of the first month the cochlear part becomes apparent (A^1) ; in the second month this part is undergoing rapid growth (B) ; early in the third month (C) it has assumed a spiral form, and lies within the spiral lamina of the cochlea, and hence is often named the spiral ganglion. The cells of the spiral ganglion send out two sets of processes—to the organ of Corti (peripheral fibres), to ganglia situated in the hind-brain (root fibres). The cochlear fibres form the lateral root of the VIIIth nerve. The vestibular ganglionic mass becomes partially subdivided into a dorsal mass—connected with the areas of sensory cells in the

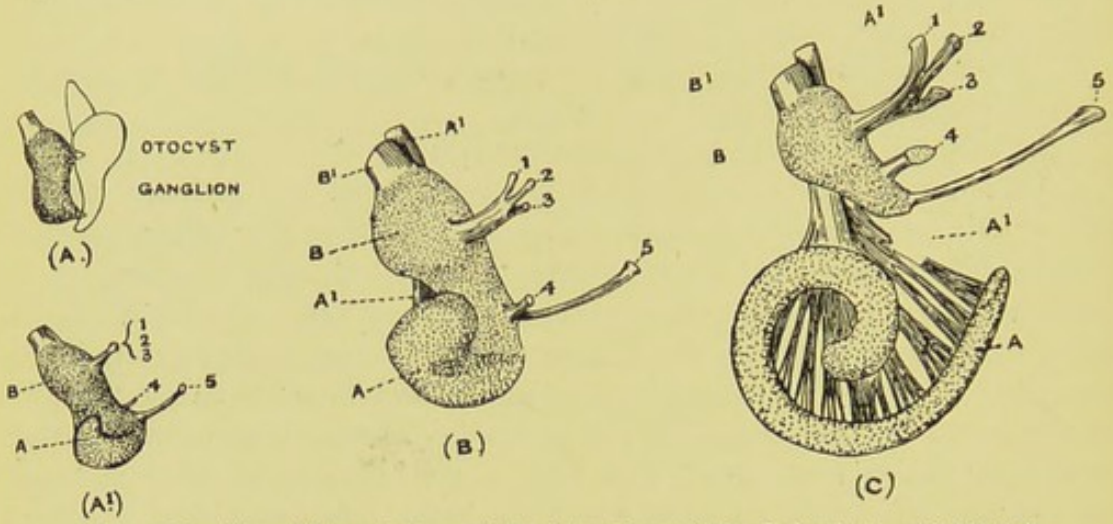


FIG. 209.—The differentiation of the Ganglion of the Labyrinth. (Streeter.) *A*. The otocyst and ganglion of a human embryo in the 4th week ; A^1. In the 5th week. The parts are those of the left side, and are viewed on their lateral aspect. *B*. From a foetus in the 7th week (16 mm. long) ; *C*. From a foetus in the 9th week (30 mm. long).

utricle and the ampullae of the superior and external semicircular canals ; the lower or ventral mass, which sends fibres to the saccule and posterior semicircular canal. The vestibular ganglion is lodged in the fundus of the internal auditory meatus. Its ingrowing or centripetal fibres form the mesial root of the VIIIth nerve. While the cochlear root enters the floor of the 4th ventricle superficial to the inferior peduncle of the cerebellum, the vestibular or mesial root passes deep to it. The lateral or cochlear root is connected with hearing, the mesial or vestibular with balancing.

Nerve Centres. (1) **Cochlear auditory.**—By the end of the first month (Fig. 210) the ingrowing root fibres of the cochlear ganglion have reached a central mass of nerve cells (central cochlear mass) developed in the alar lamina of the hind-brain. The central cochlear ganglion gives rise to the acoustic tubercle (situated on the restiform body) and a lateral accessory nucleus on the outer aspect of the restiform body. By means of the striae acousticae and lateral fillet the cochlear central ganglia are united with the superior olive, inferior corpus quadri-

geminum (mid-brain) and internal geniculate body (thalamencephalon) of the opposite side. Projection fibres connect the geniculate body with the cortex of the first temporal gyrus (see Fig. 93, p. 102). Heschl's gyri (audito-sensory) of the first temporal convolution are already apparent at the beginning of the 7th month (see Fig. 210, *A*). The cortex of these gyri, with the neighbouring area of the first temporal, receives the fibres from the internal geniculate nucleus, and forms the audito-sensory areas. It is highly probable that the cortex of the greater part of the temporal lobe forms association areas, for the interpretation of sounds. The auditory centres are necessarily connected

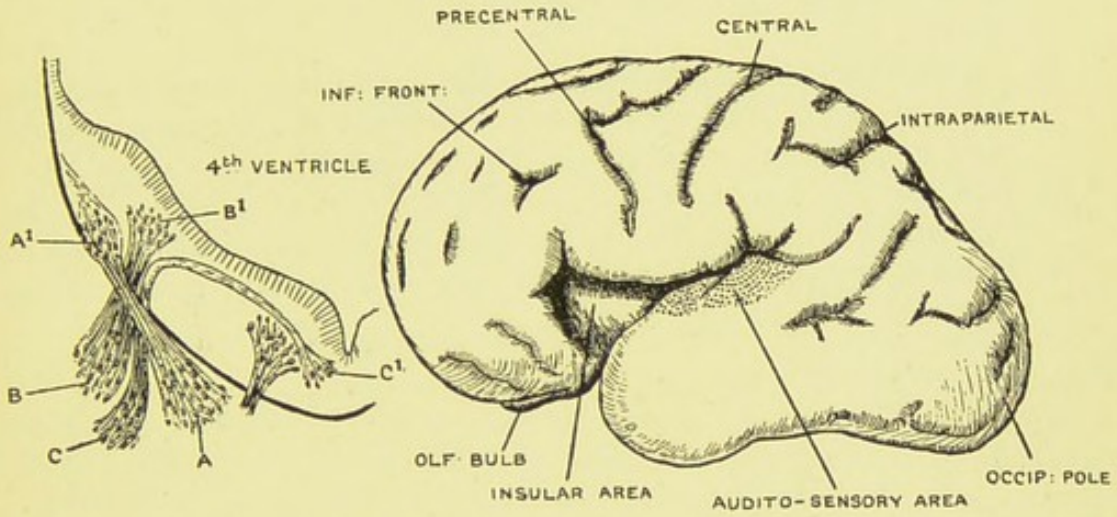


FIG. 210.—Section across one half of the Wall of the Hind-brain of an Embryo at the end of the first month. (His.) *A*. Peripheral cochlear ganglion; A^1. Central cochlear ganglion; *B*. Peripheral vestibular ganglion; B^1. Central vestibular ganglion; *C*. Geniculate ganglion of facial; C^1. Motor nucleus of facial nerve; *D*. Motor nucleus of 4th cranial nerve (trochlear). These nerves form part of the system of the 2nd or hyoid segment.

FIG. 210A.—Lateral view of the Cerebrum of Foetus in the seventh month of development. (Retzius.) The audito-sensory area on Heschl's gyri is stippled.

with the centres for sight, movement and speech, but the development of these connections is as yet imperfectly known.

(2) The ingrowing fibres of the vestibular ganglion pass beneath the inferior peduncle of the cerebellum to terminate in the nerve cells of the dorsal nucleus and Deiter's nucleus in the floor of the 4th ventricle (Fig. 210). These nerve cells and fibres are in no sense auditory, but concerned with the balancing of the body. Through the inferior peduncle of the cerebellum, the nuclei in which the vestibular root ends are connected with both the vermis and lateral cerebellar lobes. The cerebellum and acoustic ganglia arise from the same part of the hind-brain; there is a close developmental relationship between the origin of the vestibular or balancing part of the ear and the cerebellum.

Internal Auditory Meatus.—The internal auditory meatus is formed round the 8th nerve, its ganglia, and the 7th nerve. The falciform crest separates the fibres of the dorsal and ventral parts of

the vestibular nerve. The meatus also contains a prolongation of the arachnoid and subarachnoid space. Fractures of the base of the skull frequently cross the petro-mastoid in the line of the internal auditory meatus, vestibule and membrana tympani. In such cases the cerebro-spinal fluid and perilymph may escape by the external auditory meatus.

Summary.—A study of the development and evolution of the human ear leads to the following conclusions :

(1) That the otocyst was originally a surface-sense organ connected with the balancing of the body ; it was encysted above the first visceral cleft, and part of it became sensitive to sound waves.

(2) Parts of the dorsal laminae of the hind-brain were connected with it, and from those were developed the acoustic ganglia and nuclei, and probably also the cerebellum.

(3) The first and part of the second clefts were modified in air-breathing forms, to become air passages for transmitting sounds.

(4) Parts of the skeletal bases of the first and second visceral arches became the auditory ossicles.

CHAPTER XV.

PHARYNX AND NECK.

Evolution of the Pharyngeal Region.—In the latter part of the first month and opening part of the second the neck of the human embryo undergoes a very remarkable transformation. In the 4th week the representatives of branchial arches are plainly to be seen in the region of the pharynx (Fig. 37, p. 39); the elevation caused by the heart reaches forwards almost to the mandibular arch; properly speaking, there is no neck at the 4th week; as in a fish, the head is fixed directly to the body. By the end of the 6th week (Fig. 39, p. 40) all traces of the branchial arches have disappeared; the head of the embryo is now extended and lifted away from the thoracic region, which now contains the heart. As the branchial arches begin to disappear in the 4th week, a pouch is growing out from the floor of the pharynx to form the larynx, trachea, bronchi and lungs. In the passage from the first to the second month of development we see the human embryo evolve from a stage in which the parts are adapted for a branchial respiration, as in fishes, to a higher one in which its parts are fitted for breathing air. Pharyngeal glands, such as the tonsil, thyroid and thymus, originally developed in connection with the visceral or gill arches, become modified in structure and position to suit the new conditions of life. With the evolution of the mammalian method of mastication and swallowing, the pharynx, originally a respiratory structure, was further modified. The tongue became differentiated from parts in the floor of the pharynx, and muscles, which were at first designed to move the branchial arches, became converted into muscles of deglutition.

Pharynx of the Embryo.—There is very little resemblance between the pharynx and neck of a human foetus in the third week and that of the adult (Figs. 152 and 153, p. 160). Indeed, at the third week the human pharynx resembles closely that of a fish (Figs. 211, 212). In both the human foetus and fish the pharynx is bounded by **visceral** or **branchial arches,** which are separated by depressions (human

embryos) or clefts (fishes); in both the heart is situated under the pharynx, and from the ventral aorta, aortic arches pass up on each side, one in each visceral arch, to terminate in the dorsal aortae. In fishes the

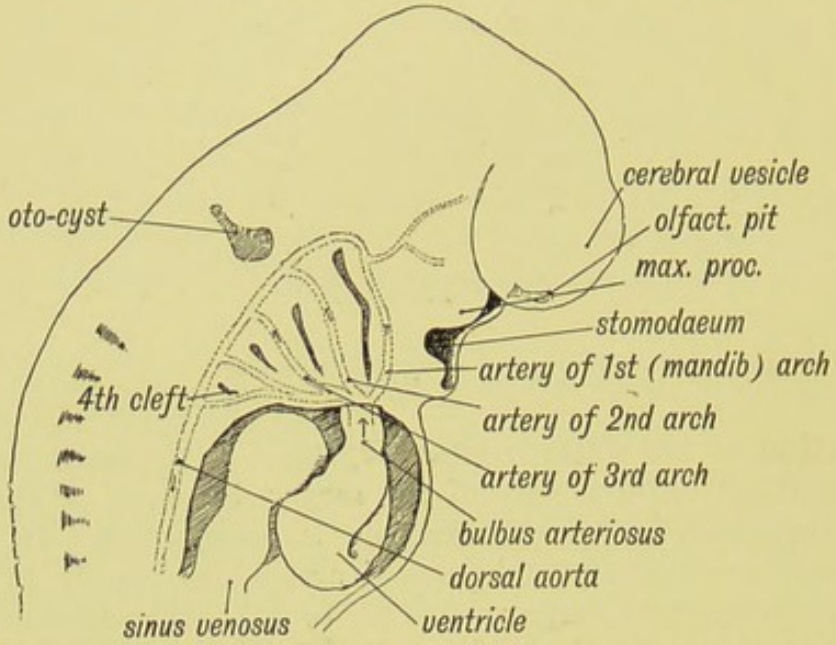


FIG. 211.—Showing the Visceral Arches and Cleft-depressions in the Pharyngeal Wall of a Human Embryo at the beginning of the 4th week. Each Visceral Arch contains an Aortic Arch. (After His.)

aortic arches give off vessels to the gills, in which the blood is arterialized. In the human embryo the blood passes directly through the aortic

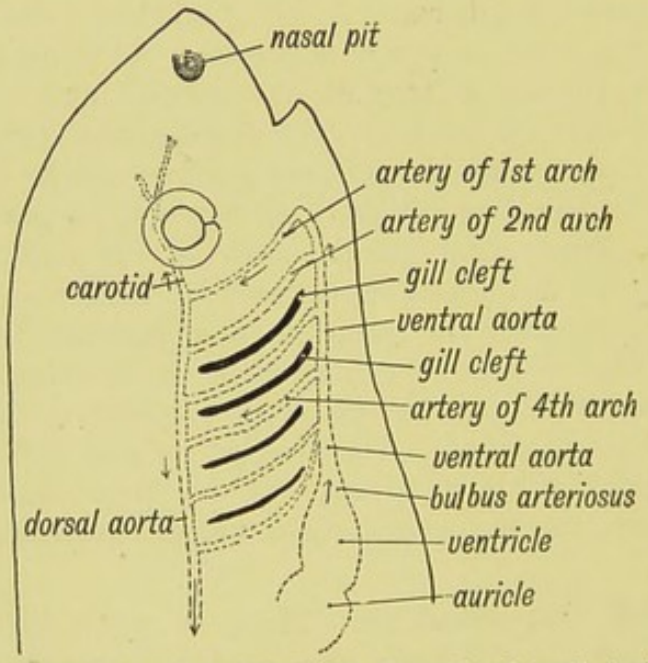


FIG. 212.—Showing the position of the Heart, Visceral and Aortic Arches in a Fish. (Diagrammatic—after Gegenbaur.)

arches. The walls of the pharynx were, therefore, primarily respiratory in function.

A considerable part of the human neck lying in front of the vertebral

column and between the mouth above and the thorax and clavicles below, with the bounding walls of the adult pharynx, is formed from the foetal visceral arches. A knowledge of the transformation of the foetal to the adult pharynx is of the utmost practical importance : it explains the occurrence of fistulae and cysts found in the neck ; it accounts for the peculiar courses taken by nerves, such as the recurrent

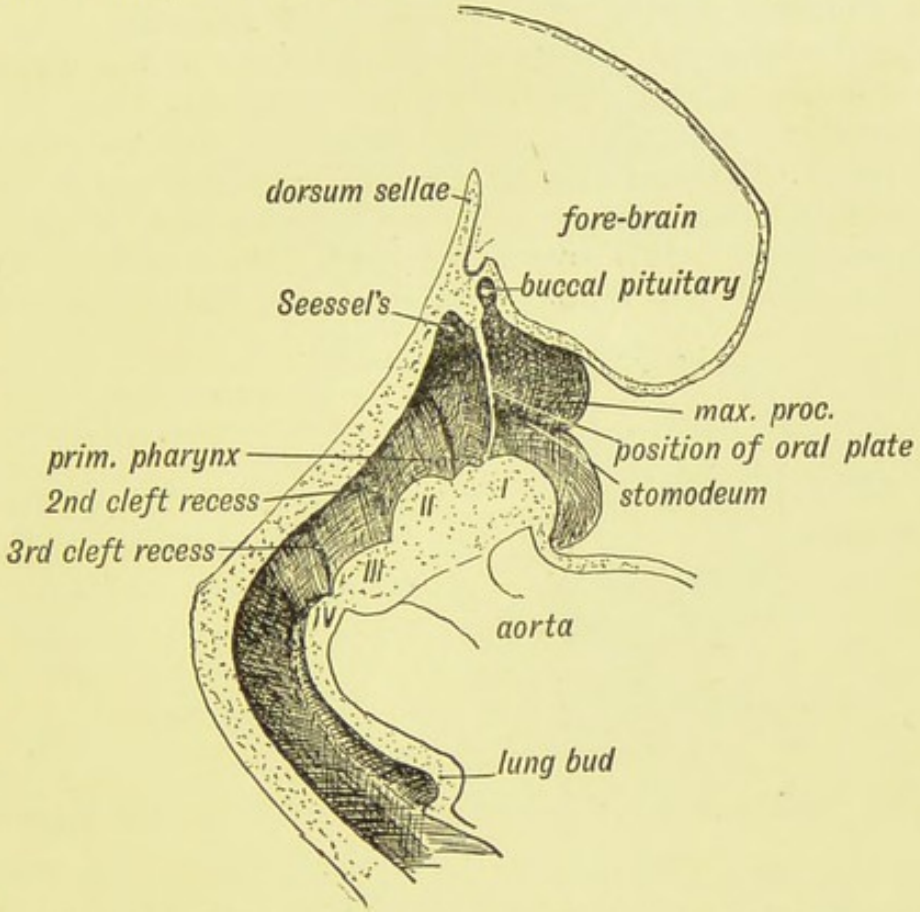


FIG. 213.—Showing the Primitive Pharynx of a 3rd week Embryo in Sagittal Section, bounded by the Visceral Arches. (After His.)

laryngeal and phrenic ; it explains the peculiar distribution of nerves to the pharynx ; and throws light on the nature and anomalies of the thymus, thyroid and tonsil. As may be seen from Fig. 211, the floor of the pharynx of the human embryo rests on the dorsal wall of the pericardium ; in the adult the pharynx and pericardium are separated by the whole length of the neck.

The Visceral Arches.—The visceral arches bound and form the whole thickness of the wall of the primitive pharynx, which is flattened dorso-ventrally, so that its cavity forms a transverse cleft when seen in cross-sections of the embryo. Four arches, each bounded behind by a depression, are to be recognized superficially on each side of the pharynx of the fourth week human embryo (Fig. 211), but behind the 4th cleft are fifth and sixth arches which, however, never become raised or superficially differentiated from the body wall behind. Sagittal and coronal sections of the primitive pharynx (Figs. 213 and

214) give a better idea of the arrangement and constitution of the visceral arches than can be had from a surface view. They are developed round the most anterior part of the fore-gut, which forms the lining membrane of the primitive pharynx. The pharyngeal lining membrane, therefore, is the same as that of the alimentary canal from which spring all the organs and glands of digestion and assimilation.

The Visceral Clefts.—The epithelium or **hypoblast,** which lines the primitive pharynx, covers the inner aspects of the arches and passes outwards in the recesses between them and there comes in contact with the epithelial covering of the body (**epiblast**) which dips in to meet it. The membrane thus formed by the union of the epiblast and hypoblast in the recesses between the arches, may be named the "cleft membrane." It is never ruptured nor disappears in the development of mammals; in fishes it disappears and real clefts are formed

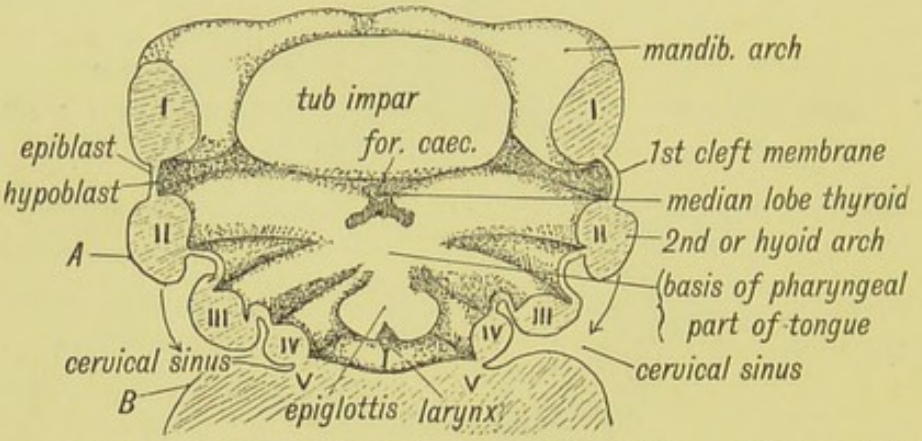


FIG. 214.—Showing the Floor of the Pharynx of a 4th week Human Embryo. (After His.)

between the arches. On the outer side of the membrane is the "external cleft depression": on the inner side, the "internal cleft recess" (Fig. 214). From the hypoblastic lining of these cleft recesses we shall see that the tonsil, thyroid and thymus arise: from the external depressions are formed the various branchial cysts and fistulae, which occasionally occur in the neck of the adult. Each arch contains, as may be seen from Fig. 215:

(*a*) A skeletal basis of **cartilage**; (*b*) an **aortic** or **vascular arch**; (*c*) a **larger nerve** along its anterior border and a **smaller** along its posterior; (*d*) a **muscle element.**

In Fig. 121 (p. 135) a schematic transverse section of a vertebrate embryo has already been given to show the relationship of the tissues of a branchial arch or branchiomere to the segments of the head.

The first visceral arch is known as the mandibular, the second as the hyoid. The remaining four are **branchial** arches, having been at one stage of evolution devoted solely to the purpose of carrying gills. The hyoid arch is specialized in fishes, to protect the branchial arches, and assist in the circulation of blood through the gills and water through

the pharynx. The mandibular arch bounds part of the buccal cavity in all vertebrates, and forms part of the apparatus of mastication.

Formation of the Cervical Sinus.—The first arch especially, and also the second, grow and increase at a much greater rate than

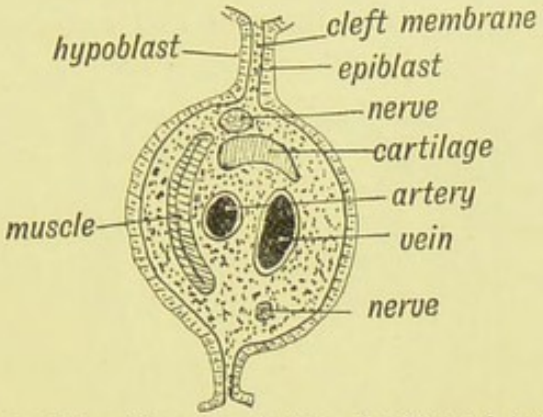


FIG. 215.—Schematic Section of a Visceral Arch.

the branchial arches. The second arch (hyoid) which in fishes forms the operculum for the gills, grows over and buries the third and fourth

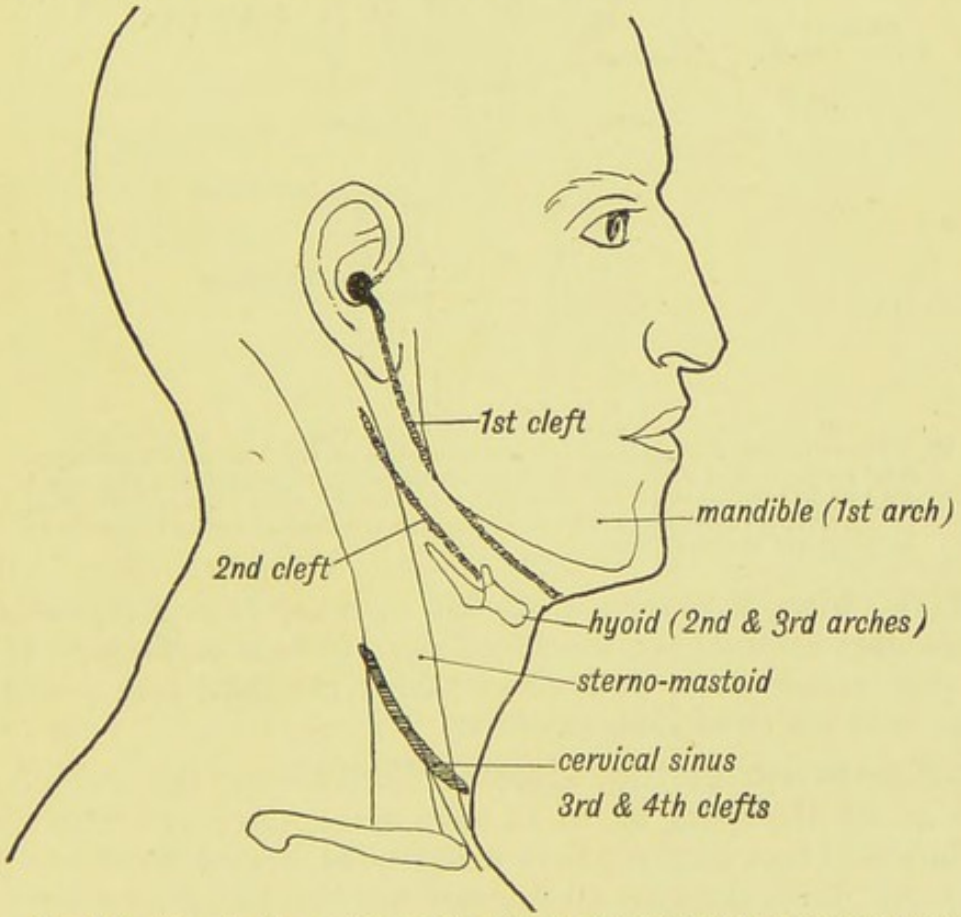


FIG. 216.—Showing the position of the External Cleft Depressions in the Adult.

in the human embryo. As it covers them over and comes in contact with the body wall behind the sixth arch (see *A* and *B*, Fig. 214), the

epiblast covering the branchial arches and clefts is buried. The epiblast so enclosed forms the lining of the cervical sinus. It usually disappears, but may remain and form a cyst in the neck, which opens some distance above the sterno-clavicular joint. It may be drawn out into a trumpet-shaped tube, which ends in contact with the tonsillar recess and passes between the internal and external carotid arteries

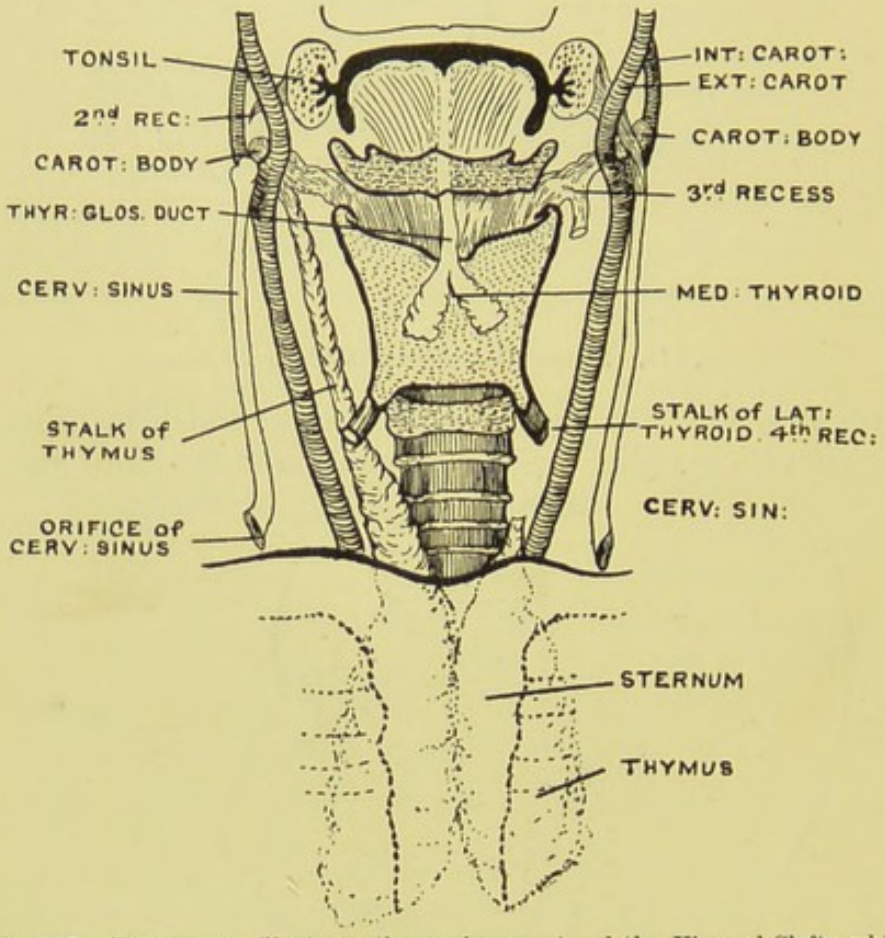


FIG. 217.—Diagram to illustrate the various parts of the Visceral Clefts which may persist. The 2nd inner cleft recess gives rise to the tonsil; the recess may be in contact with an epithelial tube derived from the cervical sinus. The 3rd inner recess gives rise to the thymus and carotid bodies; the 4th to lateral parts of the thyroid.

(Fig. 217). Often the orifice is marked by a tag of skin representing a rudimentary external ear, which encloses a piece of cartilage.[1] If the outer cleft depression in front of or behind the third arch persist, it must open in the cervical sinus.

What becomes of the Visceral Clefts.—By the end of the second month the clefts, or, to be more exact, the representatives of clefts in the human embryo, have disappeared, except the upper part of the first. From the external depression of this part a solid ingrowth

[1] For an account of the various developmental anomalies of the pharyngeal region see Keith, *Brit. Med. Journ.* 1909, Aug. 7th, 14th, 21st. For a description of its development see J. Ernest Frazer, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 156; H. Fox, *Amer. Journ. Anat.* 1908, vol. 8, p. 187.

of epithelium takes place which, ultimately becoming canaliculized, forms the **external auditory meatus.** In connection with the upper or dorsal parts of the first and second cleft depressions the **Eustachian tube** and **tympanum** are formed, the **membrana tympani** remaining approximately in the position of a cleft membrane.

If traces of the other clefts remain as fistulae or cysts they will occur in the positions shown in Fig. 216. Part of the second cleft is marked in the goat by an opening and auricular appendage. As already pointed out, superficial remnants of the second and third clefts are rare; they are usually included with the cervical sinus beneath the hyoid operculum.

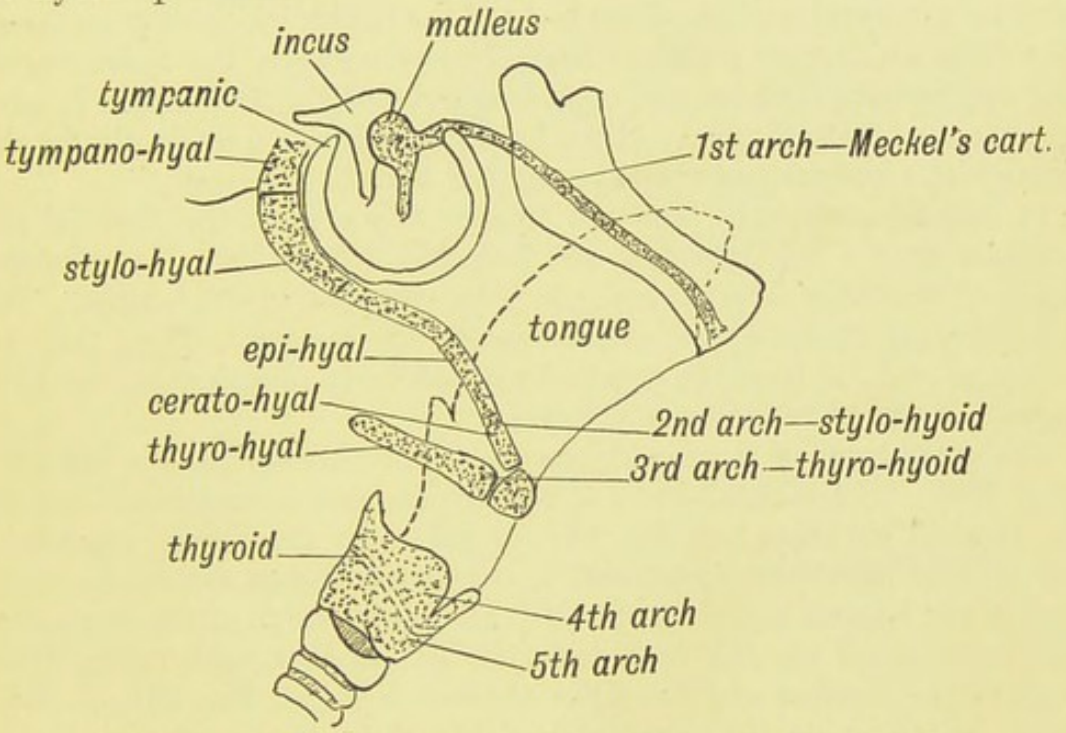


FIG. 218.—Showing what becomes of the Cartilages of the Visceral Arches.

Within the pharynx traces of inner cleft recesses are to be seen besides the Eustachian opening (Fig. 217). The **tonsil** is developed in the second cleft; the anterior pillar of the fauces represents the position of the second arch. The **lateral recess of the pharynx** (fossa of Rosenmüller), behind the Eustachian tube, although sometimes regarded as a derivative of the second cleft, is, as we have seen (p. 209), a secondary formation. The **pyriform fossa,** at each side of the laryngeal aperture, represents the position of the fourth and fifth clefts (see Fig. 198).

The Cartilages of the Arches.—The history of the skeletal basis of the first arch (Meckel's cartilage) has been already traced (p. 156 and Figs. 143 and 144).

The cartilage of the 2nd or **hyoid** arch forms (Fig. 218):

(1) The **tympano-hyal,** embedded in the petro-mastoid, and was originally continuous with the ear ossicles (Fig. 202).

(2) The **stylo-hyal** (Fig. 218), which ossifies in the early years of life and becomes joined to the tympano-hyal to form the styloid process.

(3) The segment below, the **epi-hyal,** becomes ligamentous, and forms the stylo-hyoid ligament, but it also may become ossified.

(4) The lowest segment, the **cerato-hyal,** forming the small horn of the hyoid.

The **epi-hyal** lies behind and outside the tonsil, and when ossified has been excised under the belief that it was a foreign body. The body of the hyoid (**basi-hyal**) probably represents the fused ventral parts (copulae) of the **2nd and 3rd cartilages.**

Mr. Parsons [1] has drawn attention to the fact that there is a ridge of bone on the upper surface of the body of the hyoid, which may occasionally form an almost separate bar. It lies between the lesser horns, and appears to represent the copula or body of the 2nd arch. It may be separated from the body of the hyoid by a foramen evidently for the passage of a remnant of the thyro-glossal duct.

It will be seen later that the tongue arises from the floor of the pharynx in the field between the 2nd and 3rd arches. The skeletal bases of their ventral parts come to form the bone of the tongue. The skeletal part of the hyoid arch suspends the tongue. There may be a process of bone from the concavity of the body representing the hyo-lingual of lower vertebrates (Parsons).

The **great horn** of the hyoid represents the cartilage of the **3rd arch** (Fig. 218). The skeletal bases of the 4th and 5th arches unite to form the thyroid cartilage (see Fig. 331, p. 336). In the lowest mammals, the thyroid shows an upper and lower segment, and a vascular foramen in the human thyroid frequently marks the union of the two parts. The cartilage of the 6th arch gives rise to the arytenoid, cricoid, and rings of the trachea and bronchus on each side (see Fig. 331, p. 336). Even in mammals the cartilages of the three last branchial arches remain subservient to the purposes of respiration, just as in vertebrate animals in which these arches carry gills.

The Nerves of the Visceral Arches.—The 3rd division of the 5th nerve is, as has been already seen, the principal nerve of the first or mandibular arch. The nerve for the second or hyoid arch is represented by the 7th and 8th (facial and auditory, Fig. 219). The nerve of the 3rd arch is the glosso-pharyngeal, that for the 4th is the superior laryngeal branch of the vagus, and for the 5th and 6th the inferior laryngeal (Fig. 219).

Each nerve of a visceral arch supplies (1) the muscles of the arch, (2) the pharyngeal lining and cleft recess in front of the arch. The chorda tympani and great superficial petrosal nerves represent the sensory branches of the facial to the first cleft.

The relationship of the nerves to the visceral arches is shown in

[1] F. G. Parsons, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 279.

Fig. 220, in a human embryo of four weeks, which was investigated by Prof. Streeter. The position of these nerves in the adult is diagrammatically represented in Fig. 219. The Vth nerve and Gasserian ganglion are seen to lie at the base of the mandibular process. The ganglion of the VIIth and VIIIth nerves lie at the base of the hyoid (second) arch, in front of the otic vesicle, the fibres of the facial having

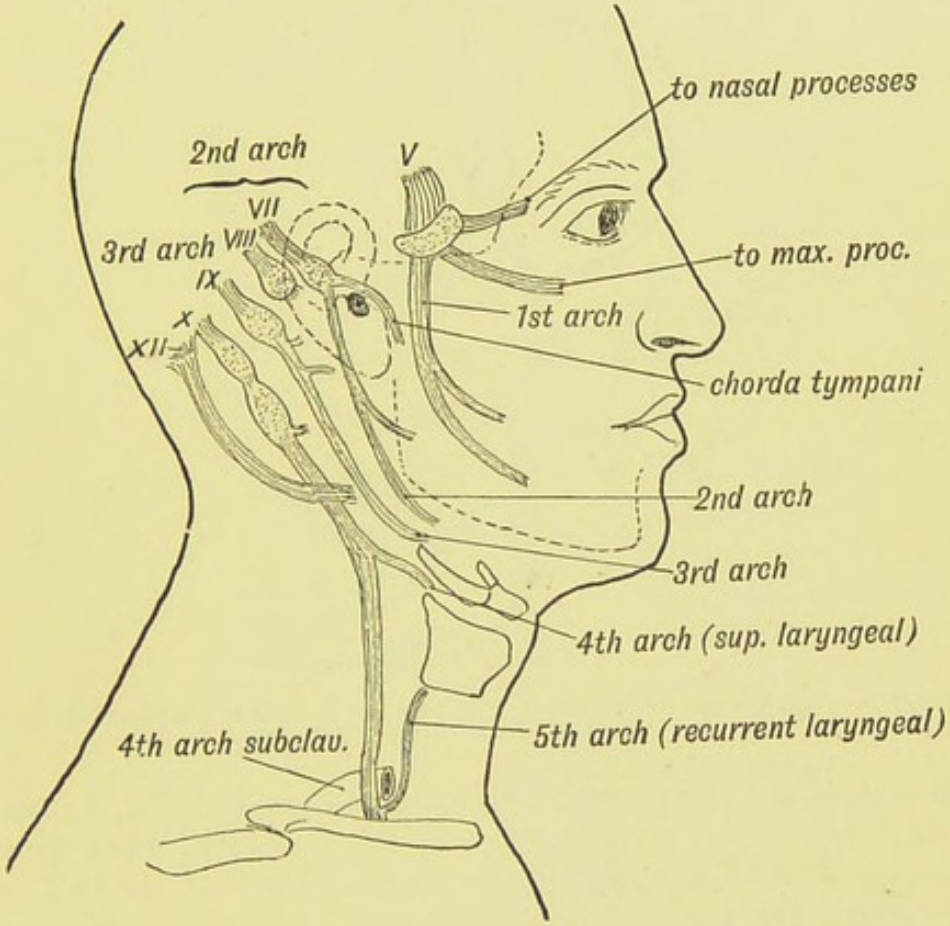


Fig. 219.—Showing what becomes of the Nerves of the Visceral Arches.

already entered the arch. The glosso-pharyngeal and its ganglia lie behind the otic vesicle and at the base of the third arch. The large ganglionic mass of the vagus lies over the bases of the fourth, fifth and sixth arches—or rather the tissue representing these arches. At this stage—the 4th week—the ganglion of the vagus and its issuing fibres rest on the dorsal wall of the pericardium, the heart being quite close to the source of its nerve fibres.

What becomes of the Aortic Arches—the Arteries of the Visceral Arches.—In Fig. 211 is given the foetal arrangement of the aortic arches, and in Fig. 221 the vessels in the adult which are formed from them. The primitive aorta in the embryo divides into two trunks, which run forwards along the floor of the pharynx, one on each side, lying between the ventral ends of the visceral arches. These

may be termed the right and left **ventral aortic stems.** From these stems six arteries (aortic arches) pass upwards, one in each visceral arch, to terminate in the right and left **dorsal aortae,** which run backwards to join together and form one vessel at the 4th dorsal vertebra—the descending thoracic aorta. The aortic arches are formed at a very early date. At the beginning of the 3rd week the first or mandibular

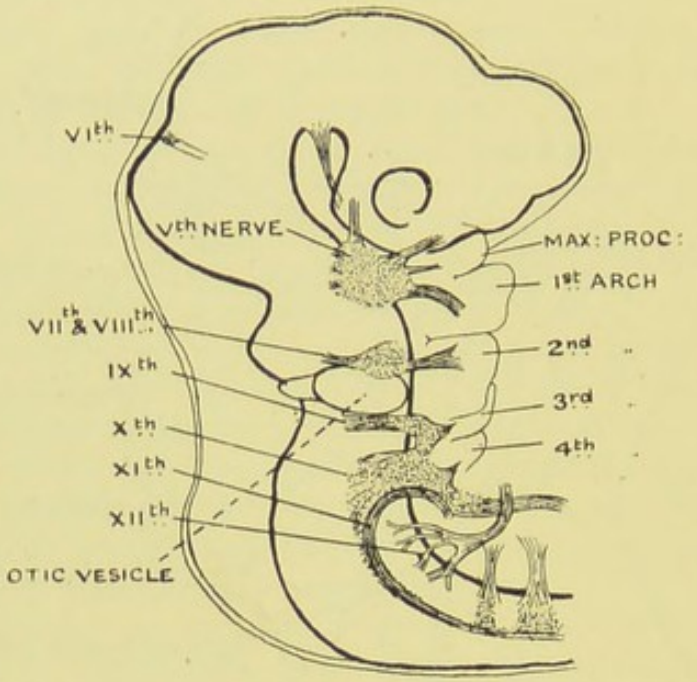


FIG. 220.—The Visceral Arches and their Nerves and Ganglia in a Human Embryo of the 4th week. (Professor Streeter.)

aortic arch is already present; the second (hyoid), third, fourth, fifth and sixth appear in succession, but by the 4th week, when the 6th or pulmonary arch [1] has appeared, the first and second are in a process of atrophy. The aortic arches are formed by the union of a network of blood spaces which are developed within each visceral arch.

The 1st and 2nd aortic arches do not persist in any vertebrate; they disappear almost as soon as formed in the human embryo. The third remains as the first part of the internal carotid, the fourth forms the 1st and 2nd stages of the right subclavian. On the left side the fourth aortic arch forms that part of the arch of the aorta between the origin of the left carotid and entrance of the ductus arteriosus. The right and left fifth arch, or, to be more accurate, the sixth, for a transient arch appears between it and the fourth, give off vessels to the lungs which are developed in close connection with these arches. This arch on the left side persists as part of the right pulmonary artery and **ductus arteriosus** (Fig. 223). On the right side the dorsal part disappears, the remaining segment joining in the formation of the right

[1] For recent literature on 6th arch and 5th cleft recess see Frank Reagan, *Amer. Journ. Anat.* 1911, vol. 12; J. Tandler, *Anat. Hefte*, 1909, vol. 38, p. 393.

pulmonary artery. When it is remembered that the 6th or pulmonary arch lies at the level of the larynx in the 4th week, and that, owing to the development of the neck, it has almost reached its final position in

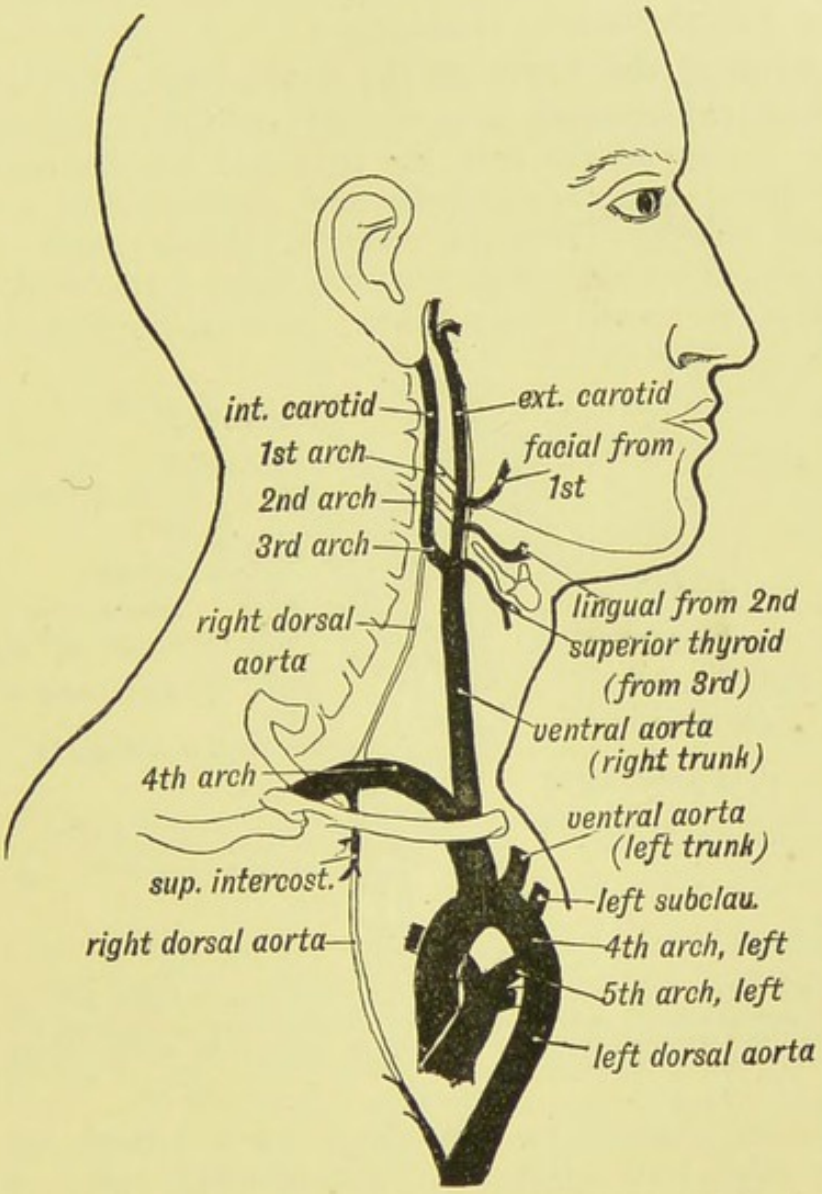


FIG. 221.—Showing what becomes of the Aortic Arches in the Adult. Only the shaded parts persist. The position of the 1st and 2nd aortic arches should be indicated above and below the position of the external auditory meatus.

the 7th week, the rapid transformation of the parts in the region of the pharynx in the second month will be realized.

Subclavian Arteries.—The visceral arches with their arteries are well developed before the limb buds appear. When, at the end of the third week, these buds grow out to form the upper extremities, the artery which supplies each bud springs from the dorsal aortae representing a segmental branch of that vessel. The embryonic or primitive subclavian is the artery of the 6th cervical segment, being situated at

a considerable distance behind the 6th aortic arch. As the aortic arch-system is elongated to form the great vessels of the neck, the origin of the subclavian comes to lie opposite the 4th arch (Fig. 222). This artery forms the entire subclavian on the left side, but only its second and third stages on the right.

The Arch of the Aorta on the Right Side.—In birds it is the 4th right arch which forms the aortic arch, and this occasionally happens in man. In amphibians both the right and left 4th arches persist. The two dorsal aortae in which they end, unite together, as they do in the human embryo, to form the descending thoracic aorta. The primitive subclavian arteries spring from the dorsal aortae above the point where these two vessels fuse together. In the latter part of the second

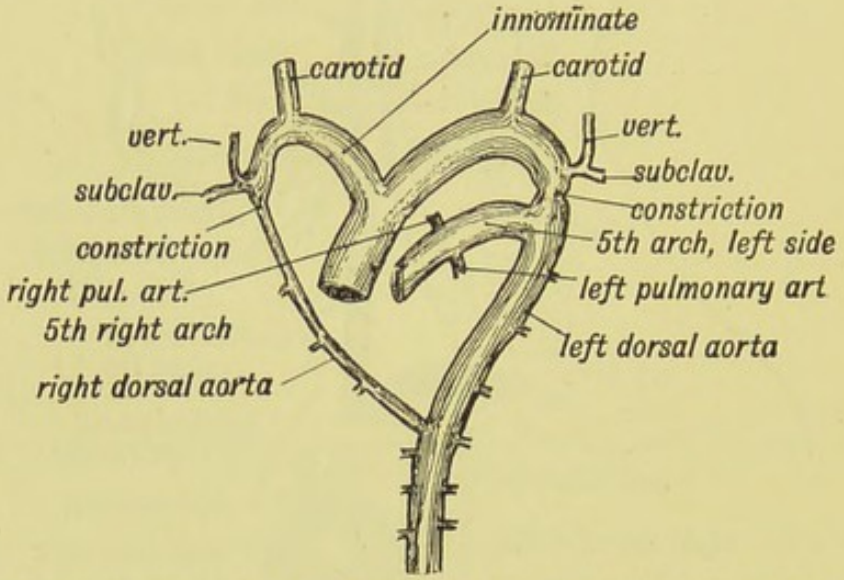


FIG. 222.—The condition of the Right and Left Dorsal Aortae in a 6th week Human Foetus. (After His.) The right arch disappears beyond the origin of the right subclavian; a constriction may appear at the corresponding point on the left side.

month the short part of the right dorsal aorta, between the origin of the right subclavian artery and point of aortic fusion, disappears, and then the subclavian artery appears as if it arose from the 4th right arch. The communicating arterial twig, which is often seen uniting the superior intercostal artery of the right side with the artery of the lower spaces, is formed by a secondary anastomoses, and does not represent the right dorsal aorta (see E. Pearce Gould, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 329).

Not unfrequently the right subclavian arises, not from the innominate, which represents the right ventral aortic stem, but as the last of the great branches which arise from the arch of the aorta (Fig. 223). In such cases two things have happened: (1) the 4th right aortic arch has been obliterated, (2) the right dorsal aorta has persisted (Fig. 223).

Cases are found in which the permanent aorta is very much constricted

at or near the point of entrance of the ductus arteriosus (see Fig. 222). It will be noticed that the corresponding part of the right dorsal aorta is obliterated. Such a constriction on the left side is to be regarded as corresponding to that on the right side, and indicates a partial attempt to produce a right aortic arch.

Dorsal Aortae.—It will be noticed that the parts of the dorsal aortae between the 3rd and 4th arches disappear (Fig. 223). The

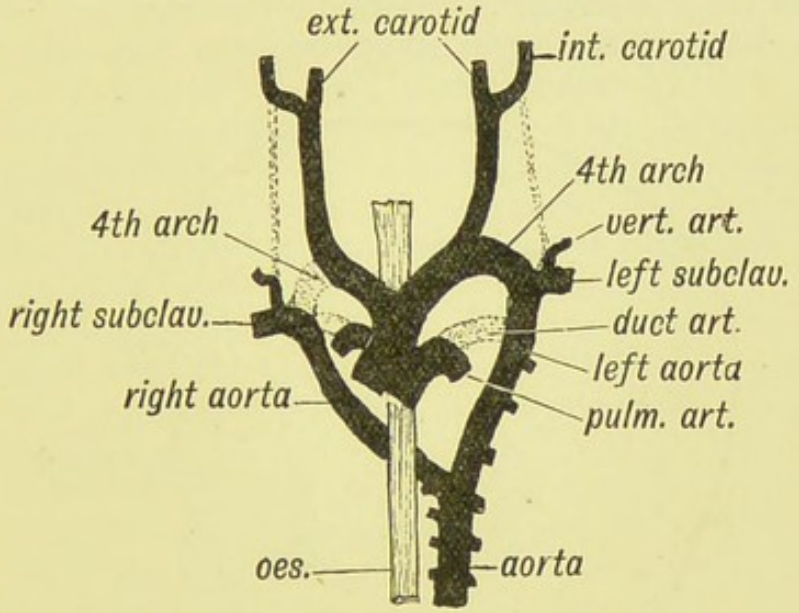


FIG. 223.—Diagram showing the manner in which the Right Subclavian may arise as the last branch of the Arch of the Aorta. The parts of the aortic arch system which become obliterated are stippled.

ventral aortae persist as the innominate, the common carotid and external carotid arteries. With the marked elongation of the cervical region and the development of the lungs in the second month, the primitive position of the aortic arches is greatly disturbed. The heart, being the pump of the lungs, must accompany these organs. The ventral aortae become elongated into the common carotid and innominate arteries (Figs. 221, 223). The 4th aortic arch, which should lie opposite the upper part of the thyroid cartilage, comes to lie at the level of the 1st rib on the right side and within the thorax on the left, while the last aortic arch dragging the nerve of its segment in front of it (the recurrent laryngeal) comes to be situated within the thorax.

Muscles of the Visceral Arches.[1]—Within each visceral arch a muscle plate is formed—recalling in mode of appearance the muscle plates which develop in connection with each vertebral somite. The muscles arising in each arch are supplied by the nerve of that arch; hence from the nerve supply alone one could infer the derivation of the musculature of the pharyngeal region. The muscles become

[1] See references, p. 135, under Edgeworth.

differentiated in the latter part of the second month. All the muscles supplied by the facial nerve—the platysma, muscles of expression, the stapedius, stylo-hyoid, posterior belly of the digastric, etc.—are derived from the muscle plate of the 2nd or hyoid arch. The muscles of mastication, with the tensors of the palate and tympanum, the anterior belly of the digastric and mylohyoid, are derived from the muscle segment of the mandibular arch. The stylo-pharyngeus is derived from the 3rd arch. The musculature of the soft palate and the constrictors of the pharynx are derived from the third and fourth arches. The musculature of the larynx comes from the fifth and sixth arches.

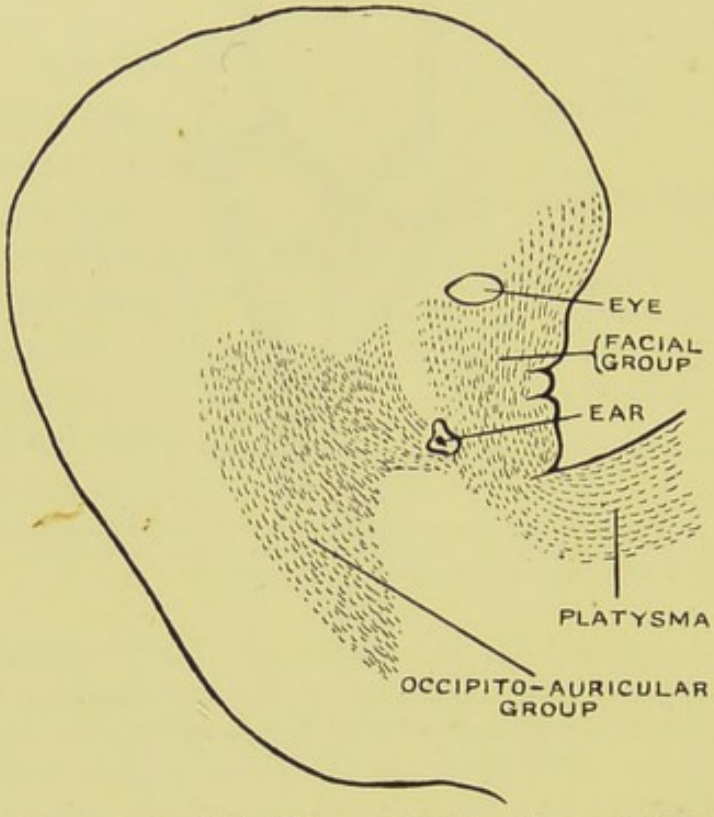


FIG. 224.—The expansion of the Platysma Sheet in a Human Foetus of 6 weeks. (Futamura.)

The Platysma and Muscles of the Face and Scalp.[1]—The platysma myoides, the muscles of the face, scalp and external ear, are derived from the muscle plate of the second or hyoid arch. They are supplied by the facial, the nerve of this arch. The muscle bud, from which the whole platysma sheet is developed, is still confined to the area of the hyoid arch at the end of the first month. During the third month the bud spreads out and forms a continuous muscular hood over the head and neck. To this hood or sheet, which is composed of two layers, a deep and superficial, the name of **platysma sheet** may be given. It is developed in the superficial fascia. During its expan-

[1] R. Futamura, *Anat. Hefte*, 1907, vol. 32, p. 479; 1906, vol. 30, p. 433.

sion or migration the platysma sheet separates into three main divisions —a part for the neck—platysma colli; for the ear and occiput—the occipito-auricular; and the facial division—for mouth, nose, orbits and forehead (Fig. 224). The muscles become differentiated during the 3rd month.

In man, the platysma sheet has undergone marked retrograde changes in the neck, scalp and external ear, but over the face it has become more highly specialized and differentiated than in any other animal. From this sheet are derived the epicranial aponeurosis, the occipitalis and frontalis muscles. On the face the platysma sheet forms the muscles round the orbit, nose and mouth. The buccinator and levator anguli oris represent parts of the deeper layer of the sheet. The transversus nuchae, fibres occasionally seen in man passing from the middle line of the neck behind, towards the ear and cheek, represent fibres constantly developed in lower primates, and better still in rodents and carnivora as the *sphincter colli* and *sterno-facialis*.

The muscles supplied by the facial nerve are peculiar in that they are the physical basis into which many mental states are reflected and in which they are realized. Through them mental conditions are manifested. It is found that the differentiation of this sheet into well-marked and separate muscles proceeds *pari passu* with the development of the brain. The more highly convoluted the brain of any primate, the more highly specialized are its facial muscles. It is remarkable that the sheet should arise from a visceral arch, which originally was closely connected with the function of respiration. To some extent the platysma does come into play during forced respiration even in man.

STRUCTURES DEVELOPED FROM THE WALLS OF THE PRIMITIVE PHARYNX.

The Tongue and its Development.[1]—The tongue is developed in the floor of the primitive pharynx between the ventral parts of the 1st, 2nd and 3rd visceral arches (Fig. 227). Two parts are to be recognized in the tongue. The **buccal part** (Fig. 225) is situated in front of the foramen caecum and the V-shaped groove. It is covered by papillae, concerned in mastication and liable to cancer. The second or **pharyngeal part,** bounding the buccal wall of the pharynx (Fig. 225), is covered by glandular and lymphoid tissue and concerned with swallowing.

The **buccal part** arises during the 3rd week from the mandibular or 1st arch and the 1st interbranchial space by the upgrowth of a tubercle, the **tuberculum impar** (Fig. 227). This was at one time believed to give rise to the whole of the buccal part of the tongue, but researches made by Kallius and others have clearly demonstrated that in the 4th

[1] E. Kallius, *Anat. Hefte,* 1910, vol. 41, p. 173, etc.; J. L. Paulet, *Archiv. f. Anat. u. Entwick.* 1911, vol. 76, p. 658; also reference on p. 226, under Frazer.

week there arise from the mandibular arch, on each side of the tuberculum impar, right and left lingual buds which fuse with and bury the median element. Hence the buccal part of the tongue is bilateral in origin, and as its nerve supply shows, is entirely derived from the mandibular arch. In the 7th week the tip of the tongue is bifid, because the lateral buds are imperfectly fused (Paulet). The bilateral origin of the tongue explains the occasional occurrence of a bifid tip and the formation of cysts in the median raphe. Besides the lingual nerve, the chorda-tympani—the branch of the facial nerve which enters the mandibular arch—also supplies the buccal parts with sensory fibres.

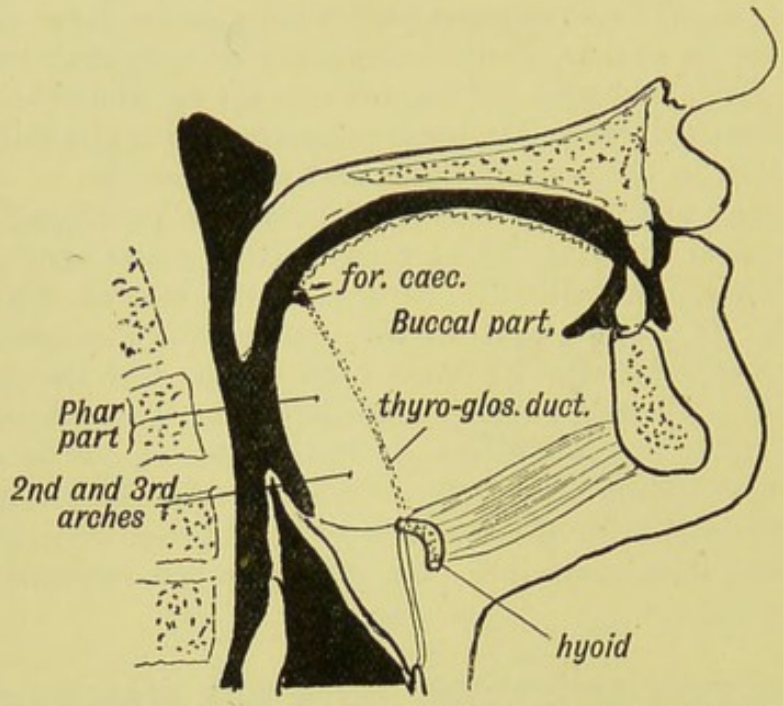


FIG. 225.—Showing the Buccal and Pharyngeal parts of the Tongue.

Until the 6th week the buccal part of the tongue, still separated from the pharyngeal part by a depression in the floor of the pharynx, from which the median thyroid bud arises, remains attached to the mandibular arch. In the 6th week the tongue becomes separated from the arch by the downgrowth of an epithelial plate ; in this way the tongue becomes separated from the alveolar ridge of the mandible. In the floor space between the tongue and mandible are developed the submaxillary and sublingual glands. Not unfrequently part of this glandular field may be imperfectly separated from the tongue, and in this manner various peculiar congenital malformations of the tongue are produced (see Fig. 226).

The **pharyngeal part** of the tongue is derived from the fused ventral ends of the 2nd and 3rd arches, in which, as we have already seen, the body of the hyoid is developed. The glosso-pharyngeal, the nerve of the 3rd arch, or more strictly of the 2nd cleft, supplies it. The V-shaped

groove (sulcus terminalis) marks the union of the buccal with the basal or pharyngeal part. From the hypoblast, which lines the depression between those two parts, arises, by a process of outbudding, the middle lobe or isthmus of the thyroid gland (Fig. 231).

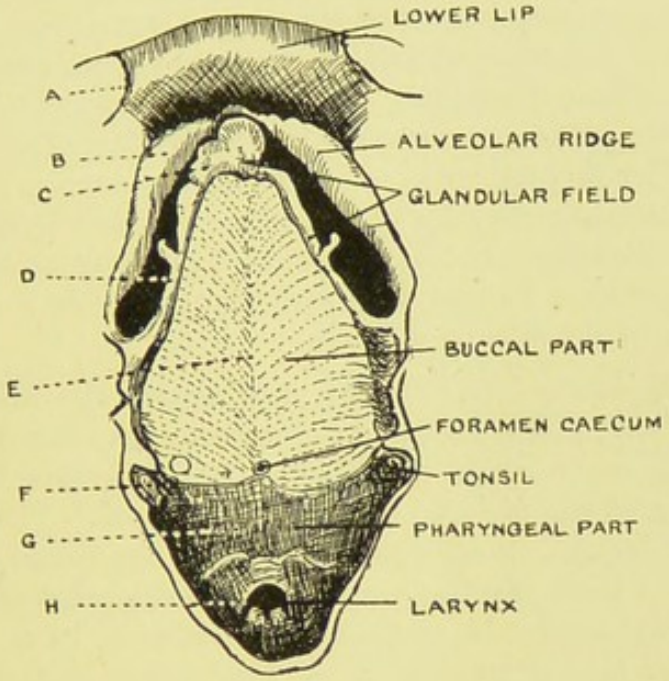


FIG. 226.—Upper Surface of the Tongue of a Child in which the glandular tissue, which forms the sublingual and submaxillary glands, has been imperfectly separated from the tongue by the down-growth of the mandibulo-lingual plate of epithelium. *A*, lower lip; *B*, alveolar ridge; *C*, glandular tissue (sublingual); *D*, submaxillary; *E* buccal part of tongue; *F*, tonsil; *G*, pharyngeal part of tongue; *H*, opening of larynx.

The Musculature of the Tongue.—The muscles of the tongue do not arise within the visceral arches, but are of extraneous origin.

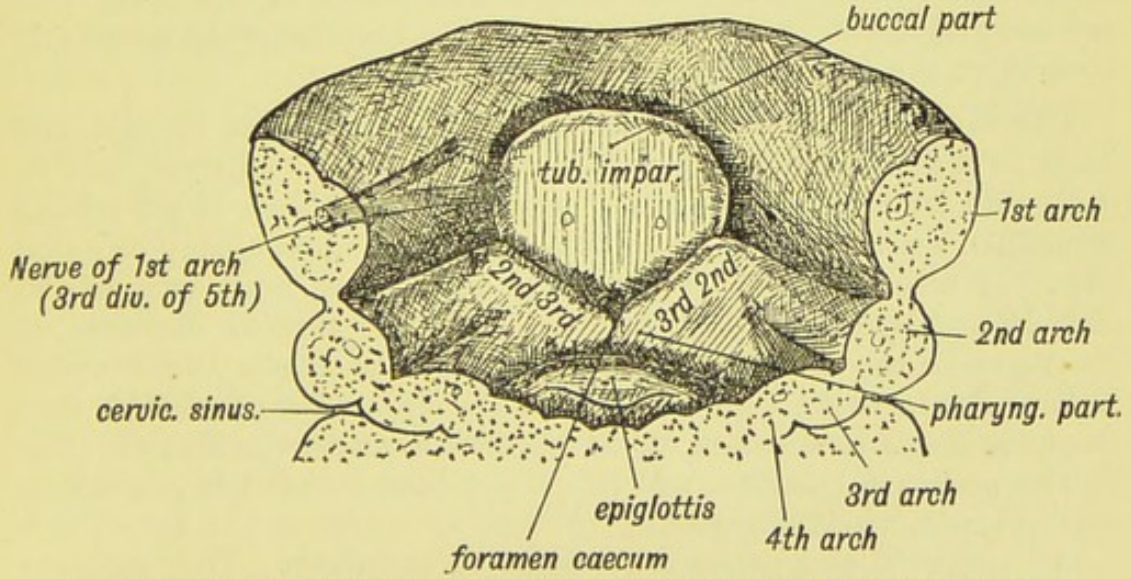


FIG. 227.—Showing the Origin of the Tongue in the Floor of the Primitive Pharynx. The condition represented is from an embryo in the 6th week. (After His.)

It has been shown that the head is probably composed of nine segments. From the muscle plates of the three posterior of these segments processes arise and grow downwards and forwards until they reach the basis of the tongue derived from the three visceral arches, carrying their nerves with them—the hypoglossal or 12th cranial nerve (Fig. 220). Hence, while the sensory nerves of the tongue come from the nerves of the 1st, 2nd, and 3rd visceral arches, its motor fibres are derived from the posterior cephalic segments. The primitive muscle of the tongue is the genio-hyoid ; the genio-glossus is a derivative of it, and so is the hyo-glossus. The lingual muscles are already recognizable in the 6th week, but the intrinsic muscles of the tongue, which have much to do with its fine movements, are later in point of differentiation—appearing in the fourth month. The sense of taste is present in a child born at the 8th month of development.

Lingual Papillae.—The filiform papillae are the first to appear, then the fungiform, a few of which, along the posterior border of the buccal part, become enlarged and sink to form circumvallate papillae, round the bases of which taste buds are developed. The papillae are confined to the buccal or masticatory part of the tongue. It will be observed that the taste papillae are situated at the brink of the pharynx (Fig. 225), at which the food is seized and carried away by the involuntary muscles. At the lateral margins of the buccal part of the tongue, just in front of the anterior pillars of the fauces, the fungiform papillae are arranged in a series of laminae, recalling and corresponding to the **papillae foliatae** of low primates and of rodents. Between the papillae foliatae occur taste buds. On the under surface of the tongue at birth, on each side of the sublingual papillae and over the position of the ranine artery, are two fimbriated folds of mucous membrane, the **plicae fimbriatae,** structures which are well developed in lemurs. Their function and meaning are unknown, but they may be connected with the sense of taste. A remnant of the plicae fimbriatae can commonly be seen on the under surface of the human tongue.

The Epiglottis.[1]—The origin of the larynx, trachea, bronchi and lungs as a depression and bud from the floor of the pharynx will be dealt with later (p. 335) ; but the origin at the 3rd week of the furcula (Fig. 231), a process from which the epiglottis is derived, may be noted here. It arises from the 4th visceral arch. The upper part of the thyroid cartilage also arises from the 4th. The superior laryngeal is the nerve of the 4th arch, hence it supplies the epiglottis and upper part of the larynx. It is possible, as Mr. Frazer has suggested, that the furcula and tuberculum impar represent a median part of the floor of the primitive pharynx which has not been invaded by, or differentiated into, visceral arches.

The epiglottis and palate are peculiar to mammals. They separate

[1] J. Schaffer, *Anat. Hefte*, 1907, vol. 33, p. 455 (Evolution of Epiglottis).

the respiratory passage from the mouth. In all mammals the epiglottis lies within the naso-pharynx in contact with the soft palate, but with the acquisition of speech in man this relationship is lost.

Origin of the Salivary Glands.[1]—In the depression between the tongue and the mandible, formed by the opening out of the linguo-mandibular plate of epithelium, there appear two linear furrows (Fig. 228). From the hypoblast of the inner, by a process of budding, arises the submaxillary gland and duct; the sublingual arises by a number of buds from the outer groove (Fig. 228). The depression from which

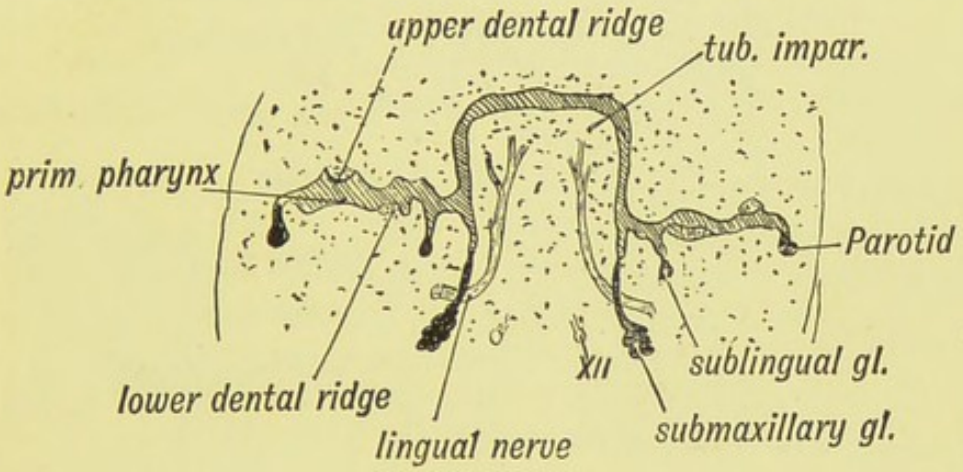


FIG. 228.—Showing the Origin of the Submaxillary and Sublingual Glands from furrows between the gum and tongue during the 6th week. (After His.)

they arise probably represents the first cleft recess; they are supplied by the chorda tympani, which corresponds to the recess. The **parotid gland,** which is the first of the salivary glands to be developed (5th week), springs as a bud from the angle between the mandibular and maxillary processes. Its duct is formed first as a groove, which later becomes enclosed to form a canal. It grows backwards in the connective tissue over the masseter, and at birth is comparatively superficial in position, but as the mandible and external auditory process grow, it sinks inwards to surround the styloid process, pushing the deep cervical fascia beneath it. In this way the stylo-maxillary ligament is formed from the fascia pushed in front of it. Its nerves are derived from the 3rd division of the fifth (auriculo-temporal). Salivary glands are accessory to the function of mastication, and hence are developed only in mammals.

Seessel's Pocket.—In the middle line of the roof of the pharynx (Fig. 229), just under the basi-occipital, there is a depression or recess of mucous membrane which receives this name. Its embryological significance is doubtful. Lymphoid tissue is developed in its walls

[1] See reference under Paulet, p. 235; also W. Rubashkin, *Anat. Hefte*, 1912, vol. 46, p. 343.

immediately after birth, and in the mucous membrane round it. It may be a remnant of the pharyngeal opening of the notochord (see p. 49). It is developed behind the oral plate. The adenoid tissue of the naso-pharynx continues to increase in amount until the age of

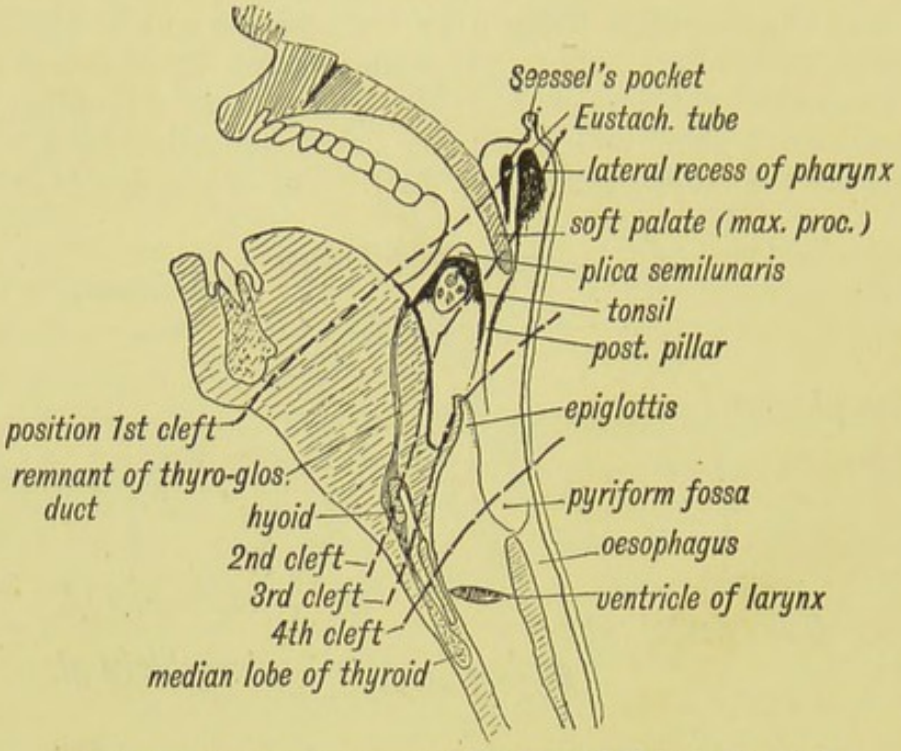


FIG. 229.—Showing the position of the Visceral Clefts in the Adult.

puberty, when it begins to undergo a slow process of atrophy (Symington).

The Tonsil.[1]—The tonsil arises comparatively late in foetal life from that part of the second cleft recess which is left between the soft palate and the tongue. In the 4th month eight or ten isolated buds of hypoblast push out from this recess or pocket into the mesoblastic tissue in the wall of the pharynx (Fig. 230). The buds afterwards canaliculize and form the crypts and glandular tissue of the tonsil. Follicles of lymphoid tissue—for the tonsil must be regarded as a lymphoid structure—begin to collect round these glandular buds in the last month of foetal life.

Concerning the origin of the lymphoid cells, both of the tonsil and the thymus, there are two quite distinct theories. The more recent (Gulland's) is that the epithelial (hypoblastic) cells, which form the glandular buds of the tonsil, give rise to broods of lymphoid cells; the older, that these lymphoid cells arise from the blood or surrounding connective tissue, creep in and form follicles round the glandular hypoblastic buds.

[1] For an account of the comparative anatomy and development of the tonsil see paper by Seccombe Hett and Butterfield, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 35.

A fold of mucous membrane, the **plica triangularis** (Fig. 230), passes from the lower part of the tonsil to the anterior pillar of the fauces. It represents the anterior or inner margin of the recess in which the tonsil is developed. Although present in the foetus, it commonly disappears in the adult. Its attachment to the tonsil marks a line of separation between an anterior and posterior group of tonsillar outgrowths (Fig. 231). The recess above the tonsil, sometimes crossed by a fold—the plica semilunaris—is a remnant of the recess of the second cleft in which the tonsil is developed (Fig. 230). In many mammals the tonsillar recess assumes the form of the finger of a glove, the blind end reaching almost to the angle of the jaw.

The tonsil is part of a great lymphoid system stationed along the alimentary canal. It reaches its fullest growth in youth, as is the

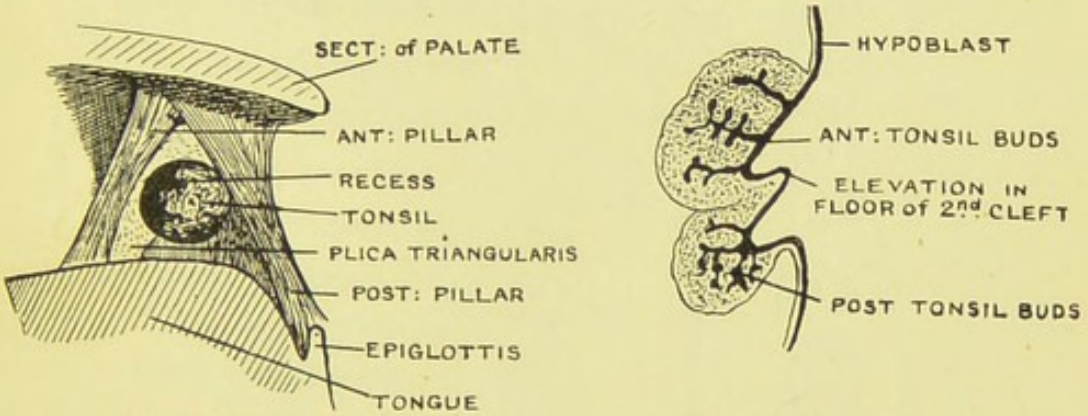


FIG. 230.—The Tonsil in a Human Foetus of 8 months. (Hett and Butterfield.)

FIG. 231.—Section across the 2nd cleft recess showing the Outgrowth of the Tonsillar Buds. The elevation between the anterior and posterior groups forms the lower part of the plica triangularis. (After Hammar.)

case with the lymphoid system generally; when active growth of the system is over, and especially in the years of decay, it becomes markedly reduced in size. The upper part of the 2nd cleft recess is included with the 1st in the Eustachian tube (Frazer). The lower part of the 2nd recess, containing the tonsil, is separated from the Eustachian segment by the growth backwards of the soft palate in the latter part of the second month. Occasionally the tonsillar recess projects outwards, and comes in contact with a tubular fistula representing the cervical sinus (see Fig. 217, p. 226).

The Pharyngeal Recess and Pharyngeal Tonsil.—At each side, the roof of the pharynx is produced outwards, behind the Eustachian tube and levator muscles of the palate, to form the **lateral recesses** of the pharynx. In the recess, and especially on the posterior wall of the pharynx between the recesses and also in and round Seessel's pocket, there is developed a submucous carpet of lymphoid tissue, the **pharyngeal tonsil,** which may become hypertrophoid. The lymphoid tissue of the naso-pharynx, when hypertrophoid, may press on and obstruct the Eustachian tube and respiratory space (see Fig. 229).

The Lingual Tonsil.—That part of the tongue (pharyngeal) produced between the 2nd and 3rd arches is studded with mucous glands which are surrounded by nodules of lymphoid tissue—the collective glandular mass receiving the name of lingual tonsil. It will thus be seen that from the 2nd cleft is produced a circum-pharyngeal ring of lymphoid tissue of great physiological and pathological importance.

The Thymus.[1]—The thymus arises in the same manner as the tonsil, only from the 3rd instead of the 2nd cleft (Figs. 232, 233 and 234). The 3rd cleft is represented in the adult by the space in front,

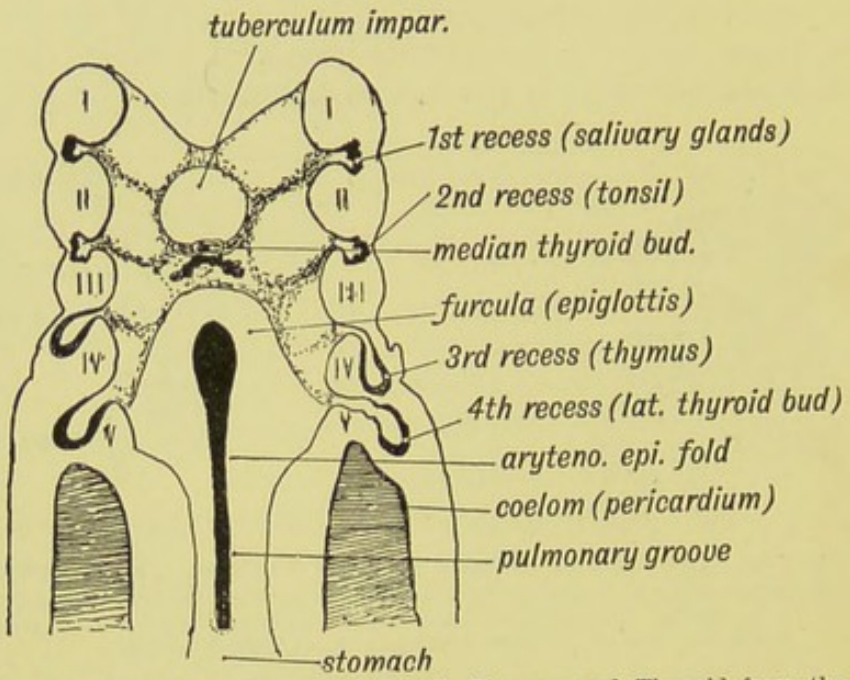


FIG. 232.—Showing the origin of the Tonsil, Thymus and Thyroid from the Internal Cleft Recesses during the 4th week. (After His.)

and on each side, of the epiglottis. It is crossed by the posterior pillars of the fauces, which represent a continuation of the palatal processes. The hypoblast in the 3rd cleft recess thickens, becomes pushed out as a minute pouch (4th week), shaped like a Florence flask, opposite the space between the 3rd (internal carotid) and 4th (arch of aorta) vascular arches (Fig. 217, p. 226). The neck of the glandular hypoblastic pocket becomes separated from the pharynx in the 6th week and usually disappears, but a strand of tissue frequently persists and represents the stalk of the outgrowth (Fig. 233). By a species of secondary budding the outgrowth becomes broken up into islands or separated acini. By a process of division the hypoblastic epithelium gives rise to meshwork of united cells (syncytium), in which broods of lymphoid cells arise during the 3rd month. The lymphoid cells—lymphocytes—become aggregated into follicles, where the production

[1] T. H. Bryce, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 91; P. Stohr, *Anat. Hefte*, 1906, vol. 31, p. 409; J. A. Hammar, *Ergebnisse der Anat.* 1909, vol. 19, p. 1 *Anat. Hefte*, 1911, vol. 43, p. 201 (Thymus).

of lymphocytes is continued. All trace of the original epithelial cells disappears. The concentric bodies, known as the corpuscles of Hassall,[1] were at one time supposed to represent remnants of the epithelium, but they are now known to be produced from single cells, which divide without a separation of the daughter cells thus formed. Hassall's corpuscles also arise from capillaries, some of which, after invading the thymus, become broken up into segments. The endothelial cells lining those segments may proliferate, occlude the lumen and thus give rise

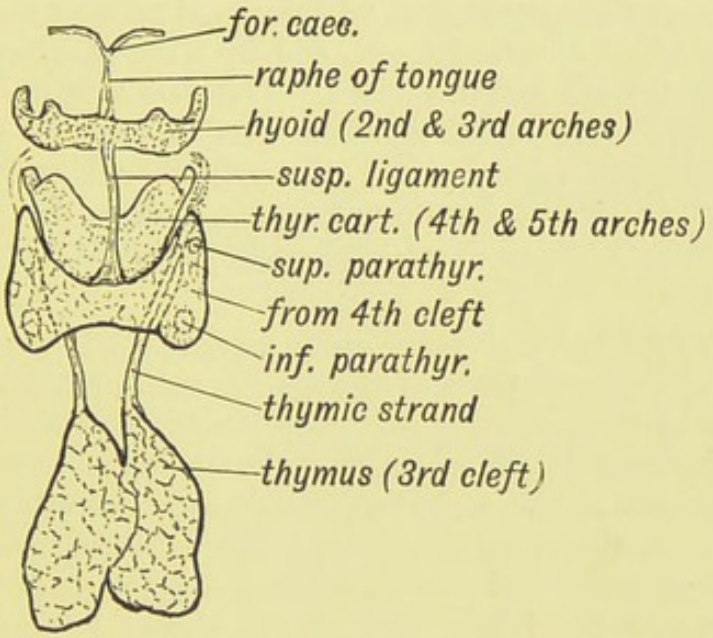


FIG. 233.—Diagram of the Thyroid and Thymus. The three parts of the thyroid body are indicated by a stippled line; the position of the parathyroids on the posterior aspect of the lateral parts is indicated.

to a Hassall's corpuscle (Nussbaum) (see also p. 320). The surrounding mesoblast supplies connective tissue stroma and capsule of the thymus. The lateral lobes come together under the ventral aortae and pericardium and ultimately assume a thoracic position along with these structures. The pointed upper extremity of each lateral lobe can be traced upwards in the fully developed foetus, under the lateral lobes of the thyroid towards the thyro-hyoid membrane (Fig. 233). These apical strands represent the stalk of the thymic buds. In its growth backwards it crosses dorsal to the lateral thyroid buds which arise from the 4th cleft (Fig. 233).

While Beard regards the thymus as the parent source of all the white blood corpuscles of the body, many interpret the appearances in quite an opposite manner and are of opinion that the leucocytes are brought within the hypoblastic element of the thymus along with the mesoblastic invasion of that element. Professor Bryce has demonstrated

[1] Dr. E. T. Bell defends the theory of their Epithelial origin, *Amer. Journ. of Anat.* 1906, vol. 5, p. 30.

that, white blood corpuscles appear in vertebrate embryos before any are seen in the thymus.

The thymus reaches its fullest growth in early childhood (3rd or 4th year), and continues large as long as the body is in a state of active growth. It begins to shrivel up when maturity is reached, and only a remnant is left as a rule, less remaining in men than in women. It receives its blood supply from the 4th aortic arches through the internal mammary. In manner of origin it resembles the tonsil; indeed it may be regarded as a buried tonsil.

There is a profuse production of lymphoid cells in the gill clefts of fishes, many of which wander out, and by their phagocytic properties help to keep the gill surfaces clean. This fact throws some light on the origin of so much lymphoid tissue from the second and third cleft recesses in higher animals. All these lymphoid structures of the pharynx are at their fullest development during the years of most active growth. In the adult, and especially in the old, they are markedly reduced in size.

The Thyroid.—At a very early period (3rd week), while the buccal and pharyngeal parts of the tongue are appearing as elevations on the floor of the primitive pharynx, the hypoblast in the middle of the furrow between those two parts of the tongue proliferates and forms a solid outgrowth. The bud thus formed grows downwards and backwards and soon bifurcates (Fig. 232). The bifurcated extremity, after redivision during the 2nd month to form a network of acini, becomes the **isthmus** and the larger part of the lateral lobes of the thyroid (Fig. 233). The stalk of the bud represents the thyro-glossal duct, the buccal opening of the duct remaining as the foramen caecum. The connective tissue and vessels of the thyroid are derived from the surrounding mesoblast; only the glandular elements arise from the hypoblast of the pharynx.

The median thyroid is present in all vertebrates and, although it arises in a manner which suggests that at one time it was a gland of the mouth, yet in no animal yet discovered does the duct persist. Its early origin in the embryo (3rd week) and its universal distribution in vertebrates point to the antiquity and importance of its function. We now know that many of the duct glands have a double function, separating both external and internal secretions. It is reasonable to suppose that, as regards the thyroid, its excretory function has been lost.

Thyro-glossal Duct.—In the great majority of subjects the thyro-glossal duct or tract completely disappears at the commencement of the 2nd month of development; the foramen caecum marks one extremity, while a ligament or a **pyramid** of thyroid tissue prolonging the isthmus towards the hyoid bone often marks the other extremity (Fig. 233). The pyramid of the isthmus may carry on it a detached

part of the thyroid-hyoid muscle—the **levator glandulae thyroideae.** The body of the hyoid bone is developed in the track of the thyro-glossal duct (Figs. 233, 234) and splits it up. Remnants of the duct or of secondary detached acini of the thyroid may persist and form cysts or thyroid tumours in the base of the tongue above the hyoid, and commonly between the genio-glossus muscles. They may also occur between the hyoid and thyro-hyoid membrane. The supra-hyoid or infra-hyoid bursae may also become cystic, and may be mistaken for thyro-glossal cysts (see Fig. 234).

In lower vertebrates the two lobes of the thyroid are stationed under the mandible. It is not uncommon to find in the right submaxillary

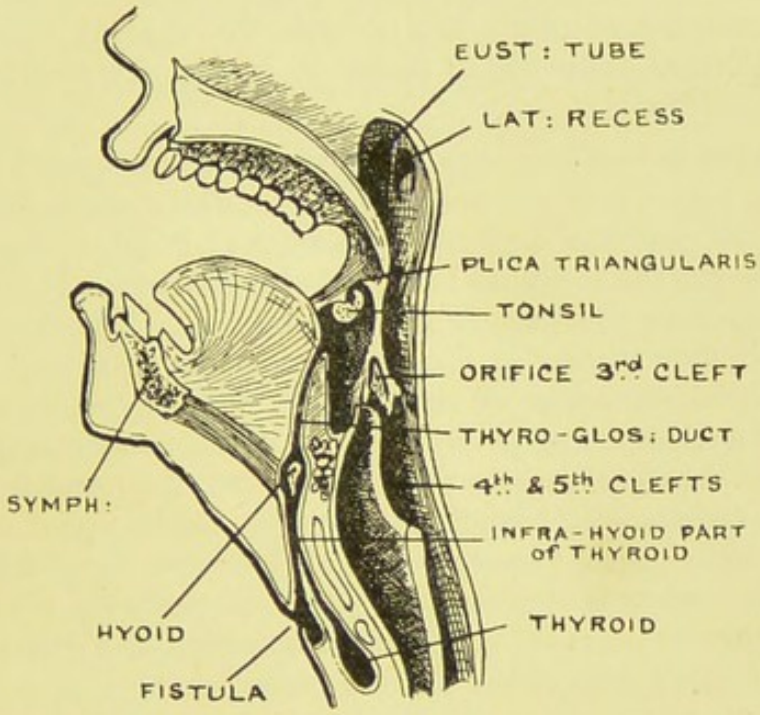


FIG. 234.—Section of the Pharynx to show the Track of the Median Thyroid Outgrowth. In rare cases there is a fistula connected with the thyroid, which opens in front of the larynx. The point of origin of the thymus outgrowth from the 3rd cleft may be marked by a recess containing lymphoid tissue as is represented in the figure. The pyriform fossa occurs at the site of the 4th and 5th clefts. The group of mucous glands in front of the epiglottis may give rise to cystic tumours.

region of man a thyroid tumour or cyst, evidently arising from an arrest in the descent of a part or of the whole of a lateral lobe. Aberrant masses of thyroid are often met with in the neck, and frequently become the site of cystic tumours. Occasionally the lumen may persist in the median thyroid and open as a fistula in front of the larynx (Fig. 234).

The **lateral lobes** of the thyroid are developed in part from the inner recess of the 4th cleft, the position of which is marked in the adult by the pyriform fossae (see Figs. 229 and 234), but a large part is derived in common with the isthmus from the median outgrowth (Fig. 233). These pockets, like the thymic of the 3rd cleft, soon lose their connection with the hypoblastic lining of the pharynx, and become isolated buds

which divide and re-divide until a collection of isolated acini is formed. The lateral lobes come in contact as they grow with the median lobe, under the laryngeal and tracheal groove in the floor of the primitive pharynx. In the blood supply of the thyroid one can see evidence of the complex origin of the body. The median outgrowth is mainly supplied by the superior thyroid arteries, while the inferior, derived from the vessel of the fourth arch, supply the lateral outgrowths. It is only in mammals that a thyroid element arises from the 4th clefts; it cannot be traced as a separate element after the 3rd month. Indeed, Soulie and Verdun deny that there is an element derived from the 4th cleft in mammals. In the process of development minor buds of the thyroid may become detached. These form **accessory** thyroid bodies. In manner of origin and growth the thyroid resembles the tonsil and thymus, but unlike these it is not transformed into a lymphoid structure.

Para-thyroids.[1]—There are usually two para-thyroid bodies on each side, an upper and a lower (Fig. 233). Both are usually applied to the deep or posterior aspect of the thyroid body, the upper being situated amongst the terminal branches of the superior thyroid artery, the lower amongst the branches of the inferior. They are flattened bodies, about 6 to 8 mm. in diameter, yellowish in colour when contrasted with the substance of the thyroid, but they cannot be recognized with certainty except by their microscopical structure. The upper are developed as outgrowths from the 3rd, the lower from the 4th inner cleft recesses. In structure they are made up of reticulating columns of cells, with vessels arranged between the columns, thus resembling in structure the carotid body, and probably also in nature and origin the medullary part of the supra-renal. Their presence is essential to the function of the thyroid body.

Carotid Bodies.—The carotid body occurs at the inner side of the fork between the internal and external carotid arteries. The commencement of the internal carotid represents the artery of the 3rd arch; that of the external carotid, the ventral aortic trunk. The body is developed in the wall of the pharynx at the ventral end of the 3rd cleft with the thymic outgrowth (see Fig. 217, p. 226). It receives a large supply of nerves from the superior cervical ganglion, and it contains a rich network of vessels. Swale-Vincent regards it as similar in nature and origin to the coccygeal body and medulla of the supra-renal (see p. 389).

[1] For a full account of the comparative anatomy of the parathyroids see Dr. Forsyth's Memoir in *Journ. Anat. and Physiol.* 1908, vol. 42, pp. 140, 237. He found that the parathyroids are irregular in number and often aberrant in position, and that it is very difficult to distinguish microscopically between embryonic thyroid tissue and adult parathyroid tissue. The parathyroids were discovered by Sandstrom in 1880. See also F. D. Thompson, *Phil. Trans.* 1911, Ser. B, vol. 201, p. 91.

CHAPTER XVI.

ORGANS OF DIGESTION.

Divisions of the Alimentary Tract.[1]—It is always advantageous to approach the development of every system of the body by a recapitulation of the various evolutionary stages, so far as these stages are known to us. As regards the evolution of the various parts of the alimentary system, comparative anatomy does not help us greatly, because in even the lowest forms of vertebrates the main parts are already present—the mouth, oesophagus, stomach, liver, small intestine and large intestine. In tracing the development of the earliest digestive cavity (archenteron) of the human embryo (p. 30), we saw that its origin was similar to that of the lower invertebrates and that its first mouth apparently became converted into the primitive streak and blastopore. A new mouth is formed by the breaking down of the bucco-pharyngeal membrane (oral membrane, Fig. 235) early in the third week; we shall see that a new vent or anus is formed at a later stage in the development of the human embryo—namely, at the commencement of the 3rd month. To understand these peculiar facts comparative anatomy has failed to help us, because we know nothing of the early forms of those animals in which the mouth and anus of vertebrates were evolved. There are other reasons why comparative anatomy does not help us to understand the early stages in the development of the alimentary system. They will be understood by a reference to Fig. 235. In the human embryo a large part of the alimentary cavity has been specialized and precociously developed to form the yolk sac for the nourishment of the embryonic tissues; the embryonic adaptations mask and obliterate the ancestral stages. With the development of the cephalic and caudal folds of the embryonic plate the archenteron becomes differentiated into three parts (Fig. 238)—the **Mid-gut**, which represents the body and chief part of the primitive cavity; the **Fore-gut**[2] and **Hind-gut**. There can be no doubt

[1] For recent literature on development of alimentary system see A. Oppel, *Ergebnisse der Anat.* 1905, vol. 15, p. 207; 1906, vol. 16, p. 216.

[2] O. Grosser, *Verhand. Anat. Gesellsch.* 1911, p. 173 (Origin of Fore-gut).

these represent three functional divisions. The mid-gut is supplied by the superior mesenteric artery and serves for one kind of digestion and absorption; the hind-gut, supplied by the inferior mesenteric artery, is mainly excretory in nature; the fore-gut, separated by the outgrowth of the liver from the mid-gut, is supplied mainly by the

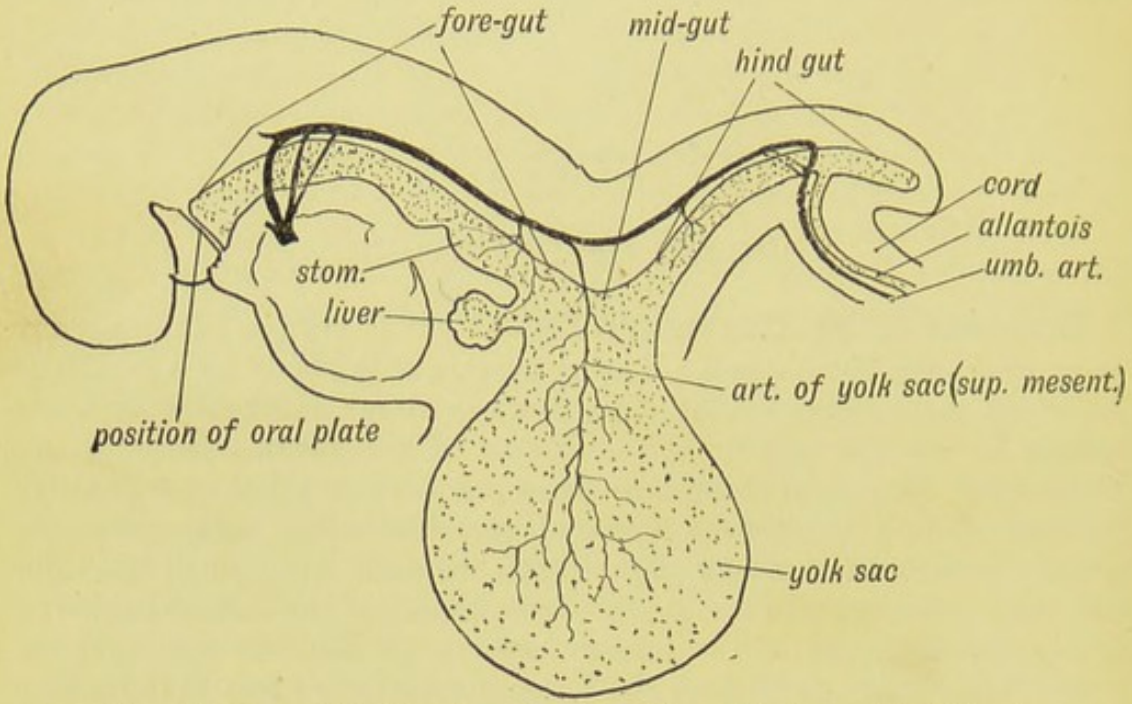


FIG. 235.—The Form of the Alimentary Canal in a Human Embryo of the 3rd week.

coeliac axis and serves the preparatory purposes of digestion. The pharynx, respiratory tract, oesophagus, stomach, liver and pancreas represent parts of the fore-gut. The hind-gut gives rise to the colon from the splenic flexure to the anus; the allantois, bladder and urethra are also separated from its hinder end—the cloaca.

Differentiation of Parts.—How rapidly the various parts of the alimentary system are differentiated during the 3rd week of development will be seen by comparing Figs. 236 and 237. Fig. 236, which represents the alimentary tract of a human embryo near the beginning of the 3rd week, shows the pharynx large, the lung bud beginning to arise from its floor; the oesophagus and stomach and first part of the duodenum scarcely marked off from one another. The evagination to form the liver indicates the junction of the fore-gut with the mid-gut. The latter division is in wide communication with the yolk sac. The various parts of the hind-gut are clearly indicated. The condition towards the end of the 3rd week is shown in Fig. 237. The oral membrane is gone; the pharynx is relatively smaller; the outgrowth of the pulmonary system is now very apparent, the oesophagus and stomach are longer and narrower; the liver outgrowth has become massive; the mid-gut is tubular, and the neck of the yolk sac reduced

to a duct (vitello-intestinal duct). The parts of the hind-gut have assumed a more definite shape.

Primitive Mesentery and Coelom.[1]—It will be remembered that almost as soon as it appears, the mesoblast is cleft into two layers—an outer applied to the epiblast to form the somatopleure or body wall, and an inner to the hypoblast or archenteron to form the visceral wall or splanchnopleure. The cavity formed by the cleavage of the mesoblast is the coelom. Originally the cavity was designed for the purposes

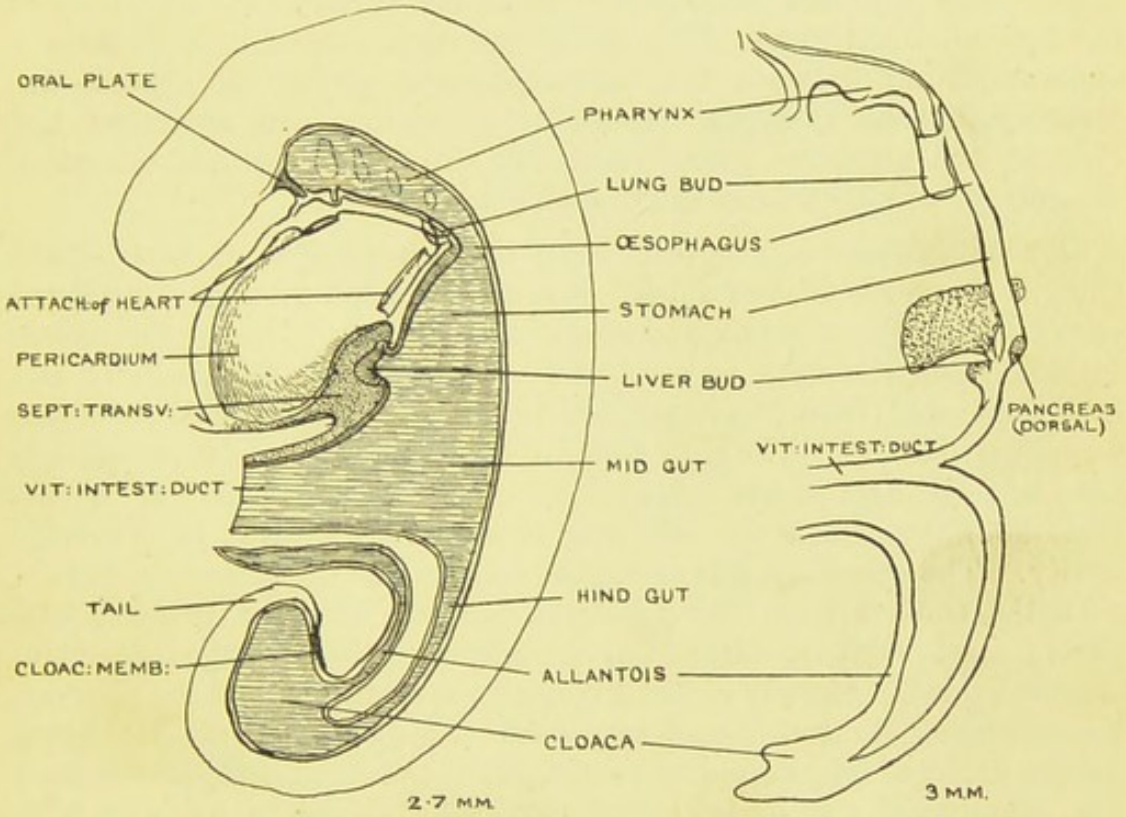


FIG. 236.—The Alimentary System of a Human Embryo 2·5 mm. long, and near the commencement of the 3rd week of development. (Professor Peter Thompson.)

FIG. 237.—The Alimentary System of a Human Embryo 3 mm. long, and about the end of the 3rd week of development. (After Professor Broman.)

of excretion; its wall also served as the nidus for the reproductive cells. In vertebrates the coelom came to serve the purposes of a large bursa, in order that the muscular movements of the digestive canal, lungs and heart might proceed without undue friction. Hence the alimentary canal is developed within the cavity of the coelom; it is situated within the median partition, which separates the right coelomic space from the left. The median partition suspends the alimentary canal to the dorsal or vertebral wall of the body cavity, and forms the **primitive dorsal mesentery**; the part of the median partition which fixes the tract to anterior or ventral wall of the body cavity forms the

[1] Broman, *Ergebnisse der Anat.* 1905, vol. 15, p. 332.

primitive ventral mesentery. This mesentery disappears from the mid- and hind-gut, and hence the right and left coelomic spaces in the abdomen are thrown into one, and form the peritoneal cavity. The only parts of the alimentary canal which never come to lie within the coelom are the anterior part or pharynx and the most posterior part of the cloaca. The anterior part of the coelomic space forms the cavity of the pericardium, which lies beneath the pharynx (Fig. 236); it is separated from the peritoneal space by a transverse partition—the **septum transversum**,[1] already well marked at the beginning of the 3rd week. The primitive oesophagus crosses the upper or dorsal border of the septum transversum (Fig. 241). At each side of it is situated a communication between the pericardial and peritoneal spaces—the **pleuro-peritoneal passages.** These two passages are separated not only by the primitive oesophagus, but also by the primitive median mesentery, which encloses the oesophagus (Fig. 241).

Oesophagus.—In the 3rd week the oesophagus of the human embryo resembles that of a fish; it is merely a sphincter or constricted part between the pharynx and stomach (Fig. 236). During the second month, when the neck is being differentiated, and the pharynx and head separated from the heart and thorax, the oesophagus undergoes a rapid elongation. The chief cause of the elongation of the oesophagus is to be sought for in the development of the lungs and pleural cavities (Fig. 239), by which the stomach is forced backwards in the body cavity. The oesophagus is of double origin; the upper part is derived with the trachea from the hinder part of the pharynx (paratracheal part); the lower part arises from the primitive alimentary canal (retro-tracheal part). Already in the 3rd week the hinder part of the pharynx is undergoing elongation and separation (Fig. 237); in the 4th week, by the union of lateral fold or partitions, the trachea is separated from the oesophagus. It is not uncommon for children to be born with these two parts irregularly separated (Fig. 240). The paratracheal part ends blindly, and is surrounded by striated pharyngeal musculature; the retrotracheal part opens from the trachea, and is covered by non-striated muscle.[2] The oesophagus is at first lined by columnar ciliated epithelium, but in the 2nd month, as it elongates, the epithelium proliferates, forming several irregular layers, which almost occlude the lumen of the tube for a time. In the 5th month glands are formed in the submucous tissue. At the beginning of the 2nd month the oesophagus is only 2 mm. long; at birth it measures 100 mm. (4 inches). Its commencement is surrounded by a sphincter formed by part of the inferior constrictor of the pharynx; above this sphincter, in later life, a pouch (**retropharyngeal diverticulum**) may arise; such pouches are never congenital in origin. At the lower end

[1] P. Thompson, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 170.

[2] See Keith, *Brit. Med. Journ.* 1910, 1. p. 301. For development of mucous membrane see F. P. Johnson, *Amer. Journ. Anat.* 1910, vol. 10, p. 521.

the oesophagus is also closed by a sphincter. The muscle coats are differentiated in the 3rd month, the circular first, the longitudinal later.

Development of the Liver.[1]—Before proceeding to describe the development of the stomach, it is convenient to deal first with the liver, because the manner in which that viscus arises gives the key to the complicated developmental changes of the abdominal viscera. The human liver in its development repeats broadly the forms met with in ascending the animal scale. In amphioxus the liver is merely a caecal diverticulum of the digestive canal; in amphibians it is a modified

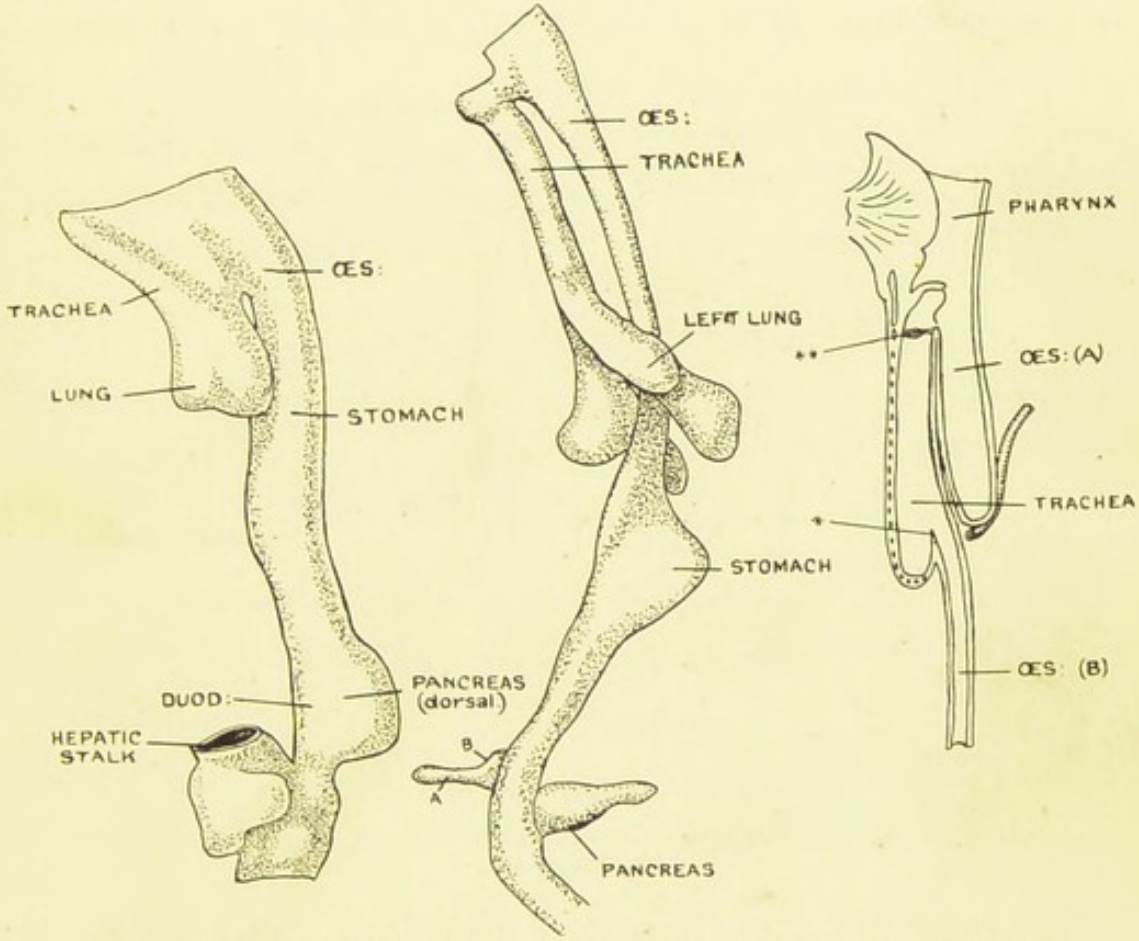


FIG. 238.—Fore-gut of an Embryo in the 3rd week of development. (Broman.)

FIG. 239.—Fore-gut of an Embryo in the 4th week of development. (Broman.)

FIG. 240.—Irregular Separation of the Trachea and Oesophagus. The upper or pharyngeal part of the oesophagus forms a blind sac; the lower part passes from the trachea to the stomach. The normal trachea—oesophageal septum—is marked *; the abnormal septum **.

tubular gland—the hepatic cells being arranged in cylinders around the bile ducts. In mammals the tubular arrangement is lost and a lobular form substituted. In every case it is so placed that the blood, laden with the products of absorption from the alimentary tract or from the placenta, must come into intimate relationship with the hepatic tissue before passing into the general circulation of the body.

[1] O. Charnock Bradley, *Journ. Anat. and Physiol.* 1908, vol. 43, p. 1; F. P. Mall, *Amer. Journ. Anat.* 1905, vol. 5, p. 227.

To understand the development of the liver, the condition of parts at the commencement of the third week must be studied. At that time, the anterior wall of the yolk sac and that part of the fore-gut which becomes the stomach, lie in the septum transversum, or to be more accurate, in the substance of the dorsal and ventral mesentery which have not yet been differentiated from the septum transversum (Figs. 236, 241). When the liver bud grows out, it springs from the junction of the fore-gut and yolk sac (Fig. 241) ; and spreads into the tissue which becomes the ventral mesentery of the fore-gut. The part of the gut from which it springs afterwards becomes the second stage of the duodenum. It is at first a hollow, fold-like diverticulum of

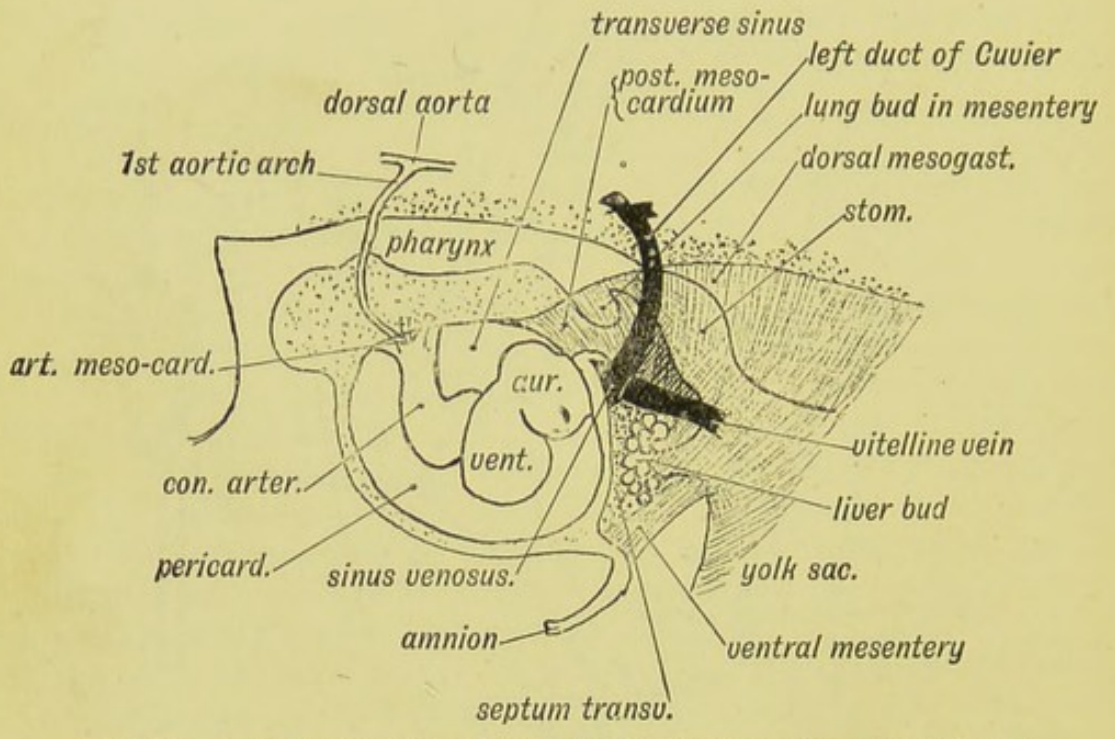


FIG. 241.—The Mesentery of the Fore-gut and its Contents, viewed from the left side (schematic).

the gut hypoblast ; from the upper or cranial end of the diverticulum arises the outgrowth of liver tissue ; its lower or caudal end becomes the gall bladder and main bile ducts (Fig. 238). The diverticulum is surrounded in the mesogastrium by a mass of mesoblastic cells which form the vessels, capsule and connective tissue of the liver. From the hollow hepatic diverticulum arise right and left solid processes of hypoblastic cells, which invade and form masses round the right and left veins from the yolk sac—the vitelline veins (Figs. 241, 242). Professor Bradley [1] has pointed out that the right and left masses do not correspond to the right and left lobes of the fully formed liver ; the separation between the right and left lobes is formed late, and has no functional significance. A line from the fundus of the gall bladder

[1] *Journ. Anat. and Physiol.* 1908, vol. 43, p. 1.

to the caval impression divides the liver into embryonic and functional right and left halves (Cantlie).

The hepatic buds are developed just behind the sinus venosus and between both the vitelline and umbilical veins which are also situated in the ventral mesentery (Figs. 241, 242). The veins are broken up by the ingrowth; from them starts an invasion of venous capillaries which, with the surrounding mesoblast, penetrates the liver buds and breaks the solid processes of hypoblast into reticulating cylinders. According to F. T. Lewis the hepatic processes perforate and proliferate

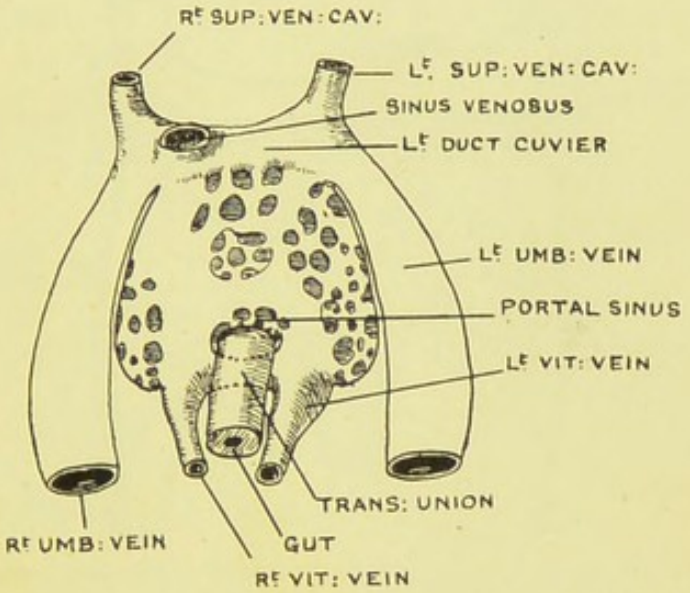


FIG. 242.—The Liver Mass invading the Vitelline Veins during the 3rd week of development. (Professor Mall.)

within the lumina of the vitelline veins, the venous capillaries thus arising directly from venous spaces. Secondary processes arise from the primary hepatic reticulating cylinders and form smaller and smaller meshes of hepatic cells. The earlier cylinders show as many as three or four cells on section, with, in their midst, a bile duct. The later-formed cylinders are composed of a single or an irregular double row of cells. During the 3th and 4th months of foetal life there is a particularly active growth in the liver, which comes to occupy the upper half of the abdominal cavity. By the third month after birth the hepatic lobules, with the intra- and sub-lobular arrangement of portal and hepatic veins, have appeared. The subcapsular layer of hepatic tissue retains the foetal arrangement, growth evidently taking place chiefly in this layer. The bile ducts probably represent the lumina of the original tubular hepatic buds.

Veins of the Liver.—Within the liver the two vitelline veins are divided into afferent or distributing vessels and efferent or collecting vessels (Fig. 242). In the 4th week a number of remarkable changes occur: (1) The left umbilical vein, which opens

at first in the left duct of Cuvier, establishes a communication with the portal sinus in the transverse fissure of the liver (Fig. 243); (2) the right umbilical vein disappears; (3) a new channel—the *ductus venosus*—is opened between the portal sinus and the inferior vena cava; the right vitelline vein, all except its terminal part, becomes obliterated (Fig. 243).

Gall Bladder and Bile Ducts[1] (Fig. 253).—The hepatic diverticulum, from which the liver buds arise, may be regarded as a

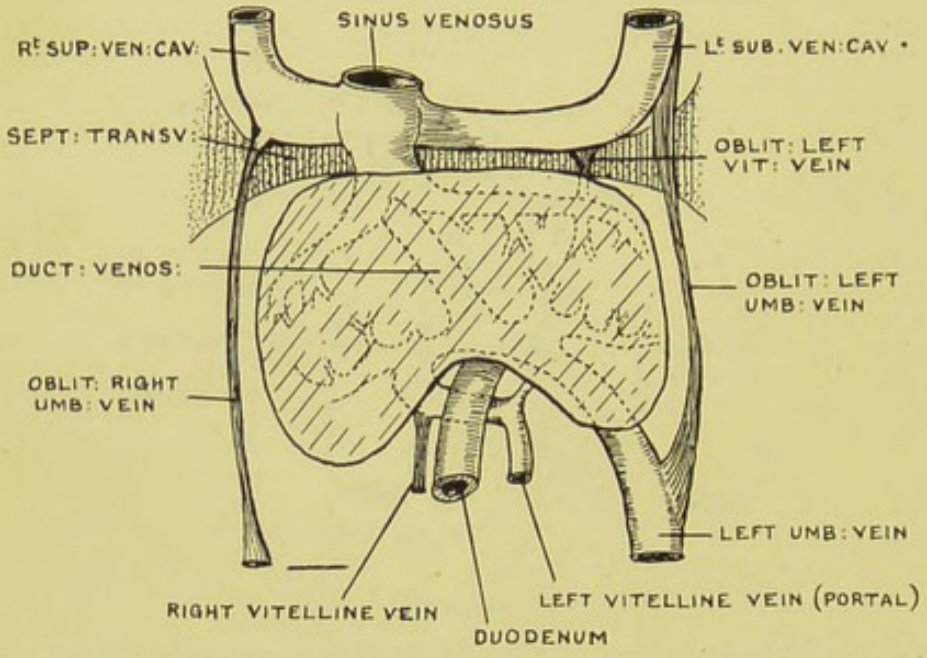


FIG. 243.—Diagram to show the Transformation in the Veins round the Liver at the end of the first month of development. (After Professor Mall.)

direct extension of the wall of the fore-gut. From its hinder part (Fig. 238) are developed the common bile duct, the gall bladder, and the cystic duct, formed at the junction of the gall bladder and common bile duct. The hepatic ducts arise within the stalks of the solid hepatic buds. At first the gall bladder lies in the ventral mesentery (gastro-hepatic omentum)—a position which is permanent in some vertebrates and may occur as a rare anomaly in man. In the second month it becomes included and buried in the hepatic tissue; at a later date it assumes its superficial position. The lumen of the ducts is occluded by an epithelial proliferation until the 3rd month. Occasionally the bud for the gall bladder divides, giving rise to a bifid or double gall bladder. Round the termination of the common bile duct a sphincter is developed from the musculature of the duodenum. The manner in which the common bile duct, hepatic artery and portal vein come to occupy the free edge of the ventral mesogastrium will be described in another paragraph.

[1] A. Pensa, *Anat. Anz.* 1912, vol. 41, p. 155.

Separation of the Liver from the Septum Transversum.—As the liver buds develop, the dorsal and ventral mesenteries of the fore-gut, in the substance of which the liver and stomach are formed,

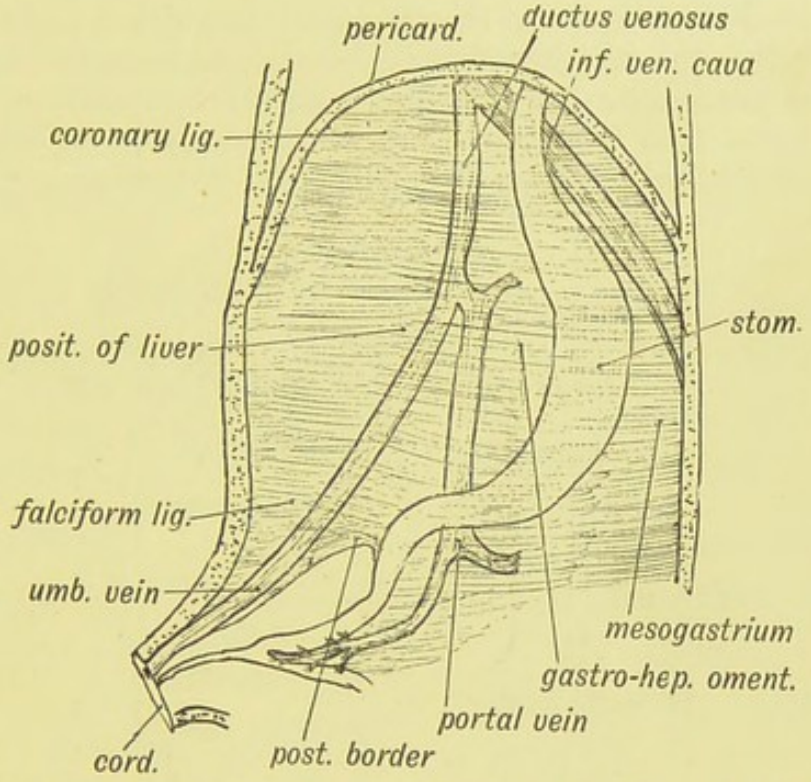


FIG. 244.—The origin of the Peritoneal Ligaments connected with the Liver. Diagram of the foetal relationship of the ventral mesentery to veins and the stomach, the liver being removed.

become differentiated from the tissues of the septum transversum. The typical arrangement of these membranes, as seen in reptiles, is shown in Fig. 244. In the dorsal mesentery (mesogastrium) lie the inferior vena cava and arteries of the fore-gut; in the ventral

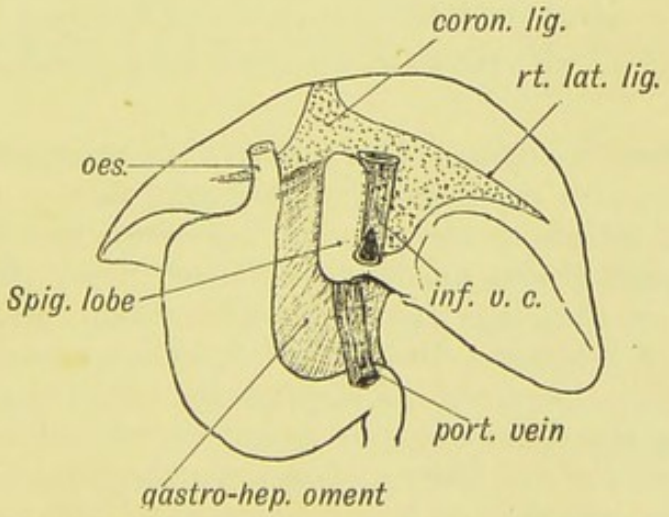


FIG. 245.—The Liver viewed from behind to show its relationship to the Gastro-hepatic Omentum, part of the Ventral Mesentery.

mesentery (gastro-hepatic omentum) are contained the terminal parts of three veins—the umbilical, portal and inferior vena cava, the last vessel reaching the ventral mesentery by passing to the right of the oesophagus. The liver develops within both ventral and dorsal mesenteries, but that part of the mesentery in which it and the inferior vena cava lie—the **mesohepaticum**—becomes separated from the part which is occupied by the bile ducts, portal vein and the stomach. Broman found that this separation, which occurs in all higher vertebrates, takes place towards the end of the 3rd week in the human

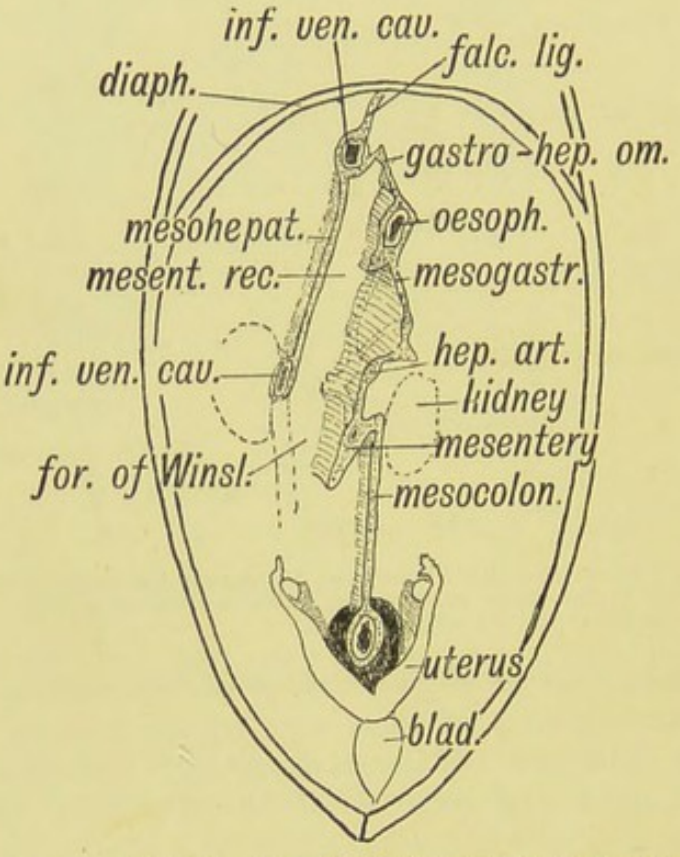


FIG. 246.—Diagram of the Primitive Attachments of the Visceral Mesenteries to the Posterior Wall of the Abdomen as seen in a Low Primate (Lemur Coronatus). The condition illustrates the earlier developmental phases of the human foetus.

embryo, by the development of a recess in the mesentery—the **Mesenteric Recess**—which commences to the right side of the duodenum, and extends forwards to the septum transversum (see Fig. 246). The **mesenteric recess** (bursa omentalis, Broman) forms the vestibular or hepatic part of the lesser sac of the peritoneum, and extends from the foramen of Winslow to behind the Spigelian lobe of the liver (see Fig. 247). When the liver and stomach are removed in the course of dissection, the attachment of the mesohepaticum will be seen to bound the hepatic part of the lesser sac on the right, while on its left side, the dorsal mesogastrium has been evaginated to form the main body of the lesser sac (Fig. 247). Thus it will be seen that the dorsal and ventral

mesenteries of the fore-gut are split into a right lamina—the mesohepaticum, and a left lamina—the mesogastrium—by the development of a recess which forms the earliest and first part of the lesser sac (see Fig. 246). The mesenteric recess during the 3rd and 4th weeks, before the diaphragm has been formed, extends forwards in the mesentery of the oesophagus almost to the right lung bud—a condition which is constant in reptiles. When the lungs expand and the diaphragm

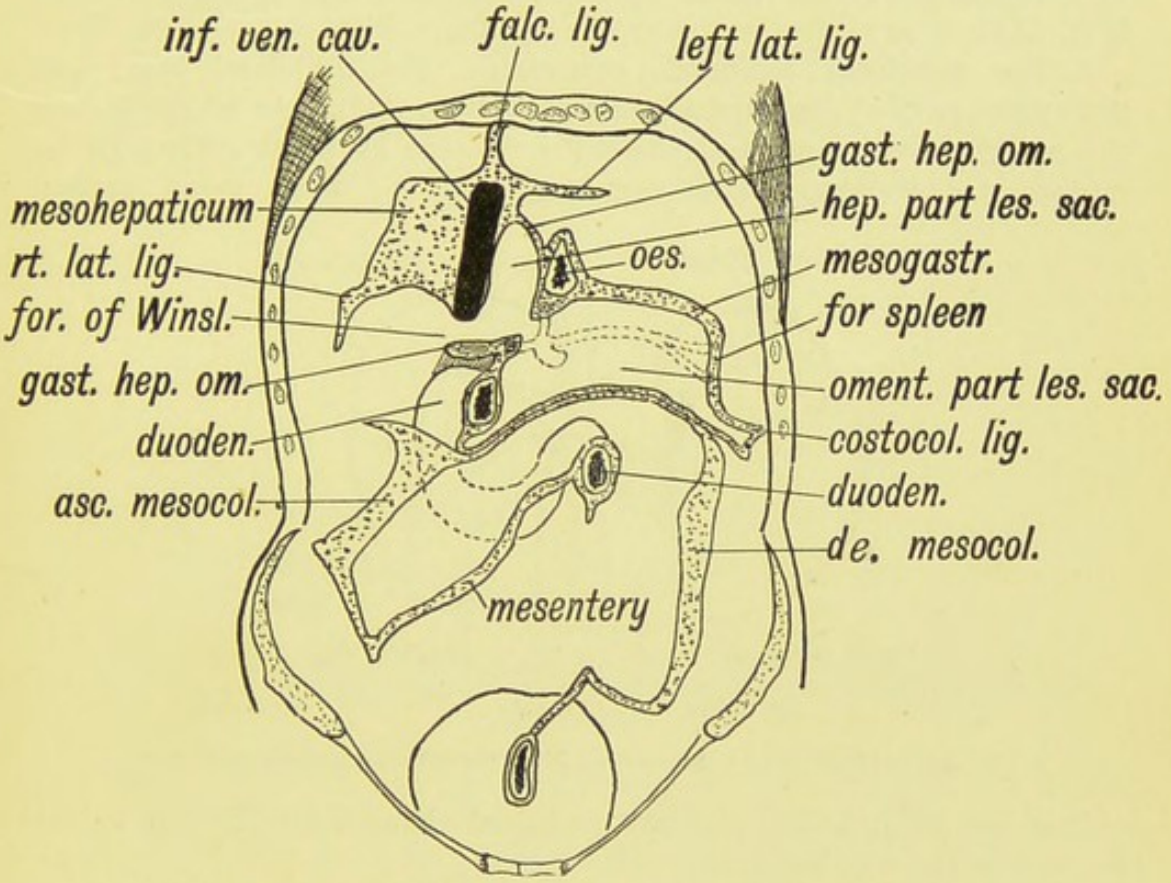


FIG. 247.—Diagram of the Attachments of the Visceral Mesenteries to the Posterior Abdominal Wall of an Adult. The three chief modifications seen, when compared with Fig. 246, are (1) the extensive adhesion of the mesogastrium, (2) of the mesocolon, and (3) mesentery of small intestine, to the posterior wall of the abdomen.

is formed the apical part of the mesenteric recess is cut off and left within the thorax—to the right of the oesophagus, and just above the diaphragm. To this detached part, Broman has given the name of **infra-cardiac bursa.** It usually disappears at the end of foetal life.

The Ligaments of the Liver.—When the liver separates from the septum transversum at the beginning of the 3rd month of development, it is attached to the walls of the abdomen by peritoneal ligaments derived from the dorsal and ventral mesenteries of the fore-gut (Figs. 244, 245). These are the following:

1. **The gastro-hepatic omentum** is that part of the ventral mesentery which passes from (1) the oesophagus, (2) lesser curvature or ventral

border of stomach, and (3) first stage of duodenum to (1) the diaphragm, (2) the posterior part of the longitudinal fissure of the liver, the ductus venosus lying within its hepatic attachment, and (3) the transverse fissure of the liver (Fig. 245). The portal and umbilical veins lie in the ventral mesentery (Fig. 244); the hepatic artery passes by it to the liver. The right or free border of the gastro-hepatic omentum, with the falciform ligament containing the remnant of the umbilical vein, represents the posterior border of the primitive ventral mesentery (Fig. 244).

2. **The falciform ligament,** containing the umbilical vein, also represents part of the ventral mesentery (Fig. 244). At an early stage the umbilical veins reached the sinus venosus by passing through the septum transversum. The terminal parts of both veins become

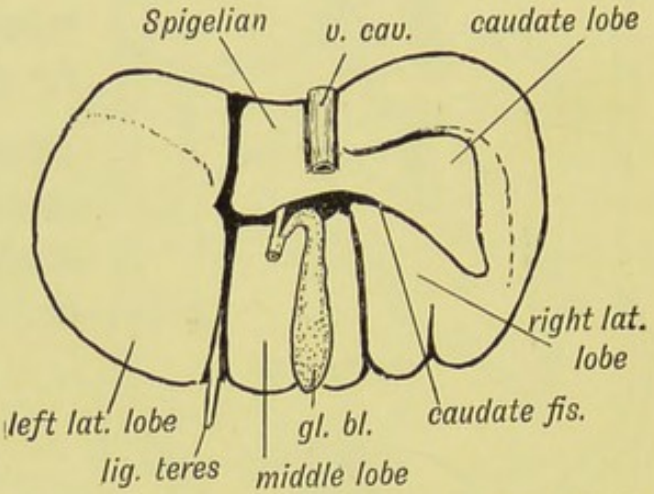


FIG. 248.—Diagram of a Mammalian Liver viewed from behind and below.

obliterated (Fig. 243); the new terminal channel for the left vein is formed in the ventral mesentery.

3. **The coronary, the right and left lateral ligaments, and the attachments to the vena cava and diaphragm.**—These ligaments, which are the chief hepatic bonds, are derived from the mesohepaticum in the early part of the 3rd month, when the liver is being separated from the diaphragm by invading pockets or recesses of peritoneum. It would be extremely convenient to retain the term mesohepaticum to designate the bonds between the liver and diaphragm in the adult, looking on the right and left lateral ligaments as merely processes of the mesohepaticum (Fig. 247).

Morphology of the Liver.[1]—The liver of orthograde (upright) animals (man, anthropoids) differs widely in form and lobulation from that of mammals generally, but Professor Arthur Thomson has shown

[1] I have dealt with some of the factors which determine the shape of the liver in lectures on enteroptosis; see *Lancet*, 1903, March 7th and 14th. For recently reported case of malformation of liver see E. Barclay Smith, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 346.

that traces of the fissures and lobes of the typical mammalian liver can be seen in the human organ. The liver of a dog or dog-like ape consists of three main lobes—right, middle and left—and two accessory lobes—the caudate and Spigelian (Fig. 248). In man the right and middle lobes have fused, but traces of the fissure which separates them (the right lateral fissure) are frequently to be seen in the liver of the newly born child (Fig. 249). The **caudate lobe** has been reduced in man to a vestige, but in the third month foetus it is of considerable size (Fig. 249). It projects from the liver at the upper boundary of the

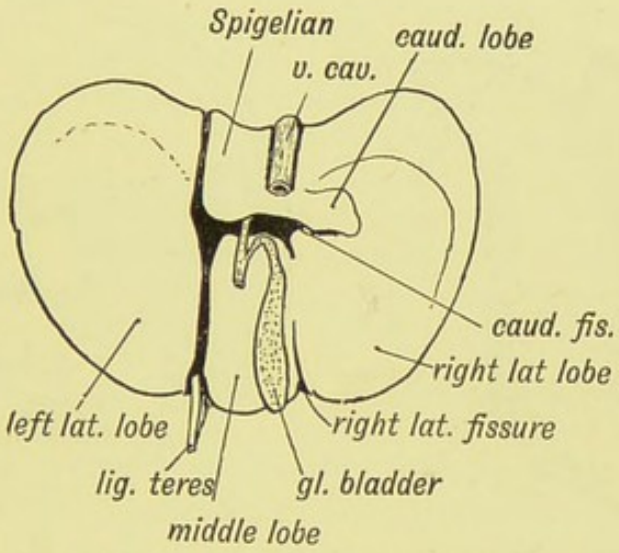


FIG. 249.—The Lower Surface of the Liver of a Human Foetus during the 3rd month, showing Vestiges of Fissures and Lobes of the typical Mammalian Liver.

foramen of Winslow; in many animals it rivals the right lobe in size. The caudate fissure separates the caudate from the right lobe, and a trace of this fissure is very frequently to be seen in the human liver (Fig. 249). Irregular lobulation of the liver is not uncommon; a form in which the gall bladder is deeply buried in an abnormal fissure of the liver is occasionally seen, but the explanation of such anomalies has not yet been investigated.

Changes in the Liver after Birth.—During foetal life the liver increases rapidly in size in comparison with the other abdominal organs. At birth it occupies nearly half of the abdominal space, and measures $\frac{1}{13}$th of its final volume. The left lobe is nearly equal to the right in size, and reaches to and may overlap the spleen. Up to the time of birth nucleated red blood corpuscles multiply within it. After birth two factors come into operation which lead to a diminution in size and change of shape. It is supplied before birth by placental instead of portal blood; at birth, its blood-forming function ceases; its rate of growth becomes proportionately less than that of other abdominal organs. The stomach, formerly empty, is now filled, and presses the liver towards the right side, causing a change in shape and partial

atrophy of the left lobe. Riedel's lobe is a linguiform prolongation of the right lobe below the 10th right costal cartilage caused by compression. It is never present at birth.

The Stomach.—The stomach is developed out of that part of the fore-gut which lies between the oesophagus and pharynx in front, and the yolk sac, duodenum and liver bud behind (Fig. 236, p. 249). Its form at the end of the first month is shown in Figs. 237 and 239. At first its dorsal and ventral mesenteries are undifferentiated from the

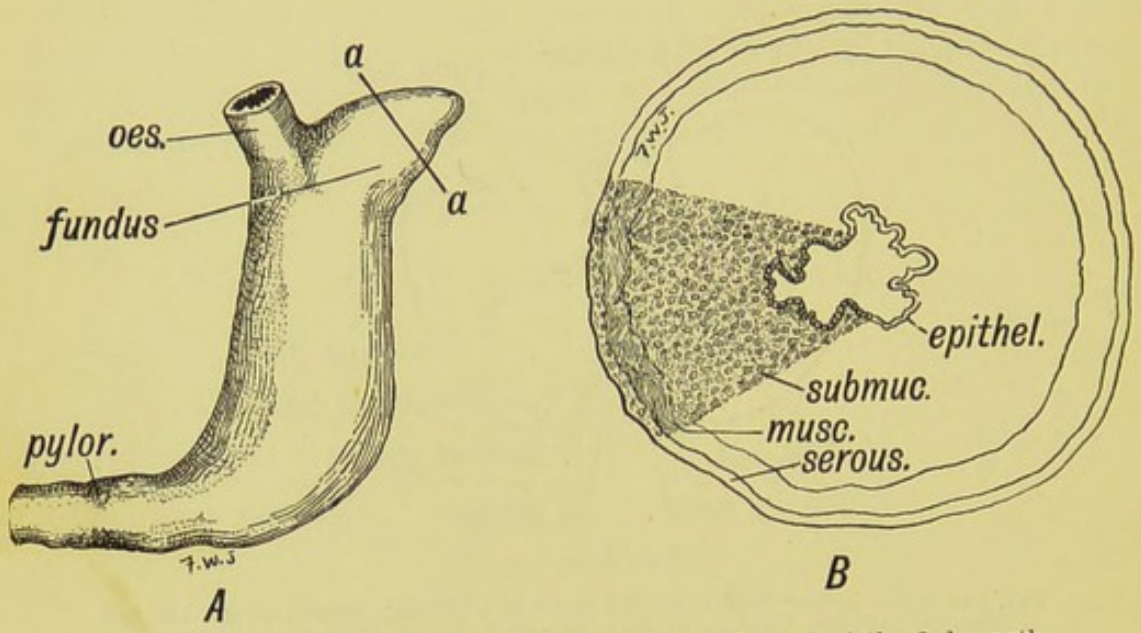


FIG. 250, *A*.—Stomach of a Human Foetus about the end of the 3rd month, showing the outgrowth of the Fundus of the Stomach. (F. W. Jones, *Proc. Anat. Soc.* 1901.)

B.—Section across the Fundus (the line of section is indicated in *A*), showing the differentiation of the four coats of the Stomach. (F. W. Jones, *Proc. Anat. Soc.* 1901.)

septum transversum. When in this condition, the stomach is situated below the lower cervical and upper dorsal region of the spine. In the 4th week the gastric part of the fore-gut shows a dorsal bulging—the greater curvature. As the liver and gut are developed, the stomach separates itself from the septum transversum and comes to be suspended from the dorsal wall of the coelom by the **dorsal mesogastrium** (Fig. 244). The gastro-hepatic omentum is part of the **ventral mesogastrium.** The oesophageal end of the stomach lies between the spinal fibres of the diaphragm which develop in its mesentery ; the outgrowth of the liver bud fixes its pyloric end in the ventral mesogastrium. Three changes quickly ensue, the one being partly dependent on the other :

(1) The dorsal border of the stomach, to which the dorsal mesogastrium is attached, grows more rapidly than the ventral border to which the ventral mesogastrium is attached. The **greater** and **lesser curvatures** are thus produced.

(2) The **fundus** of the stomach is produced as an outgrowth from the

dorsal border, its origin being similar to that of the caecum from the small intestine (Fig. 250, *A*).

(3) While the ventral mesogastrium attached to the lesser curvature undergoes a relatively slow growth, the dorsal mesogastrium is affected by a very rapid expansion. Because of the discrepancy in the growth of these two membranes, the greater curvature of the stomach becomes freely movable, while the lesser curvature remains relatively fixed.

The three factors just enumerated lead to a rotation of the stomach, the greater curvature moving to the left, while the surfaces, formerly right and left, carrying the corresponding vagus nerves, become posterior and anterior. The rotation is already evident at the end of the first month of development (Broman). All of these changes are adaptations to allow the stomach to expand when filled and contract when emptied. As the stomach fills, it is the greater curvature which expands; the lesser curvature remains relatively fixed. By the commencement of the 4th month the stomach is demarcated into a wide, vertical, **cardiac** part, and a narrower horizontal or **pyloric** part. The pyloric sphincter becomes differentiated towards the end of the 2nd month, and it is then possible to see a distinction between pylorus and duodenum.

Differentiation of the Coats of the Stomach[1] (Fig. 250, *B*). —A section of the wall of the stomach at the end of the 3rd month of foetal life shows (1) the epithelium (hypoblast) as a single layer, (2) an extremely thick submucous layer, (3) muscular, and (4) peritoneal coats. In the 4th month the gastric glands are formed by the infolding of the epithelial layer to form depressions or pits. From these pits solid processes grow within the submucous coat, thus forming the epithelial bases of the gastric glands. In the 5th month the mucous membrane of the pyloric part of the stomach cannot be distinguished from that of the duodenum, except by the thickening of the circular muscular coat which forms the sphincter of the pylorus.

The Spleen.—**The spleen** appears in the dorsal mesogastrium above the cardiac end of the stomach (Fig. 251) and grows out on the left surface of the mesogastrium (Fig. 252). It appears at the beginning of the 2nd month by a localized growth of the mesoblast in the mesogastrium. The thickening becomes vascularized. The coelomic mesothelium, which covers this thickening on the left aspect of the dorsal mesogastrium, rapidly proliferates, the deeper cells invading the vascular basis of the spleen. The tail of the pancreas (Fig. 251) reaches its point of origin. The splenic artery is one of the vessels of the mesogastrium (Fig. 252); its branches end in the developing tissues of the spleen and greater curvature of the stomach. The splenic blood spaces are formed during the earlier part of the 3rd month by a dilatation of the capillaries, and perhaps also from veins which, in the developing spleen, are lined by a layer of columnar cells. The trabecular and

[1] See reference under Johnston, p. 250.

muscular tissues, and the capsule, are derived from the mesoblast of the dorsal mesogastrium. Small masses of splenic tissue (accessory spleens) are occasionally formed in the dorsal mesogastrium near the hilum of the spleen. In the 3rd month the surface of the spleen is nodular and deeply incised; about the middle of foetal life the fissure begins to disappear; only on the anterior or gastric border do they persist. The spleen differs from a lymph gland in that its spaces are formed by dilatations of blood vessels in place of lymph vessels. Lymphoid nodules appear in the spleen about the 6th month.

The gastro-splenic omentum is that part of the dorsal mesogastrium which unites the spleen to the stomach (Figs. 251 and 252). It becomes

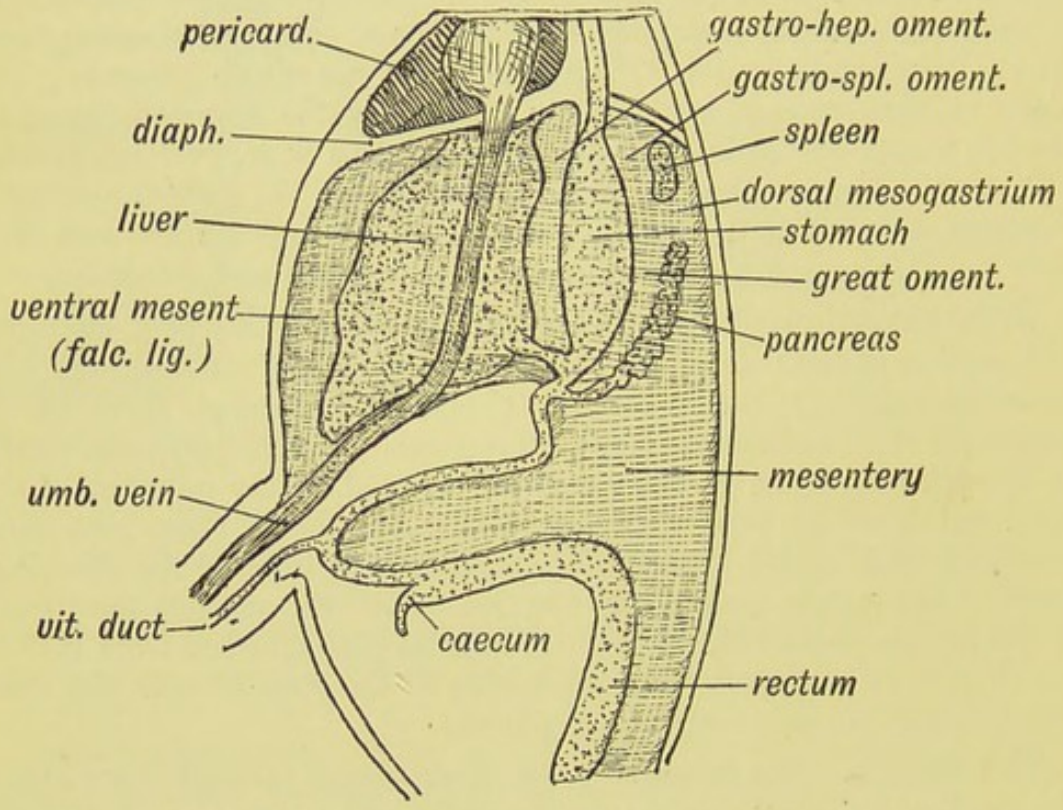


FIG. 251.—The Relationship of the Spleen, Pancreas and Liver to the Mesogastrium in the Embryo.

elongated and stretched as the stomach rotates, and as its greater curvature is developed. The spleen comes to lie against the posterior (right) surface of the cardiac end of the stomach. The dorsal part of the mesogastrium between the roof of the coelom and the spleen becomes the **lieno-renal ligament.** The rotation of the stomach also leads to the spleen being thrust towards the left side: the dorsal or renal surface of the spleen becomes applied to the peritoneum covering the anterior surface of the left kidney and supra-renal body (Fig. 252). The part of the mesogastrium between the spleen and oesophagus adheres to the diaphragm and forms the suspensory ligament of the spleen. The manner in which the dorsal mesogastrium becomes

applied and adherent to the posterior wall of the abdomen during the 2nd and 3rd months will be described in connection with the secondary attachments of the peritoneum and mesenteries.

The Pancreas.[1]—**The Pancreas** appears during the 3rd week as two processes of hypoblast from that part of the gut which afterwards

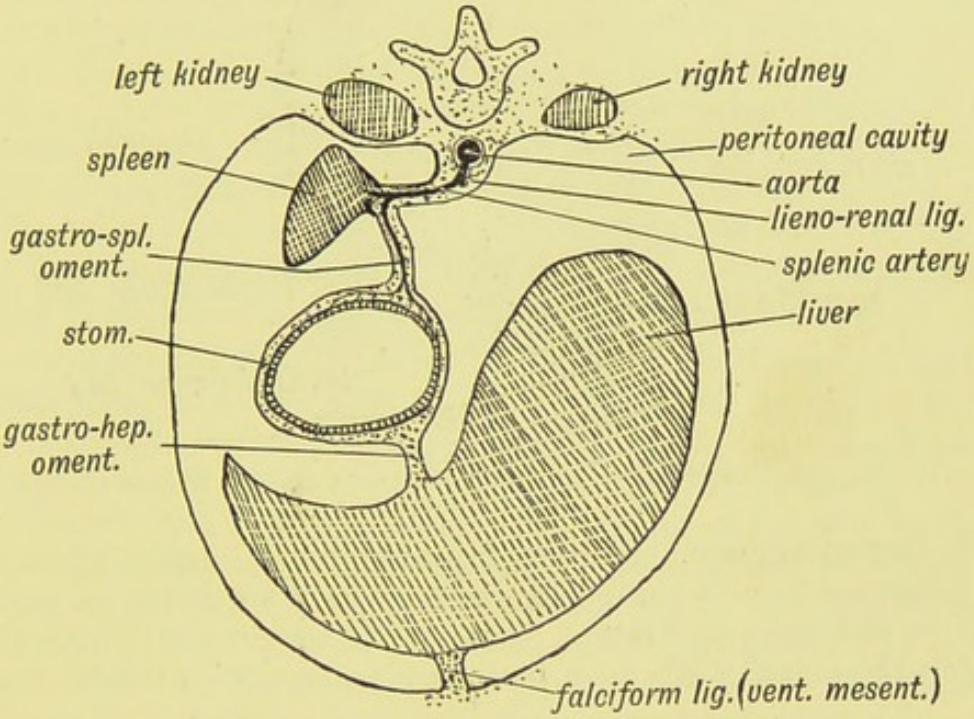


FIG. 252.—A Diagrammatic Transverse Section of the Mesogastrium viewed from behind.

becomes the second stage of the duodenum (Fig. 257). The pancreatic buds develop within the ventral as well as within the dorsal mesentery for, at their points of origin from the duodenum, these two mesenteries are continuous. Of the two buds, one is a minor process which springs from the ventral aspect of the duodenum in common with the hepatic diverticulum. This ventral bud forms only the lower part of the head of the pancreas (Fig. 254). The greater part is formed from a process which springs from the dorsal border of the duodenum, nearer the stomach than the ventral process, and grows into the dorsal mesogastrium above the stomach until it reaches the spleen (Fig. 255). It unites in the mesogastrium with the ventral bud. In many animals it sends a process within the gastrohepatic omentum, round the bile duct, almost to the transverse fissure of the liver. A representative of this omental lobe is occasionally present in man (Fig. 254). The ducts of both processes may persist, the duct of the dorsal bud (duct of Santorini) opening half an inch above the opening of the bile duct; the duct of the ventral bud (Wirsung's) terminates with the common

[1] For development of pancreas: F. W. Thyng, *Amer. Journ. Anat.* 1907, vol. 7, p. 489.

bile duct (Fig. 254). The terminal part of the duct of Santorini commonly becomes obliterated, and even if it persist, the secretion from the dorsal bud reaches the duodenum mostly through the duct of the ventral bud—the duct of Wirsung. A third pancreatic bud has been observed

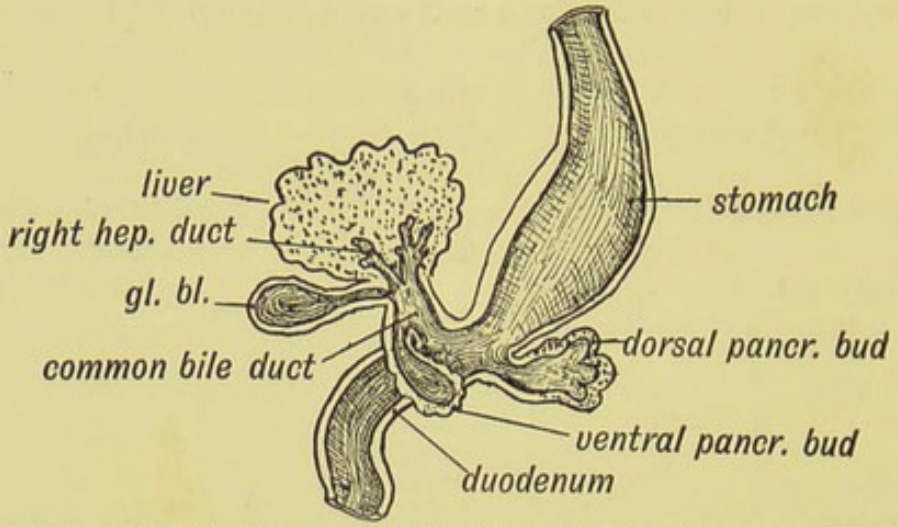


FIG. 253.—The Pancreatic and Hepatic Processes of a 4th week Human Embryo. (After Kollmann.)

in the human embryo. It arises from the ventral aspect of the gut, and corresponds to a third bud observed in the development of the pancreas in lower vertebrates. Occasionally the duct of Wirsung does not join the common bile duct, but opens separately on the duodenum.

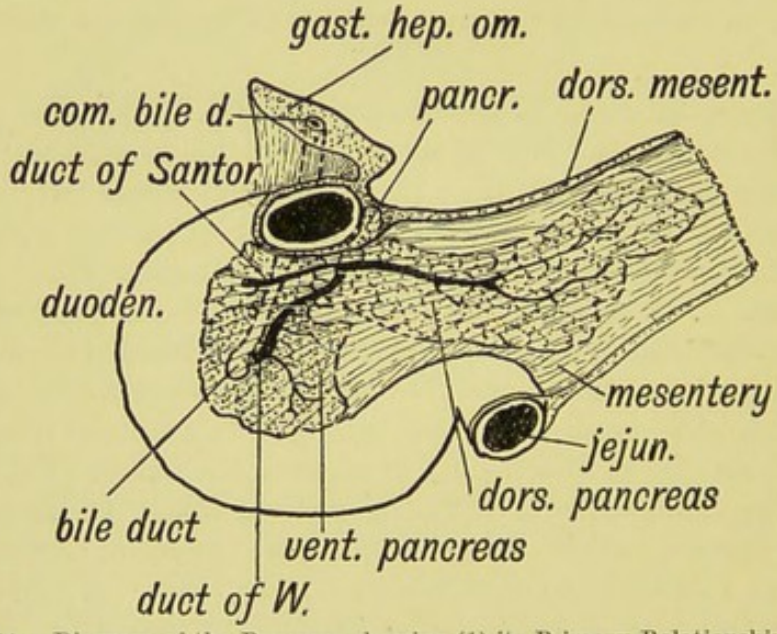


FIG. 254.—Diagram of the Pancreas showing (1) its Primary Relationship to the Dorsal and Ventral Mesenteries; (2) the parts formed from the Ventral and Dorsal Outgrowths; (3) the Formation of the Duct of Wirsung (Duct of W.) by a union between the Ducts of Dorsal and Ventral Buds.

The developing pancreatic processes are at first hollow, like the primary liver process, but the secondary processes are solid and cylindrical. They divide and re-divide, acquire lumina, and form an acino-

tubular gland. Some of the acini, already distinguished by the staining reaction of their cells, become partially or entirely separated from the duct-system and form the **islands of Langerhans.**[1] Rennie, from a study of these in fishes, concludes they are permanent bodies, while the investigations of Dale led him to regard them as temporary in nature, representing resting acini. The semi-isolated acini, of which there are several hundreds, are found in all parts of the pancreas, and represent for us the first stage in the separation of an ordinary duct gland into parts—a part connected with an external secretion, the other with a highly important internal secretion. We see from the example of the pancreas how ductless glands like the thyroid and pituitary may have arisen from duct glands by atrophy of the excretory part. The capsule and connective tissue of the pancreas are derived from the mesoblast of the dorsal mesentery (Fig. 251).

Relationship of the Pancreas to the Peritoneum and Vessels.

1. **In the Embryo.**—The pancreas develops between the layers of the dorsal mesogastrium, to a slight extent only within the ventral mesogastrium (Fig. 255); it is completely surrounded by peritoneum, and it lies with its tail directed forwards against the spleen and its head on the dorsal bend of the **duodenal loop.** It is parallel to the great curvature (dorsal border) of the stomach. This is the relationship during the 5th and 6th weeks. The dorsal mesogastrium is then attached in the middle line, in front of the aorta. The coeliac axis (Fig. 255) is the artery of the mesogastrium and of the structures which it contains. It supplies the fore-gut and its derivatives, between the septum transversum in front and yolk sac behind. The coronary artery passes direct to the cardiac end of the stomach; the splenic is a short vessel ending on the cardiac dilatation of the stomach and supplying the spleen; the hepatic passes on the right side of the pancreas to the duodenum and pyloric end of the stomach, and ends in the liver by passing through the ventral mesentery.

2. **In the Adult.**—The development of the great omentum and the rotation of the stomach to the left, lead to the pancreas being pressed against the left side of the posterior wall of the abdomen. That part of the dorsal mesogastrium which lies between the stomach and pancreas becomes elongated enormously, during the 4th and 5th months, to form the **great omentum,** and hence the two anterior layers of the great omentum are attached to the great curvature of the stomach and to the gastro-splenic omentum (Fig. 255). The two posterior layers of the omentum end on the lower (formerly ventral) border of the pancreas. The great omentum is well developed in all mammals, its origin being probably related to that of the diaphragm. Its exact function is unknown, but it is connected with the absorption, and perhaps also with the secretion, of peritoneal fluids. The duodenal

[1] K. A. Heiberg, *Ergebnisse der Anat.* 1909, vol. 19, p. 939.

loop, with the head of the pancreas in its concavity, is also pressed against the posterior abdominal wall. During all the changes which take place in the position of the pancreas and spleen, owing to the rotation of the stomach and intestine, one structure remains fixed, and that is the coeliac axis. The part of the mesogastrium in which the spleen and tail of the pancreas are situated becomes greatly drawn out. Both structures, instead of being situated near the middle line dorsal to the stomach, come to occupy a situation in front of the left kidney, the pancreas thus coming to lie across, instead of along, the

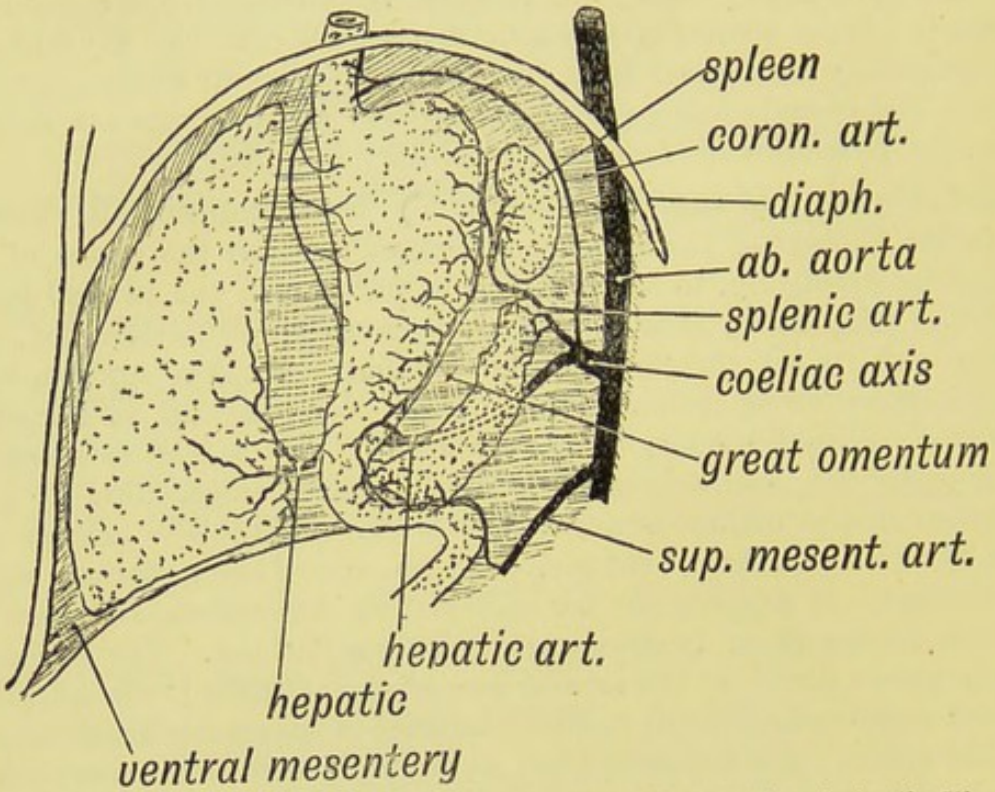


FIG. 255.—The Arrangement of Vessels in the Dorsal Mesogastrium during the 5th week (diagrammatic).

abdominal cavity. The mesogastrium is ballooned out towards the left side to form the lesser sac of the peritoneum, and as the splenic artery lies in the mesogastrium it also is drawn towards the left, circumventing the lesser sac of the peritoneum (Fig. 256).

In the 5th week the pancreas lies between the layers of the dorsal mesogastrium and the extension from these layers which forms the mesentery of the duodenal loop (Figs. 254, 255); thus right and left surfaces are covered by peritoneum. The left surface, which becomes anterior, retains its covering, but the right aspect of the pancreas and duodenal loop become applied to the posterior abdominal wall in front of the aorta, crura of the diaphragm and left kidney (Fig. 247). The peritoneal covering on the right aspect gradually disappears, and thus in the adult the pancreas comes to appear as if it lay behind and outside the cavity of the peritoneum. The complete application and fixation

of the pancreas and duodenum to the posterior abdominal wall only occur in animals adapted to the upright posture (see Figs. 246, 247, 256).

The part of the dorsal mesogastrium between the pancreas and aorta (Fig. 256) is also applied to the posterior abdominal wall, and forms the posterior lining of the lesser sac.

The Lesser Sac is composed of two parts, a vestibular or hepatic part formed from the recessus mesentericus (Figs. 246, 247) and an omental or gastric part formed by the evagination of the dorsal mesogastrium. These two parts communicate at an isthmus or constriction caused by the coronary and hepatic arteries (Fig. 256). The hepatic

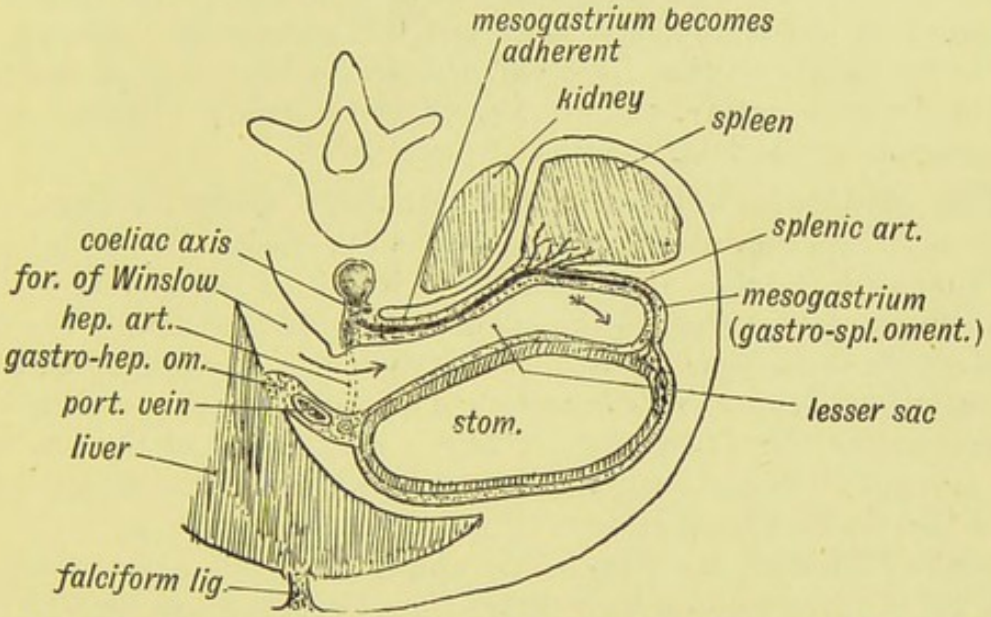


FIG. 256.—Diagram to show the Formation of the Lesser Sac of the Peritoneum from the Dorsal Mesogastrium.

recess or pocket separates the Spigelian lobe of the liver from the right crus, and permits the liver to glide during the respiratory movements of the diaphragm (Fig. 247). The gastric part isolates the stomach, allows it to contract, expand and move during digestion and respiration. In the anterior wall of the lesser sac are situated (Fig. 256): (1) the gastro-hepatic omentum or ventral mesentery, which is at first vertical and median; (2) the stomach; (3) the gastro-splenic omentum, a part of the dorsal mesentery; (4) the two anterior layers of the great omentum, also parts of the dorsal mesentery.

In its posterior wall are situated: (1) the lieno-renal ligament (dorsal mesentery); (2) the dorsal mesentery of pancreas; (3) two posterior layers of the great omentum.

Process of Peritoneal Fixation.—The embryological process which leads to the adhesion of the pancreas, dorsal mesentery of the stomach and mesentery of the duodenum to the posterior wall of the abdomen can be best studied during the 3rd, 4th and 5th months of foetal life,

but it is also to be seen at work at, and even after, birth. The applied peritoneal surfaces become adherent by the proliferation and union of lining cells of the opposed layers of peritoneum, the tissue changes being very similar to those which occur during inflammatory states. The process may be described as a physiological inflammation. The secondary adhesion of the mesenteries of the abdominal viscera are apparently related to posture; the degree of adhesion is much more extensive in man than any other animal, with the exception of the great anthropoid apes. Man and the anthropoids are distinguished from all other animal forms by the upright posture of their bodies. The peritoneal adhesions which occur from the 3rd month onwards must be regarded as adaptations to the upright posture. The suspensory ligament of the spleen, the right and left **costo-colic** ligaments, the peritoneal bands passing from gall bladder to the colon or omentum are of the same nature, and are formed by secondary adhesions of the peritoneum in the later months of foetal life.[1]

The Mid-gut, Yolk Sac and Meckel's Diverticulum.—The yolk sac reaches its maximum size in the 4th week. In the 3rd week the umbilicus extends along the whole length of the abdomen, from the septum transversum to the allantois (Fig. 236, p. 249). The neck of the yolk sac completely fills it. The vitelline arteries, which afterwards form the superior mesenteric, end on its walls; the vitelline veins commence on them (Fig. 235, p. 248). By the end of the 3rd week the mid-gut is demarcated, and the neck of the yolk sac drawn out to form the vitello-intestinal duct (Fig. 237, p. 249).

In the **fifth week** the form of the alimentary tract is that shown in Fig. 257. The condition then differs from that shown in the 3rd week in the following points:

(1) The production of the mid-gut as a **U-shaped loop** from the archenteron.

(2) The formation within the umbilical cord of a long neck to the yolk sac—the **vitello-intestinal duct**; Meckel's diverticulum is formed by a persistence of the intra-abdominal part of the canal. Normally the duct becomes occluded, and shrivels up during the 7th week; this is the case in all mammals, but in birds the yolk sac is large at the time of hatching, and part of it always persists as an intestinal diverticulum.

(3) The yolk sac, by the constriction of the umbilical orifice and formation of the cord, comes to lie on the placenta (Fig. 257). The neck of the yolk sac, the vitello-intestinal duct, lies within the umbilical cord. By the sixth week the sac is in a state of retrogression. The U-shaped intestinal loop, which is formed from the mid-gut, is at first really extra-abdominal, being situated in a funnel-shaped cavity formed

[1] For many details connected with the formation of these adhesions see papers by Dr. Douglas G. Reid, *Journ. of Anat. and Physiol.* vols. 44, 45, 46, 1910-1912.

by an extension of the coelom—the **umbilical coelom**—within the umbilical end of the cord. The vitelline artery, afterwards the superior mesenteric, is the artery of the U-shaped loop ; it terminates at the vitello-intestinal canal—the elongated neck of the yolk sac (Fig. 40).

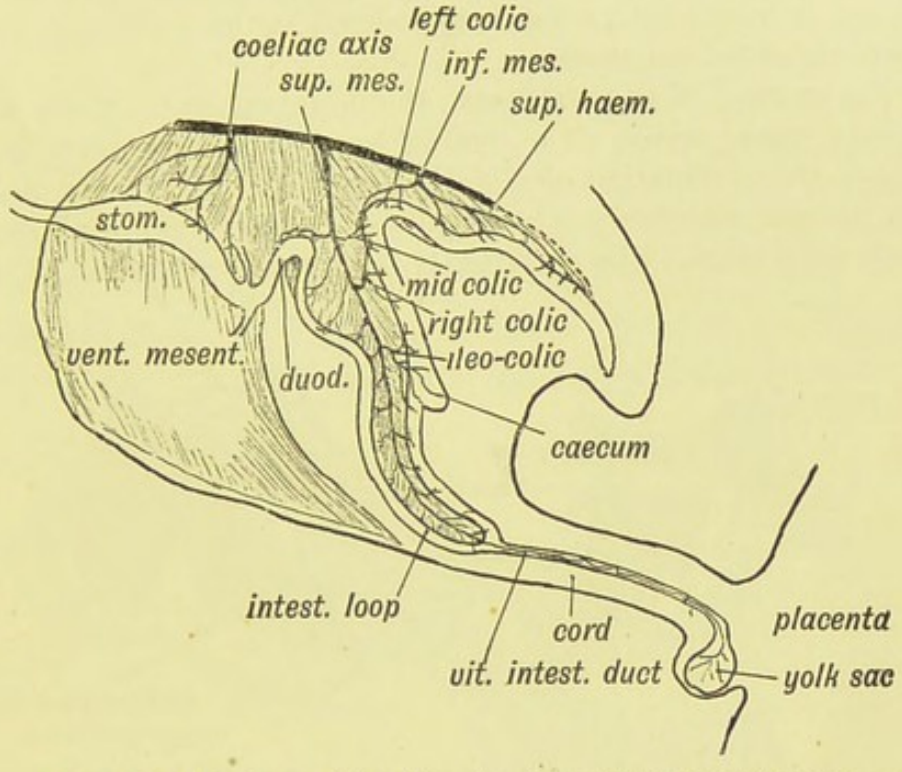


FIG. 257.—The Form of the Alimentary Canal during the 5th week.

Persistence of Certain Embryonic Structures.[1]—Many of the features seen in the human embryo at the stage of development reached during the fifth or sixth weeks may persist.

(1) The most common structure to remain is the intestinal end of the neck of the yolk sac—**Meckel's diverticulum.** It occurs in 2 per cent. of subjects, and commonly forms a finger-like sac on the free border of the ileum from two to four feet above the ileo-caecal orifice. Hence we know that this part of the ileum forms the apex of the U-shaped loop of intestine. The point on the ileum at which the canal of the yolk sac was attached is frequently the seat of a narrowing, which may be more or less marked. This forms a favourable site at which intussusception of the bowel occurs. The diverticulum varies in length and shape ; its blind end is frequently bulbous and the site of secondary diverticula. Occasionally pancreatic masses are developed at its extremity. It is lined by a glandular epithelium similar to that of the ileum. Frequently a fold of the mesentery descends to it (Fig. 259).

[1] For an account of the structure of the yolk-sac see papers by Dr. H. E. Jordan, *Anat. Anzeiger*, 1907, vol. 31, p. 291 ; 1910, vol. 37, p. 56. For an account of Meckel's diverticulum and of malformations of the bowel see Keith, *Brit. Med. Journ.* 1910, vol. 1, p. 301.

In the mesenteric fold there is usually to be found a vestige of the artery of the yolk sac (Fig. 257). The attached base of the mesenteric fold may atrophy, while the free margin forms a cord, under which a loop of bowel may become strangulated (Fig. 259).

(2) The vitello-intestinal duct may remain patent, and, when the cord is cut at birth, form a fistulous opening at the umbilicus, by which the contents of the ileum escape.

(3) The artery of the yolk sac, the terminal part of the superior mesenteric, may persist as a fibrous band which stretches from the mesentery at the situation of a Meckel's diverticulum to the umbilicus. Over it the gut may become strangulated. The young of all carnivora are born with thread-like remains of both artery and vein, stretching

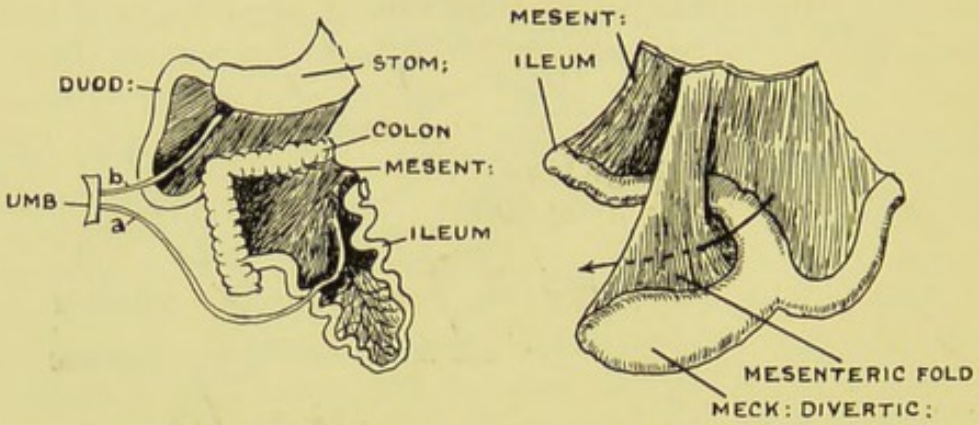


FIG. 258.—Fibrous Remnants of the Artery (*a*) and Vein (*b*) of the Yolk Sac in a Kitten.

FIG. 259.—Meckel's Diverticulum provided with a Mesentery. The arrow marks the site at which an aperture may be formed in the mesenteric fold.

from the umbilicus to the mesentery (Fig. 258). A remnant of the vein is rarely seen in the human subject. The vitello-intestinal duct may also be reduced to a fibrous structure, over which a loop of intestine may fall and thus become strangulated.

(4) The U-shaped loop, instead of retreating within the abdomen at the beginning of the third month, may remain within the umbilical funnel of somatopleure. This gives rise to a **congenital umbilical hernia.** Such herniae occur in all degrees; they may contain a piece of intestine, or almost the whole of the abdominal contents. In such cases the somatopleure, or belly wall, which forms the covering of the hernia, is commonly thin and transparent. The intra-abdominal migration of the bowel is due to the rapid extension of the lumbar and dorsal regions of the spine and growth of the body walls which commence with the third month of foetal life.

Congenital Diverticula.[1]—During the third month numerous outgrowths of intestinal epithelium are formed, which perforate the

[1] For literature on congenital diverticula see F. T. Lewis and F. W. Thyng, *Amer. Journ. Anat.* 1907, vol. 7, p. 505.

muscular coat. They usually disappear, but may give rise to diverticula. Frequently masses of pancreatic tissue are attached to them (Lewis and Thyng).

Congenital Occlusion of the Duodenum.[1]—The part of the duodenum behind the opening of the bile ducts, which marks the junction of fore-gut with the mid-gut, may be partially or completely closed—a rare occurrence. After the liver and pancreatic buds grow out, this part of the duodenum becomes occluded by the proliferation of the epithelium lining the gut (Tandler). The meaning of the proliferation is unknown. The proliferation of the intestinal epithelium—in the second month—is not confined to the duodenum; hence congenital occlusions may occur at any part of the intestine.

Duodeno-jejunal Loop and Junction.—The junction between the duodenal and U-shaped loops becomes the most fixed point in the whole

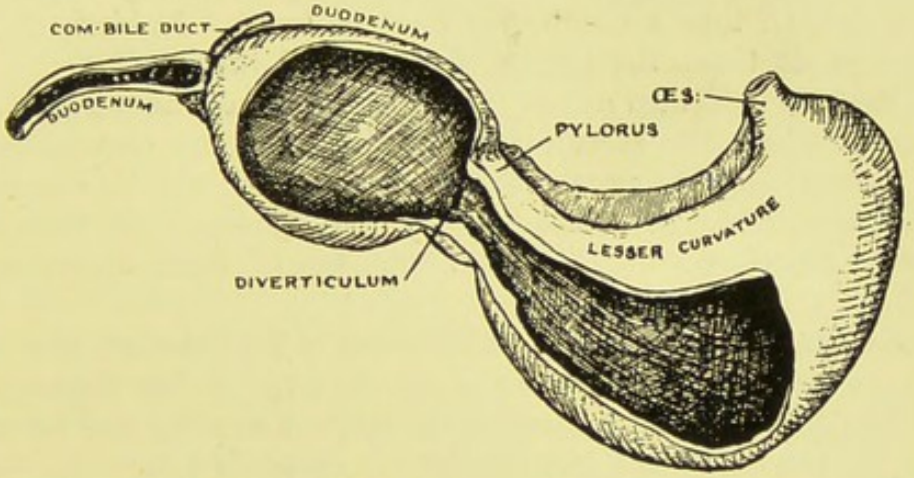


FIG. 260.—Congenital Occlusion of the Duodenum.

intestinal tract (Fig. 257). Within its dorsal mesentery a band of non-striated fibres is developed which binds the junction to the right crus of the diaphragm. The **suspensory band** [2] is generally known as the muscle of Treitz. The functional meaning of the duodeno-jejunal loop and its muscular band is unknown, but they are found in all the higher vertebrates.

Villi of the Intestine.[3]—In the 3rd month the circular muscular coat becomes differentiated, and the hypoblastic lining of the small intestine becomes thrown into longitudinal ridges, with depressions between them which sink into the thick submucous stratum. Towards

[1] For congenital occlusions see H. Forssner, *Anat. Hefte*, 1907, vol. 34, p. 1.

[2] A. Low, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 93; P. T. Crymble, *Brit. Med. Journ.* 1910, ii.

[3] W. A. Hilton, *Amer. Journ. Anat.* 1901, vol. 1, p. 459 (Dev. of Villi and Valvulae Conniventes).

the end of the 4th month the glands of Lieberkuhn are developed from the depressions. The villi arise by subdivision of the ridges (Berry). Peyer's patches begin to form in the 7th month, and are apparent to the naked eye in the 1st month after birth. The **valvulae conniventes** arise as folds of the mucous membrane in the 8th month, thus increasing the surface for absorption. They are formed first in the duodenum ; their development gradually ceases at the upper part of the ileum.

DERIVATES OF THE HIND-GUT.

At the beginning of the 2nd month the hind-gut is almost equal in length to the mid-gut, but its calibre is less. Indeed, it is not until the 5th month that the hind-gut is marked off from the mid-gut by its greater diameter. By the end of the 2nd month the anterior (jejeunal) limb of the intestinal loop has grown very rapidly, and become thrown into a number of distinct loops. At birth the small intestine is six times the length of the large bowel.

The Rectum is formed out of the posterior end of the hind-gut. The manner in which the rectum is separated from the cloaca, the anal canal formed, and the permanent anus produced, will be described in connection with the perineum and urogenital passages, for their history is closely associated with the development of these structures (see p. 370).

The Descending Iliac and Pelvic Segments of the Colon are also formed out of the hind-gut. The artery of the hind-gut is the inferior mesenteric (Fig. 261). Hence it supplies the rectum, sigmoid and descending colon. In the fifth week the hind-gut is suspended from the front of the aorta and spine by the dorsal mesentery of the hind-gut. This becomes transformed into the meso-rectum, meso-sigmoid and descending meso-colon. The angle between the hind-gut and U-shaped loop becomes the splenic flexure (Fig. 257). At the commencement of the third month, when the intestine takes up its permanent position within the abdomen, the U-shaped loop becomes twisted round on the axis of the superior mesenteric artery (Fig. 261), so that the part of the hind-gut which forms the splenic flexure is turned forwards and to the left until it touches the spleen (Fig. 267). It carries its artery, the left colic, with it. At this time the anterior limb of the U-loop elongates much more rapidly than the posterior limb, and is produced into coils of small intestine—the jejunum and ileum—which press the descending meso-colon against the kidney and the parietal peritoneum covering the left kidney (Fig. 262). The left surface and layer of the meso-colon adheres to the pre-renal layer of the peritoneum, both layers subsequently being absorbed. Thus the descending meso-colon, originally situated in the middle line, comes to be attached in the left lumbar region (compare Figs. 246, 247).

The Intersigmoid Fossa.—The sigmoid flexure, which is made up of the pelvic colon and part of the iliac segment, after the rotation of the gut, forms a loop, with its convexity directed towards the liver.

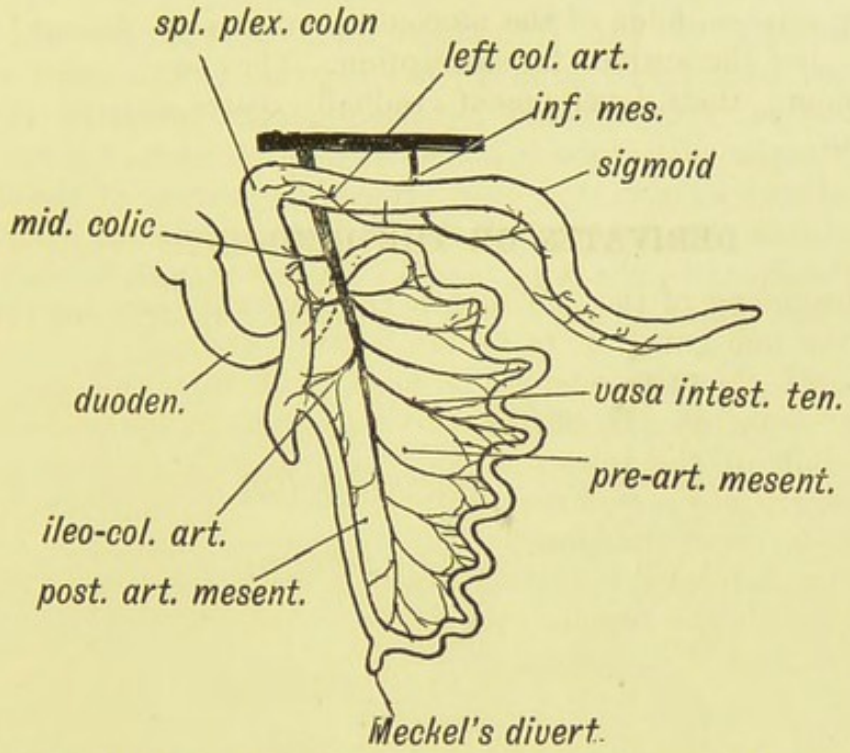


FIG. 261.—The Mesentery of the Hind-gut. The position assumed by the colon after the rotation of the gut has taken place.

The meso-sigmoid is originally attached in the middle line, but the pressure of the developing loop of small bowel pushes it against the posterior abdominal wall and left iliac fossa. It may become completely adherent like the descending meso-colon, or only partially.

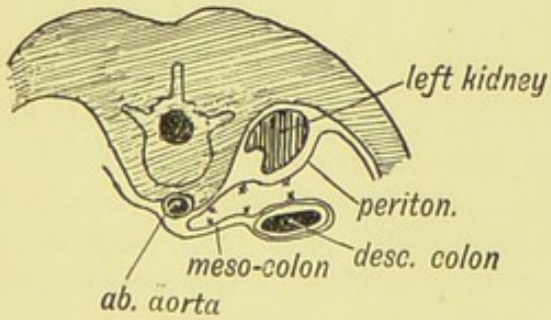


FIG. 262.—Diagram to show how the descending Meso-colon becomes applied to the Parietal Peritoneum of the left Lumbar Region.

When the sigmoid is lifted up a recess or fossa may be apparent beneath the meso-sigmoid, to the outer side of the left common iliac artery, which is due to a failure of adhesion between the meso-sigmoid and parietal peritoneum. It occurs opposite the convexity of the sigmoid loop (Fig. 247). At birth the meso-sigmoid is relatively extensive;

the sigmoid loop lies with its convexity towards the right side of the abdomen, and well above the pelvis. During adolescence the sigmoid grows more slowly than the rest of the colon. It sinks within the pelvis, and forms the greater part of the pelvic colon.

Morphology of the Ileo-colic Part of the Bowel.[1]—In all vertebrates, from fishes upwards, the junction of the small with the great intestine is demarcated by the **ileo-colic sphincter,** developed from the circular coat of the bowel.[2] As a rare abnormality the caecum may be absent in man, the only external indication of the ileo-colic junction being the presence of the ileo-colic sphincter. This is the normal condition in the frog, and in several mammals such as the racoon. The sphincter marks the junction of two different functional

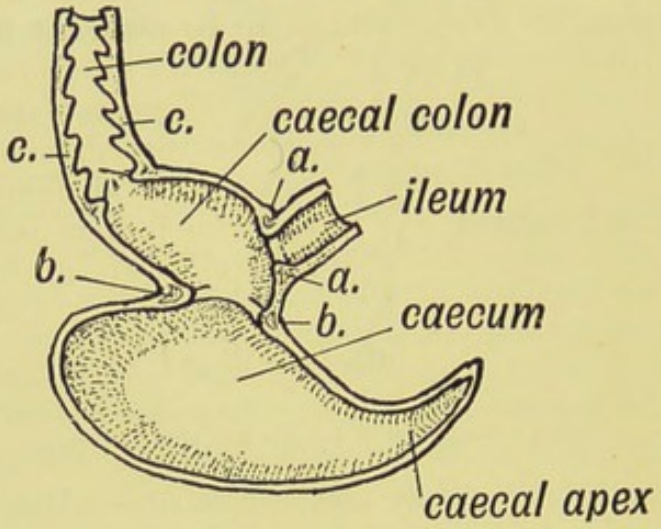


FIG. 263.—Diagram to show the parts of a typical Mammalian Caecum. Five parts are shown in the figure: (1) the termination of the ileum; (2) the caecal colon in which the ileum ends; (3) the caecum which opens from the caecal colon; (4) the apex of the caecum; (5) the commencement of the ascending colon. At three points the circular muscular fibres are thickened to form sphincters: (*a*) ileo-colic junction; (*b*) at the junction of caecum and caecal colon (in man *a* and *b* are combined in the ileo-caecal orifice and its rectinacula); (*c*) in the first part of the ascending colon.

segments of the alimentary tract. Villi, which are originally developed in the great bowel, disappear in the later months of foetal life. The proximal part of the colon from which the caecum is developed forms the caecal colon (Fig. 263); it is frequently demarcated from the ascending colon by a thickening of the circular muscular coat—the

[1] For recent literature on shape and development of caecum and appendix see R. J. A. Berry and L. A. H. Lack, *Journ. Anat. and Physiol.* 1905, vol. 40, p. 248 (Nature of Appendix); F. G. Parsons, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 30 (Age Changes in Shape of Caecum); R. J. A. Berry, "Intercolon," *Med. Journ. Australia,* 1907, June 20 (Nature of Appendix); G. S. Huntingdon, *The Anatomy of the Human Peritoneum and Abdominal Cavity,* 1903; H. A. Kelly and E. Hurdon, *The Vermiform Appendix and its Diseases,* 1905.

[2] Keith, "Anatomical Evidence as to the Nature of the Caecum and Appendix," *Proc. Anat. Soc.* Nov. 1903.

caeco-colic sphincter (Fig. 263, *c*)—which can commonly be recognized in the bowel of man. The caecum is developed as a diverticulum of the caecal colon. In all vertebrates its submucous coat is rich in lymphocytes, which in mammals collect in the form of solitary follicles more or less closely crowded together. R. J. Berry found that in the primates there is a tendency for the lymphoid tissue to be aggregated in the apex of the caecum. In man, in anthropoids, and a few other forms, the lymphoid tissue becomes richly developed in the distal part of the caecum, which has a narrow lumen, strong muscular coat, and is of great functional activity during digestion. This highly specialized part of the caecum is the appendix ; it is well developed in man, and is certainly not a vestigial structure. The lymphoid tissue undergoes a great reduction in size and growth when the period of adolescence is past. Thus there are five structures to be observed in the ileo-colic region of a typical mammal (Fig. 263) : (1) an ileo-colic sphincter, (2) a caeco-colic sphincter, (3) a caecal segment of the colon, (4) a caecum, the distal part of which may be specialized to form (5) an appendix. Further, a study of the comparative anatomy of this region shows that the caecum is largest in vegetable-feeding animals, and that there is a correlationship between the development of the stomach and caecum. In the horse, for instance, the caecum and caecal colon are complicated, the stomach simple ; in the ruminants the stomach is complex, the caecum comparatively simple. In animals which live on a flesh diet the caecum is small.

Development of the Colon and Caecum.—Towards the end of the first month of foetal life an elevation appears on the free border of the posterior limb of the U-shaped loop (Fig. 257). The elevation contains a diverticulum of the caecal colon, which forms the caecum and appendix. It continues to grow outwards and forwards in close contact with the free border of the ileum. At first the colic part of the intestinal loop and the caecal process are not of larger calibre than the small intestine, but in the fifth month the colon and caecum undergo an enlargement, but the terminal or apical part of the caecum retains its foetal dimensions, and forms the appendix. As the superior mesenteric (vitelline) artery descends in the loop, it gives off three branches to the posterior limb—the middle colic, right colic and ileo-colic arteries (Figs. 261 and 265). The mesentery of the U-shaped loop may be divided into two parts, the fate of the two parts being different :

1. The mesentery of the anterior limb in front of the superior mesenteric artery—forms the **pre-arterial part.** This gives rise to the greater part of the mesentery of the small bowel.

2. The mesentery of the posterior limb, behind the artery—is the **post-arterial part.** It forms the mesentery of the ascending and transverse colon, and also the lower part of the mesentery of the small bowel.

At the seventh week the great growth of the anterior limb, to form the coils of the jejunum and ileum, causes the U-shaped loop to rotate

so that the splenic flexure of the colon comes against the spleen. This brings the transverse meso-colon, containing the middle colic artery, against the part of the meso-gastrium which forms the great omentum (Figs. 267, 261). These two layers adhere ; thus the transverse colon is formed by the fusion of a part of the dorsal meso-gastrium with the mesentery of the posterior limb of the U-shaped loop (Fig. 247). The rotation places that part of the loop mesentery which forms the ascending meso-colon against the duodenum, and at the same time the duodenal loop is pressed into its permanent position in front of the right kidney and inferior vena cava. The caecum thus comes to be

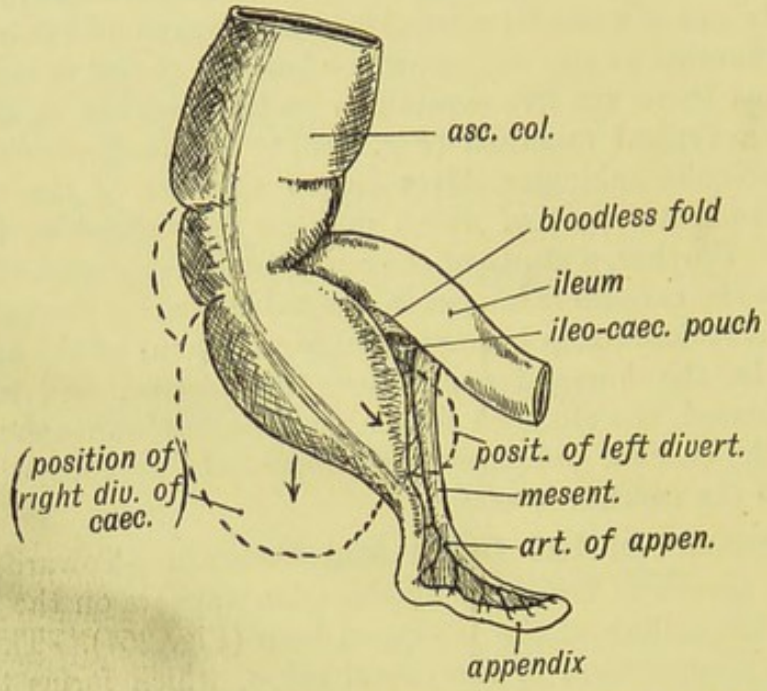


FIG. 264.—Diagram of the Apex of the Caecum at the time of Birth and the Diverticula which may be produced in the Fundus of the Caecum afterwards.

situated in the majority of foetuses in front of the right kidney, near the gall-bladder, and there it remains until about the time of birth, when both the caecum and ascending colon undergo a gradual migration towards the right iliac fossa. The cause of this migration is probably due to a functional elongation of the proximal part of the colon, but it occurs only in animals adapted to the upright posture. Thus the attachment of the ascending meso-colon is formed by a secondary adhesion to the parietal peritoneum during the migration of the colon and caecum. The appendix, during the migration, may be caught behind the colon, thus assuming a **retro-colic position** ; it is then lodged and fixed in the ascending meso-colon. The peritoneal adhesions, which are formed in the 4th and 5th months of foetal life, between the transverse meso-colon and great omentum, and especially the adhesions which the ascending colon forms just before and after birth, as the caecum assumes its position in the iliac fossa, are subject to a

great range of variations, and many peritoneal folds and recesses may be formed. The object of all of them is to give a fixation of the viscera to the abdominal wall—a fixation which occurs only in orthograde primates. Dr. Douglas Reid has described the various foetal adhesions in recent volumes of the *Journal of Anatomy and Physiology*.

The Appendix.—At first, and until the fifth month, the caecal diverticulum is of the same calibre throughout, but from that month onwards, the appendix remains small while the caecum grows, keeping pace in diameter with the colon. At birth the appendix is still the tapered apex of the caecal diverticulum (Fig. 264), but during childhood, an outer, or an inner, sacculation, or both together, arise in the

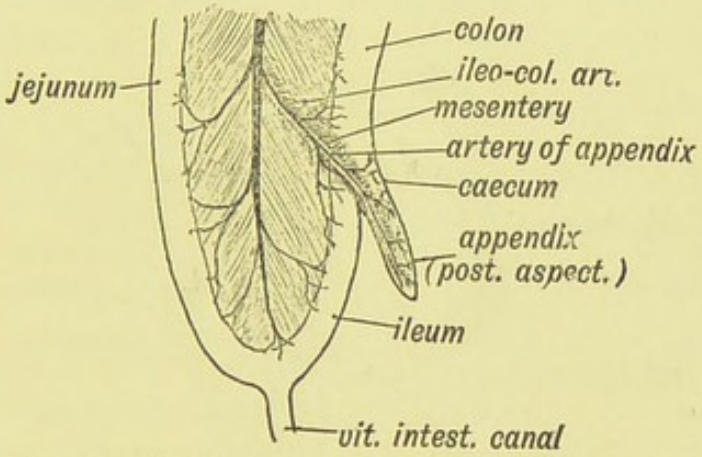


FIG. 265.—The Appendix and Peritoneal Folds at the end of the 2nd month of Foetal Life. The intestinal loop is viewed from the left side.

fundus of the caecum and thrust the appendix backwards and to the left into an asymmetrical position.[1]

Although a distinctly marked appendix is only seen in man, the anthropoids, lemur, opossum and certain rodents, still a corresponding lymphoid structure is present generally in mammals. The appendix is a lymphoid diverticulum of the caecal apex (R. J. Berry). It must be regarded as a lymphoid structure, and although it can be dispensed with, is not therefore to be regarded as vestigial in nature any more than is the tonsil. The caecum is longest, as is also the bowel, in herbivorous animals.

Ileo-caecal Valves.—At the ileo-colic junction, the development of villi ends. In the higher primates the junction is invaginated within the caecum, in the form of two lips or valves. The invagination becomes apparent in the human foetus of the 3rd month. Within these folds are (1) the ileo-colic sphincter ; (2) muscular bands developed in the **retinacula** from the circular musculature of the caecum and representing the **mid-caecal** sphincter of the typical caecum (Fig. 263). These bands serve in the emptying and filling of the caecum. Only

[1] See F. G. Parsons, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 30.

to a slight extent can the ileo-colic lips serve as mechanical valves; they assume a valvular form when dead and dried.

Ileo-caecal Fossae.—When the caecal diverticulum grows out from the hinder limb of the U-shaped loop it carries with it three folds (see Fig. 266):

1. **The ileo-colic fold,** a process from the right side of the mesentery containing the anterior caecal artery; in a small proportion of cases this fold forms the mesentery of the appendix; [1]
2. **The bloodless fold,** a process from the coat of the ileum;
3. **The mesentery of the appendix,** a process from the left side of the mesentery, containing the artery to the appendix (Fig. 265).

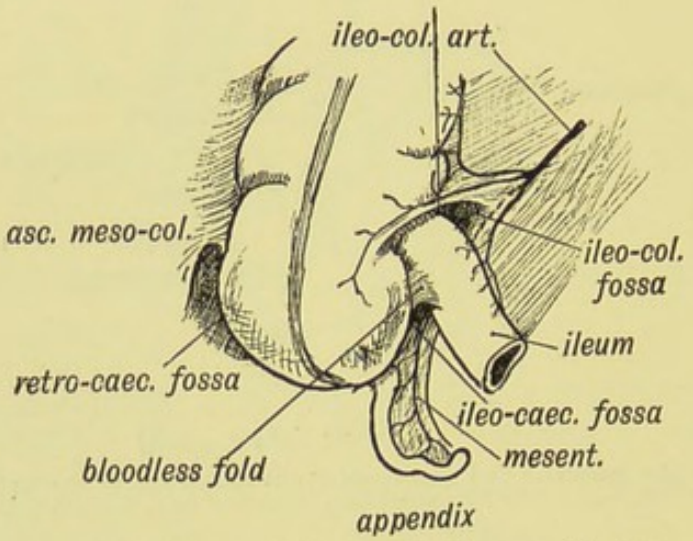


FIG. 266.—Peritoneal Fossae in the Ileo-caecal Region.

These three folds give rise to three **fossae** (Fig. 266):

1. **The ileo-colic,** between the termination of ileum and ileo-colic fold;
2. **The ileo-caecal,** between the bloodless fold and mesentery of the appendix;
3. **The retro-caecal,** between the mesentery of the appendix and commencement of the ascending meso-colon.

The caecum and appendix are made up of bilateral halves; there are right (anterior caecal fold) and left (mesentery of appendix) mesenteries. In birds the appendix is divided; it is occasionally double in malformed human infants.[2] There is no reason to suppose, however, that the appendix was ever double in the evolution of the mammalia.

The Duodenum.—The part of the duodenum above the entrance of the common bile duct is formed from the fore-gut, the part behind from the mid-gut. The liver and pancreatic buds arise from its ventral

[1] See Dr. Geo. M. Smith, *Anat. Record*, 1911, vol. 5, p. 549.

[2] Dr. F. Wood Jones, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 193.

border at the junction of these two parts. At first it is entirely covered by peritoneum and suspended by the mesentery, in which it forms a minor loop (Figs. 255, 257). In its concavity rests the head of the pancreas (Fig. 254).

In the 7th week the U-shaped loop of intestine rotates so as to bring the ascending colon, with its mesentery, against the duodenal loop, which, with the head of the pancreas, is thus pressed against the right kidney and inferior vena cava (Fig. 267). The peritoneum covering the right aspect of the head of pancreas, and the duodenal loop, adheres to the parietal peritoneum covering the kidney and disappears. The transverse meso-colon gains an attachment to the front of the duodenum (Figs. 246, 247).

The duodeno-jejunal fossa is formed as the U-shaped loop of bowel rotates, dragging the transverse meso-colon after it (Fig. 267). The

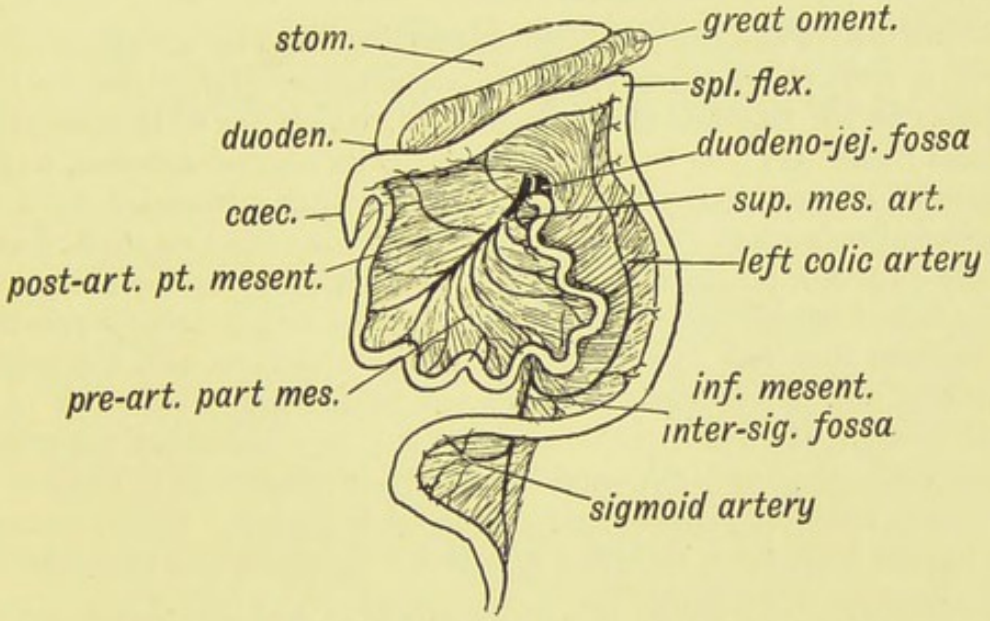


FIG. 267.—To show the Rotation of the Intestinal Loop and Formation of the Duodeno-jejunal Fossa.

inferior mesenteric vein passes forwards along the dorsal mesentery to the splenic vein, which is then also in the dorsal mesentery (Fig. 279, p. 290). The mesentery of the hind-gut is stretched as the ascending colon migrates to the right; the inferior mesenteric vein checks it and gives rise to a fold, which forms the left boundary of the fossa (Fig. 267). The fossa is occupied by the bend of the intestine at the duodeno-jejunal junction; it forms a bursa for this knuckle of the gut.

The mesentery of the small gut is formed out of the primitive mesentery of the U-shaped intestinal loop, chiefly from that part of it (the pre-arterial) which lies between the superior mesenteric artery and the anterior limb of the loop (Fig. 261). After the rotation, the aspect of the mesentery, which was directed towards the right, becomes left and

anterior. During the rotation of the gut the superior mesenteric artery comes to lie in front of the third stage of the duodenum. At first the mesentery is attached in front of the spine only at the origin of the superior mesenteric artery (see Figs. 246, 247). Its oblique attachment to the posterior abdominal wall, from the duodenum to the right iliac fossa, is a secondary adhesion, formed after the rotation of the gut and during the 4th and 5th months, and this extensive attachment is found only in animals adapted to the upright posture. The last part of the mesentery to become adherent to the posterior wall of the abdomen is that in the angle between the ileum and ascending colon. Not unfrequently this part remains free, and it is then possible for a **volvulus** to form by a rotation of the ileo-colic loop.

By the rotation of the U-shaped loop, the small intestine becomes confined in a bursa or peritoneal compartment formed by the mesentery of the large bowel (Fig. 247).

Abnormal Fixation of the Mesentery.—The rotation of the bowel is subject to three forms of disturbance, giving rise to three varieties in the fixation of the mesentery, which are of importance to medical men. (1) The bowel may undergo its normal rotation, but the process of adhesion may fail; the bowel is thus suspended by a free fan-shaped mesentery. It may undergo a twist round its stalk, formed by the superior mesenteric artery, and thus give rise to obstruction of the bowel (complete volvulus). (2) It may not undergo a rotation; the caecum then lies on the left side of the abdomen, and the colon—ascending and descending—are situated behind and to the left of the small bowel. (3) The rotation may occur in a direction opposite to the normal—the duodenum and mesentery coming to lie in front of the transverse colon in place of being situated behind it. Several cases of this nature have been recorded of late by surgeons and anatomists.

Meconium.—At birth, the great intestine and the ileum are distended by meconium, a black, semi-fluid substance secreted by the liver and mucous membrane of the bowel. Dr. A. Low found that the meconium reaches the ileo-colic junction in the 4th month, the rectum in the 5th. The meconium passes quickly along the jejunum. At birth the lower part of the ileum and whole of the great intestine are distended with it. By the 3rd or 4th day after birth all the meconium has been passed, a fact which may be utilized to prove that a child had lived for a certain time after birth.

CHAPTER XVII.

CIRCULATORY SYSTEM.

Early Stages in the Evolution of the Heart.—In Ammoecetes, the larval form of the lamprey, is represented the most primitive form of heart in vertebrate animals. Even in this early vertebrate form the heart consists of four chambers (Fig. 268) : (1) Sinus venosus, receiving

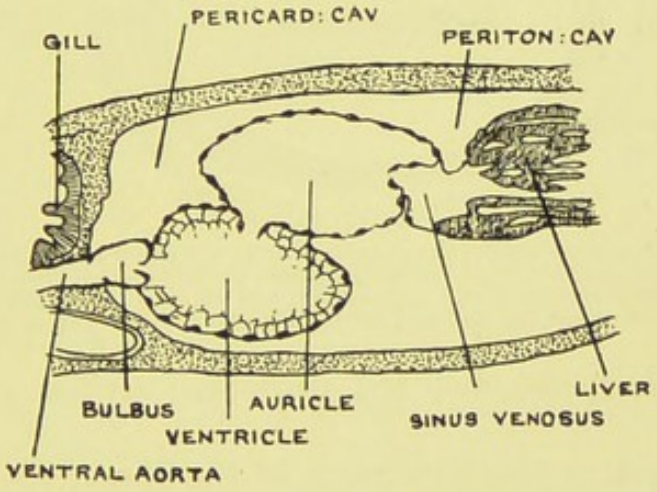


FIG. 268.—The Heart of Ammoecetes seen in a Median Section. (After Vialleton.)

the portal blood through the liver ; (2) auricle ; (3) ventricle ; (4) bulbus cordis, from which the primitive ventral aorta passes out to distribute the blood in the branchial chamber. The primitive heart is thus a pump which forces the portal blood through the respiratory system. It is clear, then, that the early evolutionary stages of the heart must be sought for amongst invertebrate forms, but these stages are as yet unknown. When the heart appears in the human embryo towards the end of the second week, it is double—consisting of a right and left cardiac tube. We therefore suppose that originally there were right and left hearts, which had been differentiated in the walls of the right and left vessels, conveying the blood from the alimentary to the respiratory systems. In Fig. 269 the left side of such a primitive circulation

is represented. The left heart forces the blood along a primitive dorsal aorta to the capillary system of the archenteron. An afferent (primitive portal) vessel conveys the blood back to the heart. When the head and tail folds are produced in the embryonic plate at the beginning of the 3rd week (see Fig. 269), the right and left cardiac tubes are thrust under the fore-gut, where they speedily become fused into a median heart. In its origin the heart is thus made up of symmetrical halves derived from the corresponding sides of the body. When formed, the heart is suspended within the anterior part of the coelomic space—which becomes the cavity of the pericardium. In

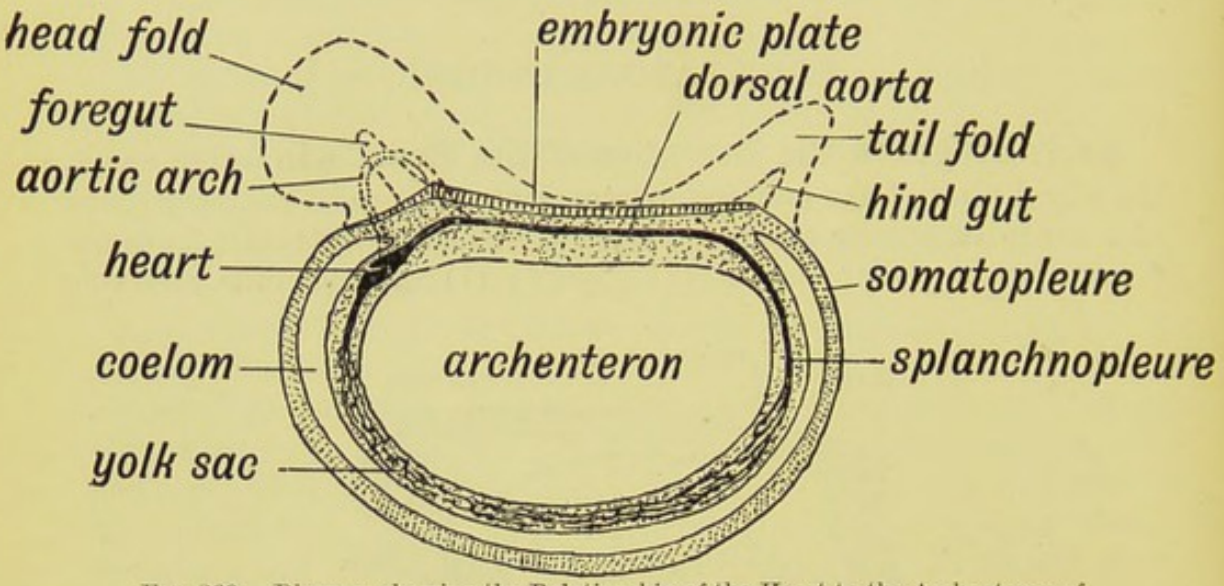


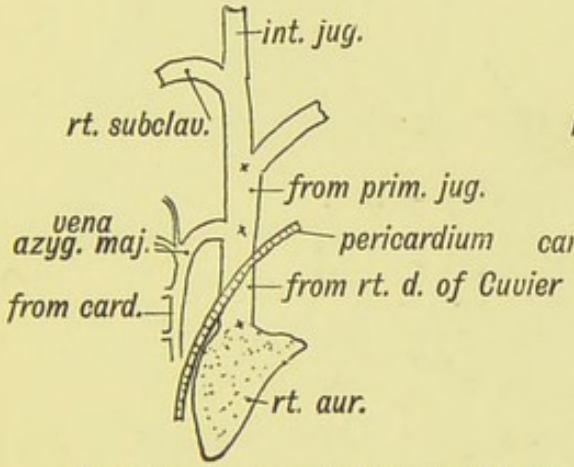
FIG. 269.—Diagram showing the Relationship of the Heart to the Archenteron of the Developing Ovum. The outgrowth of the head fold is indicated carrying a process (fore-gut) of the Archenteron and also the Aorta and Heart. The outgrowth of the tail fold and hind-gut is also shown. (After A. Robinson.)

Ammoecetes the pericardial and peritoneal cavities are continuous (Fig. 268).

Later Stages in the Evolution of the Heart.—So long as the heart is merely a pump for the gills, it retains the simple structure seen in Ammoecetes—but with the origin of a pulmonary system a series of most remarkable changes occur. The pulmonary system in the human embryo takes on its definite form during the second month; at the same time the heart is undergoing a series of changes, which converts it into a double pump, one for the lungs, another for the body. We know that these evolutionary changes occurred slowly, for in amphibia the heart has reached that point in evolution where a single ventricle can serve both the respiratory and systemic circulations. The evolution of a pulmonary system also led to a series of changes in the arrangements of veins. Amongst the most remarkable of these is the formation of a new passage, by which the blood of the abdomen can pass direct to the heart—the inferior vena cava. In the human embryo of the first month the heart and great veins are

arranged as in a fish; in the second month they take on the definite mammalian form.

Fixation of the Heart.—At the beginning of the 3rd week (Fig. 241, p. 252) the heart lies free within the pericardium, with its two extremities fixed to the wall of that cavity. Its anterior or arterial extremity perforates the dorsal wall of the pericardium to give off the aortic arches in the floor of the pharynx. The venous or posterior end is fixed to the septum transversum, the embryonic partition, which is formed between the pericardial and peritoneal cavities (Fig. 236, p. 249). The fate of the aortic arches, which convey the blood from the ventral to the dorsal aorta, has been already traced (p. 229). We now propose, before surveying the complicated changes which ensue in the



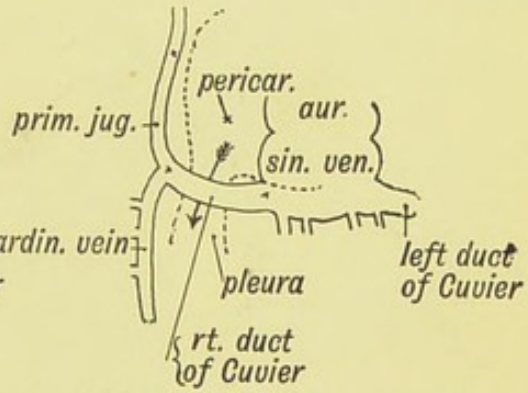


FIG. 270.—The Superior Vena Cava of the Adult.

FIG. 271.—The Embryonic Venous Trunks out of which the Superior Vena Cava is formed. The arrow is in the communication between the pericardial and pleuro-peritoneal cavities.

heart itself, to trace the evolution of those great venous channels which convey the blood to the heart—the venae cavae.

1. The **superior vena cava** arises from the following foetal vessels (Figs. 270 and 271):

(*a*) The part above the entrance of the vena azygos is the terminal part of the right primitive jugular or anterior cardinal vein;

(*b*) The part below the entrance of the vena azygos major arises from the right duct of Cuvier. The condition of these venous trunks, the anterior and posterior cardinal veins and ducts of Cuvier, in a human embryo of the 3rd week, is shown in Fig. 271. The condition shown is retained permanently in fishes.

The anterior cardinal or primitive **jugular vein,** which drains the anterior half of the body on each side, with the **posterior cardinal vein,** which drains the posterior half of the body, receive a tributary (segmental vein) from each body segment. The cardinal veins lie in the mesoblast on the dorsal side of the coelom, at the junction of the splanchnopleure and somatopleure (Fig. 272). By their union they

form on each side the **duct of Cuvier**, which conveys the blood to the sinus venosus—a contractile chamber opening into the primitive auricle. The sinus venosus remains as a separate chamber of the heart in lower vertebrates, but in the course of mammalian development it becomes partly merged in the right auricle of the heart.

It is important to notice how the ducts of Cuvier reach the sinus venosus (see Fig. 272). They pass from the dorsal to the ventral surface of the body in the *somatopleure* or body wall, and enter the ventral mesentery or **mesocardium** of the heart to reach the sinus venosus, thus encircling the coelom. The transverse folds by which the ducts of

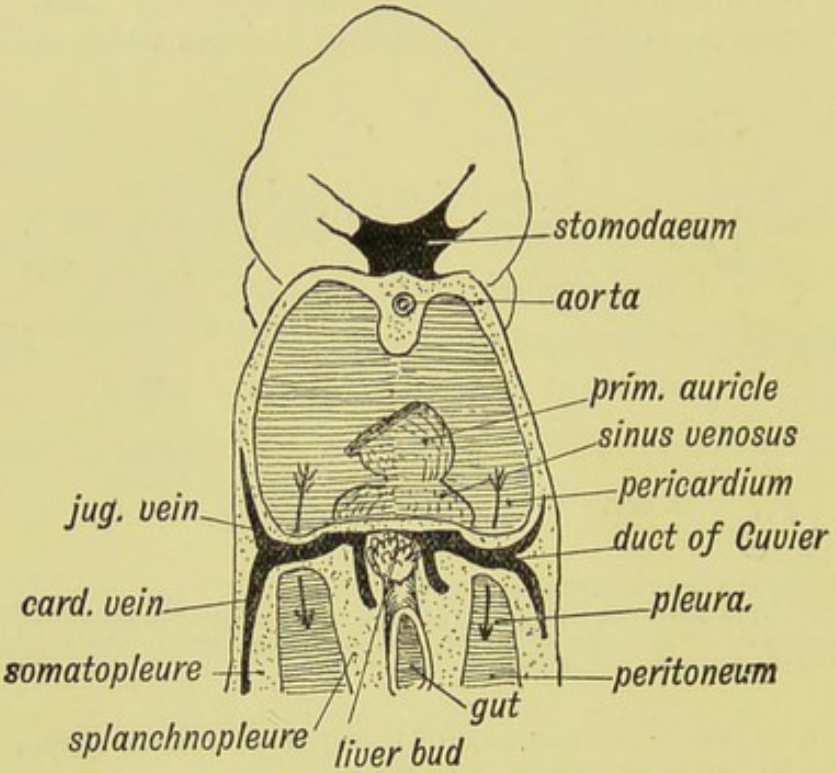


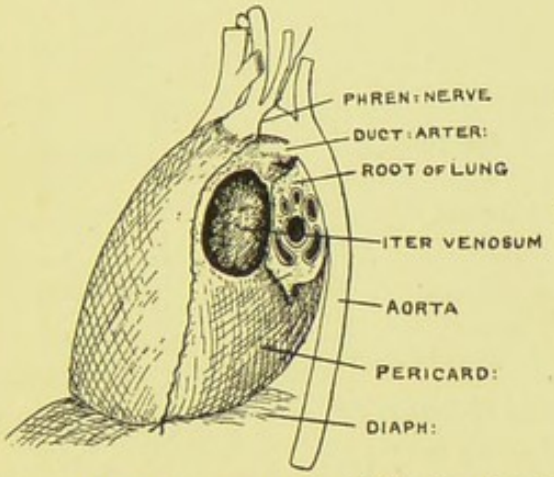
FIG. 272.—Diagram to show the manner in which the Ducts of Cuvier encircle the Coelom at the junction of the Pericardial and Peritoneal Passages at the 3rd week. (After His.)

Cuvier reach the sinus venosus from the body wall form the **septum transversum** (Fig. 272).

We have already seen that the pericardial and peritoneal cavities communicate at the dorsal or oesophageal margin of the septum by the right and left **pleural (pleuro-peritoneal) passages.**[1] The exit from the pericardial cavity to the pleural passage is surrounded by the great venous channels—the ducts of Cuvier; hence the exit is named the **iter venosum** or pericardio-pleural junction. Ultimately, by the end of the 4th week, the part of the coelom lying in front of the ducts of Cuvier and septum transversum is cut off from the rest; the part so

[1] In a former passage I have applied the usual term "pleuro-peritoneal" to these passages, but it is both convenient and accurate to restrict this term to the posterior end of the passage—where pleura passes into peritoneum.

cut off forms the pericardium. Thus the ducts of Cuvier are instrumental in separating the pericardial from the pleural cavity. If the primitive pleuro-pericardial communication (iter venosum of Lockwood) persists between them, it occurs as a foramen in the pericardium behind the part of the superior vena cava derived from the duct of Cuvier. On the left side the duct of Cuvier atrophies, and the iter venosum, if it persists, is then represented by an aperture in the pericardium in front of the root of the left lung (Fig. 273). The ducts of Cuvier, and



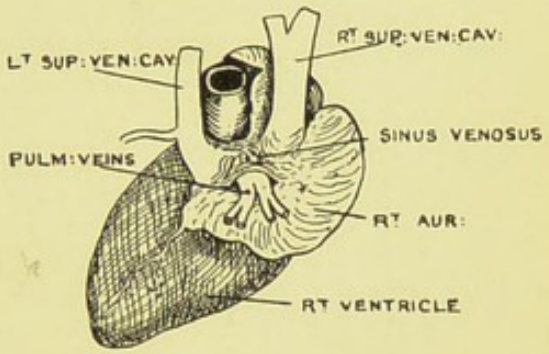


FIG. 273.—Heart of a Child, showing an Abnormal Aperture in the Pericardium in front of the root of the Left Lung, representing a patent Iter Venosum or Pericardio-pleural Junction of the Embryo. The left auricle is seen within the aperture.

FIG. 274.—Abnormal Heart of a Child seen from behind, showing Persistence of the Left Duct of Cuvier, absence of the Inferior Vena Cava, and Pulmonary Veins terminating in the Sinus Venosus. A similar condition is seen in certain fishes.

the folds of the somatopleure in which they lie, are separated from the body wall and buried deep in the thorax by the development of the lungs and pleurae.

2. **The Vestigial Fold and Oblique Vein of Marshall.**—In the human embryo, during the 3rd week, and for some weeks afterwards, there is a right and left duct of Cuvier and corresponding cardinal veins (Fig. 276). A left superior vena cava is present and may persist (Fig. 274). The vestigial fold and oblique vein of Marshall (Fig. 275) are all that usually remain of the left superior vena cava. The right superior vena cava, within the pericardium, passes in front of the right pulmonary vessels, and is bound to them by a mesentery or fold of serous pericardium; the left has a similar relationship (Fig. 275); when it disappears the pericardial reflection remains in front of the left pulmonary vessels as the vestigial fold. The intra-pericardial part of the left vena cava or duct of Cuvier becomes the oblique vein (Fig. 275): it turns round the left auricle to terminate in the left horn of the sinus venosus (coronary sinus). The extra-pericardial part of the left duct of Cuvier joins the superior intercostal vein (Fig. 275). Both right and left superior venae cavae persist in some lower mammals, and

occasionally this is also the case in man (Fig. 274). The left superior vena cava begins to atrophy when the common auricular chamber is divided into a right and left compartment at the beginning of the 2nd month.

The **left superior intercostal vein** represents the following embryonic vessels (see Fig. 275) :

(*a*) Anterior part of the left posterior cardinal vein ;
(*b*) The extra-pericardial part of the left duct of Cuvier ;
(*c*) The terminal part of the left primitive jugular vein.

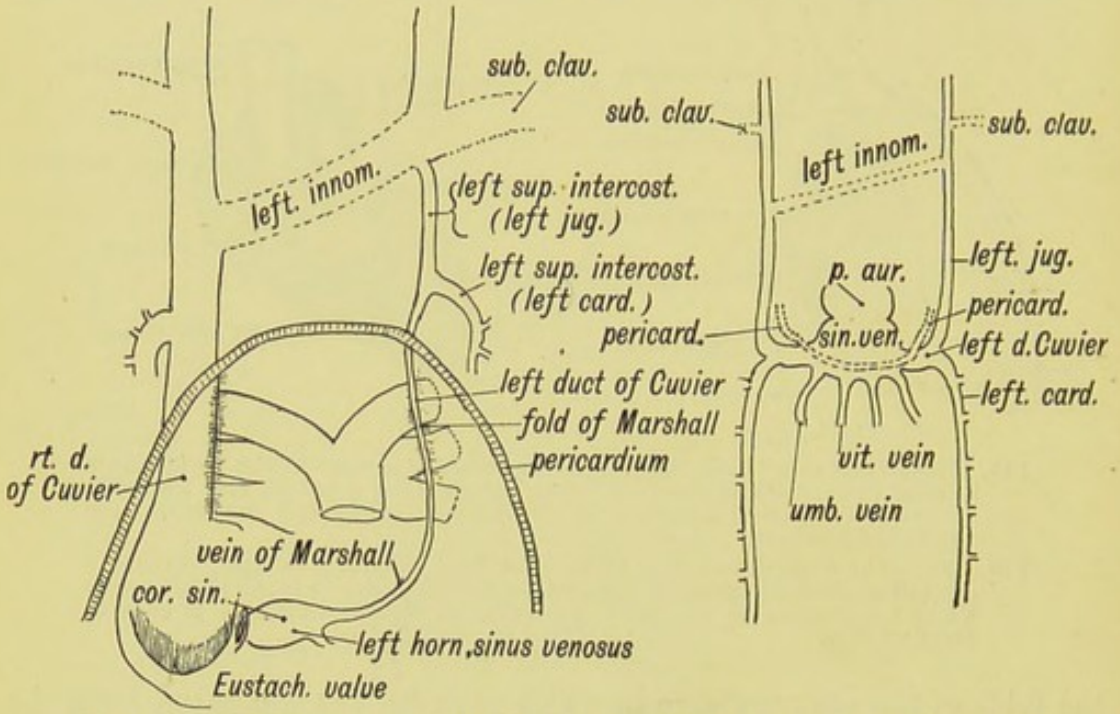


FIG. 275.—The Remnants of the Left Superior Vena Cava, derived from the Structures shown in Fig. 69.

FIG. 276.—Diagram of the Sinus Venosus and Ducts of Cuvier of the Human Embryo about the 3rd week.

3. **The Left Innominate Vein** opens up as a channel of communication between the two primitive jugular veins, the left superior vena cava undergoing a simultaneous process of atrophy (Fig. 275).

4. **The Subclavian Veins** are developed in the 4th week with the outgrowth of the fore-limb buds ; they open into the primitive jugulars (Fig. 276). The subclavian vein represents a segmental tributary of the primitive jugular.

5. **Jugular and Cerebral Veins.**—In the first month each anterior cardinal vein commences in a corresponding primitive cerebral vein.[1] Each primitive cerebral vein passes along the base of the skull, receiving the veins from the fore-, mid- and hind-brains, and makes its exit by the jugular foramen, where it becomes the jugular or anterior

[1] For a full account of the development of the intra-cranial sinuses see monograph by Professor Mall, *Amer. Journ. Anat.* 1904, vol. 4, p. 1.

cardinal vein. The primitive cerebral veins form the cavernous sinus and the vestigial petro-squamosal sinuses. An efferent channel leaves the skull at the Glasserian fissure, where it enters the external jugular vein. It is not uncommon in adult subjects to see the petro-squamosal sinus, which ends behind in the lateral sinus, also send out an emissary vein by a foramen at the root of the zygoma—a remnant of the embryonic condition. As the cerebrum expands in the 2nd and 3rd months, the longitudinal, lateral and petrosal sinuses are formed as new channels, the primitive cerebral veins being reduced to form the petro-squamosal sinuses.

Veins formed from the Posterior Cardinals of the Embryo.[1]—Each posterior cardinal vein receives on its own side—(*a*) A branch from each body segment from the lower cervical to the last caudal. These become the intercostal, lumbar and sacral veins. (*b*) The segmental veins of the intermediate cell mass, which become the supra-renal, renal, spermatic, and ovarian veins. (*c*) When the hind-limb buds grow out, their veins join that part of the cardinal veins which become the common iliac. The lateral sacral, ilio-lumbar and ascending lumbar veins are anastomotic channels formed between the segmental veins.[2]

The posterior cardinal veins are divided into **pre-nephric** and **post-nephric** parts by the development of the Wolffian body or mesonephros. That body actually grows into, and breaks up a part of the cardinal vein into, a "renal portal" circulation, so that the venous blood from the posterior segments of the body passes through, and is elaborated by the mesonephros, as Shore found to be the case in the frog (Fig. 278). A communication quickly opens up between the post-nephric and pre-nephric section of each vein.

From the **right cardinal vein** are formed (1) the vena azygos major; (2) the post-renal or post-nephric part of the inferior vena cava (Fig. 277).

The part above the entrance of the right renal becomes the vena azygos major; the part below, the inferior vena cava. Hence it is that the origin of the vena azygos can commonly be traced to the renal vein. The ascending lumbar vein, which also ends in the vena azygos major, is, as already mentioned, a new anastomotic channel.

From the **left cardinal** arise (Fig. 277)—(1) Part of the left superior intercostal vein; (2) left superior azygos vein; (3) left inferior azygos, which commences in the left renal vein, and also receives the left ascending lumbar. The post-nephric part of the left cardinal disappears in higher mammals; occasionally it persists in man, and very frequently in the rabbit.

[1] See F. T. Lewis, *Amer. Journ. Anat.* 1901, vol. 1, p. 229.

[2] For literature and description of cases of abnormal development of the posterior cardinal veins, see Dr. Gladstone's article in *Journ. Anat. and Physiol.* 1912, vol. 46, p. 220; J. Cameron, *ibid.* 1911, vol. 46, p. 416.

The greater part of the **left common iliac** vein arises, like the left innominate, as a communicating channel between the posterior cardinals. It is formed as the post-nephric part of the left cardinal becomes obliterated (Fig. 277).

The Inferior Vena Cava.—The transformation of the cardinal system and the development of a new caval channel to convey the

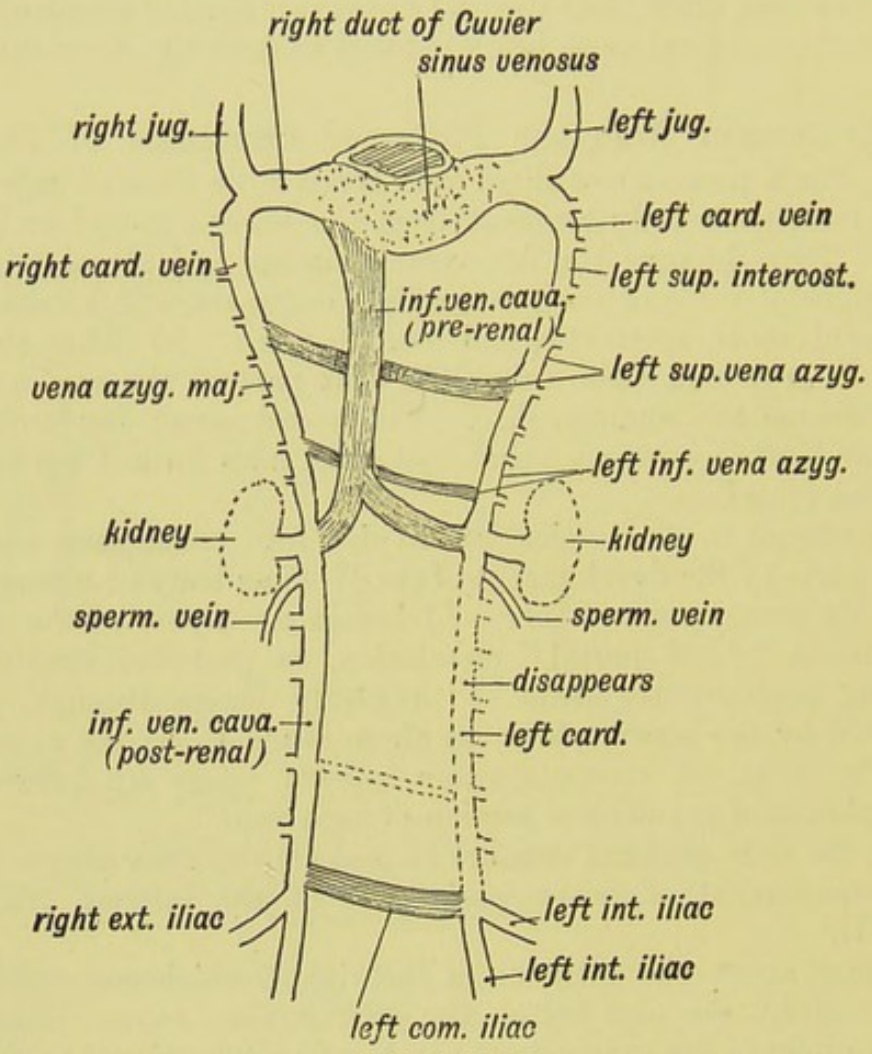


FIG. 277.—The Remnants of the Posterior Cardinal Veins in the Adult. The new channels are shaded. (After Hochstetter.)

blood in the systemic veins of the abdomen direct to the heart, take place at the beginning of the 2nd month as the pulmonary system begins to develop. With the evolution of lungs, respiratory movements of the body wall were introduced—a new force which was utilized to assist the return of the venous blood to the heart. Three parts are to be recognized in the inferior vena cava: (1) a post-renal part, formed from the post-nephric part of the right cardinal (Fig. 278); (2) a supra-diaphragmatic part, formed from the terminal part of the vitelline veins which are situated in the ventral mesentery of the fore-gut (Fig. 243); (3) a pre-renal or new part, which is formed as a com-

municating channel in the dorsal mesentery of the fore-gut between the post-renal and supra-diaphragmatic parts. The pre-renal part is formed at the commencement of the 2nd month, when the cardinal veins are broken up by the development of the mesonephros; in this way the blood from the posterior part of the body is short-circuited to the heart (Fig. 278).

The Portal Vein.—**The Portal Vein** is formed out of the terminal parts of the two vitelline veins. They end in the posterior chamber

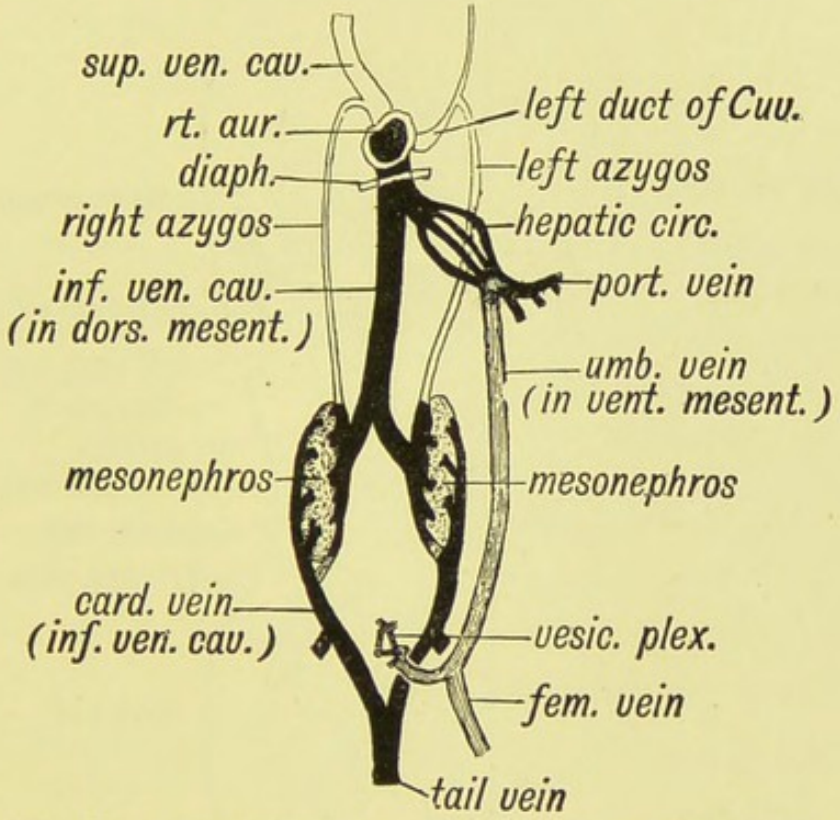


FIG. 278.—The Arrangement of the Cardinal, Umbilical and Inferior Caval Veins in Lower Vertebrates. The venous blood from the posterior part of the body passes through either the renal or hepatic circulations before reaching the heart. (After Hochstetter.)

of the tubular heart of the embryo—the **sinus venosus.** The vitelline veins, right and left, arise from ramifications on the yolk sac and pass in the ventral mesentery of the fore-gut to the sinus venosus (Fig. 279) The nutriment within the yolk sac is thus carried to the heart and distributed by the heart to the tissues of the embryo and yolk sac. With the differentiation of the gut from the yolk sac, the parts of the vitelline veins, at first situated on the yolk sac, fuse together in the dorsal mesentery. Thus while the terminal parts of the vitelline veins lie in the ventral mesentery of the fore-gut, the three tributaries of the portal vein—the splenic vein from the fore-gut, the inferior mesenteric from the hind-gut, and the superior mesenteric from the mid-gut (Fig. 279)—lie in the dorsal mesentery. They are developed as tributaries of the vitelline veins, for we have already seen that the veins

of the yolk sac may persist as a cord which joins the superior mesenteric vein below the pancreas (see Fig. 258, p. 270). The duodenum forms a loop between the vitelline veins (Fig. 280), and hence on either side of the 1st and 3rd stages of the duodenum the vitelline veins remain separate, while in front, between and behind these stages, they are united by anterior, middle and posterior junctions (see Fig. 280).

The portal sinus in the transverse fissure of the liver is formed out of the anterior junction of the right and left vitelline veins in the ventral

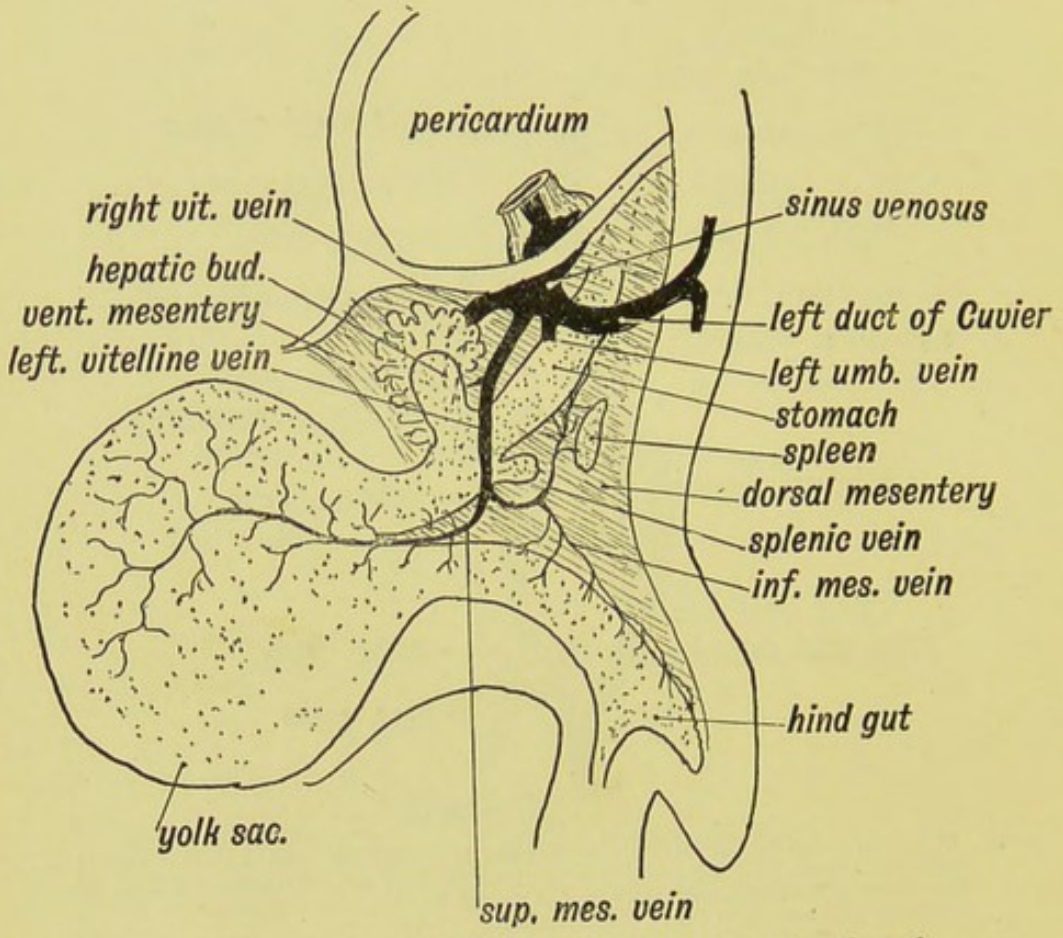


FIG. 279.—The Left Vitelline Vein of an Embryo of the 4th week.

mesentery (Figs. 279, 242); the part of the portal vein in the gastro-hepatic omentum (ventral mesentery), and behind the 1st stage of the duodenum, is formed from the right vitelline vein; the corresponding part of the left vein disappears; the commencement of the portal vein—in the neck of the pancreas—represents the middle junction of the two vitelline veins (Fig. 280); the terminal part of the superior mesenteric vein, which in the adult lies in front of the 3rd stage of the duodenum, represents a part of the left vitelline vein—the corresponding part of the right disappears (Fig. 243, p. 254). To understand the transmutation which leads to the formation of the portal vein, it must be remembered (1) that the duodenum forms at first a free loop, the right surface of which afterwards becomes applied to the posterior wall

of the abdomen ; (2) the pancreas is developed in its dorsal mesentery ; (3) the ventral mesentery, in which the liver is developed, is attached to the anterior part of the loop (Fig. 279).

The Hepatic Veins are formed out of the terminal parts of the vitelline and umbilical veins. Those veins end at first in the sinus venosus (Figs. 280, 242, 243). The liver is developed between and around the

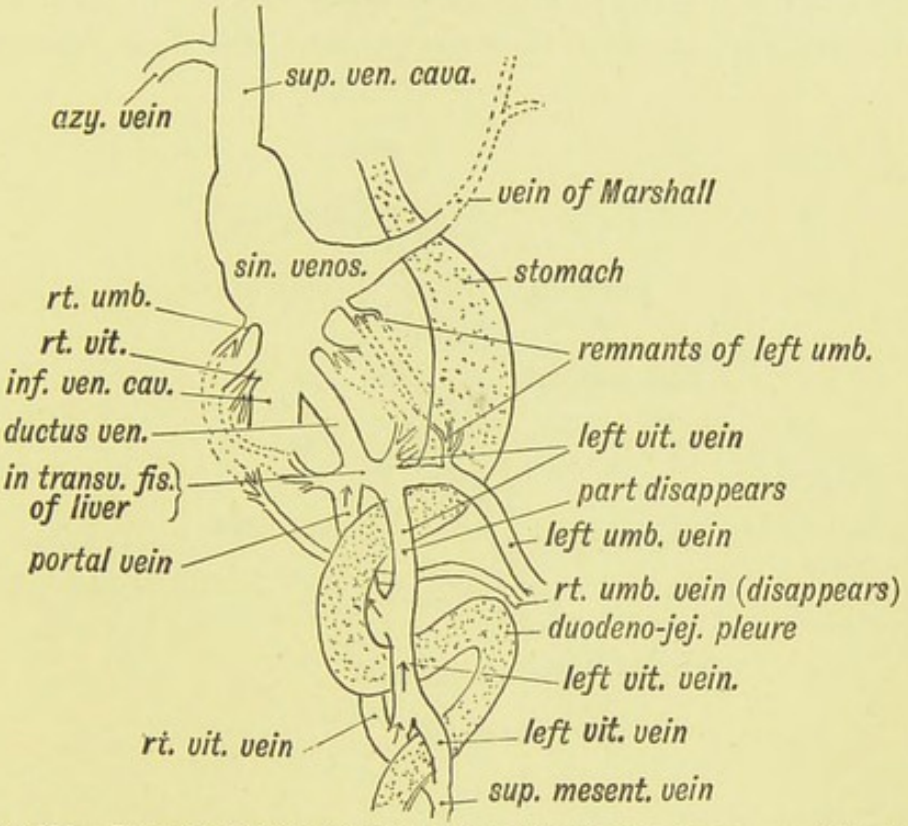


FIG. 280.—Diagram showing the Formation of the Ductus Venosus, and the fate of the Umbilical and Vitelline Veins. The arrows show the parts of the vitelline veins which become the portal vein.

vitelline and umbilical veins, near their termination in the sinus venosus. The hepatic buds perforate and develop within the venous channels (F. T. Lewis). The veins are broken up and a fine intra-hepatic venous network takes their place. Thus it comes about that the vitelline veins are transformed into the veins of the portal and hepatic circulation. All the foetal and umbilical blood is at first poured through the liver.

The Ductus Venosus is a new channel formed in the 5th week between the portal sinus and the terminal part of the right vitelline vein, whereby the greater part of the umbilical blood is short-circuited to the sinus venosus without passing through the liver. After birth, when a short circuit is no longer required between the placental circulation and heart, it becomes reduced to a fibrous cord. It occupies the posterior part of the longitudinal fissure of the liver and lies within the hepatic attachment of the gastro-hepatic omentum (Fig. 245).

The Umbilical Veins.—The umbilical vein at birth consists of two parts : (1) A part within the umbilical cord ; (2) another within

the body, enclosed in the falciform ligament and anterior half of the longitudinal fissure of the liver. It joins there the ductus venosus and portal sinus (Fig. 281). The condition of the umbilical veins in a human embryo of three weeks is shown in Fig. 282, and the arrangement of the representative of this vessel in the adult forms of lower vertebrates—the lateral vein—is shown in Fig. 278. In the body stalk the umbilical veins have already fused, but in the body wall and ventral mesentery, in which they pass to reach the sinus venosus, they

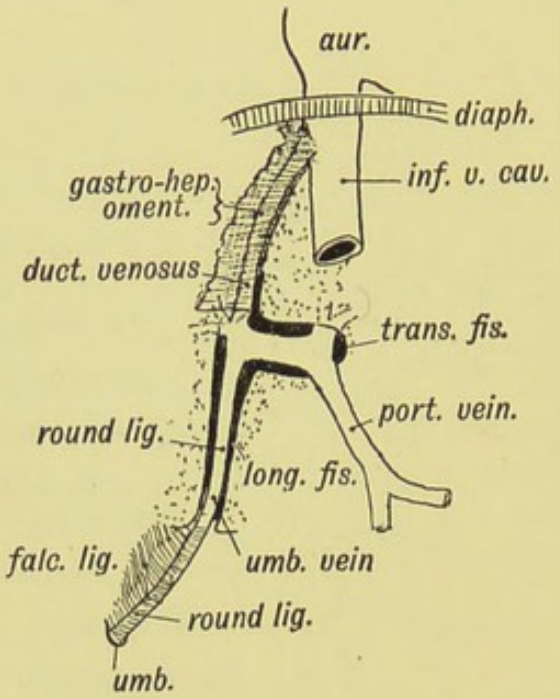


FIG 281.—Diagram of the Remnants of the Umbilical Vein in the Adult—viewed from behind.

remain separate. With the differentiation and closure of the umbilicus, the parts of the body wall in which the umbilical veins are situated are drawn out to form the umbilical cord. The intra-embryonic parts then lie within the ventral mesentery of the fore-gut, lateral and ventral, to the vitelline veins. By the umbilical veins the blood is returned from the placenta to the heart. In nearly all vertebrate embryos the vitelline veins are the first of all the vessels of the body to be developed, but in the Higher Primates, including man, this appears not to be the case. Professor Eternod found that in a human embryo, of about 14 days, the umbilical veins and the venous sinuses of the chorion were already in process of formation, while the vitelline veins had not yet appeared. We have already seen (Chap. II.) that the Higher Primates are remarkable for the precocious development of the chorion; this early differentiation of the chorion is attended by an equally early formation of the umbilical vessels, which return the blood from the chorion to the heart.

The outgrowth of the liver-bud within the ventral mesentery breaks up not only the vitelline veins, but also the umbilical at their junction with the sinus venosus (Figs. 242, 243, p. 253). The intra-embryonic part of the **right** umbilical vein atrophies, while the **left** enlarges. With the terminal parts of the vitelline veins the opposite is the case. Thus the umbilical blood as well as the vitelline comes to be poured into the

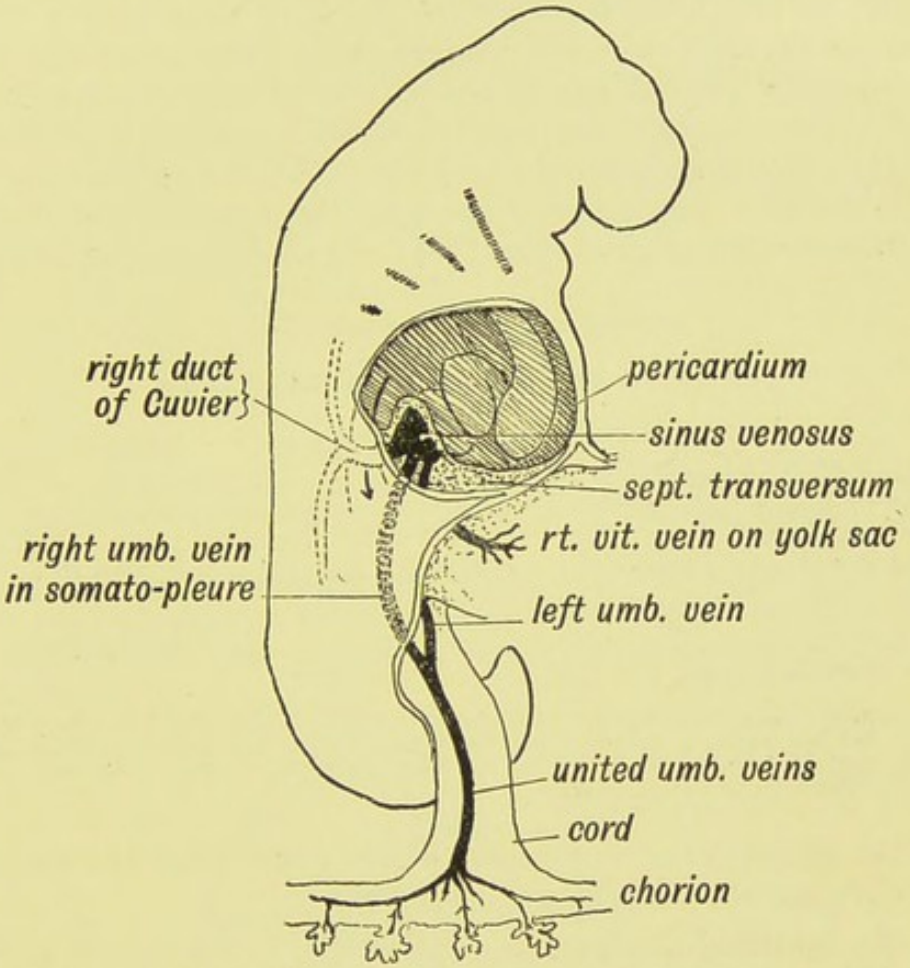


FIG. 282.—Diagram of the Right Umbilical Vein in an Embryo of 3 weeks, before the Outgrowth of the Liver-Bud. (Modified from His.)

liver. The left umbilical vein within the body remains permanently; when its terminal part is broken up by the outgrowth of the liver it becomes united with the portal sinus. The left umbilical vein thus comes into communication with the ductus venosus (see Figs. 280, 281).

Nature of the Umbilical Veins.—In lower vertebrates part of the venous blood from the posterior region of the body passes into the renal-portal circulation; part (from the limbs—pelvis and *bladder*) passes by the **lateral veins** through the belly wall and ventral mesentery to the hepatic-portal circulation (Fig. 278). It will be remembered that the allantois is an extra-embryonic part of the bladder, which plays a leading part in the vascularization of the placenta. The part of the umbilical vein which afterwards forms the round ligament in the

falciform ligament represents the terminal part of the united lateral veins of lower vertebrates; the part within the umbilical cord and placenta corresponds to greatly enlarged tributaries to the bladder.

DEVELOPMENT OF THE HEART.

Origin of the Cardiac Tubes.—We have already seen that the heart arises as right and left cardiac tubes situated on the wall of the archenteron, at each side of the part which is destined to form the fore-gut. Two elements are included in the formation of each cardiac tube: (1) a lining membrane which forms the endocardium, and probably arises as a linear invagination of the hypoblast or endoderm which lines the archenteron (Fig. 283); (2) an ensheathing layer, from

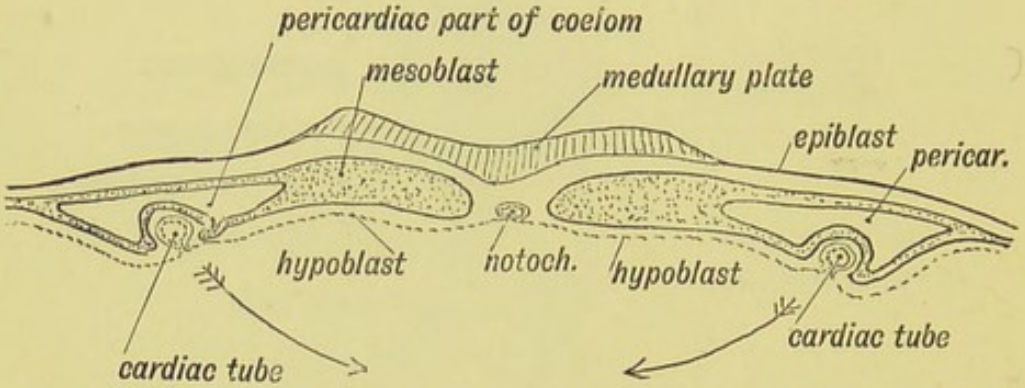


FIG. 283.—Transverse Section of Embryonic Plate showing the Right and Left Cardiac Tubes situated in the Splanchnopleure. The arrows indicate the approximation of the sides of the body wall which takes place after the outgrowth of the fore-gut.

which the musculature is formed, which arises from the splanchnopleure covering the archenteron (Fig. 283).

The Pericardial Coelom.—In Fig. 308, p. 313, a section across the head fold of a salamander embryo is shown, developmental changes being much more clearly marked in the embryos of lower than of higher vertebrates. The mesoblastic plate on each side is cleft to form the cavity of the coelom. At each side of the fore-gut the somatopleure and splanchnopleure, which form the outer and inner walls of the coelom, have fused to form the mesoblastic basis of the visceral arches. Below the pharyngeal part of the fore-gut, the coelom remains open and forms the pericardial cavity. Beneath the fore-gut, the right and left layers of the splanchnopleure, with the cardiac tubes, have met and fused (Fig. 284). The heart is thus suspended in a mesentery, forming the **dorsal** and **ventral mesocardium.** In mammalian embryos the ventral mesocardium is never formed (Robinson), and the dorsal mesocardium disappears, except over the posterior segment of the heart—the sinus venosus. A diagrammatic section across this part of the dorsal mesocardium, showing the stage reached in the 3rd week, is

given in Fig. 285. It is continuous with the ventral mesentery of the fore-gut; at each side of it is the pleural passage. The lung buds lie in the mesentery of the fore-gut between the pleural passages;

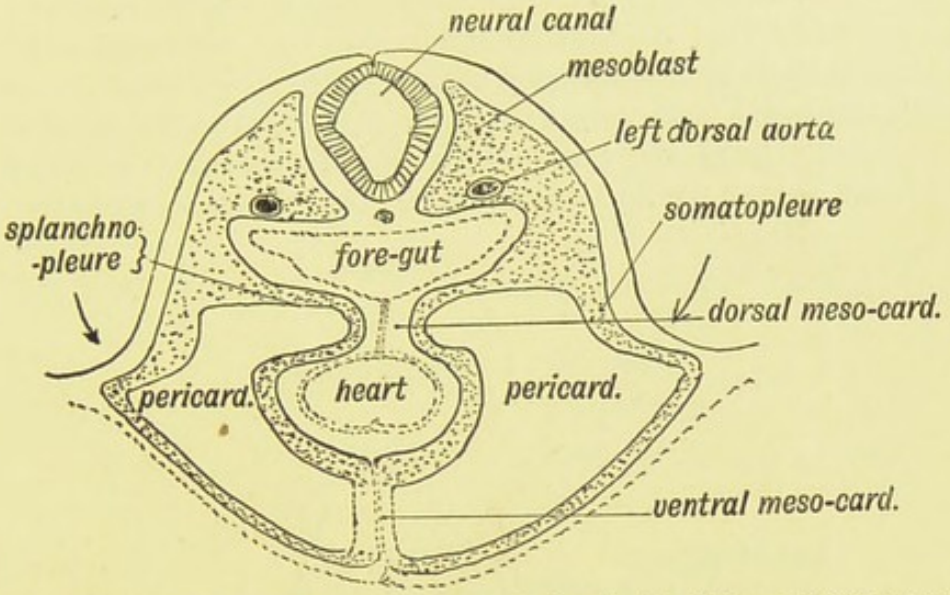


FIG. 284.—Illustrating the manner in which the Cardiac Tubes and Splanchno-pleures were formerly supposed to become fused together under the Fore-gut.

when the pulmonary veins are developed, they reach the sinus venosus through the dorsal mesocardium. The sinus venosus lies in the transverse septum with the dorsal mesocardium attached to its upper surface (Fig. 285).

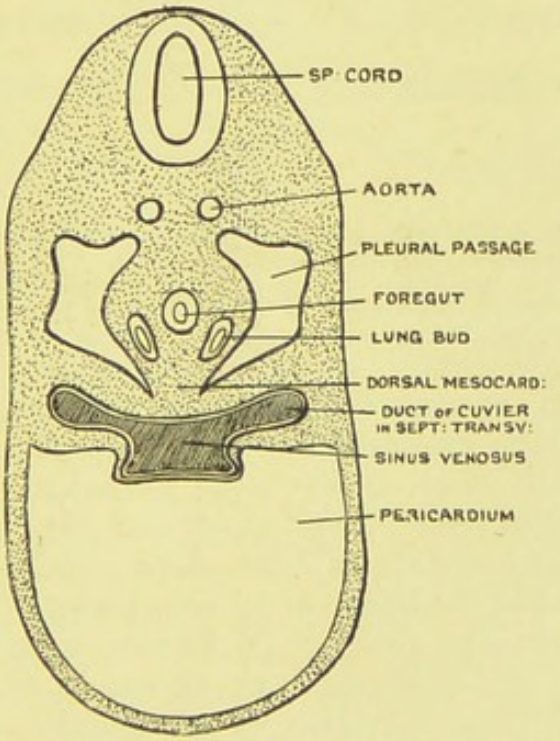


FIG. 285.—Diagrammatic Section across an Embryo of the 3rd week to show the relationship of the Sinus Venosus to the Septum Transversum and Dorsal Mesocardium.

Demarcation into Chambers.—In the third week the heart undergoes **three important changes** :

(1) The dorsal mesocardium disappears, and the heart, all but the anterior and posterior extremities, is left free in the anterior expansion of the coelom. This can best be understood by a reference to Fig. 241. The heart is there seen suspended between the fore-gut and ventral wall. The tubular heart is formed behind by the union of the right and left vitelline veins from the yolk sac, and ends in front as the first or mandibular aortic arches, which, as is also the case with the aortic

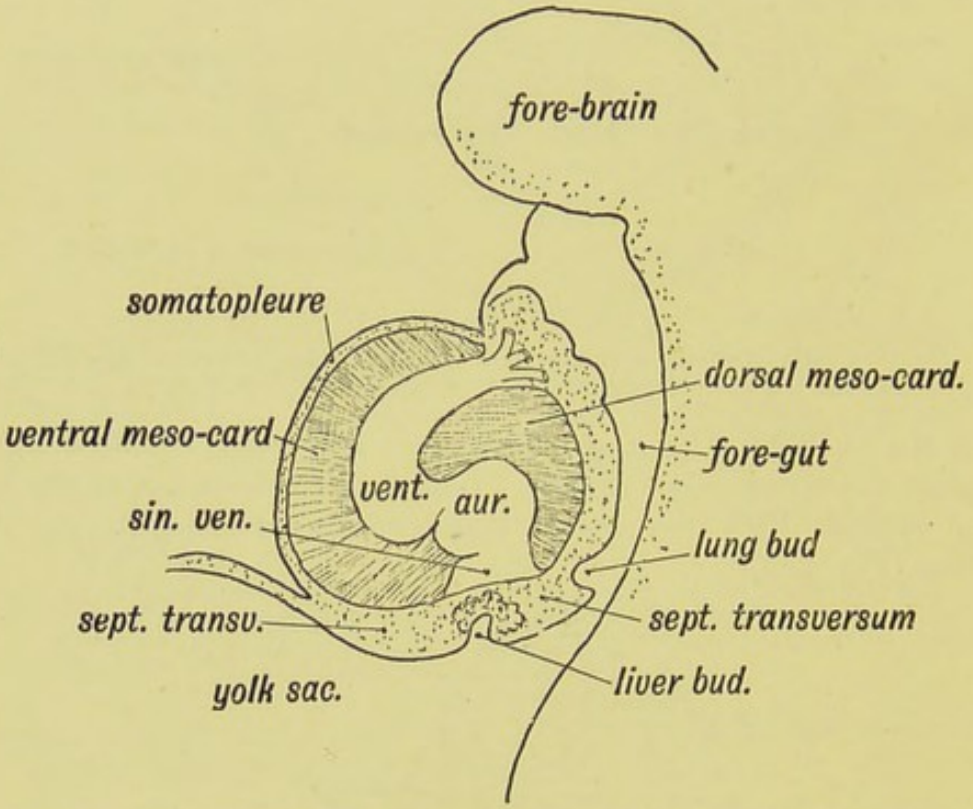


FIG. 286.—Lateral View of the Heart and Pericardium to show the Attachments of the Dorsal and Ventral Mesocardia (schematic). The ventral mesocardium, although not formed in the human heart, is represented to give a clear conception of the relationship of the heart to the ventral mesentery of the fore-gut.

arch of the hyoid segment, have only a very transient existence. The posterior end of the mesocardium, both the ventral and dorsal parts, persists—the part which encloses the sinus venosus, and this part forms an element in the septum transversum (Fig. 286).

(2) The tubular heart shows demarcations into four segments which can be recognized in the hearts of all vertebrates (Fig. 288) : (*a*) Sinus venosus ; (*b*) Primitive auricle ; (*c*) Primitive ventricle ; (*d*) Bulbus cordis. In this condition (third week) the human heart is exactly like that of a fish (Figs. 211, 212), viz. a tubular four-chambered heart which pumps blood into the branchial or aortic arches.

(3) The disappearance of the mesocardium allows the heart to become

twisted and bent. Two chief bends are formed which materially help to give the heart its adult shape (Fig. 289) :

(*a*) **The Ventricular Bend.**—The ventricular part of the tube is bent into a V-shaped piece, the apex of the V-shaped loop being turned towards the right.

(*b*) **The Auriculo-ventricular Bend.**—The ventricular part is bent in front of the auricular so that the auricle becomes dorsal to the ventricle.

Meaning of the Cardiac Bends.—The cardiac bends are due to the asymmetrical development of the auricular and ventricular chambers on the cardiac tube (Fig. 288). They are not accidental twistings due to the fact that the cardiac tube suddenly becomes too long for its

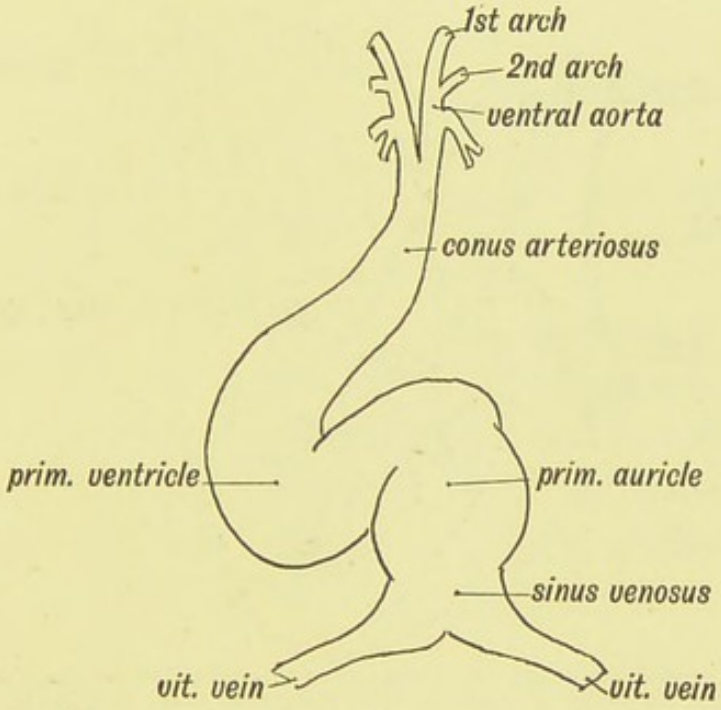


FIG. 287.—The Primitive Divisions of the Embryonic Heart.

chamber, but are the result of a regular series of growth changes, which lead to the formation of the chambers of the adult heart. As may be seen from the diagram given in Fig. 288, the auricles arise chiefly from the dorsal wall of the primitive cardiac tube, while the ventricles arise mainly by an evagination and growth of the ventral and lateral aspects of the ventricular segment of the primitive cardiac tube. Indeed, we shall see that in the 2nd and 3rd months the lesser curvature of the ventricular bend becomes arrested in growth, then absorbed, so that the auricular and aortic orifices at the beginning and end of the ventricular segment are brought together, the one in front of the other (see Fig. 302). The arrest of growth affects the right aspect of the ventricular segment much more than the left, hence the primitive ventricle is bent towards the right side (Fig. 289). Valves are developed at the juncture of the venous and auricular segments, of the auricular

and ventricular, and at the ventricular and aortic by infoldings or cushions of the endocardium (Fig. 288). Part of the auricular segment remains between the primitive auricle and ventricle to form the **auricular canal** (Fig. 208, II.). This is enveloped by an upgrowth of the base of the primitive ventricle.

The Sinus Venosus.—The sinus venosus, the first chamber of the foetal heart, is formed by the union of the vitelline veins ; the umbilical veins and ducts of Cuvier come subsequently to open in it (Fig. 289). The sinus is embedded in the septum transversum (Fig. 289). The ducts of Cuvier reach the sinus from the somatopleure by passing

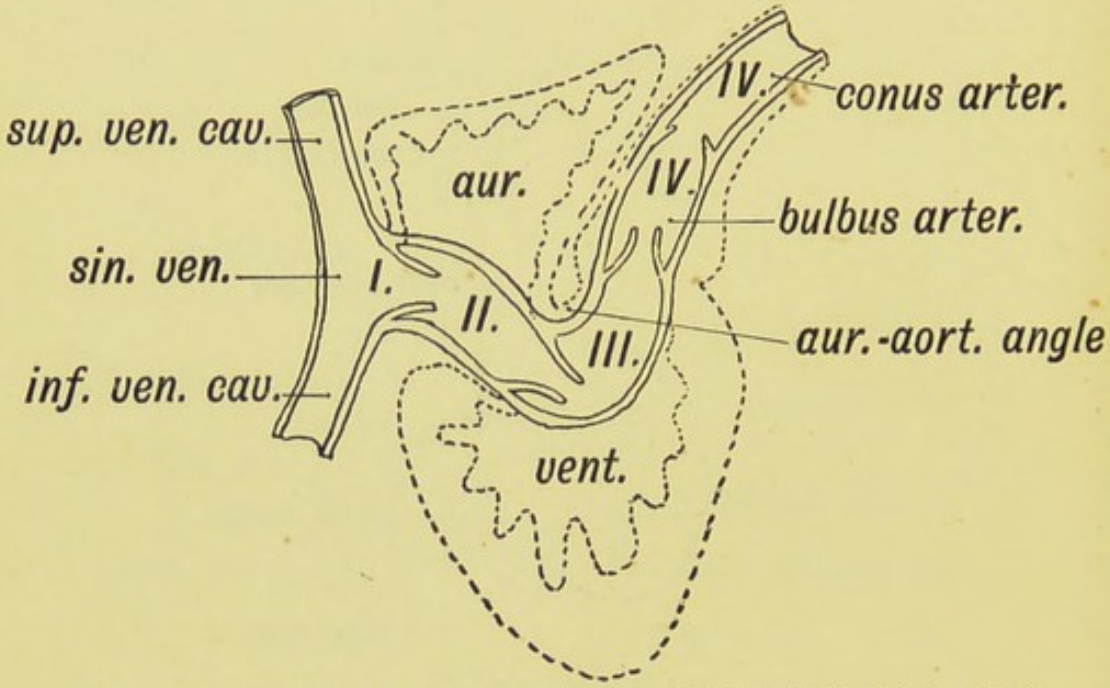


FIG. 288.—Diagram of the four Segments of the Primitive Cardiac Tube. I. The venous segment. II. The auricular segment ; on its dorsal aspect the auricle proper is developed ; the venous valves are shown between the venous and auricular segments. III. The ventricular segment, the ventricle proper being developed from its ventral aspect ; the ventricular segment is separated from the auricular by the auriculo-ventricular and from the next segment by the aortic valves. IV. The bulbo-aortic segment.

through the septum. In fishes and in the human embryo the sinus serves as a reservoir during systole of the auricle ; the systolic wave always commences in the sinus venosus. The right and left **venous valves** (Fig. 291) at the juncture of the sinus and auricle prevent the regurgitation of blood during systole of the auricle. These valves become more or less atrophied when the right and left sides of the heart are completely separated by the formation of septa.

Fate of the Sinus Venosus (Fig. 290).—Since the sinus venosus plays such a dominant part in the physiology of the heart of lower vertebrates, it is extremely important that we should follow its fate in the human heart. It becomes submerged chiefly in the right auricle, the sulcus terminalis (see Fig. 293), marking the line at which it became

included by the upgrowth of auricular tissue. Already, at the end of the first month, its orifice has come to occupy a position in the posterior or dorsal wall of the right part of the common auricle (Fig. 291). The part which it forms of the right auricle is indicated by the entrance of the following vessels which primarily terminate in the sinus :

(1) The superior vena cava (the right duct of Cuvier) ;

(2) The inferior vena cava, which also opens into the sinus ;

(3) The oblique vein of Marshall (left duct of Cuvier), which opens into the left horn of the sinus venosus. The left horn of the sinus becomes the coronary sinus. The sulcus terminalis is marked on the

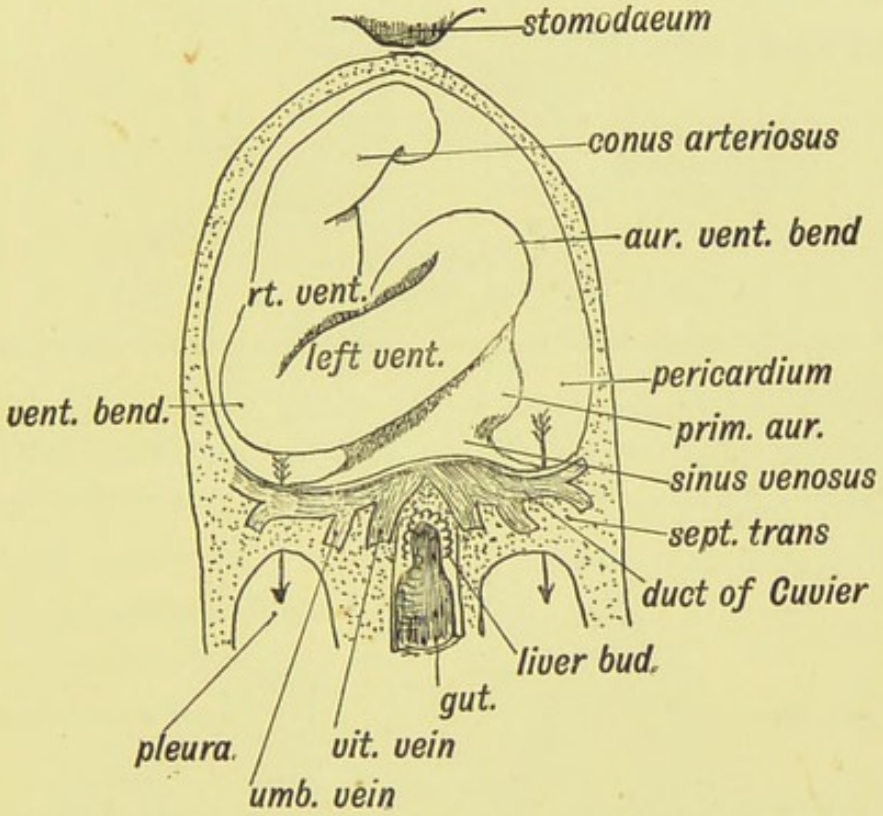


FIG. 289.—Showing the two chief Bends which occur in the Heart during the 3rd week.

interior of the right auricle by a strong muscular band (taenia terminalis), which runs down on the anterior wall of the right auricle from the superior to the inferior vena cava, and indicates the junction of the primitive auricle with the sinus venosus (Fig. 292). The musculature which surrounds the terminal part of the superior vena cava, and that contained in the wall of the coronary sinus, represents the musculature of the sinus. Elsewhere the muscle of the sinus appears to be replaced by that of the auricle.

The Valves of the Sinus Venosus.—Right and left lateral valves (venous valves) guard the entrance of the sinus to the primitive auricle and prevent the regurgitation of blood when the auricle contracts (Fig. 291). The valves meet above and form a **superior fornix** in front of the superior caval opening ; they meet below in an **inferior fornix,**

which, owing to the great shortening of the ventral part of the auricular segment, reaches the base of the ventricle, and actually fuses with

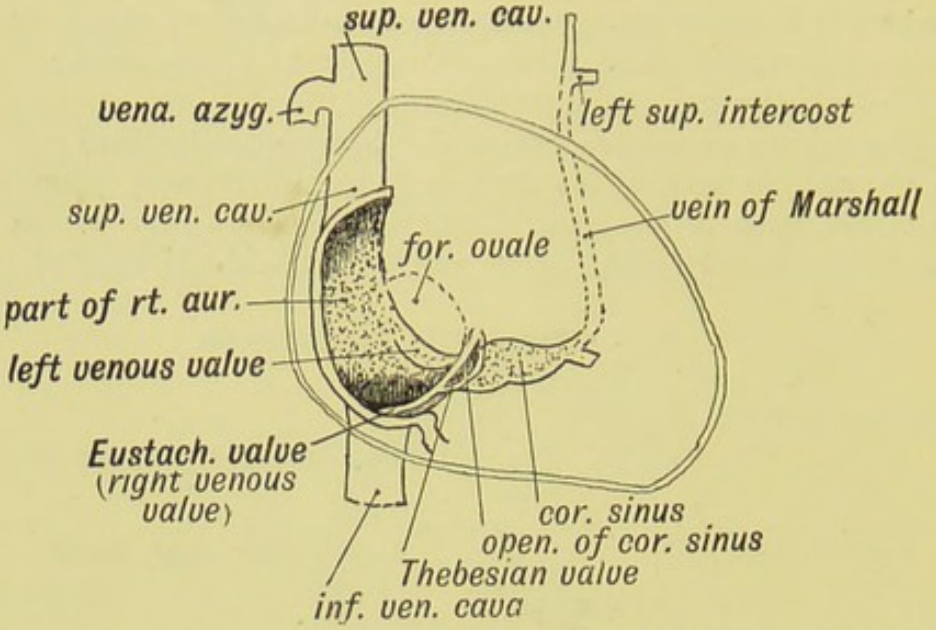


FIG. 290.—Showing the part of the Right Auricle formed from the Sinus Venosus.

the posterior endocardial cushion (Fig. 298). That has an important bearing on the origin of the auriculo-ventricular (A.V.) bundle within the auricular canal. Along the base of each valve is arranged a band

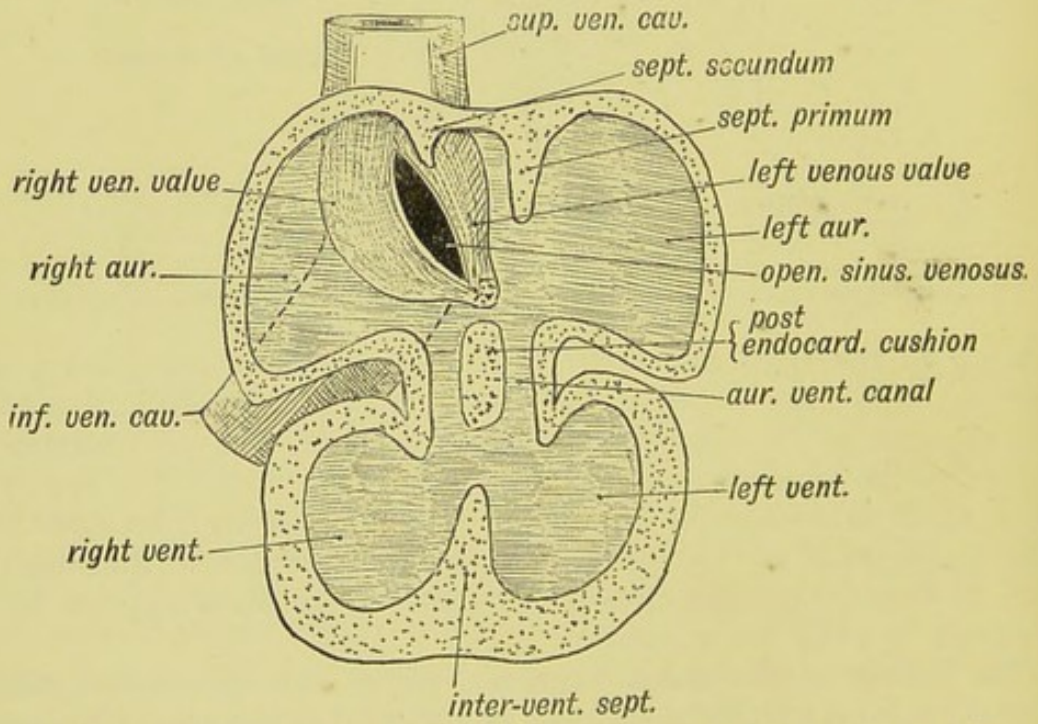


FIG. 291.—Sections of the Heart of a 5th week Human Foetus showing the Right and Left Venous Valves which guard the Entrance of the Sinus Venosus into the Primitive Auricle. The septum secundum is not yet developed ; that indicated is in reality a section across the upper fornix of the venous valves. (After His.)

or taenia of the auricular musculature. Thus each valve consists of a membranous marginal part and a muscular basal part. The right valve in the adult heart becomes (Fig. 292) (1) the Thebesian and (2) Eustachian valves; (3) the musculature at its base forms the taenia terminalis. The left valve becomes (1) a fretted membrane on the septal margin of the inferior caval orifice, (2) a band of musculature accompanying this remnant (Fig. 292).

The Limbic Bands.[1]—Two inflections of the wall of the sinus venosus are formed (*a*) between the superior and inferior caval orifices, (*b*)

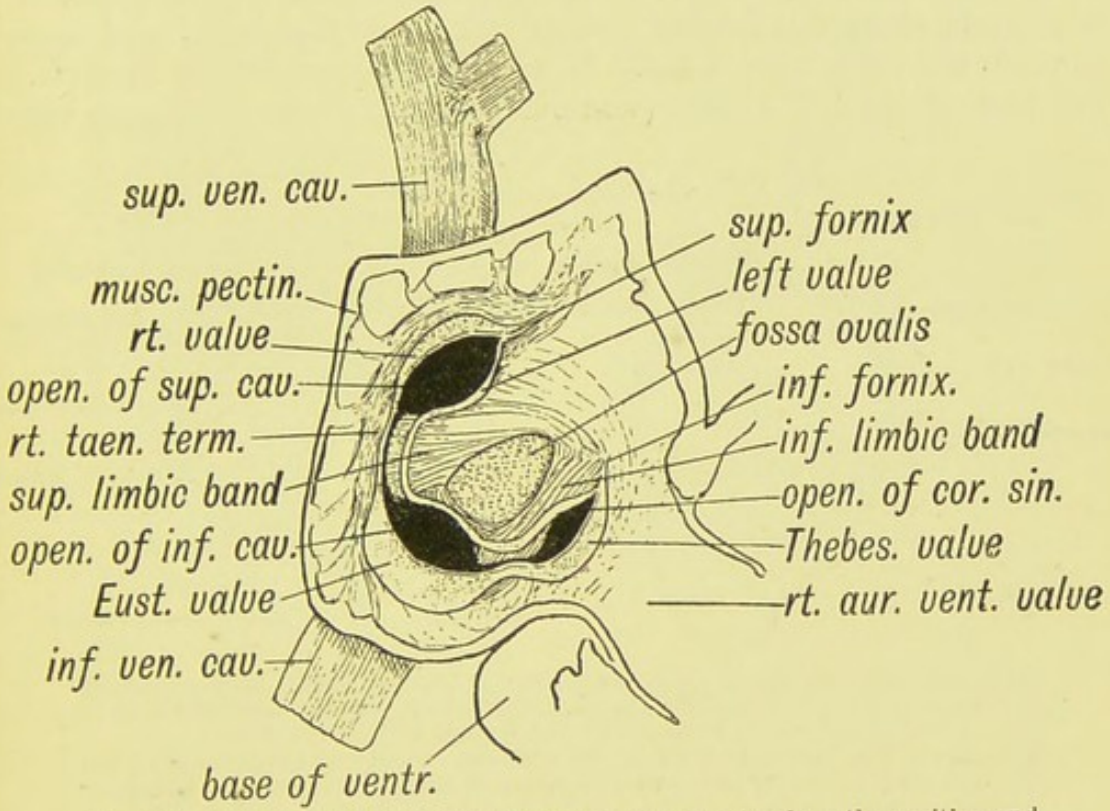
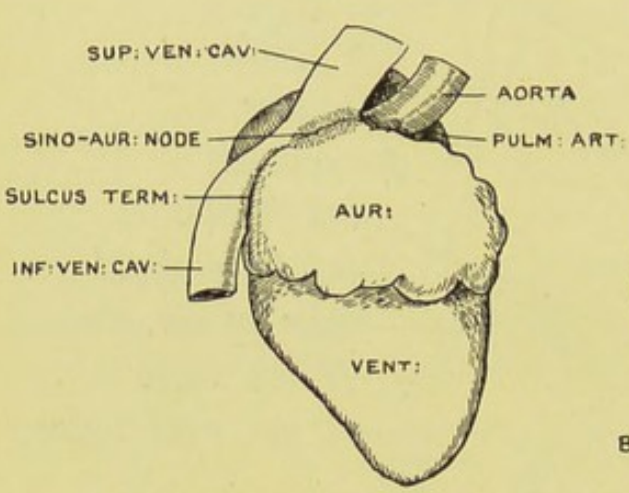


FIG. 292.—Diagram of the Right Auricle thrown open to show the position and relations of the Right and Left Venous Valves and the manner in which they are broken up by the Superior and Inferior Limbic Bands.

between the inferior caval orifice and that of the coronary sinus. In these inflections bands of auricular musculature cross, forming the upper and lower limbic bands (Fig. 292). Thus the mechanical valves which prevent regurgitation in auricular systole are replaced by a muscular mechanism which serves the same purpose. In amphibians and reptiles, where the division of the heart is incomplete, over-pressure in the right side is relieved by the escape of blood to the left side of the heart; but in birds and mammals such an adjustment is impossible, hence the mechanical venous valves are replaced by a "safety mechanism," which will allow regurgitation from the auricles to the veins if the right side becomes over-distended.

[1] Keith, *Proc. Anat. Soc.* Nov. 1902; *Lancet*, Feb. 27th, March 5th and 12th, 1904; *Journ. Anat. and Physiol.* 1907, vol. 42, p. 1.

Sino-auricular Node.[1]—The musculature of the sinus venosus of fishes is made up of small peculiar fibres rich in nuclei and in nerve supply. It has, more than all the musculature of the heart, the power of automatic rhythmical contraction. In human and mammalian hearts the sinus musculature is replaced by fibres similar to those of the auricle—all but at one place—namely along the sulcus terminalis, which marks the junction of the sinus and auricle, the sino-auricular node, found beneath the sulcus terminalis immediately in front of the superior vena cava of the human heart (Fig. 293). In lower mammals like the mole, the sino-auricular tissue is more extensive ; it extends along the greater part of the sulcus terminalis, and passes towards the pulmonary veins. In amphibia and reptiles it extends to the part of the left auricle (vestibule), in which the pulmonary veins



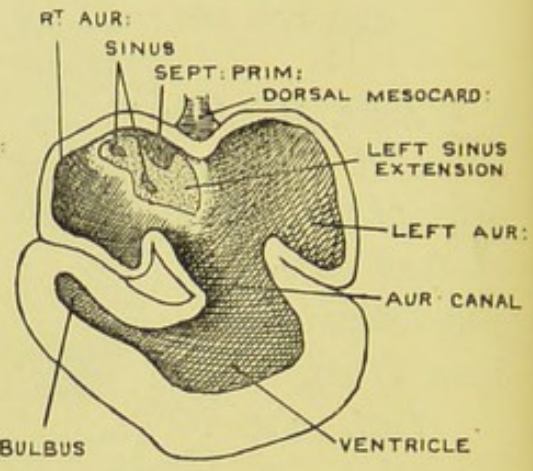


FIG. 293.—Human Heart at the beginning of the 3rd month of development to show the position of the Sino-auricular Node. The unsubmerged strip of sinus venosus is seen between the superior and inferior venae cavae.

FIG. 294.—The Posterior Wall of the Common Auricle of an Embryo of the 4th week, showing the Left Extension of the Sinus Venosus. (His.)

terminate. In the lowest mammals—monotremes—the muscular tissue of the node assumes a peculiar form.[2] Thus the higher in the animal scale one ascends, the greater is the reduction of the sino-auricular nodal tissue. It is in reality a neuro-muscular tissue, and is well defined by the 5th month of development. Dr. T. Lewis found that the contraction of the heart spread from the sino-auricular node, and gave it the name of the " pace-maker " of the heart.

Formation of the Right Auricle.—The right auricle is formed by the combination of three parts : (1) the right primitive auricle which appears as a diverticulum from the right dorso-lateral aspect of the auricular segment of the cardiac tube (Fig. 288) ; it forms the appendix and all that part of the right auricle which is furnished with musculi

[1] Keith and Flack, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 172 ; W. Koch. *Verhand. Deutsch. Path. Gesellsch.* 1909, p. 85.

[2] Dr. Ivy Mackenzie, *Verhand. Deutsch. Path. Gesellsch.* 1910, p. 90.

pectinati. (2) The auricular canal (Fig. 288) which forms the inner layer of the right auriculo-ventricular valve, and the smooth part of the auricle above the base of that valve. The morphological and physiological junction between the auricle and ventricle is at the free margins of the auriculo-ventricular cusps. (3) The sinus venosus which forms the part of the right auricle between the remnants of the right and left venous valves (Fig. 292).

Formation of the Left Auricle.—The left auricle is also formed by the combination of three parts: (1) the vestibule which arises as an extension round the terminal parts of the pulmonary veins (Figs. 295, 296), (2) the left primitive auricle, and (3) the auricular canal, all

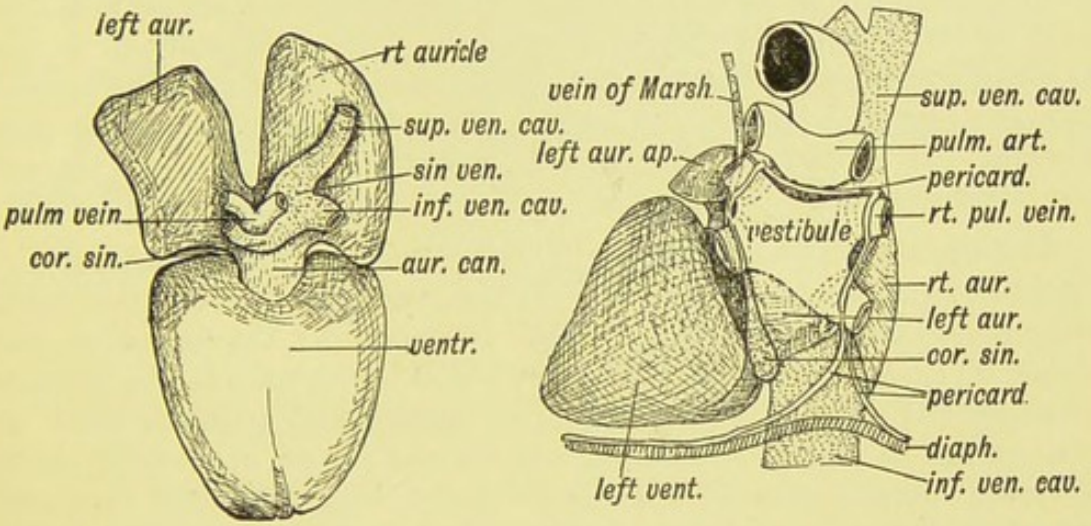


FIG. 295.—Reptilian Heart, viewed on its Dorsal Aspect, to show (1) the manner in which the Auricles arise from the Cardiac Tube, (2) the Auricular Canal, (3) the Sinus Venosus and Great Veins, (4) the Common Pulmonary Vein, which, at its termination, is embraced by the sinus venosus.

FIG. 296.—Heart of Adult viewed from behind to show the Vestibule and the other parts of the Left Auricle. The auricle was in a systolic condition. The remains of the left superior vena cava (vein of Marshall) and the attachment of the pericardium are also indicated.

of which arise in a manner similar to the corresponding part on the right side. In the human heart the vestibule forms a large part of the left auricle, the primitive auricle being reduced to form merely the appendix (Fig. 296). The vestibule is marked off from the rest of the auricle by a prominent muscular fasciculus—the taenia terminalis sinistra.

Origin of the Vestibule of the Left Auricle.—The representative of the pulmonary veins in fishes—viz. the vein of the swim bladder—ends directly or indirectly in the sinus venosus, a condition which may reappear as an abnormality in the human subject. In the Dipnoi, in which the swim bladder serves as a real lung, the pulmonary vein passes along the left wall of the sinus venosus, but opens in the left auricle near the base of the left venous valve in a manner almost identical

to that shown in some abnormal human hearts (see Fig. 274, p. 285). In the human embryo the pulmonary veins meet in the dorsal mesocardium, and open by a single orifice as in the Dipnoi. The relationship of the dorsal mesocardium to the sinus venosus has been already described (Fig. 285, p. 295). As the lungs develop they grow round and overlap the heart; the right and left pulmonary veins separate; their orifices move apart; later the right and left veins subdivide. With these changes the dorsal mesocardium is widened, and the part of the auricle in which the veins end is greatly extended to form the vestibule (compare Figs. 295, 296). It is highly probable that the vestibule of the left auricle also represents an extension of the sinus venosus. The late Professor His, who laid our knowledge of the development of the human embryo on a sure foundation of fact—he died in 1904—believed this to be the case. It is certainly so in the heart of amphibians. In Fig. 294 the sinus area will be seen to extend into the posterior wall of the left auricle. The condition is that seen towards the end of the first month, when the pulmonary veins are not yet developed.

Auricular Septa.—During the latter part of the first, and the opening part of the second month, the auricular part of the heart becomes separated into right and left chambers by the formation and union of three septa: (1) the endocardial cushions, (2) the septum primum, (3) septum secundum. Two **endocardial cushions** arise as thickenings of the endocardium, one on the dorsal or anterior wall, the other on the ventral or posterior wall; they meet and fuse, and thus divide the common auricular canal into the right and left auriculo-ventricular orifices (Figs. 291, 297). In amphibians the endocardial cushions form the dorsal and ventral cusps of the common auriculo-ventricular valve; in reptiles these two cusps fuse, and thus divide the common auriculo-ventricular orifice into right and left channels; in birds and mammals the fusion is complete. The lower fornix of the venous valves (Figs. 291, 298) becomes implanted on the posterior cushion; thus the sinus comes almost to reach the ventricular chamber. The **septum primum** (Fig. 297) is left as a crescentic fold between the primitive auricular diverticula (see Fig. 295). Its lower margin, which is covered by a thickening of endocardial tissue, stretches between the endocardial cushions; the adjacent margins of the septum and endocardial cushions fuse, but occasionally the fusion is incomplete, an inter-auricular foramen (foramen primum) being left between the base of the tricuspid valve below and septum ovale above (Fig. 297). In mammals and birds the upper part of the septum primum breaks down, the **foramen ovale** being thus formed. The part which remains forms the septum ovale. The **septum secundum** (Fig. 297) is formed by an inflection of musculature from the roof of the auricle to the right of the septum primum. It forms the annulus ovalis (limbic bands) (Fig. 292) and the musculature of the septum above the foramen ovale

(Fig. 297). The foramen ovale thus becomes bounded above by the septum secundum, below by the septum primum. In 25 per cent. of people, according to Fawcett's statistics, the foramen ovale fails

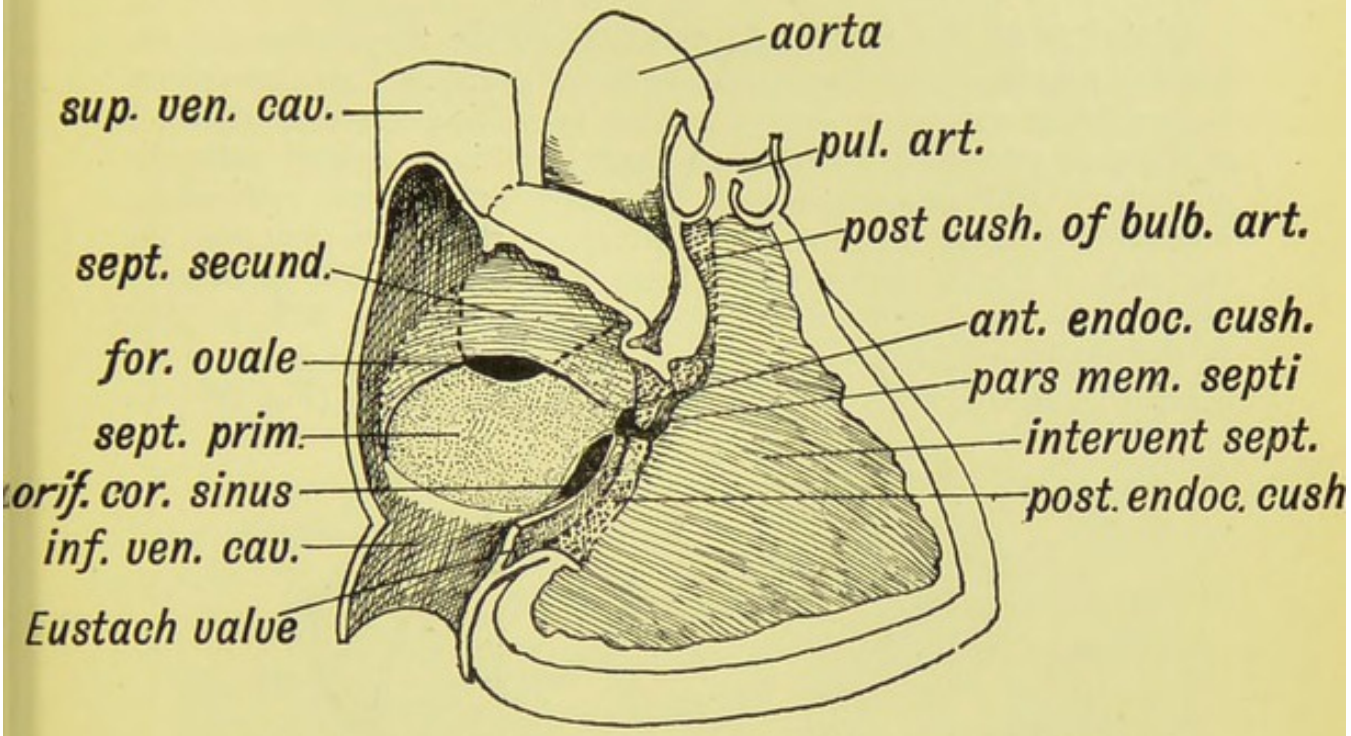


FIG. 297.—Diagram of the opened Right Auricle and Ventricle to show the parts which enter into the Formation of the Septum.

to close within the first year after birth, but even when an opening remains blood could pass from the right to the left auricle only when the pressure was greater in the right than in the left. The foramen

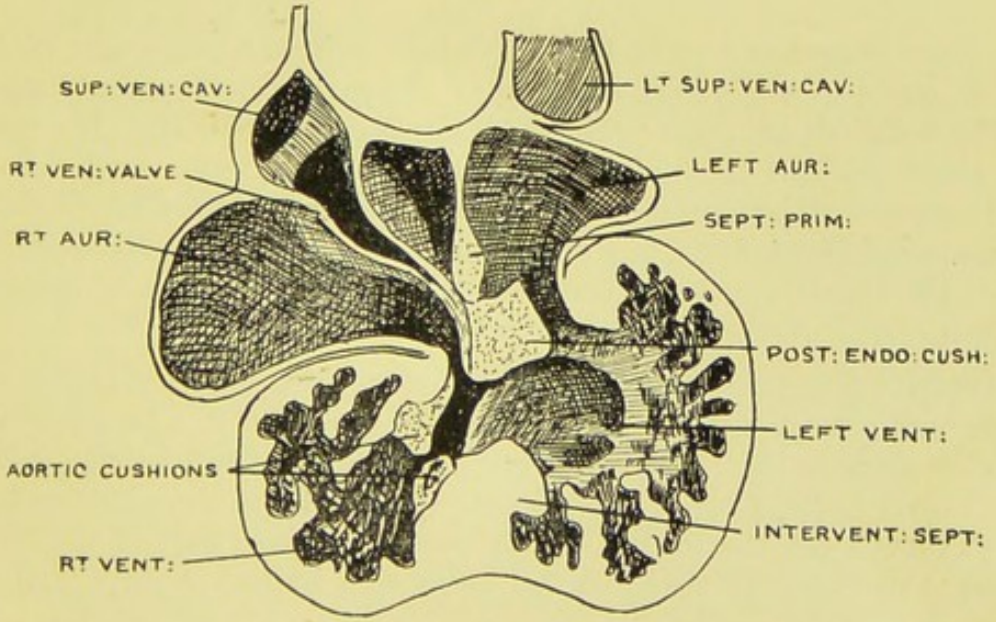


FIG. 298.—Coronal Section of the Heart of a Rabbit, illustrating the condition of parts at the beginning of the 2nd month of Human Development. (Born.)

ovale is an adaptation to the foetal type of respiration ; by it the purer blood returning from the placenta can pass from the right to the left side of the heart without passing through the lungs, which are then only partially pervious.

Division of the Conus Arteriosus.—While the division of the heart is rapidly proceeding in the auricular segment a similar process is at work in the aortic segment which lies within the pericardium—the conus arteriosus. The conus arteriosus is separated into the pulmonary and systemic aortae by dorsal and ventral endocardial ridges which are arranged in a spiral form, so that when they fuse, the last pair of aortic arches, which form the right and left pulmonary arteries, are connected with the pulmonary aorta (Fig. 223, p. 233). In the bulbus cordis, which forms the fourth and terminal cavity of the heart (Fig. 288, p. 298), four endocardial cushions appear (Fig. 299, *A*),

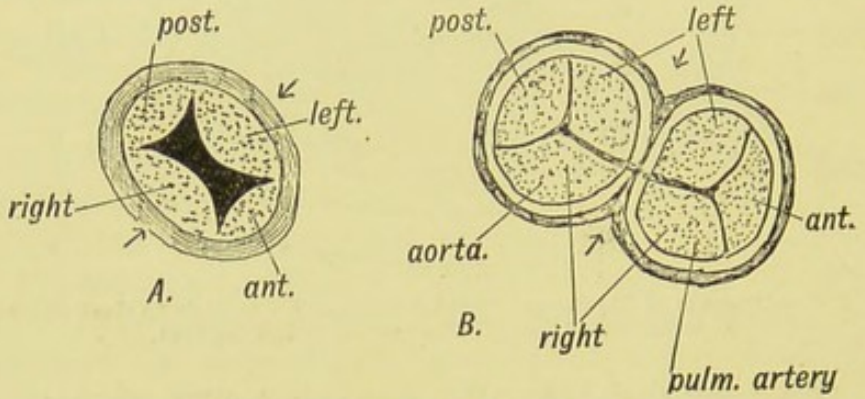


FIG. 299.—The Origin of the Semilunar Valves.

A. The four Endocardial Cushions in the conus arteriosus.
B. The division of the Lateral Cushions to form two Aortic and two Pulmonary Semilunar Valves.

the larger dorsal and ventral cushions fuse with each other, and with the spiral septa of the conus arteriosus. From the endocardial cushions of the bulb, the semilunar valves are formed (Fig. 299, *B*). If a section be made through the pulmonary and systemic aortae, two valves in one vessel will be found to be adjacent to two valves in the other ; these are formed from the dorsal and ventral endocardial cushions ; the right and left cushions become hollow, and form the two remaining valves.

Bulbus Cordis.[1]—We have seen how the first chamber of the heart—the sinus venosus—becomes included in the auricles. In a somewhat similar manner the fourth chamber of the heart—the bulbus cordis—becomes submerged in the ventricles—principally in the right ventricle. In the 3rd week the bulbus cordis forms a distinct part of the human heart. In Figs. 300 and 301 the heart of a human embryo and that

[1] See Greil, *Morph. Jahrb.* 1903, vol. 31, p. 123 ; Keith, *Lancet*, 1909, Aug. 7, 14, 21 ; Thompson, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 159.

of a shark are placed side by side. In both the truncus arteriosus (ventral aorta) are present (1); the bulbus cordis (2); it is lined with valves in the shark and surrounded by cardiac musculature; the bulbus is distinctly marked off from the ventricle at 4, and from the truncus at 3. The ventricle (5) is shaped in the shark like the stomach; in the embryonic human heart a diverticulum or evagination indicating the left ventricle has already appeared (3rd week); the auricular canal (6), the left and right auricles (7) (8) are also present. Thus

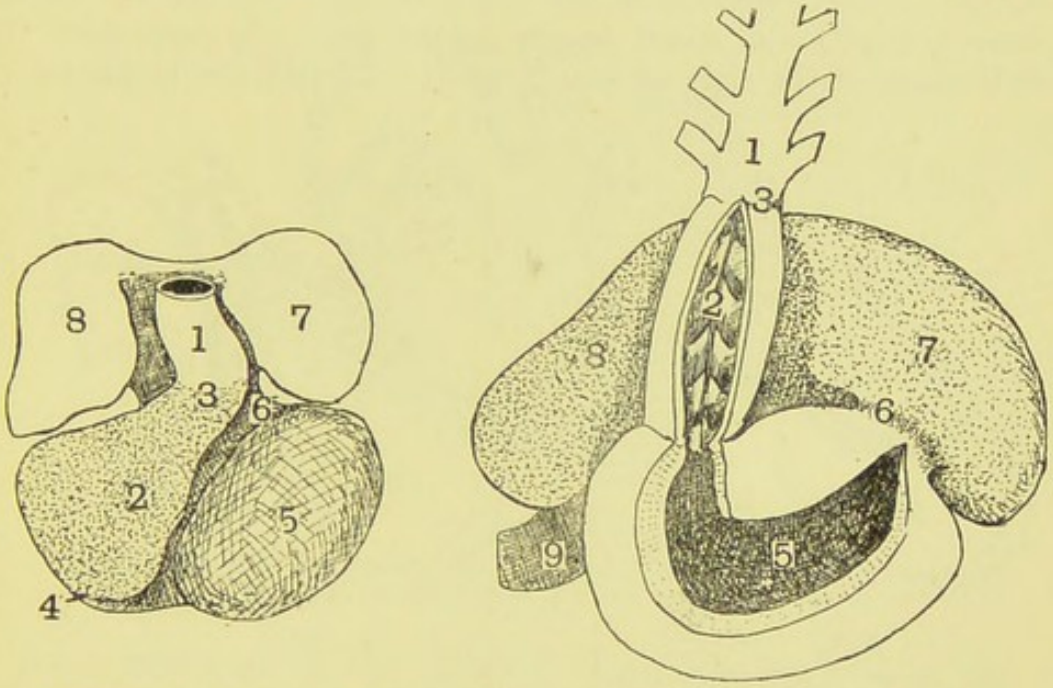


FIG. 300.—Heart of an Embryo of three weeks seen from the front. (After His.) Explanation in text.

FIG. 301.—Heart of a Shark viewed from the front.

in the human embryo all the parts of the primitive vertebrate heart are represented.

Fate of the Bulbus Cordis.—The fate of the bulbus cordis is most easily understood by a reference to such a diagram as is represented in Fig. 302, *A*, *B*. The bulbo-ventricular part of the heart in the human embryo resembles the stomach; there is a greater and a lesser curvature. In the second month the lesser curvature, represented in the diagram by a heavy black line, undergoes a process of atrophy. The result is (Fig. 302, *B*) that the cavity of the bulbus becomes thrown into that of the ventricle and the auriculo-ventricular and aortic orifices are brought side by side. At this time, when the lesser curvature is disappearing, the cavities of the ventricles are appearing by an evagination or enlargement of the ventricular wall, leaving the interventricular septum between the evaginations. The conus or truncus arteriosus is dividing then into systemic and pulmonary aortae. Thus it comes

about that the cavity of the bulbus cordis is converted into the infundibulum of the right ventricle, merely a trace extending across to the left ventricle above the interventricular septum. The importance of recognizing the bulbus cordis as a separate constituent of the heart will be realized when it is remembered that 95 per cent. of the cases of congenital malformation are the result of its imperfect transformation to form the infundibulum of the right ventricle of the heart. In nearly every case of what is described as **congenital stenosis** of the pulmonary orifice, a cavity of variable size will be found under the malformed valves representing the bulbus cordis. In fishes the bulbus is connected with the blood supply to the gills; its derivative, the infundibulum of the right ventricle, has to do with the regulation of

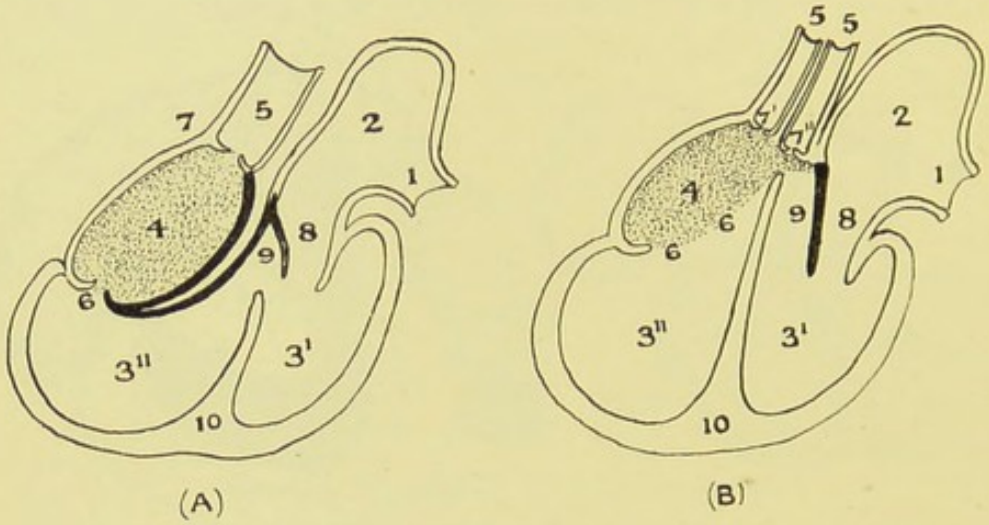


FIG. 302, *A*.—Diagrammatic Section of the Embryonic Heart in the 3rd week.
B.—Diagrammatic Section of the Foetal Heart at the 3rd month.

1, sinus venosus; 2, auricle; 3′, 3″, left and right ventricles; 4, bulbus cordis; 5, common aorta; 6, bulbo-ventricular junction; 7, bulbo-aortic junction; 8, auriculo-ventricular junction.

the blood supply to the lungs, but in neither case do we know the exact function of this part of the heart.

Formation of the Ventricles.—Along the lateral and convex aspects of the ventricular tube the musculature grows rapidly, forming a dense superficial layer and a deep sponge-work system of trabeculae, which almost fill the ventricular chamber. In the hearts of fishes and amphibians the sponge-work persists, but in birds and mammals the ventricular chambers are formed as diverticula by the absorption of the sponge-work. Between the right and left excavations, however, part of the sponge-work is left to form the interventricular septum (Fig. 303). In front the musculature of the septum is attached to the anterior cushion in the bulbus arteriosus (Figs. 297, 299); behind, it is attached to the posterior of the two endocardial cushions in the auricular canal (Fig. 299). On its upper free crescentic margin is a thickening

of endocardial tissue. The **interventricular foramen** [1] is bounded below by the margin of the interventricular septum; above, by the posterior aortic and auricular endocardial cushions (Fig. 297). The **pars membranacea septi,** which is found beneath the base of the septal cusp of the tricuspid, and below the septal cusps of the aortic valve, is formed, early in the 2nd month, by the fusion of the endocardial lips of the interventricular foramen (Fig. 297). Only in mammals and birds is the interventricular foramen closed, the foramen ovale opened and the venous valves replaced by a muscular mechanism.

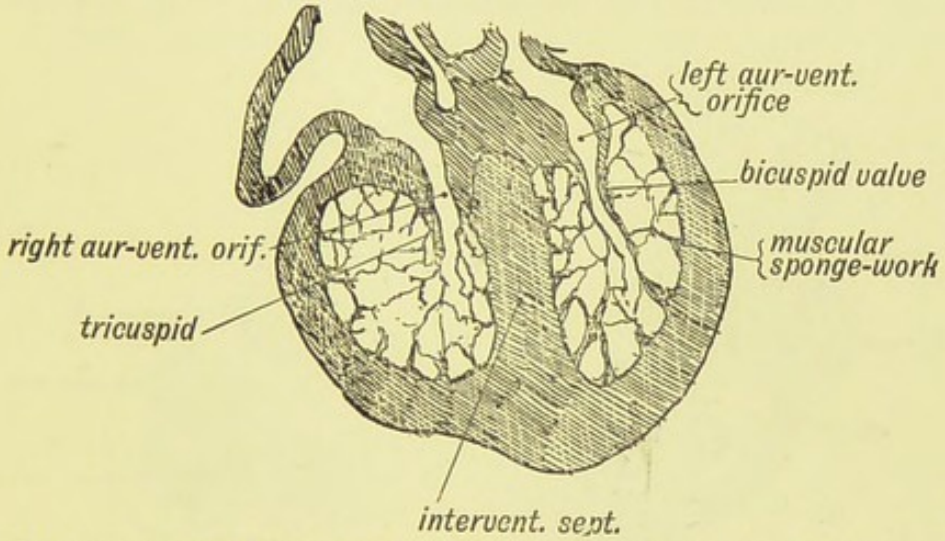


FIG. 303—Section of the Ventricles of the Foetal Heart, showing the Muscular Sponge-work within their Cavities. (After His.)

Abnormalities of the Heart.[2]—Thus six parts enter into the formation of the septum of the heart, the two interauricular septa, the endocardial cushion of the auricular canal, the interventricular septum, the endocardial cushions of the bulbus and conus arteriosus (Fig. 297). Abnormalities may result from their non-union, but by far the commonest defect found is a patency of the interventricular foramen (Fig. 306). This is accompanied in nearly every case by an arrest in the expansion of the bulbus cordis and a stenosis or narrowing at the orifice of the pulmonary artery (**congenital pulmonary stenosis**). The blood of the right ventricle is pumped into the aorta, through the interventricular foramen; blood is supplied to the lungs through the ductus arteriosus or by the bronchial arteries from the aorta.

Auriculo-Ventricular Valves.—At first the auricular canal is exposed on the surface of the heart (Fig. 294), but it soon becomes enveloped by the upgrowth and excavation of the bases of the ventricles (Fig. 303). The auricular canal, with an attenuated envelopment derived from the ventricle, thus comes to hang within the ventricular

[1] For recent account of development of ventricles see F. P. Mall, *Amer. Journ. Anat.* 1912, vol. 13, p. 249.

[2] A. Keith, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 211.

chambers and forms the lateral cusps of the tricuspid and mitral valve (Fig. 303). The septal cusps are formed from processes of the endocardial cushions (Fig. 305). The chordae tendineae, musculari papillares, columnae carneae, trabeculae and moderator band are derived from the muscular sponge-work of the ventricles.

Various maldevelopments of the heart throw light on the nature of the auriculo-ventricular valves. In Fig. 304 an abnormality of this kind is represented. The anterior and posterior endocardial cushions have not united, hence the tricuspid and mitral valves are continuous across the upper border of the septum (Fig. 305). The aperture seen

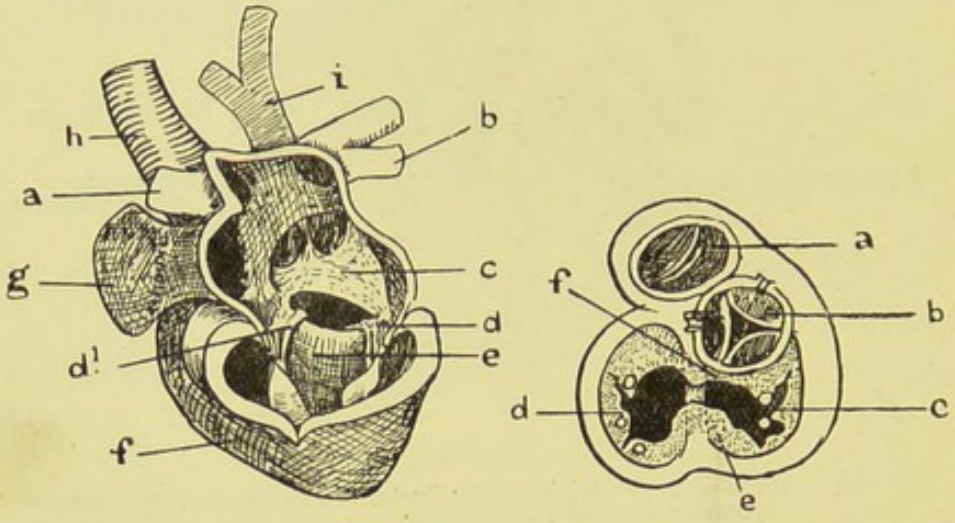


FIG. 304.—Abnormal Heart of a Child with the Left Auricle and Ventricle laid open. *a*, left ; *b*, right pulmonary veins ; *c*, septum primum ; *d*, *d'*, posterior and anterior endocardial cushions ; *e*, interventricular septum ; *f*, left ventricle ; *g*, left auricular appendix ; *h*, aorta ; *i*, sup. vena cava.

FIG. 305.—Same Heart from above. *a*, the orifice of pulmonary artery with fusion of septal cusps ; *b*, valves of aorta, with the coronary arteries rising above septal cusps ; *c*, *d*, *e*, *f*, continuity of the tricuspid and mitral valves across the upper border of septum.

above the interventricular septum is the foramen primum—not the interventricular foramen.

Purkinje System of the Heart.—About the middle of the nineteenth century, Purkinje, Professor of Anatomy at Breslau, discovered large peculiar muscle fibres beneath the endocardium of the heart of the sheep and of other ungulate animals. In 1906 Tawara showed that such fibres were connected with a muscular bundle, which rose in the wall of the auricle near the orifice of the coronary sinus and entered the ventricle along the upper border of the interventricular system.[1] In many cases of malformed heart the primitive relations of the **auriculo-ventricular** (A.V.) **bundle** may be seen (Fig. 306). It passes along the upper border of the interventricular septum below the interventricular foramen. Its left branch descends on the septum to the musculari papillares of the left ventricle ; the right division or branch passes

[1] For an account of Tawara's discovery see Keith, *Lancet*, 1906, Aug. 11.

along the moderator band, which marks the junction of the bulbus cordis with the body of the right ventricle. When it is remembered that the ventricles arise from evaginations of the ventricular tube, it will be seen that the bundle on the upper border of the septum occupies the least disturbed part of the lumen of the primitive cardiac tube.

The evolution of the Purkinje system may be realized from a study of Fig. 307. Gaskell found in 1883 that the auricles and ventricles were connected in fishes, amphibians and reptiles by the musculature of the auricular canal (Fig. 307, 4, 4), and that the wave of contraction passed from auricle to ventricle by it. The auriculo-ventricular

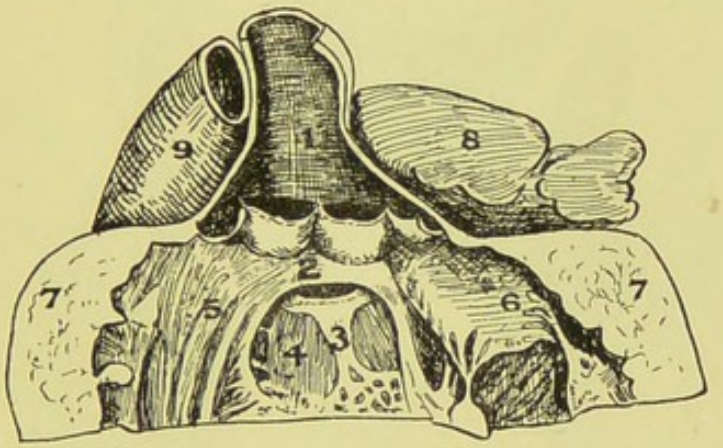


FIG. 306.—The Auriculo-ventricular Bundle in a Heart with open Interventricular Foramen. 1, aorta; 2, on the site of the pars membranacea septi; 3, left division issuing from bundle situated on the upper margin of the interventricular septum (4); 5, anterior wall of left ventricle; 6, mitral valve; 7, cut wall of left ventricle; 8, left auricle; 9, pulmonary artery.

muscular collar begins in a ring of peculiar muscle cells situated as shown in Fig. 307, 3, 3. In the mammalian heart the auriculo-ventricular muscular canal disappears—all except at the upper border of the septum, where it forms the bundle. The node in which it arises represents a remnant of the ring of peculiar auricular fibres. It is true that the sinus venosus reaches the posterior endocardial cushions (Fig. 298) near the site of the node, but it is most improbable, in the light of comparative anatomy, that the node at the commencement of the bundle should represent sinus musculature.

Changes in the Circulation at Birth.—(1) The outflow of the blood to the placenta by the hypogastric arteries and its return by the umbilical vein is arrested when the umbilical cord is tied. The umbilical vein and ductus venosus gradually become ligamentous. (2) The first breath expands not only the air spaces of the lungs, but also the pulmonary vessels, so that the pressure within them becomes less than in the aorta; hence the blood in the pulmonary aorta passes through the lungs instead of gaining the aorta by the ductus arteriosus. A section across the ductus arteriosus and aorta (Fig. 309) shows that, before

birth, the septal wall of the ductus is invaginated within the lumen of the aorta ; after birth the septal wall is bent within the lumen of the ductus, thus partly closing it. (3) The foramen ovale is closed by the pressure within the left auricle being raised by the inflow of pulmonary blood, the pressure in the left auricle then reaching a higher point than in the right auricle. The closure of the foramen is assisted by an alteration in the action of the limbic bands (Fig. 292) brought about by their indirect attachment to the diaphragm. (4) The hypogastric

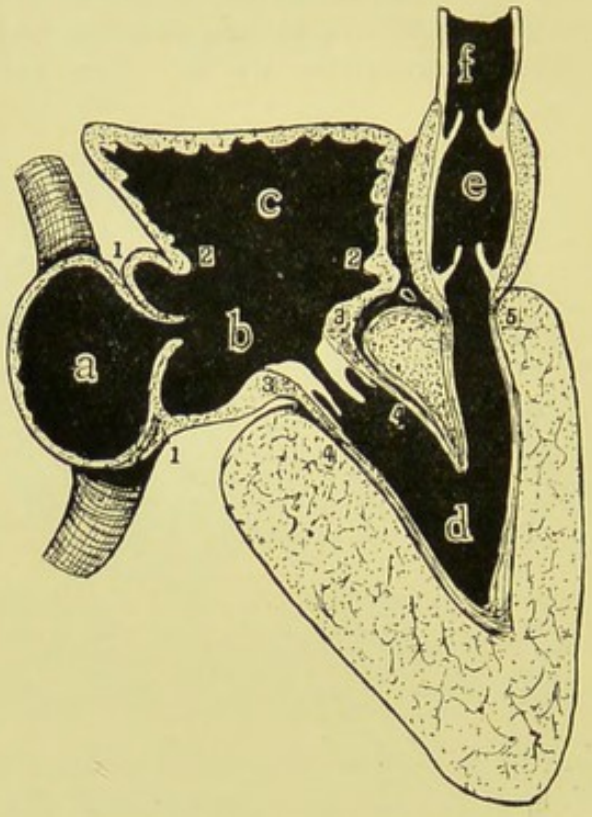


FIG. 307.—Section of a Generalized Type of Heart to show the Origin of the Auriculo-ventricular Bundle and Node. *a*, sinus venosus ; *b*, auricular canal ; *c*, auricle ; *d*, ventricle ; *e*, bulbus cordis ; *f*, aorta ; 1, 1, sino-auricular junction ; 2, 2, auricular junction with canal ; 3, auricular ring of peculiar fibres ; 4, auriculo-ventricular musculature ; 5, bulbo-ventricular junction.

arteries, beyond the origin of the vesical arteries, become reduced to cords. (5) The pressure within the aorta becomes three times that in the pulmonary arteries ; the left ventricular wall becomes three times as thick as that of the right. Before birth the ventricular pressure and ventricular walls of the right and left side were equal.

Remnants of the Foetal Circulation in the Adult.—The nature of these remnants has been already described ; they need be only enumerated here. They are :

(1) The Obliterated Hypogastric Arteries ;
(2) The Umbilicus ;
(3) The Round Ligament of the Liver ;

(4) The Fibrous Remnant of the Ductus Venosus ;
(5) The Eustachian Valve ;
(6) The Foramen Ovale ;
(7) The Fibrous Remnant of the Ductus Arteriosus.

Changes in the Position of the Heart.—The alteration of the position of the heart from a subpharyngeal position in the embryo to the thoracic situation in the adult, is brought about by two factors. First, the heart is primarily a pump for forcing the blood through the organ of respiration ; hence in the fish it lies beneath the gills, in air-breathing vertebrates it is situated close to the roots of the lungs. Secondly, in reptiles, birds and mammals a neck is developed, the head

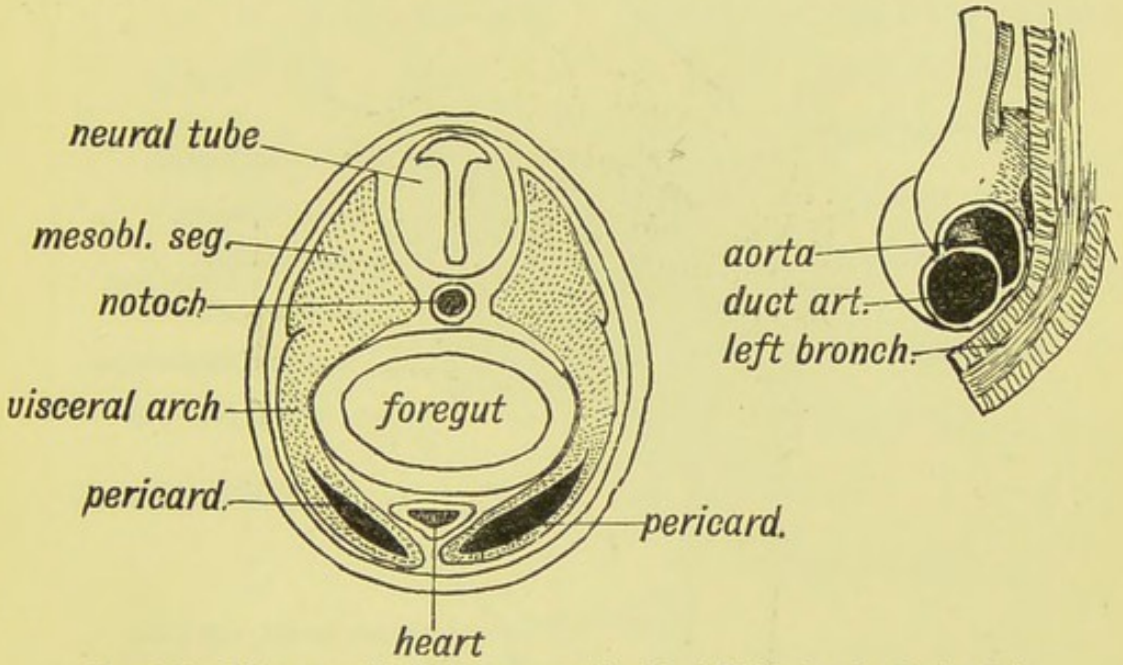


FIG. 308.—Diagrammatic Section across the Head Fold of a developing Salamander to show the relationship of the Pericardial part of the Coelom to the Heart and Fore-gut. (After C. Rabl.)

FIG. 309.—Section across the Junction of the Aorta and Ductus Arteriosus (viewed from behind) of a full time Foetus to show the Inflection of the Wall of the Ductus within the Lumen of the Aorta.

and pharyngeal region being gradually forced forwards, while the heart and pericardium come to lie opposite the middle part of the dorsal region of the spine. The neck is differentiated in the human foetus during the second month. All the structures in the neck become elongated—the oesophagus, trachea, vagus nerves, jugular veins and carotid arteries. During this change the arch of the aorta and its branches are evolved from the ventral stems of the aortae and aortic arches. In most mammals the left carotid arises in common with the aortic stem, and a reversion to this type is the commonest abnormality to which the aortic arch is liable in man (Parsons). The separation of the left carotid from the innominate in man is due to the large size of the upper aperture of his thorax. The left vertebral artery or the thyroidea ima may gain an origin from the aortic arch.

The Divisions of the Coelom.[1]—Out of the anterior part of the coelom (Fig. 310) is formed the **pericardium.** It lies beneath and behind the primitive pharynx (Fig. 311); the outer wall of the space is formed by the somatopleure of those segments which form the walls of the pharynx (Fig. 308). The pericardial part of the coelom by the third week is expanded and thrust downwards and backwards, and communicates by a narrow neck or isthmus (**iter venosum**) with the pleural passage on each side of the mesentery (Fig. 285). The duct of

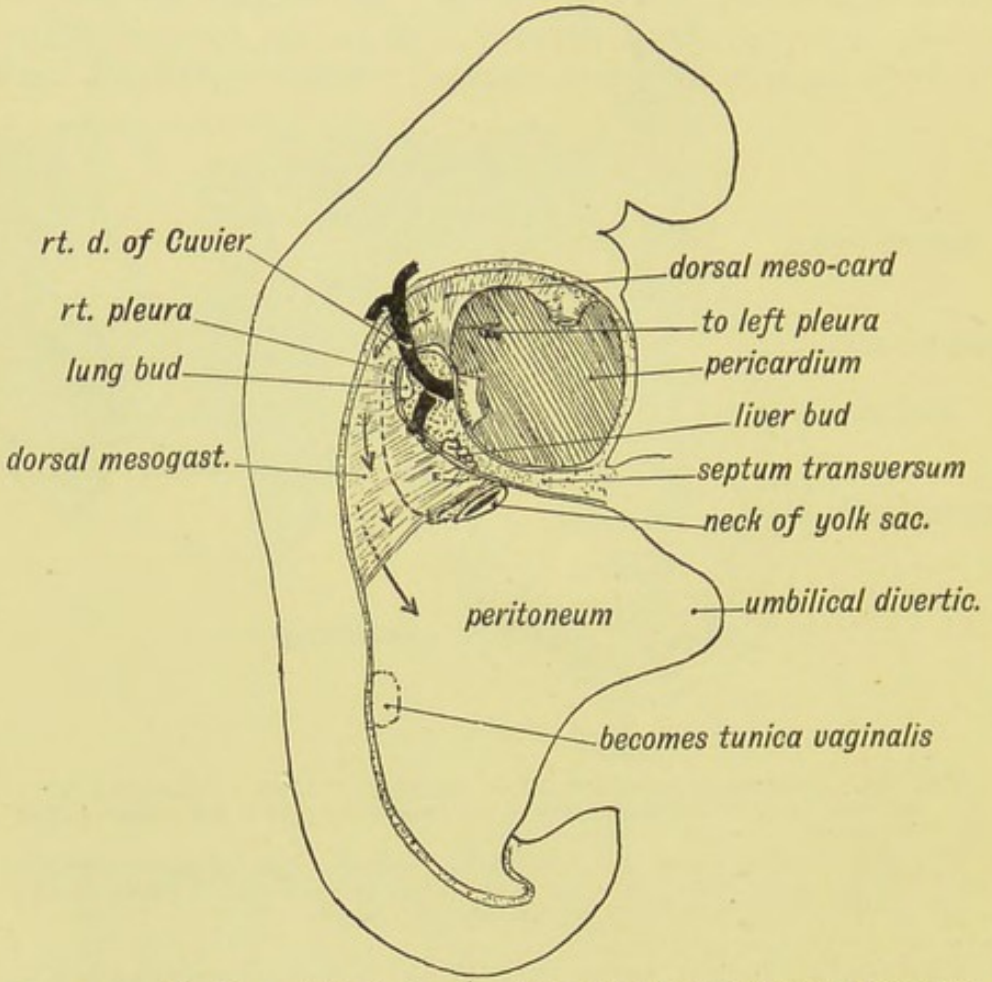


FIG. 310.—The Form of the Coelom in a 3rd week Embryo as viewed from the right side.

Cuvier encircles the neck or isthmus on each side (Fig. 310). The *itinera venosa* are situated at the upper border of the septum transversum, and separated by the posterior or dorsal mesocardium and fore-gut. This open condition of the iter venosum is permanent in many fishes. With the origin of the lungs, the pleural passage, leading from the pericardial to the peritoneal cavity, undergoes a great expansion by the ingrowth of the lung buds, which grow out against the upper border of the septum transversum (Fig. 324). Thus out of the narrow pleural passages of the right and left sides are gradually

[1] See references under Broman, p. 249.

formed the **pleural cavities.** The pleurae expand until, instead of lying as minute passages above and behind the pericardium, they come to completely cover it. The abdominal part of the coelom, separated from the pleurae by the development of the diaphragm, forms the **peritoneal cavity** ; a small part on each side is shut off in the scrotum, the **tunica vaginalis.**

The Pericardium.[1]—In Fig. 311 the relationship of the heart to the pericardium is shown during the 3rd week of foetal life, and is

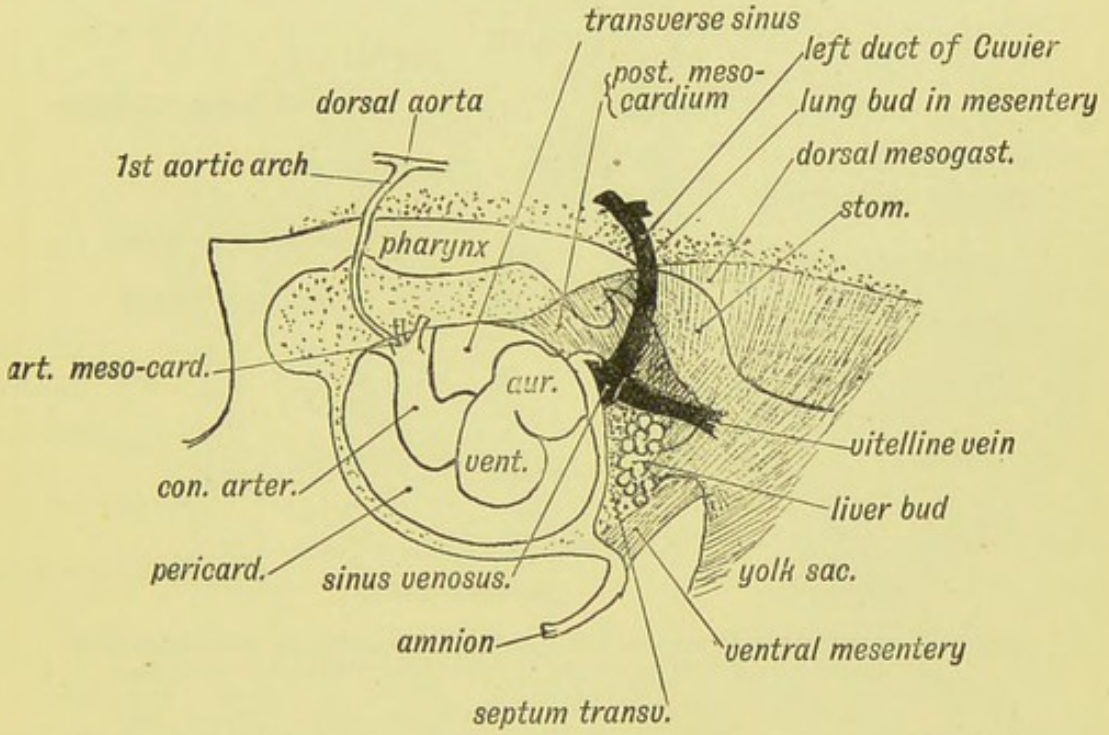


FIG. 311.—Diagram to show the manner in which the Heart is fixed within the Pericardium by the Arterial and Venous Mesocardia in a Human Embryo of 3 weeks.

similar to that of the fish (Fig. 314). The heart is tubular ; the dorsal and ventral mesocardia are absent except at two points, where the heart still remains attached. These two points are (Fig. 311) :

(1) In front where the conus arteriosus enters the ventral wall of the pharynx to divide into right and left ventral aortae from which the right and left visceral aortic arches arise. The mesocardium which binds it here may be named the **arterial mesocardium.**

(2) Behind the sinus venosus is embedded in the septum transversum, through which the great veins reach it. The mesocardium which binds it behind may be named the **venous mesocardium.** Thus the heart is fixed at two points, behind by the venous mesocardium to the septum transversum, in front to the pericardium beneath the pharynx by the arterial mesocardium.

[1] A. Keith, *Journ. Anat. and Physiol.* 1906, vol. 41 (Abnormality of pericardium).

In Figs. 312, 313 are shown the points of fixation of the heart within the pericardium of the adult. The arterial and venous mesocardia can be recognized only somewhat altered in position and form.

(1) The truncus arteriosus becomes the ascending aorta and pulmonary aorta, and these are attached together to the fibrous pericardium by the arterial mesocardium.

(2) The sinus venosus, which becomes parts of the right and left auricles, and their vessels are still attached by the venous mesocardium to the posterior wall of the pericardium, which is formed from the

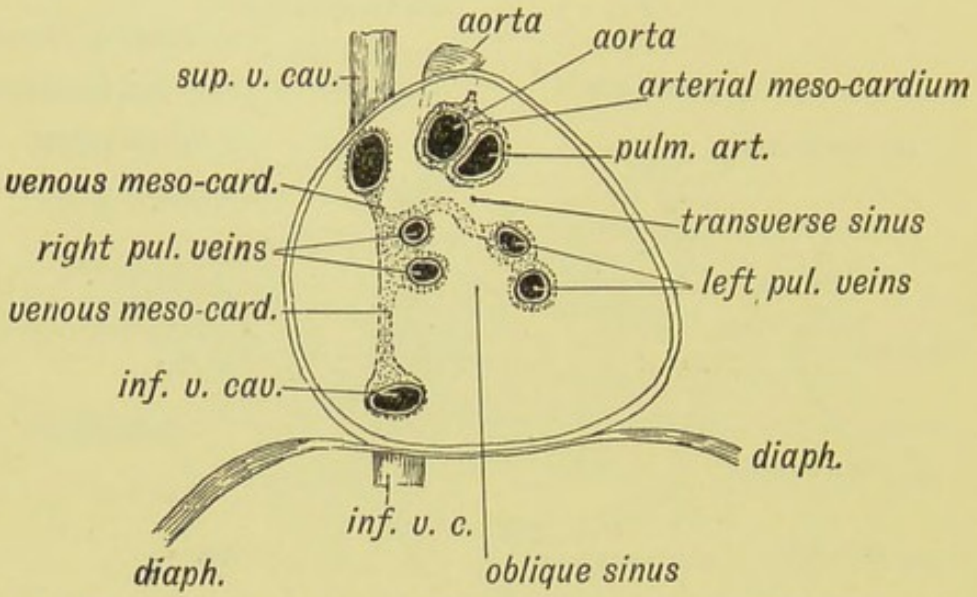


FIG. 312.—View of the Interior of the Pericardium showing the Attachments of the Heart to its Dorsal Aspect by the Arterial or Venous Mesocardia.

septum transversum. The heart has become so doubled on itself that the venous mesocardium comes almost in contact with the arterial mesocardium, the narrow space which separates them being the **transverse sinus** (Fig. 313). By comparing Figs. 311 and 313, it will be seen that the transverse sinus is formed by the breaking down of the dorsal mesocardium of the heart.

The venous mesocardium becomes much more extensive by the ingrowth and separation of the pulmonary veins. These grow in from the lungs, and pierce the pericardium to reach the left auricle (Fig. 325). They reach the auricle through the mesentery or venous mesocardium of the sinus venosus. The migration of the left pulmonary veins causes a prolongation of the venous mesocardium to the left side; when the heart is removed the venous mesocardium is seen to be F-shaped in section. The oblique sinus lies in the concavity of the pulmonary venous mesocardium (Fig. 312).

Primitive Relationships of the Pericardium.—Were one to restore the head and pericardium to the relative positions they occupy in the 3rd week of development, then the pericardium must be lifted

from the thorax and placed beneath the chin and larynx so that the septum transversum is opposite the origin of the phrenic nerve from the 4th cervical segment; the anterior border of the umbilicus is also then opposite the origin of the phrenic nerve. In the somatopleure over the pericardium and between the mandible and umbilicus are developed the depressors of the hyoid, the sternum and sternal ribs. The pericardium is therefore the coelom of the neck; its fibrous wall represents the deepest layer of the cervical somatopleure, probably corresponding to the fascia transversalis of the abdomen. With the elongation of the neck and separation of the pharynx and pericardium, the tissue of the branchial segments which surrounds the aortic arches is drawn out to form the carotid sheaths.

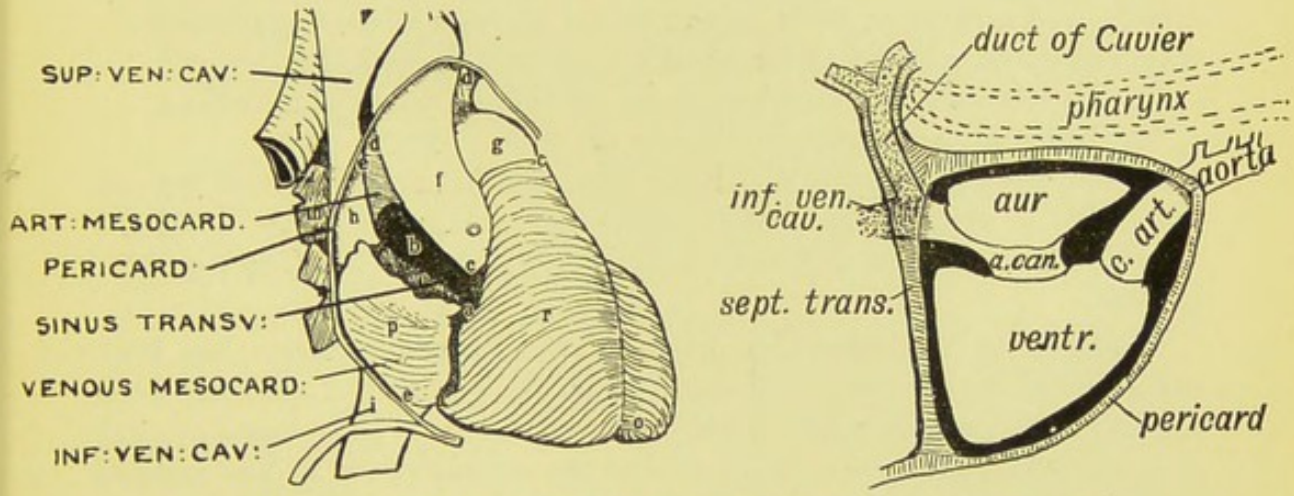


FIG. 313.—The Heart pulled forwards to show its two Attachments by the Arterial (*d*, *d*) and Venous (*e*, *e*) Mesocardia.

FIG. 314.—Diagram of the Heart of a Fish to show: (1) the Primitive Parts of the Heart; (2) the Relationship of the Heart to the Pharynx; (3) the Septum Transversum.

Ectopia Cordis.—Occasionally children are born with their hearts exposed on the surface of the chest. In extreme cases only the dorsal wall of the pericardium is present, and it is flush and continuous with the skin of the chest. In such cases there has been an early cystic condition of the pericardial coelom leading to rupture of the somatopleure on its ventral wall—in which the sternum is normally developed. In these cases the sternum is partially absent, or if present it is cleft, the right and left halves being widely parted. The pathology of the condition appears to be similar to that of ectopia vesicae.

The Dorsal Aortae.—In the 3rd week there are still two dorsal aortae. The blood passes from the two ventral aortic stems through the aortic arches to end in a dorsal aorta on each side. These run backward side by side, and at first end in the yolk sac, but with the formation of the allantois they pass out on the body stalk to the membranes and placenta. The umbilical arteries are thus the direct continuations of the dorsal aortae (Young and Robinson); later in the

3rd week the dorsal aortae are continued into the caudal region. The middle sacral artery is formed by the fusion of the two caudal arteries.

About the end of the 3rd week the dorsal aortae fuse together from about the region of the 7th cervical segment to the 4th lumbar. In front of and behind these points they remain separate.

The fate of the two dorsal aortae in front of the 4th dorsal vertebra has been already dealt with (p. 233 and Figs. 221 and 222). It remains to consider what becomes of them in the posterior extremity of the body. Following the researches of Young and Robinson, the dorsal aortae beyond the 4th lumbar segment, where they remain apart, form :

(1) The common iliac arteries ;

(2) The internal iliac—in part at least ; the external iliac, gluteal, sciatic, and pudic probably represent the arteries of the segments from which the lower limbs and genital organs are developed ;

(3) The hypogastric arteries—intra-abdominal parts of umbilical ;

(4) The umbilical arteries—in the umbilical cord.

The authors just mentioned have described in the embryos of several mammals a system of arterial arches on each side of the hind-gut resembling the aortic arches on each side of the fore-gut (see Fig. 235, p. 248).

Visceral Arteries.—The origin of the visceral arteries has been investigated by Professor Broman.[1] In the embryo of the 3rd week the dorsal aortae not only send a branch to each body-segment, but also a corresponding ventral branch to the primitive gut. The visceral arteries are thus segmental in their arrangement. The coeliac axis arises from the visceral branch of the 3rd dorsal segment, the superior mesenteric from the artery of the 6th, but it also receives contributions from the 4th and 5th. Although in the embryo the umbilical arteries appear as the continuation of the dorsal aortae, they probably represent the visceral branches of the 5th lumbar segment.

Formation of Blood Vessels.—The formation of blood vessels is best studied in the mesoblast which surrounds the archenteron, for in the human embryo, with the exception of the chorion, the yolk sac is the site of the earliest formation of blood vessels (Fig. 315). A section through the wall of the yolk sac, formed from the archenteron, shows a **blood island**—a group of round nucleated red blood cells (erythrocytes), which have been formed by the division and subdivision of certain cells (erythroblasts) in the mesoblast. The mesoblastic cells which surround the blood island become **vasoformative cells.** By their flattened processes, which appear as fibres in section, they surround, and form a containing or endothelial wall for, the erythrocytes. The blood islands, scattered over the wall of the yolk sac, become confluent by the *union and canaliculization* of intervening cells—which thus

[1] Broman, *Anat. Hefte*, 1908, vol. 36.

become vasoformative. In this manner a vascular network is produced on the yolk sac ; the manner in which the blood islands are united is typical of the manner in which new blood channels are formed. Within the body of the embryo mesenchymal (mesoblastic) cells assemble in vasoformative groups, become canaliculized and unite with neighbouring groups to form both arteries and veins. The endothelial cells of capillaries retain throughout life the vasoformative power which

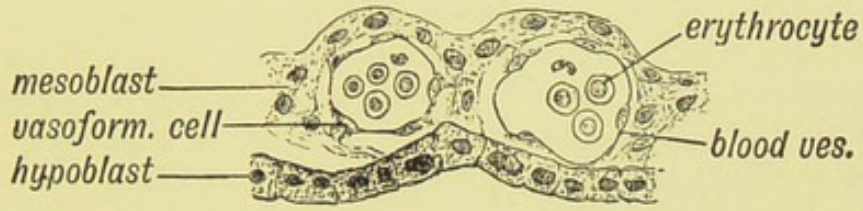


FIG. 315.—Section across the Yolk Sac, showing Blood Vessels and Nucleated Red Blood Corpuscles forming in its Mesoblastic Layer. (After Selenka.)

characterizes them during the period of development and growth. The cellular processes at the growing point of a capillary are permeable at first to the plasma only, subsequently the lumen becomes large enough to allow the blood cells to pass.

It is improbable that all vasoformative cells arise primarily, as His believed, in the mesoblast of the archenteron and from there permeate and vascularize the whole of the embryo and its membranes. In the human embryo the chorion is the first site of blood-vessel formation (Eternod, Dandy). All the vasomotor nerves escape from the dorsal region of the cord, which may be regarded as being correlated segmentally with the mid-gut.

Formation of Blood.—In the development of each system of the human body the various parts appear in the same order as they are seen to occur in ascending the scale of the animal kingdom. In many invertebrates the blood is formed by only a fluid living intercellular substance—the **plasma** ; when the human heart beats first, its lumen contains no blood cells, only plasma. In amphioxus nucleated uncoloured corpuscles appear in the plasma ; the cells which appear first (during the 3rd week) in the circulation of the human embryo are the red nucleated corpuscles (erythrocytes) formed in the blood islands of the archenteron, but these are originally formed from nucleated mesoblastic uncoloured cells (erythroblasts or haematoblasts). In all vertebrates, with the exception of amphioxus, nucleated white as well as nucleated red cells appear in the blood ; in the human embryo the white cells (leucocytes) appear somewhat later than the red. In mammals only do the nuclei disappear or become extruded from the erythrocytes, red blood corpuscles (erythroplastids) being thus formed. The erythroplastids begin to appear in the blood of the human embryo at the end of the 2nd month, and gradually replace the erythrocytes,

which cease to appear in the circulating blood some days after birth (Ham). At every period the erythrocytes are formed within a vascular wall.

The Germinal Centres for Red Blood Corpuscles.—At every period of life the red blood corpuscles (erythroplastids) arise from erythrocytes. These are formed first in the blood islands of the chorion, of the yolk sac and within vascular extensions of the vaso-formative cells throughout the body. The formation of blood corpuscles in the liver commences at the beginning of the second month of development, and ceases in the later months of foetal life.[1] The parent erythroblasts lie side by side with the liver cells. The splenic blood spaces are also sites of blood formation in the latter half of foetal life. About the middle of foetal life the capillaries of the bone marrow begin to be invaded by them, and from birth onwards the capillaries of the red bone marrow become the breeding ground of erythrocytes, from which the red corpuscles arise by disappearance of their nuclei. The genetic relationship between erythroblasts and leucoblasts is at present uncertain.

Origin of White Blood Cells.[2]—From the researches of Beard and of Gulland, which have been amply confirmed by other investigators, there can now be little doubt that the form of white blood cells known as **lymphocytes** are produced from the hypoblastic lining of the gut. The manner of their formation may be seen in a section of the thymus of an amphibian or fish which shows the production of broods of lymphocytes from the epithelial layer. The lymphocytes are produced from the basilar part of the epithelial cells by a process of division. When separated, they lie within the adjacent lymph space ; there they form germinal centres or lymphoid follicles. The lymphocytes are carried into the lymph vessels, where they form secondary germinal centres or lymphatic glands. The tonsil, thymus, Peyer's patches and solitary follicles, appear to be produced from areas of hypoblast, some of which remain superficial while others have become buried. The thymus is one of the earliest and greatest of these leucoblastic centres ; in Beard's opinion, the only centre. The tonsil is differentiated later, while the intestinal system undergoes no active growth until some days after birth.

Leucocytes are also profusely produced from (1) the endothelium of serous cavities—such as the peritoneum and pleura ; (2) from the endothelium of lymphatic vessels ; (3) from leucoblasts within bone marrow ; (4) from the endothelium of capillaries, and possibly (5) from connective tissue cells. As yet, however, these statements must be accepted with reserve. Mollier, who has recently studied the develop-

[1] See Mollier, *Archiv. für Mikroscopic Anat.* 1909, Bd. 74.

[2] See Retterer et Lelievre, *Journ. d'Anat. et Physiol.* 1912, vol. 48, pp. 14, 194 ; F. Weidenreich, *Ergebnisse der Anat.* 1909, vol. 19, p. 527.

ment of the blood corpuscles, describes the liver as the chief source of white blood corpuscles during foetal life ; later the site of their formation is shifted to the blood spaces in marrow. He regards both basophile and eosinophile leucocytes as arising in the liver from the same parent cells (haematoblasts) as give origin to the red nucleated corpuscles.

Lymphatic System.—In all vertebrate animals the plasma or lymph from the tissues of the body is drained into the veins by a special system—the lymphatic vessels. In amphibia the lymph collects in large spaces, from which it is forced into the venous system by two pairs of lymph hearts—one pair situated in the angle between the jugular and subclavian veins, the other pair between the internal and external iliac veins. In mammals the lymph hearts disappear ;

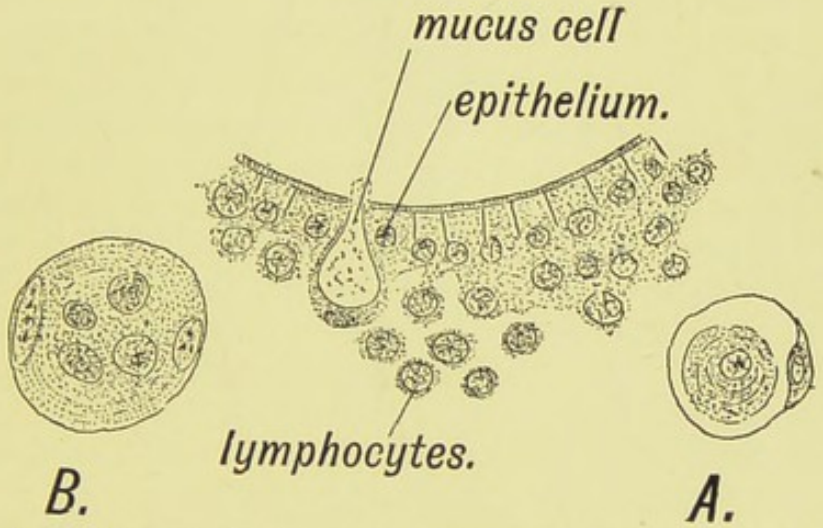


FIG. 316.—Section of a tubular part of the Thymus of a Frog, showing (1) the Production of Lymphocytes from the Thymic Epithelium ; (2) the Production of Hassall's Corpuscles. In *A* a leucocyte within the wall of a capillary has become enlarged and shows concentric striae ; in *B* the nucleus of the leucocytes has undergone division ; it completely fills the lumen of the capillary, the nuclei of which are seen in the periphery of the body. (After Nusbrum and Machowski.)

they are no longer required, for the negative pressure in the veins of the thorax, set up by the evolution of a separate respiratory cavity, is sufficient to draw the lymph into the venous system. It is remarkable, however, that Miss Sabin who, by a paper [1] published in 1902, inaugurated our knowledge of the development of the mammalian lymphatic system, found that the lymph vessels appear first at those

[1] Florence Sabin, *American Journ. of Anat.* vol. 1, 1902, p. 367. In nearly every subsequent volume will be found some of the important contributions made to our knowledge of the development of lymphatics by modern American embryologists. Professor Florence R. Sabin, *Amer. Journ. Anat.* 1901, vol. 1, p. 367; F. T. Lewis, *Amer. Journ. Anat.* 1909, vol. 9, p. 33 ; Florence Sabin, *Amer. Journ. Anat.* 1909, vol. 9, p. 43 ; Geo. S. Huntingdon and C. F. W. M'Clure, *Amer. Journ. Anat.* 1910, vol. 10, p. 177; F. T. Lewis, *Amer. Journ. Anat.* 1905, vol. 5, p. 95; G. Huntingdon, *Anat. Anz.* 1911, vol. 39, p. 385; E. R. Clark, *Amer. Journ. Anat.* 1912, vol. 13, p. 347.

four points where the amphibian lymph hearts are situated. In her opinion the lymph system begins about the end of the first month by evaginations or outgrowths from the great veins at those four points. Other investigators, such as M'Clure and Huntingdon, while they agree that the lymphatics are first apparent at those four points, regard the vessels as arising independently in the menenchymal tissue and

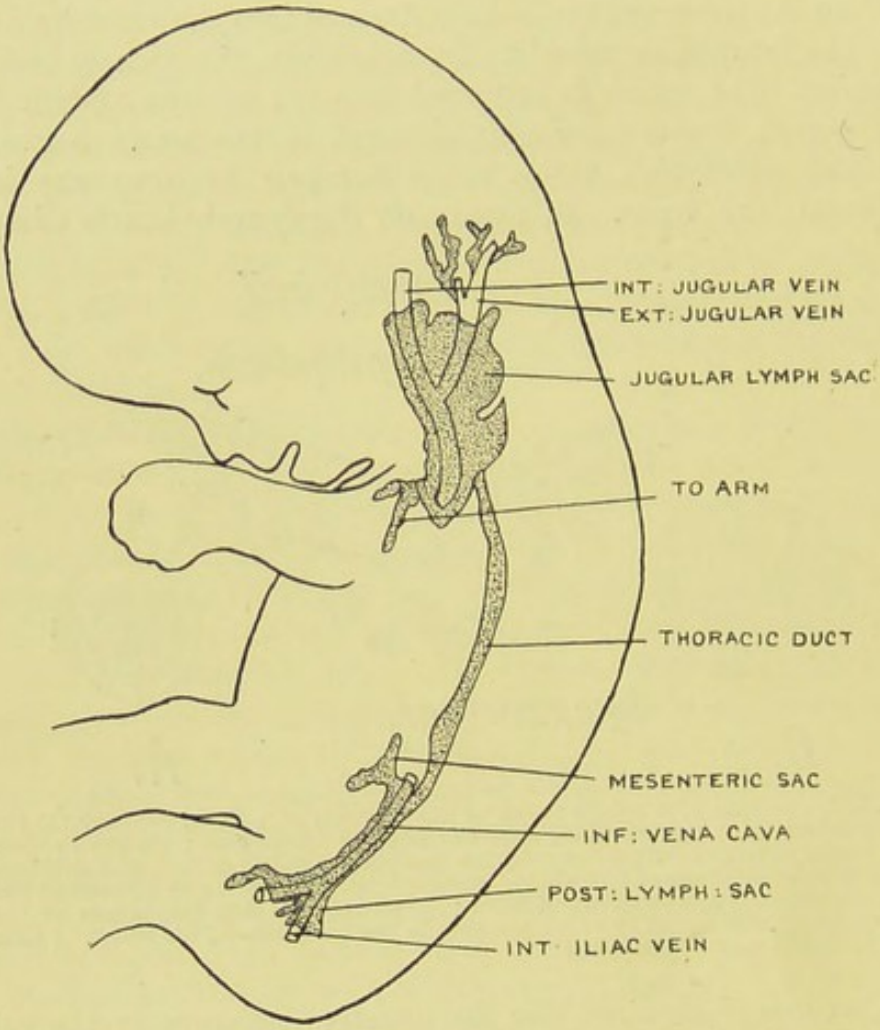


FIG. 317.—The Main Lymphatic Vessels and Sinuses of the Human Foetus at the beginning of the 3rd month. (After Prof. Florence Sabin.)

not as outgrowths from veins. They may be described as veins modified to serve as lymphatics.

The condition of the lymph system in the human embryo at the beginning of the 3rd month is shown in Fig. 317. The site of the termination of the thoracic duct is occupied by a large jugular sinus; from this sinus, vessels are growing out to the neck, head and arm of the left side. On the same side a communication has been established between the jugular sac and the posterior lymphatic sac. This communicating trunk becomes the thoracic duct. From the posterior sac outgrowths take place to form the lymphatics of the lower extremities

and pelvis; from the thoracic duct, diverticula to form the visceral and renal lymphatics are developed.

Lymphatic Glands make their appearance first as small masses or nodes of lymphocytes, which invade a plexus of lymph vessels, the vessels becoming converted into lymph sinuses. The first lymphatic nodules appear at the end of the first month; they grow in size and number during each month of foetal life. The lymphatic glands serve as germinal centres for the production of lymphocytes.

Interscapular Gland.[1]—Under this name has been included the mass of peculiar tissue which occupies the posterior triangle of the neck, and extends under the trapezius towards the posterior border of the scapula. It represents the **hybernating gland** of insectivora and bats. It begins to form in the 2nd month of foetal life at the site of the jugular lymph sac. It is composed of a stratum of three tissues —lymphoid, haemolymph (blood-forming) and fat.

Haemolymph Glands.—In the subperitoneal fat of many mammals numerous red bodies may be seen which differ from lymphatic glands in the following points: (1) the sinuses contain red blood corpuscles; (2) instead of afferent and efferent lymphatic vessels, arteries and veins open into the sinuses. They occur in the human foetus, and apparently serve the same function as the spleen (W. B. Drummond).

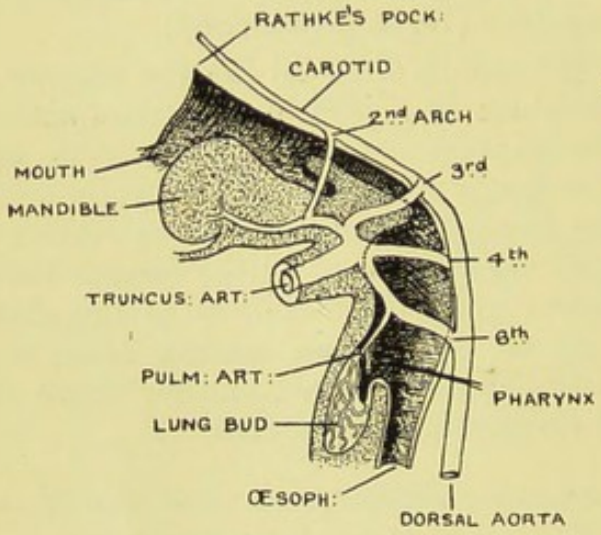
Bone Marrow.—Until the 5th month of foetal life the marrow is composed of branched cells embedded in a jelly-like matrix (primary marrow); it then assumes the appearance of lymphoid tissue, and contains leucoblasts; in the 6th month erythroblasts and erythrocytes appear in the dilated capillaries forming **red marrow** in the centres of ossification (Hammar). At birth the marrow of all the osseous tissue is red; during the years of active growth the marrow of the shafts of bones is gradually replaced by fat cells, **yellow marrow** being thus formed (Hutchison). From birth onwards the red marrow forms the only tissue in which red blood corpuscles are produced.

[1] For recent account of this structure see Bonnot, *Journ. Anat. and Physiol.* 1908, vol. 43, p. 43.

CHAPTER XVIII.

RESPIRATORY SYSTEM.

Stages in the Evolution of the Human Respiratory System.—The development of the lungs, the pleural cavities and chest wall forms one of the most complicated chapters of human embryology. The steps in the development of this system, as seen within the human embryo, are unintelligible until they are interpreted by a study of comparative anatomy, especially of those animal forms that show the



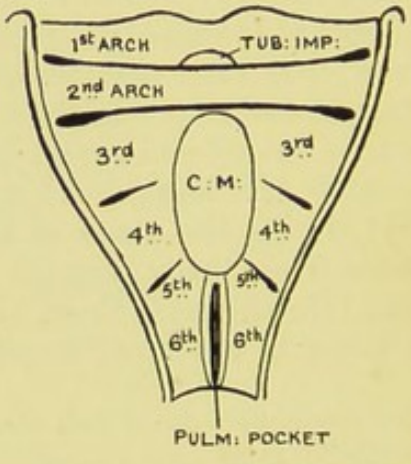


FIG. 318. Showing the Pulmonary Artery arising from the 6th of Pulmonary Aortic Arch in Human Embryo of 4 weeks. (His.)

FIG. 319.—Showing that the Pulmonary Diverticulum arises from the bases of the last or 6th pair of Visceral Arches. (Frazer.)

manner in which a purely pulmonary system arose from one which was purely branchial. Hence it is necessary to briefly recapitulate the various modifications of the respiratory system which are seen to occur in ascending from the lowest to the highest class of vertebrates. Four stages may be recognized :

Stage I.—This stage is represented in fishes, in which the respiratory system is made up of three parts : (1) **Branchiae,** in which the respiratory exchange of blood gases is effected ; (2) the swim bladder, an evagina-

tion from the oesophagus, containing oxygen, and surrounded by lymphoid tissue; (3) the musculature of the branchial arches and pharynx, which pumps water through the branchial clefts, and helps to force the blood through the branchiae; (4) nerve system with centre —both motor and sensory—in the hind-brain, and visceral nerves supplied by the vagus, and from vasomotor centres in the dorsal region of the cord. Although branchiae are never developed in the human embryo, yet the condition in the 3rd week, when the heart is sub-pharyngeal in position and the visceral and aortic arches are in process

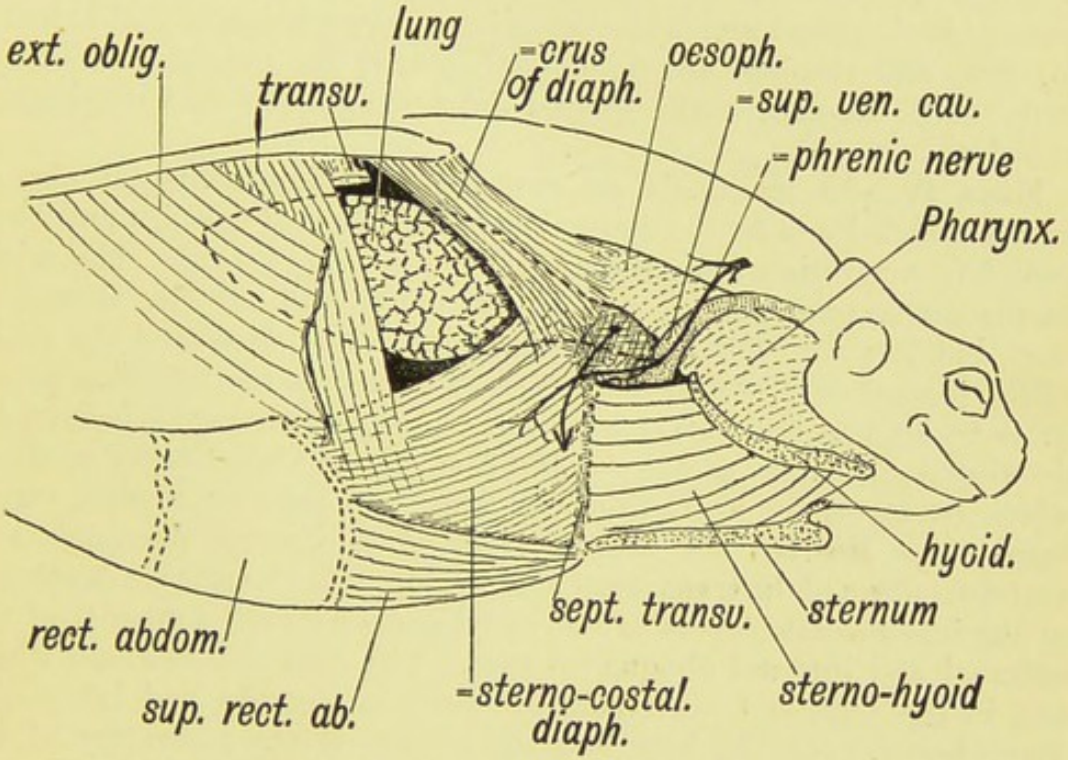


FIG. 320.—Diagram of the Lung and Respiratory Muscles of an Amphibian (Surinam toad) to show the Muscles out of which the Diaphragm is evolved and the Abdominal Position of the Lung. The arrow shows the direction in which the mammalian lung develops. The shoulder girdle and greater part of the external oblique are cut away. The heart lies above the sternum.

of development, can only be explained by the supposition that at one stage of evolution these parts had served a respiratory purpose.

Stage II.—In most amphibians four parts are to be recognized in the respiratory system. (1) The swim bladder is bifid; each half, now properly called a lung, projects within the abdominal cavity above the pericardium and liver (Fig. 320). (2) A respiratory passage leading from the pharynx to the lungs, and formed from the 2nd, 3rd, and 4th branchial (4th, 5th, and 6th visceral) arches. (3) The vascular system of the last pair of branchial arches is transferred to the surface of the lungs (Fig. 318). (4) The branchial muscles, which formerly forced water through the gill slits, now pump air into the lungs, forming thus the muscles of inspiration. The muscles of the body wall (see Fig. 320) are modified to form the muscles of expiration. Two parts of these

are specially worthy of notice, because in mammals they become the diaphragm: viz. (*a*) part of the transversalis sheet, which rises from the spine and ends in the pericardium, oesophagus and roots of the lung; (*b*) a deep lamina of the rectus abdominis which ends in the pericardium. The nerve to these muscular segments descends on the outer aspect of the superior vena cava exactly in the same manner as the phrenic nerve descends to the diaphragm (Fig. 320).

Stage III.—(1) In reptiles the lungs are abdominal in position, but an elaborate series of septa have grown up within them, thus exposing a larger vascular surface to the inspired air. (2) The respiratory passage is elongated and demarcated into larynx, trachea and bronchi. (3) Ribs and sternum are developed, so that the musculature of the body wall becomes differentiated into inspiratory and expiratory muscles.

Stage IV.—In mammals an extraordinary developmental change occurs which leads to the formation of two pleural cavities and their complete separation from the abdomen by a diaphragm. The origin of the diaphragm must be sought for, not in the reptiles, present or past, but in a very low form of amphibian. To understand the origin of the pleural cavities and diaphragm of mammals the following points must be kept in mind: (1) That the septum transversum, in its fully developed condition, as seen in the frog, is the fibrous layer of tissue which separates the heart from the liver. (2) Into the septum transversum are inserted the deepest layer of the rectus abdominis and vertebral fibres of the transversalis (Fig. 320). (3) The ribs are developed in the intermediate layers of the body wall—between segments of the external and internal oblique muscles. The muscular fasciculi which end in the septum transversum are deep to the ribs and intercostal musculature. (4) The lung buds lie at first in the mesentery of the fore-gut from which they grow outwards on each side into a narrow (pleural) passage of the coelom, which leads from the pericardium to the peritoneal cavity (Fig. 324). The passage is situated at the upper border of the septum transversum; its pericardial opening, the **iter venosum,** is closed by the superior vena cava. Now, when the lung buds grow out in the mammalian embryo, instead of growing backwards into the peritoneal cavity, behind the septum transversum, they grow outwards and forwards into the septum transversum, which becomes separated from the body wall to form the central tendon of the diaphragm and the diaphragmatic and vertebral aspects of the fibrous pericardium (see Figs. 325, 333). The lungs spread forwards, separating the ribs and intercostal musculature from the pericardium and the parts of the rectus and transversalis which now form the musculature of the diaphragm. Thus the pleural cavities are diverticula formed from the pulmonary passages of the coelom. They are new formations which appeared in mammals. The development of the diaphragm gave mammals two advantages: (1) an enormous

increase in the power of inspiration; (2) the respiratory negative pressure, which affects all the viscera within the body cavity in reptiles, became restricted to the thorax in mammals.

Morphological Parts of the Respiratory System.—It consists of (*a*) The respiratory passage which extends from the pharynx to the bronchioles of the lung. The tissues which surround this passage are derived from the coverings and substance of the 4th, 5th and especially the 6th arch. The passage is completed in mammals by the development of the soft and hard palate. (*b*) The pulmonary tissue made up of (1) a diverticulum from the fore-gut which represents the

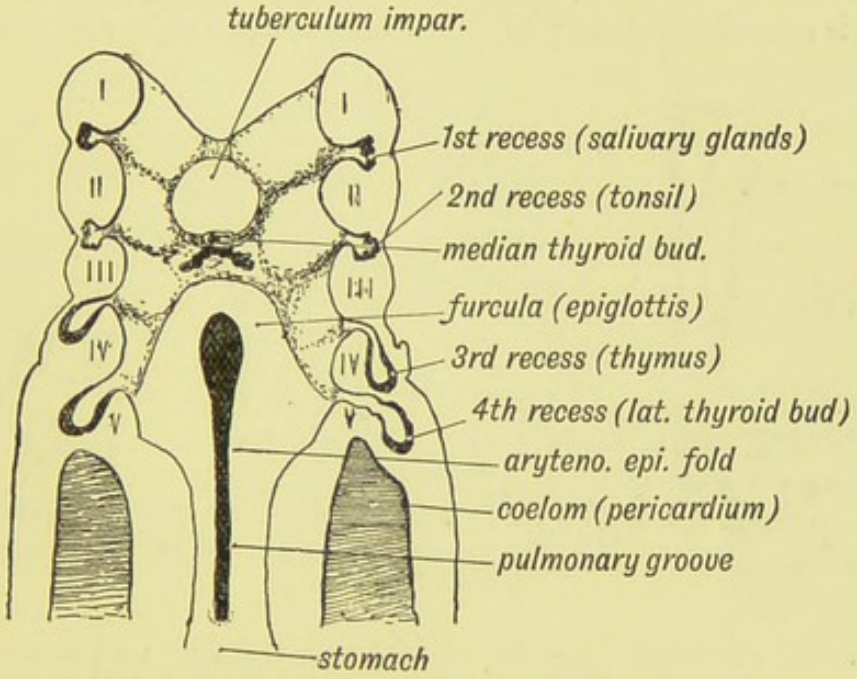


FIG. 321.—Floor of the Pharynx and Oesophagus of a Human Embryo of 3 weeks, showing the Furcula, Pulmonary Groove and Diverticulum. (After His.)

swim bladder; (2) a vascular network derived from the last pair of branchial segments (Fig. 318). The pulmonary arteries are derived from the aortic arches of these segments; the bronchial arteries are the vessels of the original diverticulum. (*c*) The respiratory muscles, sternum and ribs are formed in the somatopleure of the body wall.

Development of the Pulmonary System.[1]—In the 3rd week, towards the end of it, a deep groove appears in the floor of the primitive pharynx and oesophagus. The groove or trough-like depression of the fore-gut commences between the ventral ends of the 6th (or 5th and 6th, see Fig. 319) visceral segments and stretches almost to the stomach (Fig. 321). The **furcula,** formed from the central mass and ventral

[1] A. Oppel, *Ergebnisse der Anat.* 1904, vol. 14, p. 142, 1905, vol. 15, p. 289; J. M. Flint, *Amer. Journ. Anat.* 1906, vol. 6, p. 1; R. Mazilier, *Contribution à l'Étude de l'Embryologie du Diaphragm*; A. Greil, *Anat. Hefte,* 1905, vol. 29, p. 445 (Dev. of Amphibian Lung).

parts of the 4th segments, bounds the pulmonary groove in front (Fig. 319) ; in its anterior part, which is the most prominent, is developed the epiglottis ; the anterior parts of the lateral margins of the pulmonary groove, form the true vocal cords, for the aryteno-epiglottidean folds are secondary formations of a later date (Frazer). The posterior parts of the margins of the groove unite, and in this manner the posterior part of the groove is separated as a diverticulum on the ventral aspect of the oesophagus (see p. 250). The anterior part of the groove represents the basis of the pulmonary passage ; the posterior part, the basis of the pulmonary tissue. Two points should be noted in connection with the relationships of the oesophagus at the third week : (1) like that of a fish, it is extremely short ; (2) it lies between the right and left cavities

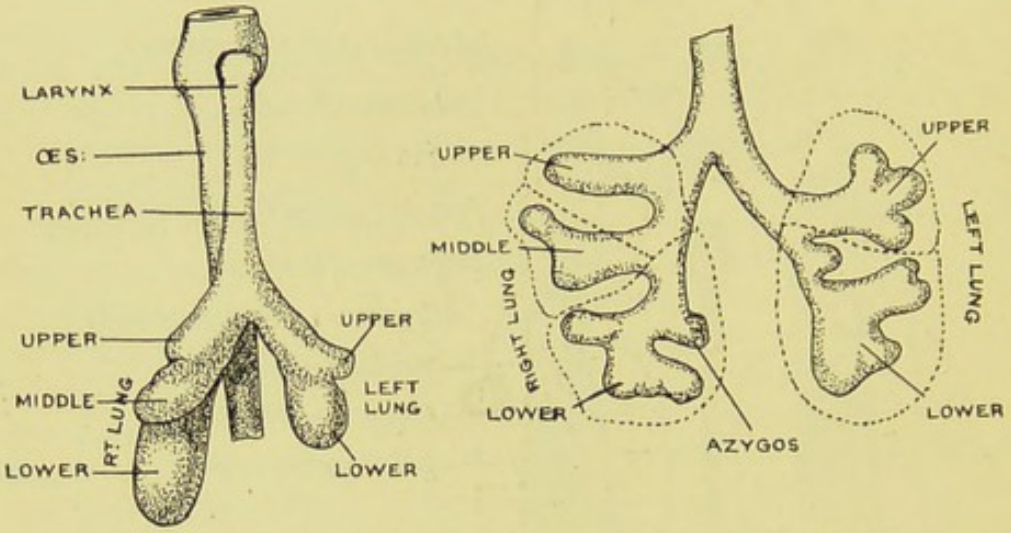


FIG. 322. The Trachea, Bronchi and Lung Buds in the 4th week of development. (After Broman, *Entwickelung des Menschen*, 1911.)

FIG. 323.—The Lobulation of the Lungs early in the 5th week. (After Merkel.)

of the coelom in the dorsal attachment of the mesocardium of the sinus venosus (Fig. 324). (3) The part of the coelom which lies at each side of the oesophagus is the narrow isthmus connecting the pericardium and peritoneal cavities which afterwards become the pleurae (Figs. 310 and 324).

When the pulmonary bud or groove is viewed from the side, its posterior extremity is seen to end in a deep pocket, the **pulmonary pocket** or diverticulum (Fig. 311, p. 315). The wall of the pocket is lined by a mass of hypoblast, which ultimately forms the epithelial lining of the whole respiratory tract, from the ciliated epithelium of the trachea to the pavement epithelium lining the alveoli of the lungs. Round the pulmonary bud is grouped a mass of mesoblastic tissue out of which the connective-tissue system of the trachea, bronchi and lungs is developed.

In the 4th week the pulmonary pocket produces a larger right and a smaller left process, the right and left **lung buds** (Fig. 322). The

median part of the pulmonary outgrowth separates from the pharyngeal floor and forms the trachea. The anterior part forms the larynx (see p. 335). The right bud forms the right lung and bronchus; the left, the left lung and bronchus. The hypoblast becomes the epithelial lining of the respiratory tract; the surrounding mesoblast forms the vessels, connective-tissue covering and coats of the respiratory tubes and lungs. As the lung buds develop the stomach is forced backwards; the oesophagus becomes elongated. The tracheal part of the bud becomes separated from the oesophagus, but both retain the

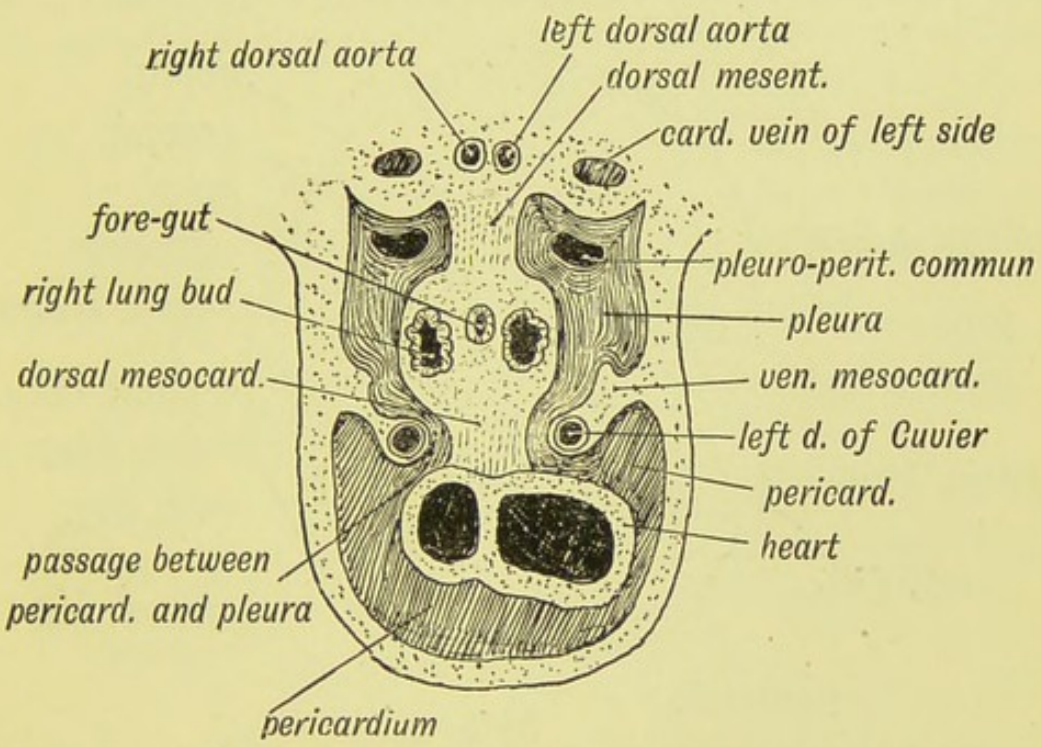


FIG. 324.—A Section of a Human Embryo to show the Relationships of the Pulmonary Buds at the 4th week, looking backwards. (After Kollmann.)

same nerve supply—the recurrent branch of the vagus—which is the nerve of the 6th arch. The rapid development of the lung during the 3rd, 4th and 5th weeks is illustrated by Figs. 238, 239, 322, 323. In the 3rd week the lung bud is a mere diverticulum; in the 4th the trachea and buds of the main bronchi are apparent; in the 5th week the secondary bronchi and separate lobes are in a process of differentiation.

In Fig. 324 the relationship of the lung buds is shown to surrounding structures during the 4th week. The following points should be noted:

(1) As the lung buds grow out they push their way into the **pleural passages**—the narrow communications between the pericardium and peritoneum. These parts of the coelom form the **pleurae.** The part of the coelomic lining which is invaginated as a covering on the lung bud becomes the visceral pleura. The invaginating or ensheathing

lining of the isthmus becomes the parietal pleura. As the lung buds grow, they distend the originally small pleural parts of the coelom until at the time of birth the right and left pleurae almost meet in front of the heart, and completely separate the chest wall from the pericardium and diaphragm. They meet after birth under the sternum, enclosing between them the anterior mediastinum.

(2) As will be seen from Fig. 310, the lung buds sprout out from the mesentery just behind the duct of Cuvier. This relationship is retained in the adult, the vena azygos major and superior vena cava lying above and in front of the root of the right lung. If the left duct

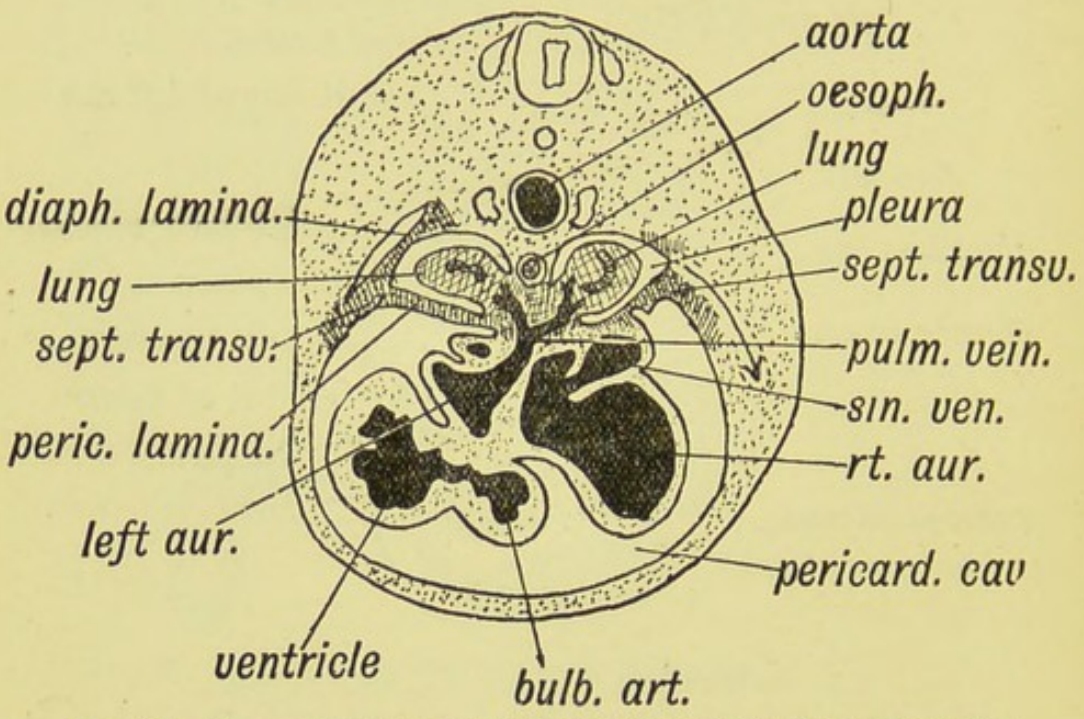


FIG. 325.—Transverse Section of a Human Embryo showing (1) the Outgrowth of the Lung Buds from the Mesentery of the Fore-gut; (2) the Separation of the Pericardium from the Body Wall and Formation of the Pleural Cavities; (3) the Separation of the Diaphragmatic Lamina from the Septum Transversum. (After Lockwood.)

of Cuvier persisted it would lie above and in front of the root of the left lung. The lung bud springs from the pulmonary diverticulum just behind the 6th visceral arch of the pharynx. The arch is involved in the formation of the pulmonary groove and pulmonary diverticulum (Fig. 319). It is from this arch (6th aortic arch) that vessels arise, permeate the lung, and become the pulmonary arteries (Fig. 318). The ductus arteriosus—part of the 6th arch—lies over the root of the left lung. At this stage (4th week) the pleural passage or cavity is still in communication with the peritoneal above the septum transversum (Fig. 324).

Formation of the Bronchi and Lungs.[1]—The bronchi are the stalks of the right and left lung buds. The right bud is the bigger;

[1] R. Heiss, *Anat. Anz.* 1912, vol. 41, p. 62 (Dev. of Lobes of Lung).

the left is probably repressed by the heart turning to the left side. The right shows three secondary buds—the forerunners of the upper, middle and lower lobes of the lung ; the left, two, which form the upper and lower lobes (Fig. 322).

The condition of the lung buds during the 5th week is shown in Figs. 323, 327. The right and left bronchi are formed, so are the chief bronchial ramifications. Each ramification ends in a bud, which divides again and again and keeps on dividing until the fourth month. The terminal buds form the bronchioles and infundibula. Each bud is solid, and carries its sheath of mesoblast ; the appearance on microscopic examination is very similar to that of a gland, such as the pancreas

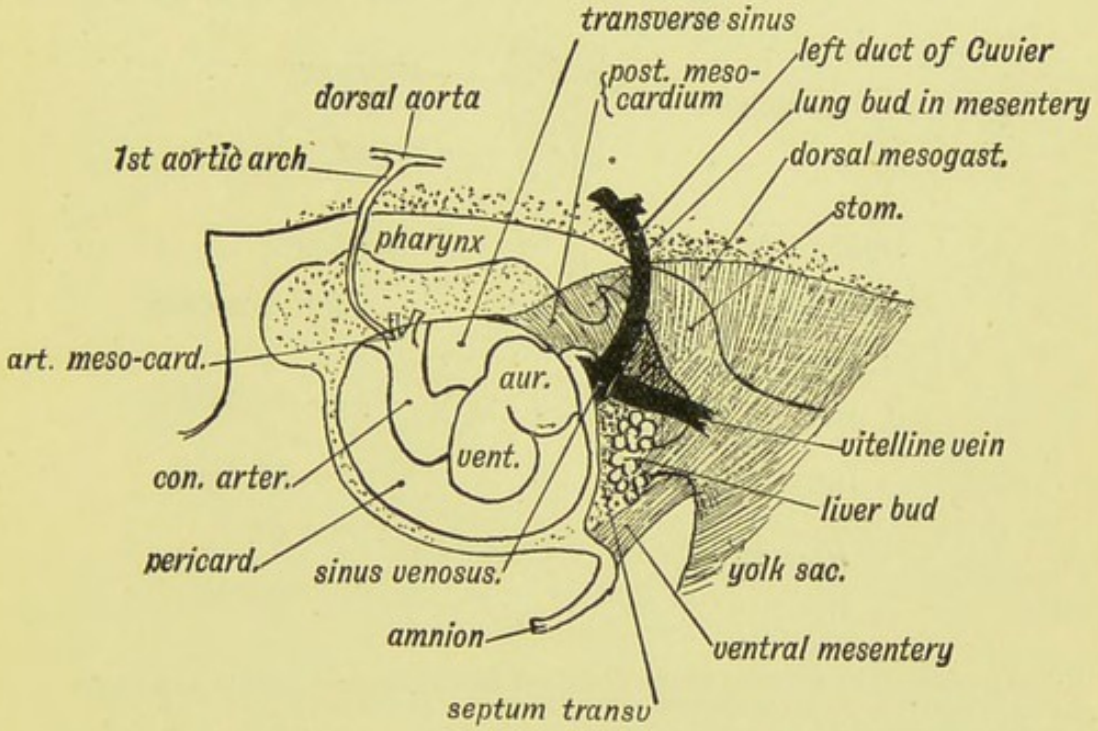


FIG. 326.—Diagram to show the manner in which the Heart is fixed within the Pericardium by the Arterial and Venous Mesocardia in a Human Embryo of 3 weeks. The "dorsal mesocardium" in the above figure forms part of the venous mesocardium.

or parotid. In the 3rd month the mesoblast between the pulmonary buds is extremely abundant ; by the sixth month it forms merely a thin stroma amongst the alveolar air sacs. At the sixth month saccular evaginations occur from the infundibula ; they form the air cells, or alveoli. Nothing is known definitely of the growth of the lung tissue after birth, but it is probably formed by outgrowths from the infundibula occupying the subpleural layer. The opinion usually held by embryologists is that the production of new alveoli ceases at the 7th month of foetal life. After that time there is merely an enlargement of the elements already formed.

Changes in the Shape of the Lung.—Even in the 5th week the lungs are merely glandular masses round the terminal parts of the

bronchial outgrowths. As in the frog, the hilum forms the apex of the lung. During the 2nd and 3rd months the lungs assume their definite shape. The upper lobe grows upwards, and an apical region is thus formed. The diaphragmatic or basal surface is at first absent, but as the pleural cavities expand and the basis of the diaphragm is stripped from the body wall, this surface appears. In the human and anthropoid foetus the diaphragmatic or basal surface becomes remarkably large. The most important change, however, relates to the anterior or ventral border of the lungs; at first situated on the dorsal side of the pericardium the lungs expand forwards until they reach almost to the lateral borders of the sternum. In man and anthropoids the ventral or sterno-costal part of the lung reaches a high degree of development.

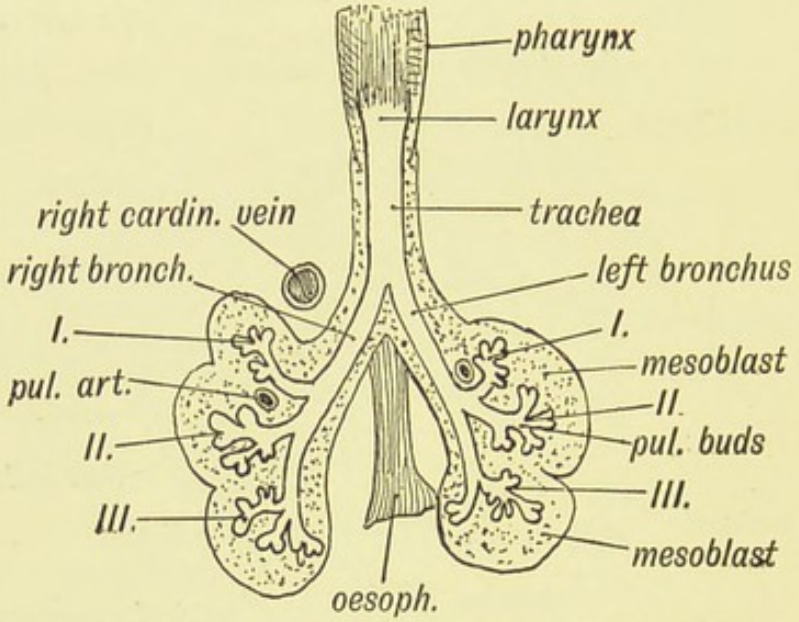


FIG. 327.—The condition of the Right and Left Pulmonary Buds in an Embryo at the end of the 5th week. (After His.)

There are certain **peculiarities in the lungs** of animals which are adapted to an upright posture (Man and Anthropoids):

(1) **Ramification of the Bronchi.**[1]—In quadrupedal mammals the main bronchus passes backwards in the lung as a main stem, which grows gradually smaller by giving off four dorsal and four ventral bronchial branches (Fig. 328). So altered are the human lungs, that the arrangement of bronchi seen in most mammals is not easily recognized in them. The ventral bronchi are larger, longer and more branched than in other mammals. In the human as in the mammalian lung the secondary and terminal bronchi are developed by a dichotomy or subdivision of the pulmonary buds.

(2) **The Lobes of the Lungs.**—In the embryonic condition (Fig. 327) it is seen that the right and left lung buds are nearly symmetrical.

[1] For a recent account of the development of the mammalian lung and bronchi: J. M. Flint, *Amer. Journ. Anat.* 1906, vol. 6, p. 1.

Aeby supposed the upper lobe of the right lung to be absent in the left; and this is also the conclusion which Flint arrived at after a minute investigation of the development of the lungs of the pig. It must be remembered that the point of origin of any bronchus may easily be moved to meet new physiological conditions. At least in the human embryo each main bronchus gives off three primary buds. All three remain separate on the right side; on the left the upper and middle primary buds arise together (Fig. 327). Hence the upper lobe of the left lung represents the upper and middle lobes of the right. In the sheep and pig the upper right lobe springs from the trachea. The

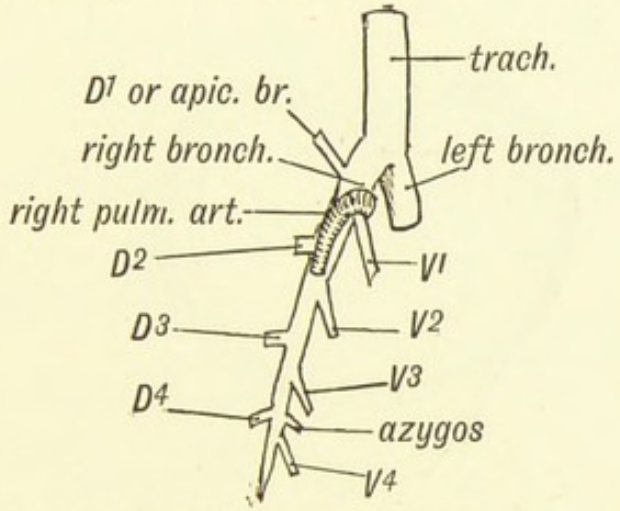


FIG. 328.—Scheme of the Bronchial Ramifications in Quadrupedal Mammals. *D*, the dorsal ramifications; *V*, the ventral ramifications.

bronchus of the upper right lobe (the reason for it is not clear) commonly lies above its artery—that is to say, it is **eparterial.** The other bronchi are **hyparterial.**

(3) **The Diameters of the Thorax.**—The peculiar branching of the bronchi in man and upright primates is due to the shape of the lungs, which in turn is due to the shape of the thorax. In quadrupedal animals, such as the horse or dog, in which the chest rests and is supported between the fore limbs, the thorax has its greatest diameter in the dorso-ventral direction (Fig. 329). In upright animals (man, anthropoids, and also in some water living mammals, such as seals, etc.) the transverse diameter becomes the greater. At birth the diameters of the child's thorax are nearly equal. The thorax is flattened by the spine becoming invaginated within it; the thorax thus comes to lie within the axis of gravity of the upright body.

(4) **The Azygos Lobe.**—On the inner side of the right lung of man the azygos lobe is frequently present, sometimes as a mere pulmonary projection or trace, sometimes as a lobule. It represents an over-development of the second ventral branch from the right bronchus (Fig. 323). It projects into and fills a slight recess between the pericardium and diaphragm, behind the intra-thoracic part of the inferior

vena cava. The lobe is always well developed in quadrupedal mammals. In them the pericardium is separated from the diaphragm by a diverticulum of the right pleura—the **sinus subpericardiacus** (Fig. 330). With the assumption of the upright posture (in man and anthropoids) the heart sinks until it rests on the diaphragm, the subpericardiac sinus and azygos lobe being thus obliterated. The reappearance of the azygos lobe as a separate structure—for a buried rudiment is always present—in man is an atavism—that is to say, a recurrence of an ancestral feature. In quadrupeds the contraction of the diaphragm is followed by an expansion of the lobus azygos and a corresponding elongation of

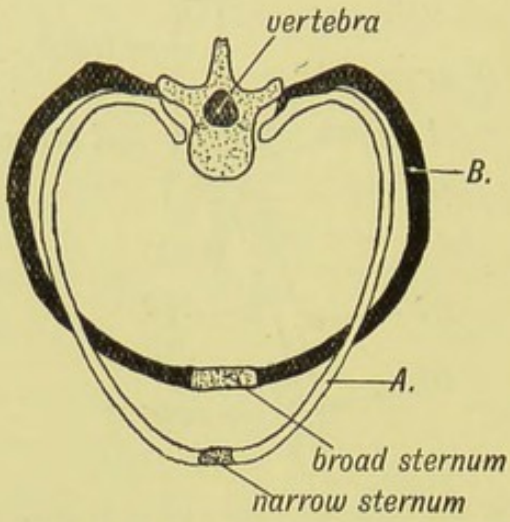


FIG. 329.—Diagrammatic Section of the Thorax of a Quadrupedal Mammal (*A*), contrasted with a corresponding section in Man (*B*).

the highly elastic intra-thoracic part of the inferior vena cava ; in man, on the other hand, the contraction of the diaphragm is followed by a descent of the heart, thus indirectly enlarging the pulmonary space.

Blood Supply of the Lung.[1]—The pulmonary aorta is formed with the ascending part of the aortic arch, out of the conus arteriosus (see p. 229). The right and left pulmonary arteries spring as branches from the right and left 6th aortic arches (Fig. 318, p. 324). They enter the lung buds, and are carried backwards with them. The pulmonary veins grow out from the pulmonary buds and enter the left auricle through the venous mesocardium about the 5th week (Fig. 325). The mesenchymatous or interstitial tissue of the lungs is supplied by the bronchial arteries of the aorta. These arteries also supply the pleura on the mediastinal and diaphragmatic surfaces of the lungs.

Changes at Birth.—When the child begins to breathe at birth, the expansion of the lungs opens up the pulmonary circulation ; the foramen ovale is closed and the ductus arteriosus begins then to be

[1] J L. Bremer, *Amer. Journ. Anat.* 1901, vol. 1, p. 137 (Dev. of Pulmonary Arteries) ; V. Federow, *Anat. Hefte*, 1910, vol. 40, p. 529 (Dev. of Pulmonary Veins).

closed, and within the 1st month becomes reduced to a fibrous cord. The ductus arteriosus represents the dorsal segment of the 6th left arch; the corresponding part of the 6th right arch disappears soon after it is formed. It is about the 4th day after birth until the whole of the lung is inflated. The first part to expand is the costo-sternal or ventral part; the second, the diaphragmatic or basal part, the apex is the third, and the dorsal border and deep part the last.[1]

The Larynx.[2]—The larynx is developed round the anterior part of the pulmonary diverticulum. The origin of the cartilages of the larynx is shown in Fig. 331. The thyroid cartilage is formed by the

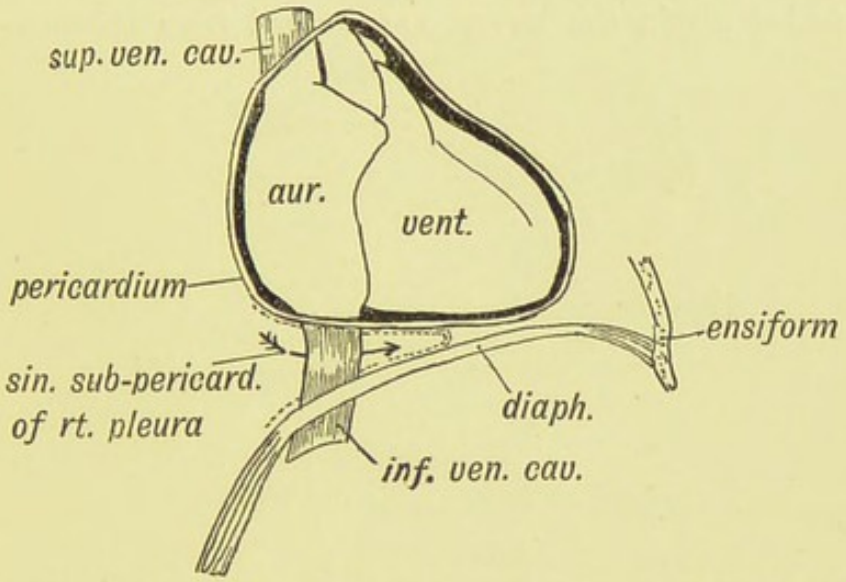


FIG. 330.—The Relationship of the Heart to the Diaphragm in Quadrupedal Mammals.

expansion and amalgamation of the skeletal bases of the 4th and 5th visceral arches (in 8th week, Kallius). The skeletal basis of the 6th or pulmonary arch in man, which forms the two lateral cartilages in the short pulmonary passage of the frog, becomes divided into a dorsal segment which forms the arytenoid cartilage, a ventral segment to form the cricoid. From the posterior part of the primitive lateral cartilage arise the rings in the wall of the trachea, chief, secondary and ultimate bronchi (Fig. 331).

Recently Mr. Frazer has made a very thorough investigation of the development of the larynx. At each side of the primary pulmonary orifice lies a mass of tissue representing the last or 6th visceral arch (Fig. 319). In this tissue develops the various parts of the larynx. The cricoid and arytenoid are the primary cartilages; they are the only ones present in the larynx of amphibia and reptiles. The thyroid

[1] For papers relating to the morphology and mechanism of the lungs see *Further Advances in Physiology*, edited by Leonard Hill, Edward Arnold 1909; also Keith, *Journ. Anat. and Physiol.* 1909, vol. 39, p. 243.

[2] J. E. Frazer, *Journ. Anat. and Physiol.* 1911, vol. 44, p 156; H. Lisser, *Amer Journ. Anat.* 1911, vol. 12, p. 27.

only appears in mammals. The true vocal cords represent the primary opening of the larynx. In the 2nd and 3rd months of human development the part of the laryngeal cavity above the vocal cords (suprarimal part) is produced by the upgrowth of the lateral masses on each side of the primary opening. In these masses are developed the arytenoid cartilages and the aryteno-epiglottidean or permanent folds which bound the lateral margins of the secondary laryngeal orifice. The epiglottis, in Mr. Frazer's opinion, is developed out of the mass of tissue (central mass) which lies behind the 2nd and 3rd arches (Fig. 319). It is possible that the 4th arch may also assist in its upbuilding. Cartilage appears in the epiglottis at the 4th month.

The muscles within the larynx are derived from the 6th visceral

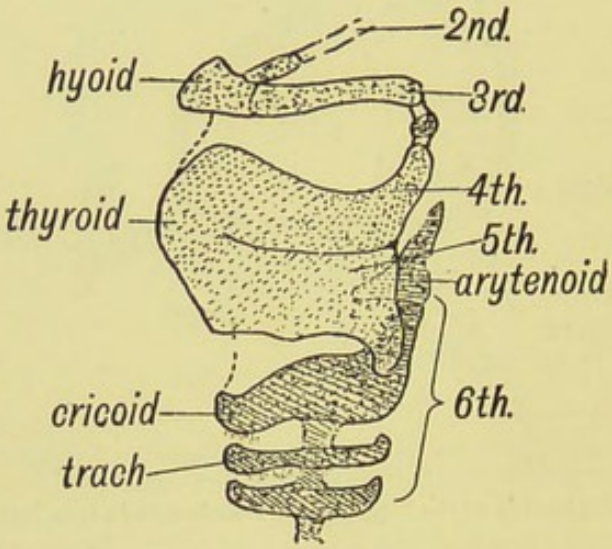


FIG. 331.—Diagram of the Cartilages of the Larynx to show the parts derived from the Skeleton of each Visceral Segment.

segment and are supplied by the inferior laryngeal nerve, while the crico-thyroid arises from the musculature of the 4th segment.

The epiglottis is developed in the furcula (Symington); in lower vertebrates its lateral margins extend into the aryteno-epiglottic folds. The cartilages of Santorini and Wrisberg, in the aryteno-epiglottic folds, are continuous with the epiglottis in many mammals (Sutton). Until the 5th month of foetal life the epiglottis lies behind the palate and within the naso-pharynx—a position which is normal for the adults of many kinds of mammals.

The purposes which the larynx serves in all air-breathing vertebrates are (1) to regulate the inflow and outflow of respiratory air, and thus the positive and negative pressure within the lungs; (2) to prevent food passing into the air passage. The production of voice which has led to a marked alteration of the human arytenoid cartilage is a secondary function. Only in man and the higher anthropoids are the true vocal cords covered by stratified epithelium; but all the

muscles of the human larynx are represented in the larynx of the ape, although in a less specialized condition.

Soon after the upgrowth of the lateral masses to form the supra-rimal cavity of the larynx, an evagination takes place above each vocal cord to form the ventricles. In the 5th month mucous glands are developed from the membrane lining the ventricles, and a little later an outgrowth is developed from their apices to form the saccules of the larynx. They project against the thyro-hyoid membrane. Occasionally the **saccule** of the larynx may protrude through the thyro-hyoid membrane, thus giving rise to an air cyst in the neck. Such laryngeal sacs are normally developed in anthropoids after birth, and attain in them great dimensions. Their function is unknown.

Diaphragm.[1]—The diaphragm constitutes one of the most pronounced structural characteristics of mammals. The ancestral mammalian types in which the diaphragm first appeared are long since extinct; we cannot study the evolution of the diaphragm among modern vertebrates. There are certain facts which throw light upon its origin, and make us certain that the diaphragm did not rise up gradually as a partition within the coelom and shut off that part which contains the lungs from the part containing the abdominal viscera. In the human embryo of the 3rd week there are only potential pleural cavities represented by the two narrow and short passages leading from the pericardium to the peritoneum. The passage lies, then, opposite the 4th and 5th spinal segments, from which the phrenic nerve arises, and from which the musculature of the diaphragm is derived. It is clear, then, that the diaphragm entered into the service of the lungs when these were situated, as in the frog, below the cervical region. In some manner, as the lungs developed and afterwards took up a thoracic position, the muscle which became associated with them in the neck accompanied them when they retreated to their new position in the thorax. If we are to find a representative of the early form of the diaphragm, it must be amongst amphibians that we should look. We can also get light on its origin by studying certain malformations to which it is liable in man.

In Fig. 332 is shown the thoracic aspect of the diaphragm of a newly born child, in which the left **pleuro-peritoneal opening** has remained patent. Through the opening the upper end of the left supra-renal body and the spleen projected within the pleural cavity, giving rise to a congenital diaphragmatic hernia. The pleuro-peritoneal opening is situated on each side, between the muscular fibres which rise from

[1] See Keith, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 243; Mall, *Bull. Johns Hopkins Hosp.* vol. 12, Nos. 121-123, pp. 158, 171; I. Broman, *Ergebnisse der Anat.* 1911, vol. 20, p. 1 (Dev. Pericardium and Diaphragm); A. Brachet, *Mem. de l'Acad. Roy. de Med. de Belgique*, 1906, vol. 19; R. Mazilier, see reference, p. 327; M. Ramstroem, *Anat. Hefte*, 1906, vol. 30, p. 669 (Distribution of Nerves in Diaphragm).

the ribs and sternum, and which form the **ventro-lateral part** of the diaphragm, and the muscular fibres which arise from the spine and arcuate ligaments, forming the **dorsal part** of the diaphragm. The phrenic nerves, when they reach the diaphragm, divide into two branches, a ventral to the right and left ventro-lateral parts (from 3rd and 4th cervical nerves), and a dorsal branch (from 4th and 5th cervical nerves) to the right and left dorsal parts. The central tendon, situated between the four parts just mentioned, makes up the fifth morphological element of the diaphragm. Each of these five parts—the central,

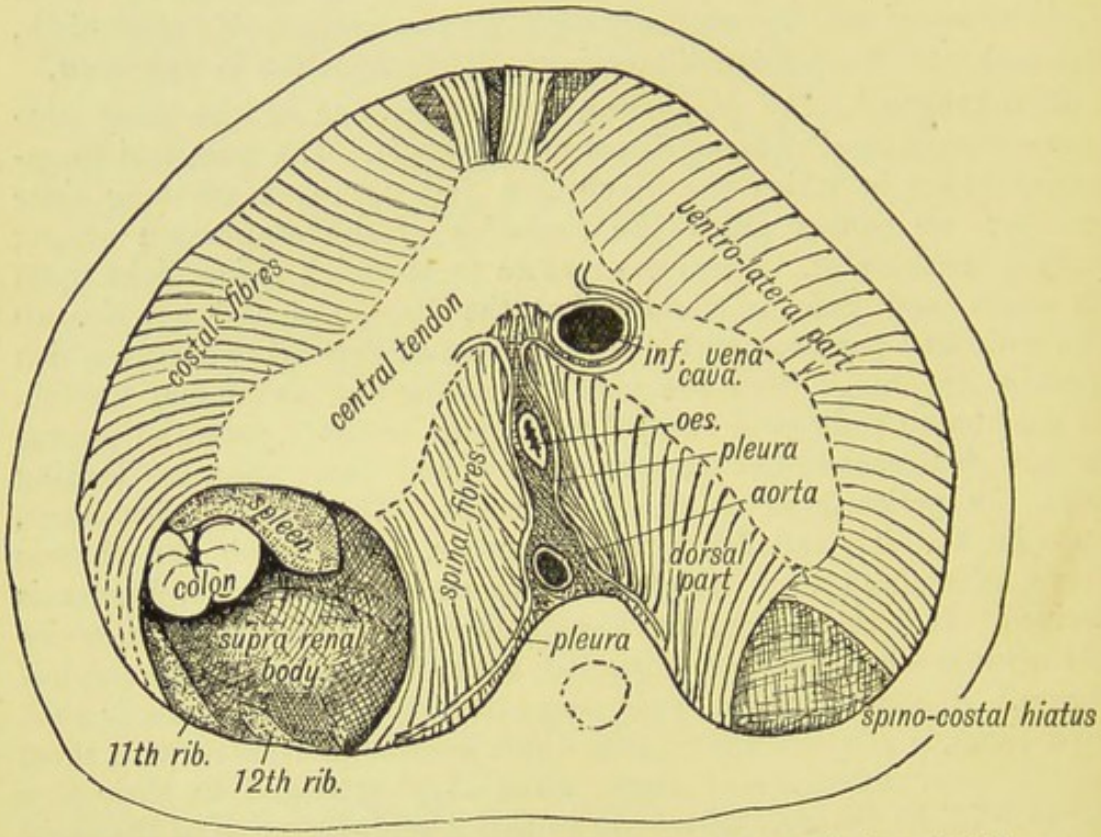


FIG. 332.—The Thoracic Aspect of the Diaphragm of a newly-born Child in which the communication between the Peritoneum and Pleura has not been closed on the left side; the position of the opening is marked on the right side by the Spino-costal Hiatus. The dorsal mesentery of the fore-gut (represented by the posterior mediastinal pleura) is also shown.

the two dorsal and two ventro-lateral, has its own developmental history.

The **central tendon of the diaphragm** is formed from the septum transversum (see Figs. 325 and 333). The manner in which that structure is cleft into its pericardial and diaphragmatic elements by the outgrowth of the two pleural passages and lung buds has been already described (pp. 326, 329). The dorsal and ventral mesentery of the fore-gut (Fig. 334) are included in the formation of the septum transversum (p. 249), and hence the structures developed in these mesenteries—the aorta, oesophagus, azygos veins, thoracic duct, vagus nerves and inferior vena cava—perforate the median or central part

of the diaphragm. The structures of the posterior mediastinum lie in the mesentery of the fore-gut (see Fig. 332).

The **ventro-lateral parts** of the diaphragm are derived from the ventral longitudinal muscular sheets which give rise to the rectus abdominis and depressors of the hyoid bone (Fig. 320, p. 325). Were the parts of this sheet restored to their embryonic relationships, then the pericardium should be placed beneath the pharynx, so that the central tendon of the diaphragm lies opposite the 4th cervical segment. The sternal and costal origins of the ventro-lateral segment of the diaphragm should be detached and the muscle placed ventrally in the

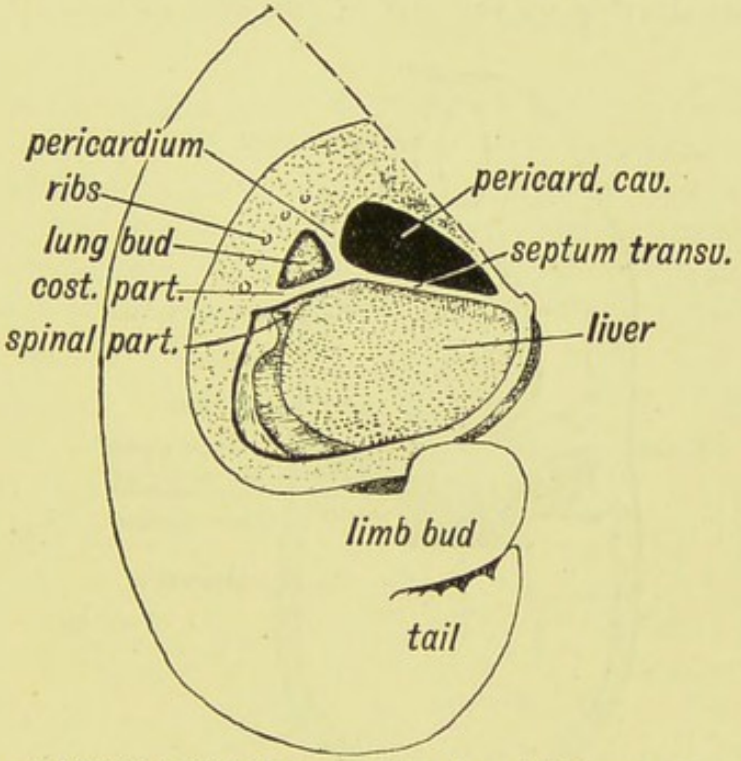


FIG. 333.—A Lateral Section along the Thoracic and Abdominal Regions of a Human Embryo in the 5th week of development, showing the Lung Bud growing within the Septum Transversum and separating it into a Pericardial and a Diaphragmatic (costal) Lamina. The arrow points to the dorsal mesentery of the fore-gut within which the crura of the diaphragm are developed. (After Mall.)

neck so that it is continuous, at its insertion to the septum transversum, with the depressors of the hyoid bone. Behind, it is continuous with the anterior end of the rectus sheet. The anterior part of the rectus sheet is divided into four strata—(1) the ventro-lateral fibres of the diaphragm, (2) the interchondral parts of the intercostals, (3) the rectus abdominis, which in all mammals, except man and the anthropoids, reaches forwards to the 1st rib, (4) the pectoralis major, minor, subclavius and that frequent human abnormality—the sternalis muscle. The development of the lung separates, from the chest wall, the deepest part of the rectus sheet to form the ventro-lateral part of the diaphragm. The ribs are formed in the chest wall and to the posterior six, this part ultimately obtains an origin (see Fig. 325).

The **dorsal parts of the diaphragm** are formed from that part of the transversalis sheet of the body wall which forms the subvertebral musculature (Figs. 320, 332). The right and left spinal parts of the diaphragm sink within the dorsal mesentery of the fore-gut, obtaining anteriorly an insertion to the pericardium and septum transversum, while posteriorly they retain an origin from the spine and costal processes. The quadratus lumborum, longus colli, the rectus capitis anticus major and minor are also derived from the subvertebral musculature.

Pleuro-peritoneal Opening.—The pleural passages, into which the lung buds develop at the end of the first month, open into the

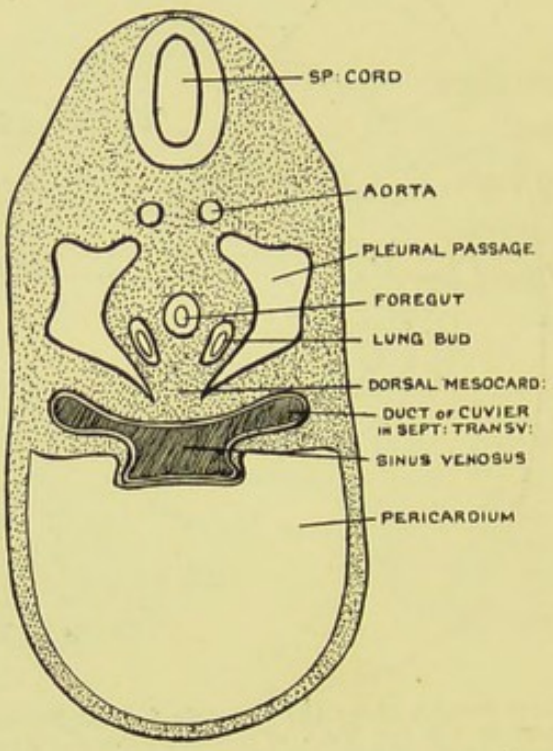


FIG. 334.—Section across Mesentery of the Fore-gut to show its relationship to the Pleuro-peritoneal Openings and Septum Transversum.

pericardium by the iterinera venosa ; behind they communicate with the peritoneum by the pleuro-peritoneal openings. These lie above the septum transversum (Fig. 334) and are separated by the mesentery of the fore-gut. In the mesentery between the openings are developed the spinal fibres of the diaphragm ; on the lateral side of each opening arise the costal fibres. The openings are closed by two factors (Fig. 332). (1) The spinal fibres migrate outwards and obtain attachment to the arcuate ligaments ; the costal fibres migrate inwards, obtaining an origin from the 11th and 12th ribs. Only in man and anthropoids does this migration occur, and the extent to which they approach each other and thus close the opening is extremely variable. (2) The collapsed condition of the lungs allows the abdominal viscera, developed

in the domes of the diaphragm, to press the spinal and costal fibres against the dorsal wall of the thorax, thus mechanically closing the aperture. The liver, especially, by its upgrowth within the septum transversum helps to close the apertures, particularly on the right side, which is seldom the site of a diaphragmatic hernia. The supra-renal bodies are also developed just behind the pleuro-peritoneal orifices, and help to close them. Indeed, the mesentery of the Wolffian body, in the anterior extremity of which the supra-renal bodies are developed, are attached along the dorsal wall of the coelom as far as the septum transversum, where it forms a fold upon the lateral or outer margin of the pleuro-peritoneal orifice, where it is sometimes named the pleuro-peritoneal membrane, and is regarded as an embryonic form of diaphragm.

Musculature of the Body Wall.—The development of the musculature of the body wall, also of the ribs and sternum, ought rightly to be included here, for all are closely related to the mechanism of respiration. The ribs have been already considered, and it will be more convenient to reserve the development of the wall of the thorax and abdomen with other correlated structures for another chapter (Chap. XXI.).

CHAPTER XIX.

UROGENITAL SYSTEM.

Evolutionary Stages.[1]—The union of the genital with the urinary system has to be sought for at a very early stage in the evolution of animals. The coelom, which it will be remembered is derived from the cavities of the primitive somites or segments of the embryo (Fig. 33, p. 34), represents the earliest excretory organ. The genital cells appeared on the walls of the coelom, and passed out from the body cavities with the products of excretion. Later, the coelom itself became specialized; in the dorsal part, at each side of the root of the mesentery, tubular evaginations (Fig. 335) were set aside for the excretion of the more solid products and glomeruli which separated the fluid or water from the blood. The urinary products were conveyed from the tubules by a nephric or Wolffian duct. The genital cells are stationed in an area of coelomic epithelium on the inner or mesial aspect of the Wolffian ridge, near the root of the mesentery (Fig. 335). Even in the lamprey, which possesses the most primitive urogenital system to be seen in the vertebrates, the stage in evolution represented diagrammatically in Fig. 335 has been already reached. It is from such a primitive arrangement that the human urogenital system has been evolved.

Succession of Renal Organs.—In the evolution of vertebrate animals there was a succession of three renal or nephric organs. Towards the end of the 3rd week of development of the human embryo, the first of these, the **pronephros,** makes a transitory appearance (Fig. 336); the second, the **mesonephros** or Wolffian body, is in process of formation; the basis of the third, the permanent renal organ, or **metanephros**, is just visible. The vestiges of the pronephros belong to the hinder cervical segments, and lie in the roof of the coelom behind the septum transversum. The pronephros represents the kidney of the lamprey; the coelomic mouth (nephrostome) of each tubule is open

[1] For references to some of the more recent papers dealing with the development and malformations of the urogenital system see Keith, *Brit. Med. Journ.* 1908, Dec. 12th, 19th, 26th.

(Fig. 335). The mesonephros corresponds to the segments of the dorsal and lumbar regions. The tissue of the permanent kidney lies ventral to the sacral vertebrae and dorsal to the cloaca. Already the Wolffian duct has reached the cloaca. It is clear that pronephros, mesonephros and metanephros are parts of the same linear series of organs. All are made up of nephric tubules opening into a common excretory duct. While in the cervical region the tubules are simple and retain their segmental arrangement, in the dorsal and lumbar region they multiply in number and complexity; in the sacral region they become exceedingly numerous and massed round a diverticulum from the Wolffian

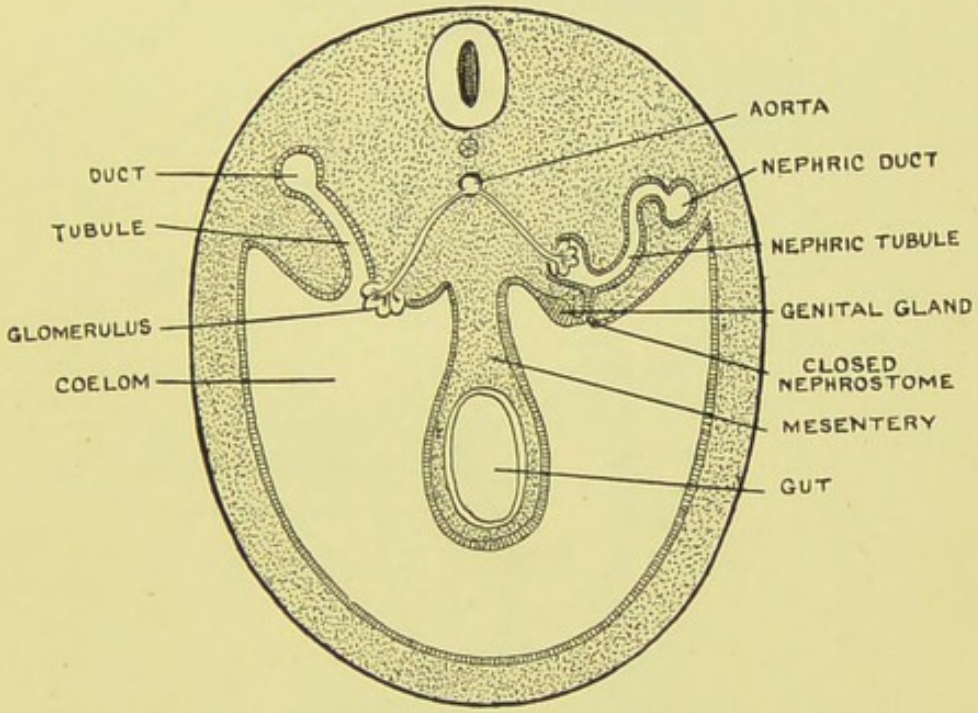


FIG. 335.—Schematic Section to show the Specialization of the Dorsal Part of the Coelom into Nephric Tubules and Glomeruli. On one side the tubule and glomerulus remain in continuity with the coelom; on the other side they are buried in the Wolffian or intermediate ridge.

duct—which forms the primitive ureter. In the second month of human development the Wolffian body is at the height of its development; in the 3rd month the permanent kidney assumes its predominant position, and its predecessor—the Wolffian body—is converted into a mere appendage of the genital system.

Evolution of the Penis.—The transformations just described are of ancient origin, but those remarkable changes which are seen to occur in the perineum of the human embryo represent much later evolutionary changes. Even in the lowest mammals—monotremes and marsupials—the rectum and urogenital ducts end in a common terminal passage—the cloaca. In the human embryo, during the first month of development, this is also the case; but in the second month changes occur which separate the rectal and urinary passages. These changes are

due to the evolution of an external or extra-cloacal penis. In Fig. 337 stages in the evolution of the penis are represented. In the tortoise the penis lies on the pubic or ventral wall of the cloaca; during copulation the open groove of the penis is converted into a canal by the application of the dorsal or opposite wall of the cloaca. In Echidna—a primitive mammal—the penis is still intra-cloacal; its groove is converted into a canal, except posteriorly, where there is still an opening between the urogenital and cloacal passages—which represents the primitive urogenital orifice, for the penile canal is a new passage. In marsupials the penis is still partially intra-cloacal, but the primitive

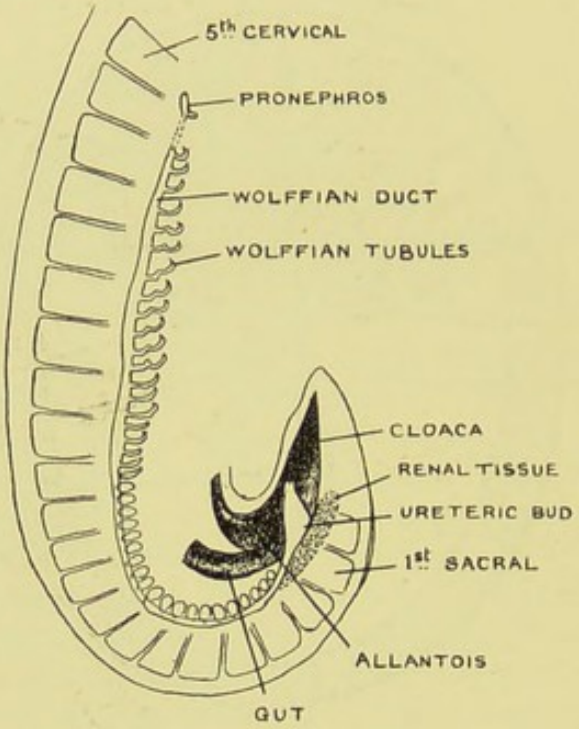


FIG. 336.—Condition of the Nephric or Renal Tissue in a Human Embryo of 3 weeks. (After Ingalls.)

urogenital orifice is closed, and the urogenital passage is now separated from that which serves for the faeces. In man the penis is completely extra-cloacal, and a perineal body separates the rectal orifice from the urogenital passage. The **metamorphosis of the cloaca** is thus a result of the evolution of the penis. The external penis appears with the evolution of a vagina, uterus and the intra-uterine nourishment of the young. The cloacal passage is seen in oviparous mammals; in viviparous mammals the penis is evolved as an intromittent organ, and the urogenital passage is separated from that of the rectum.

The Wolffian Body or Mesonephros.[1]—In lower vertebrates (Fishes and Amphibians) the Wolffian body is the functional kidney; in higher vertebrates (Reptiles, Birds, and Mammals) it is merely a temporary or embryonic structure, the renal function being taken

[1] J. B. MacCallum, *Amer. Journ. Anat.* 1901, vol. 1, p. 245 (Dev. of Wolf. Body).

over by the permanent kidney. Apparently the permanent kidney (metanephros) arose by a hypertrophy and separation of the hindermost segment of the Wolffian body (mesonephros). The presence of the mesonephros in the human embryo and in the embryonic stages of the three great classes of higher vertebrates, with the presence of many curious stages in the development of their genito-urinary system, can

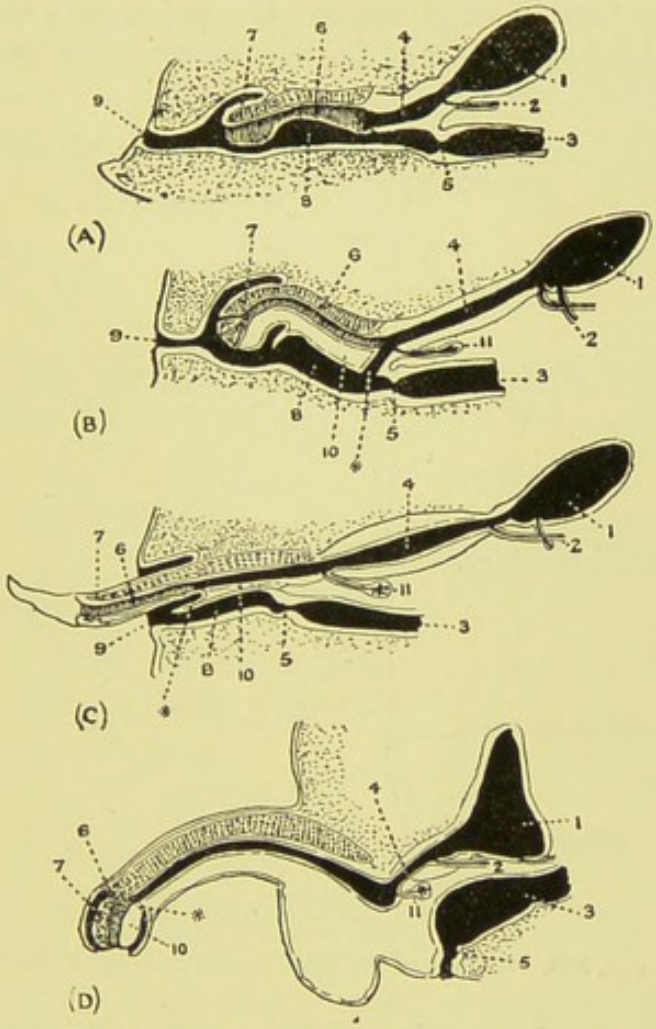


FIG. 337.—Stages in the Evolution of the Penis. *A*, stage seen in tortoise; *B*, stage seen in Echidna; *C*, stage seen in marsupial (kangaroo); *D*, stage seen in man. The phallic canal is shaded. 1, bladder; 2, Wolffian duct (vas); 3, rectum; 4, urogenital sinus; 5, anus; 6, phallic groove and canal; 7, glans; 8, cloaca; 9, cloacal orifice; 10, floor of phallic canal; 11, Cowper's glands; * position of primitive orifice of urogenital sinus.

be explained only by the fact that these higher forms are descended from ancestors of the lower.

In Fig. 338 the Wolffian body, such as occurs in the frog, is represented diagrammatically, and it corresponds in structure to the Wolffian body which appears in the human embryo. Each body is made up of a main duct and a series of tubules. In the frog, as in the human embryo, the hind-gut ends in a dilatation, the **cloaca.** In the cloaca open the rectum, allantois, and the two **Wolffian ducts**—right and left.

In the frog, the Wolffian bodies lie on each side of the spine, their anterior ends reaching forwards to the region of the heart. Each duct is joined by numerous convoluted tubules—the **Wolffian tubules.** Each tubule is furnished with a glomerulus at its blind extremity, and in most features agrees with a secretory tubule—such as is seen in the permanent kidney. These tubules secrete the urine ; the Wolffian duct conveys the urine from the tubules to the cloaca. The anterior tubules, however, lose their secretory function and become associated with the genital gland. In the male frog they convey the spermatozoa to the Wolffian duct,

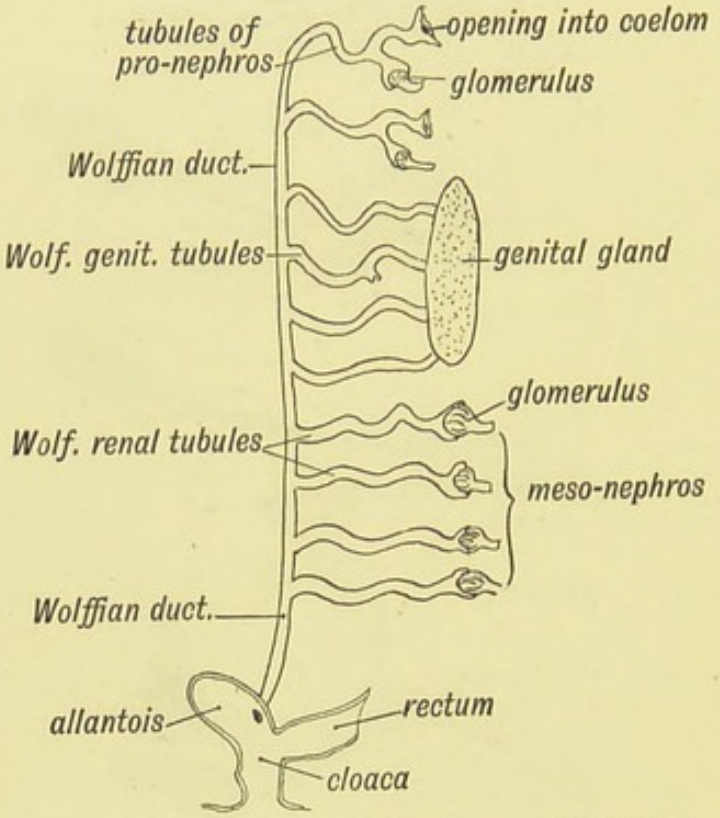


FIG. 338.—Scheme of the Wolffian Body on the right side.

which thus carries both urine and spermatozoa. In the female, the **genital** Wolffian tubules are connected with the ovary but are quite functionless (Fig. 338).

The Wolffian Body in the Human Embryo.—At the beginning of the second month of foetal life, the Wolffian body is well developed ; by the end of that month it is undergoing a process of atrophy, except those parts connected with the genital organs. It projects as a ridge from the lumbar and dorsal regions at the base of the mesentery (Fig. 339), extending, on each side of the spine, from the posterior cervical region, where the diaphragm is developed, to the pelvis behind, where the ridges become approximated. To its inner side, in the lower dorsal region, lies the **genital ridge.** The genital and the Wolffian bodies have each its own mesentery, but these two mesen-

teries have a common attachment—the common urogenital mesentery (Fig. 339). On section the Wolffian ridge is seen to be made up of convoluted tubules terminating at their blind extremities in glomeruli. The tubules open into the Wolffian duct, just as in the frog; the duct is situated in the basal or attached part of the ridge. It runs backwards in this ridge and turns into the pelvis to end with the Müllerian duct (also situated in the Wolffian ridge) in the cloaca of the hind-gut. The whole arrangement is similar to that seen in the frog. Further, as in the frog (Fig. 338), certain of the more anterior or genital tubules are connected with the genital glands, and are not, as the posterior are,

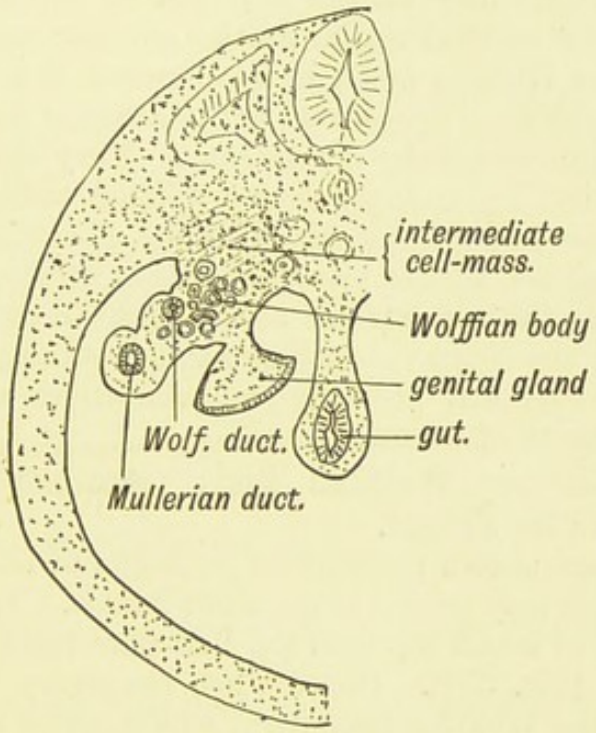


FIG. 339.—Diagrammatic Section to show the Position of the Wolffian and Genital Ridges on the Dorsal Wall of the Abdomen.

secretory in nature. If the testes were functional at this time—which they are not—the spermatozoa and urine of the Wolffian body would pass to the cloaca by the Wolffian duct.

Origin of the Wolffian Duct and Tubules.—The tubules which compose the Wolffian body are developed in the **intermediate cell mass**, and begin to form early in the 3rd week (Figs. 335, 339). The intermediate cell mass is divided from before backwards into segments; two or three tubules arise in each segment. At first they are minute transverse vesicles formed by mesoblastic cells in the intermediate mass; these vesicles become tubular; one end opens into the Wolffian duct; at the other a glomerulus is developed (see Fig. 336). The duct is developed in the outer part of the intermediate cell mass. Its anterior or cervical part appears early in the 3rd week as a solid rod of cells; the process of formation spreads backwards, and by the

end of the 3rd week it has reached the cloaca. In the posterior or pelvic end of the embryo the two Wolffian ridges, before they reach the cloaca, fuse together to form the **genital cord.** Within the genital cord the right and left ducts are situated almost side by side. The ducts soon become open, their lining epithelium being derived from the mesoblast of the intermediate ridge.

The Pronephros[1] (Fig. 338).—Even before the mesonephros (Wolffian body) there appears to have been another kidney—the pronephros. While only permanently functional in some of the lowest fishes, and even in them it is partly replaced by the mesonephros, it still appears transiently in the embryos of all vertebrates. It is developed in the cervical region at the anterior end of the Wolffian ridge. Like the Wolffian body, it is composed of a longitudinal duct and tubules; the duct appears to be an anterior prolongation of the Wolffian duct, but its tubules are different. They open into the coelom (peritoneal cavity) by trumpet-shaped ciliated ends, and are derived from invaginations of the mesothelial lining of the coelom. They are coiled and terminate in the pronephric duct, which, as already mentioned, is merely the anterior end of the Wolffian duct. A glomerulus is developed in the course of each pronephric tubule (Fig. 338). The pronephric tubules are probably representatives of the segmental (nephridial) tubules of worms.

The Fate of the Wolffian Body (mesonephros) and Pronephros.—1. In the **Female.**

In Fig. 340 are shown the various remnants of the embryonic renal formations which may persist in the adult female. The Müllerian duct, the upper part of which becomes the Fallopian tube, is situated in the Wolffian ridge (Fig. 339). Hence when the ovary and tube migrate to the pelvis, the Wolffian mesentery, which comes to form the mesosalpinx, is also drawn within the pelvis, and with it all the Wolffian remnants in the female. A hydatid attached to the mesosalpinx (part of the broad ligament) at the fimbriated extremity of the Fallopian tube (Fig. 340) represents the anterior end of the Wolffian duct and the most anterior (cephalic) of the Wolffian formation—probably the Pronephros. It certainly corresponds to the pronephric remnant found in the frog. It may become enlarged or cystic, but never to a great extent. The Wolffian duct (Fig. 340) runs towards the body of the uterus in the mesosalpinx; it reaches the side of the uterus, but from that point onwards it disappears by the commencement of the 3rd month. Occasionally, however, remnants of the lower or distal part of the duct persist. They lie in the roof of the vagina. The point of termination of the duct is sometimes represented on the trigone of the vestibule a little distance from the side of the opening of the urethra. Only the upper part of the duct (mesosalpingeal part)

[1] J. Tandler, *Anat. Hefte*, 1905, vol. 28, p. 255 (Vestiges of Pronephros).

persists in women. The uterine and vaginal segments, if they persist, get the name of **duct of Gartner.** The **genital** tubules, those attached to or connected with the ovary, persist and form the **epoophoron,** Organ of Rosenmüller, or parovarium (Fig. 340). The **renal** Wolffian tubules—those which acted as renal structures in the embryo—also persist, sometimes unconnected with the duct. They lie between the

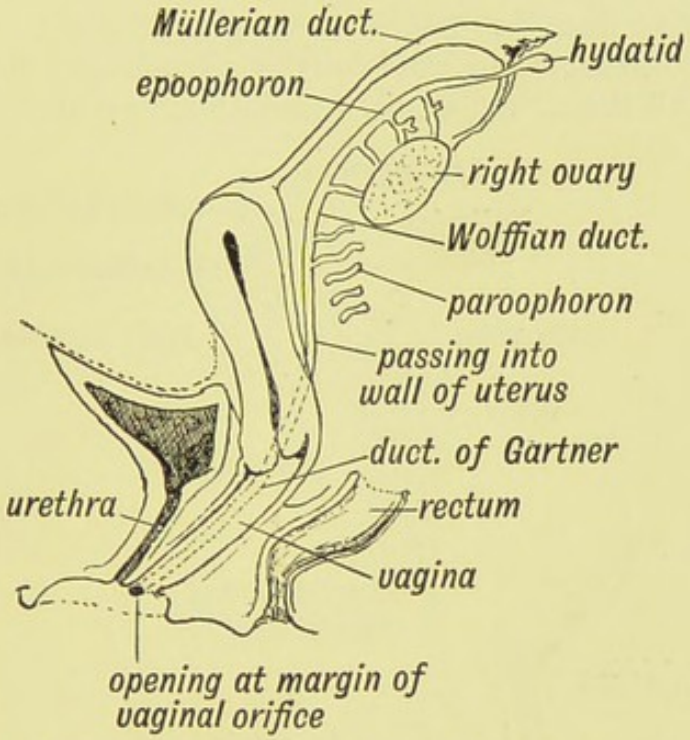


FIG. 340.—Remnants of the Wolffian Body in the Female (see also Fig. 342).

ovary and uterus and form the **paroophoron.** Fluid may collect in their cavities, and thus those vestiges may form large cysts.

2. In the **Male.**

In the male (Fig. 341) the Wolffian duct forms :

(1) The tube of the epididymis, which is coiled up in the globus major, body and globus minor of the epididymis ; [1]

(2) The vas deferens and common ejaculatory duct. The duct opens at each side of the uterus masculinus in the prostatic urethra, a site corresponding to the vestibule of the vagina in the female ;

(3) The vesiculae seminales arise from the Wolffian ducts as tubular diverticula at the end of the 3rd month ; the terminal part of the duct also becomes dilated to form an ampulla.

The stalked hydatid frequently seen on the upper extremity of the testicle corresponds to the hydatid at the fimbriated extremity of the Fallopian tube in the female, and is of similar origin (Figs. 340 and 341).

[1] J. C. Bremer, *Amer. Journ. Anat.* 1911, vol. 11, p. 393 (Dev. of Vasa Efferentia) ; Otto Petersen, *Anat. Hefte,* 1907, vol. 34, p. 239 (Dev. of Vesiculae Seminales).

The **genital tubules** of the Wolffian body become the vasa efferentia and coni vasculosi.

The **renal tubules** of the Wolffian body form :

(1) The vasa aberrantia found in the globus minor ;

(2) The paradidymis or organ of Geraldés situated in the cord above the globus major but not always present. The vas aberrans represents an elongated Wolffian tubule, which has effected a communication with the Wolffian duct, but not with the genital gland. The tubules of the paradidymis represent blind tubules, which retain the embryonic cystic form. All these tubules, both genital and renal of the Wolffian

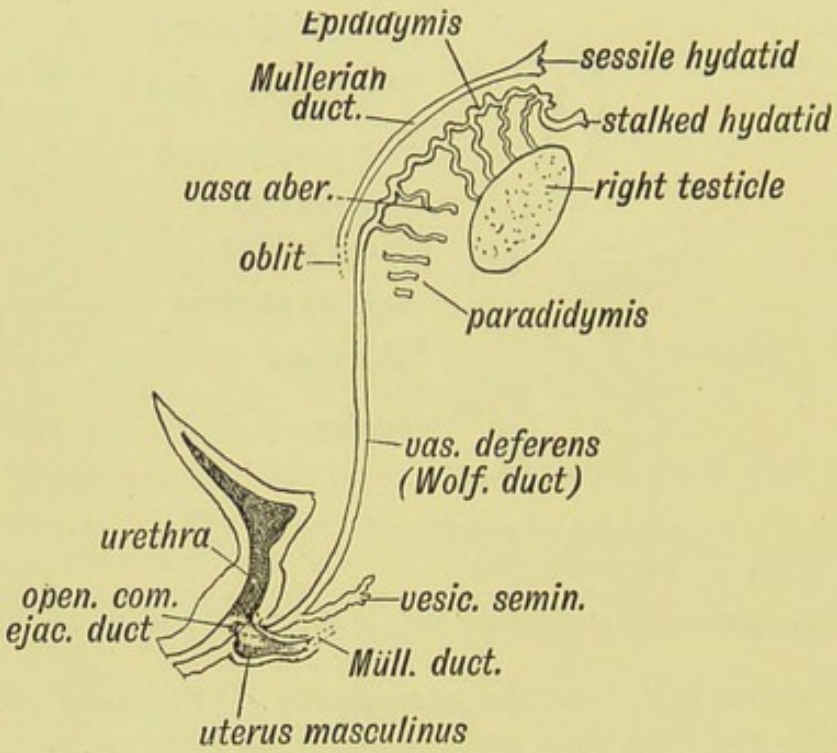


FIG. 341.—Remnant of the Wolffian Body in the Male (see also Fig. 342).

body, are situated originally in the mesentery of the Wolffian body (Fig. 339).

Thus it will be seen that while in the male the Wolffian tubules and duct become part of the genital system, in the female they become functionless and only of pathological importance. Their presence in the female is due to their being inherited from the male, just as the breasts in the male persist because of their utility in the female.

Rete Testis.—The junction between the genital tubules of the Wolffian body and the seminal tubules of the testes is effected by the development of a separate element to which the names of rete-cords or junctional cords have been given. In Fig. 342, *B*, is represented the origin of the junctional tubules, according to the account given by Dr. Allen.[1] The ovary and testis represent only the middle part of

[1] For a recent account see Bennet M. Allen, *Amer. Journ. of Anat.* 1905, vol. 5, p. 79.

the original genital ridge; the anterior and posterior parts become atrophied. In the anterior vestigial part of the ridge solid cords grow into the mesentery of the Wolffian body, and from these cords, as shown in Fig. 342, *B* (where only two cords are represented), is formed the rete testis. The rete testis effects communications with the seminal tubules by means of outgrowths, which form the vasa recti, and also with the glomerular or blind extremities of the genital tubules of the Wolffian body (Fig. 342, *C*). In the female the junctional cords are formed; vestiges usually remain. Frequently fimbriated hydatids are attached to them (Fig. 342, *A*). The majority of parovarian

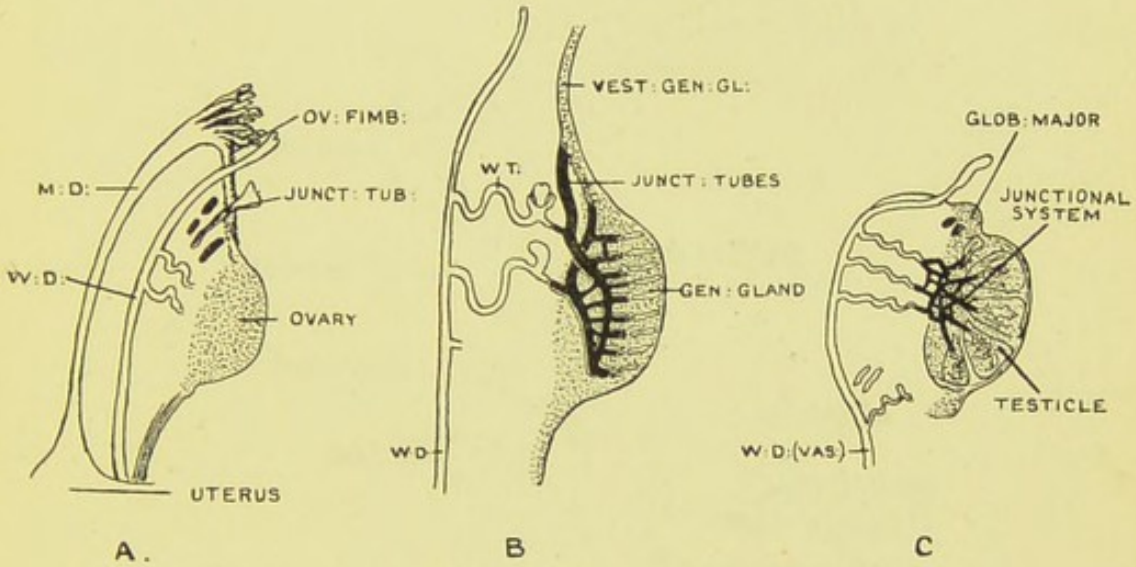


FIG. 342.—Diagrams showing the fate of the Junctional Cords in the Ovary and in the Testis. *A*, ovary and Fallopian tube, showing the rudiments of the junctional tubules in the ovario-fimbriate margin of the broad ligament; *B*, the origin of the junctional system, according to Bennet Allen; *C*, the junctional system of the testis. *M.D.* Müllerian duct; *W.D.* Wolffian duct; *W.T.* Wolffian tubules.

cysts[1] are formed from the junctional rudiments. Isolated vestiges may also be seen in the testicle between its upper pole and the globus major (Fig. 342, *C*). They also may give rise to cysts.

THE KIDNEY.

Origin of the Permanent Kidney.[2]—In Fishes and Amphibians the Wolffian body alone acts as a kidney. In Reptiles, Birds and Mammals the permanent or hind kidney appears, and supplants the Wolffian kidney. Like the Wolffian body the kidney arises by the combination of two elements which are developed separately—a duct or excretory

[1] For the pathological significance of this structure see Alban Doran, *Journ. of Obstetrics and Gynaec. of Brit. Empire*, Oct. 1910.

[2] G. C. Huber, *Amer. Journ. Anat.* 1905, vol. 4, Supplement (Dev. of Renal Tubules); A. F. Dixon, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 117 (Supernumerary Kidney); E. Muthmann, *Anat. Hefte*, 1907, vol. 52, p. 577 (Horse-shoe Kidney).

part, and a nephric or secretory part. The excretory part arises as an outgrowth from the hinder end of the Wolffian duct, and forms the ureter, the pelvis of the ureter and the collecting tubules, which compose the main part of the medullary pyramids of the kidney. The secretory part arises from the sacral segments of the intermediate cell mass at the hinder end of the Wolffian tissue ; it forms the cortex of the kidneys—the glomeruli, convoluted tubules and loops of Henle ; in short, the secretory substance of the kidney (Fig. 345). Already, at the beginning of the 4th week, the ureteric part of the kidney is apparent as a dilatation or slight evagination at the hinder end of the Wolffian duct, near the cloaca ; the nephric tissue is represented in

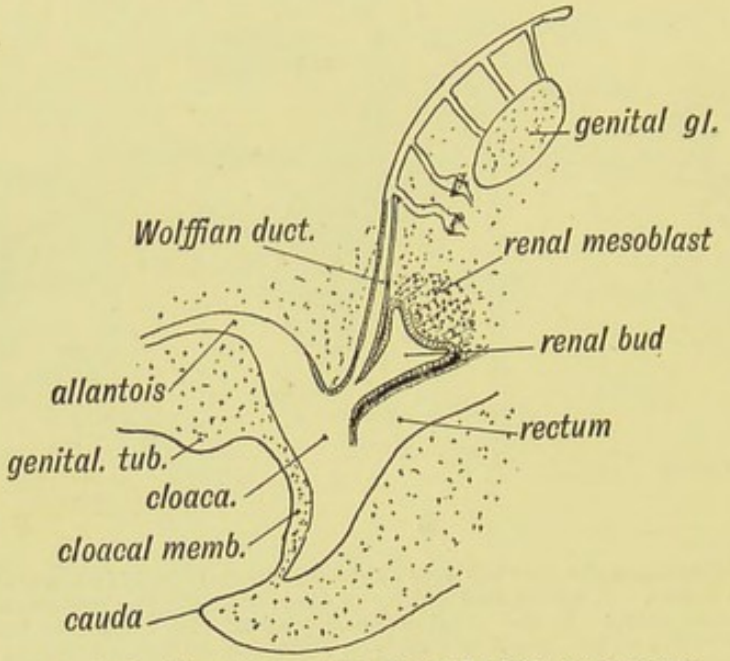


FIG. 343.—The Origin of the Renal Bud (diagrammatic).

the sacral region (Fig. 336). At the beginning of the 2nd month the ureteric bud grows out from the Wolffian duct, and presses against the nephric tissue in the sacral region (Fig. 343). By the end of the 2nd month the renal bud has ascended to the lower part of the lumbar region, passing behind—dorsal to—the Wolffian body ; the ureter and its pelvis and calyces can now be recognized (Fig. 344). They have arisen by the division and redivision of the growing end of the ureteric outgrowth. In the third month the process of outgrowth from the ureteric bud continues ; the growing end of each bud divides and redivides, and in this manner the collecting tubules of the pyramids are formed (Fig. 345, *C*). In Fig. 345, *A*, the growing extremity of such a collecting duct is represented. Near one of its terminal buds is represented one of the numerous tubule-rudiments, formed from the nephric tissue surrounding the ureteric outgrowth. Like a Wolffian tubule, it appears in a vesicular form. At one extremity it establishes a communication with the collecting tubule ; at the other a glomerulus develops

(Fig. 345, *B*). The tubule elongates, becomes convoluted, and quickly assumes the adult form represented in Fig. 345, *C*. Glomeruli appear at the commencement of the 3rd month; a capsule also becomes differentiated for the kidney from the surrounding mesoblastic tissue. Up to the time of birth, tubular and glomerular formation are seen in full activity within the subcapsular zone of the kidney. The deep tubules are the first to differentiate. Soon after birth the formation of new elements ceases; increase in size is then due to pure growth of

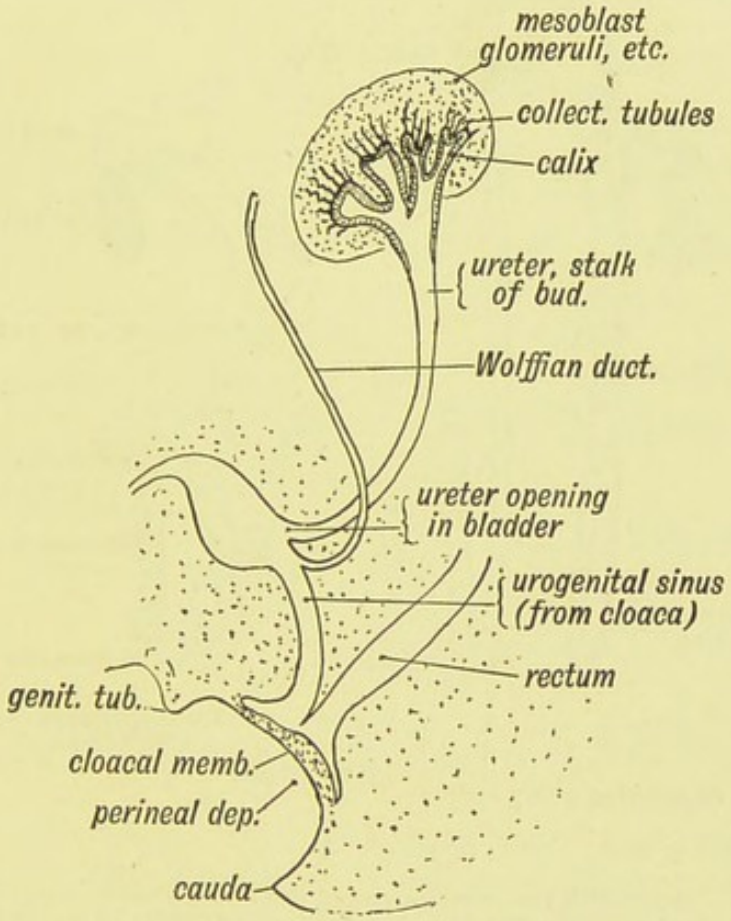


FIG. 344.—The Separation of the Wolffian Duct, Termination of the Ureter in the Bladder and Subdivision of the Renal Bud.

the parts already formed. In the 4th month the foetal kidney becomes lobulated, owing to the outgrowth of the collecting tubules being more active round certain centres. In the fissures between the lobules cortex is formed; soon after birth, as new cortical tissue is laid down, the depressions between the lobules are filled up. In many mammals (ox, bear, seal) the renal substance is broken up into numerous lobules.

The upper pole of the kidney reaches the 11th rib in the 5th month, and is then in juxtaposition with the supra-renal body, which is developed at the anterior end of the Wolffian body. As the kidney passes upwards, the Wolffian body is descending in connection with the genital glands. In the course of its ascent the kidney necessarily

alters its blood supply. It receives temporary branches from the common iliac artery and from the aorta, and also from the artery to the supra-renal body. Its definite artery is ultimately derived from the artery 2nd lumbar segment, but more than one frequently persist.

With the development of the lumbar and sacral regions of the body the ureter becomes elongated. The terminations of the ureter and Wolffian duct separate about the middle of the second month, and the

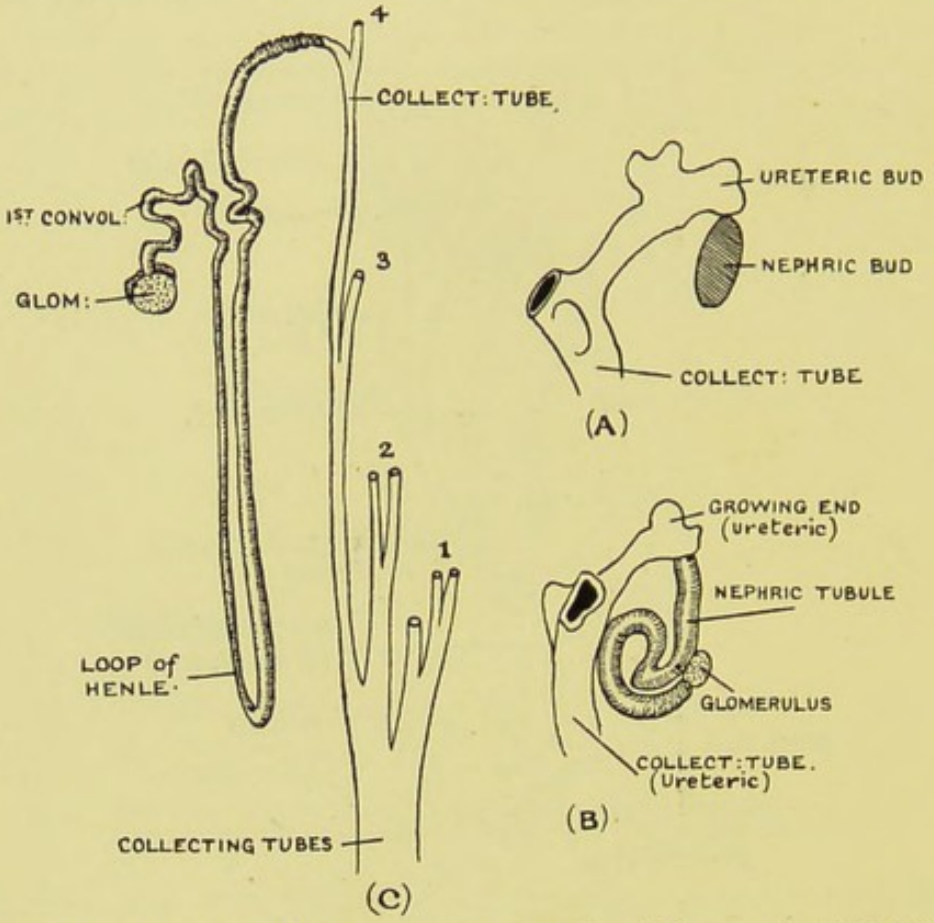


FIG. 345.—Illustrating the Development of the Renal Tissue. *A*, growing end of collecting tubule with bud of nephric tube attached to it; *B*, first stage in the development of a nephric bud into a nephric tubule; *C*, fully developed renal tubule; the part formed from the ureteric bud is represented in outline and the part from the nephric tubule is shaded. (After G. Carl Huber, *Amer. Journ. of Anat.* 1905, vol. 4, Special Supplement.)

part of the cloaca into which the ureters open forms the trigone of the bladder (Fig. 344).

As the kidney grows forwards its hilum at first looks towards the pubic region, and even when it has reached the lumbar region and the poles become upper and lower, the hilum of the kidney still looks towards the ventral wall of the abdomen. In the 4th and 5th month an anterior lip is formed to the hilum by the development of cortical tissue, and the hilum then assumes its normal form and position. The anterior lip is usually absent from **horseshoe kidneys**, in which the lower poles are united by a strand of renal tissue. In the sacral region

of the embryo the Wolffian or nephric ridges approach each other. In those cases where horseshoe kidneys are developed the nephric ridges were apparently fused at their hinder ends. Such kidneys are usually supplied with multiple arteries. The kidney may be arrested in its ascent—in the pelvis or in the lower lumbar region; it then derives its arteries from the iliac arteries or from the aorta. The ureteric bud may divide, and give rise to a forked ureter, or to double or even triple ureters. The nephric element may remain single, or it also may become divided, giving rise to two kidneys on one side.

THE MÜLLERIAN DUCTS.

The **Müllerian Ducts**[1] or **Oviducts** are present in almost all vertebrates, and convey the ova to the surface of the body. In fishes, amphibians, reptiles, birds and lower mammals (Marsupials) the ducts

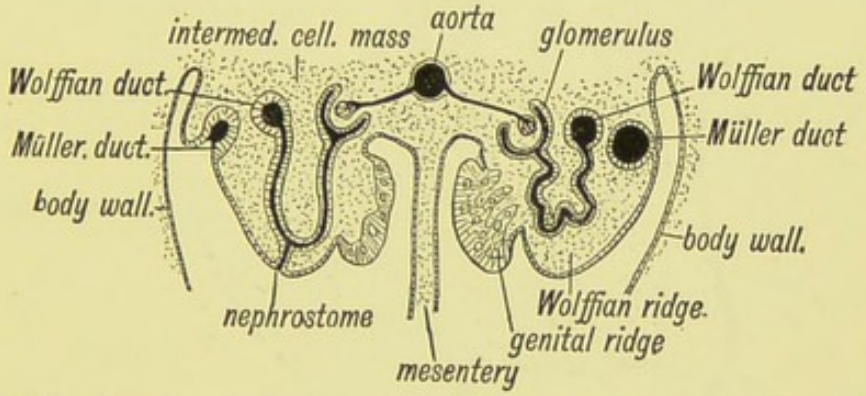


FIG. 346.—Diagrammatic Section across the Wolffian and Genital Ridges to show the Origin and Relations of the Müllerian Duct to the Duct and Tubules of the Wolffian Body. (After Pasteau.)

terminate in the cloaca. This is also the case in the embryonic stages of man and all higher mammals. The development of the duct in man is very simple (Fig. 346). It is developed on the outer surface of the Wolffian ridge, below (ventral to) the Wolffian duct, by a tubular invagination of the mesothelium of the coelom. The anterior (cephalic) end of the furrow-like invagination remains connected with the coelom and forms the ostium abdominale. It arises in a region of the coelom where many nephric tubules are invaginated, and it may represent the coelomic opening (nephrostome) of one of these tubes. Although the ostium is developed thus, the fimbriae which surround it are not formed until the 4th month, when they appear as outgrowths of the lining membrane of the tube. More than one ostium may be developed. As it passes backwards in the Wolffian ridge it lies below and internal to the Wolffian duct and comes in contact with the Müllerian duct of the opposite side in the pelvis (Fig. 348). The Müllerian duct is formed

[1] S. E. Wichmann, *Anat. Hefte*, 1912, vol. 45, p. 629 (Origin of Müller's Duct).

in the embryo later than the Wolffian duct; its posterior growing end does not reach the urogenital sinus until the 6th week, and it is nearly a month later before its lumen actually communicates with that of the sinus (Fig. 347). In fishes the Müllerian is derived from the Wolffian duct. They terminate between the openings of the Wolffian ducts in that part of the cloaca from which the trigone of the bladder is differentiated (Fig. 347). They are developed in the male as well as the female embryo.

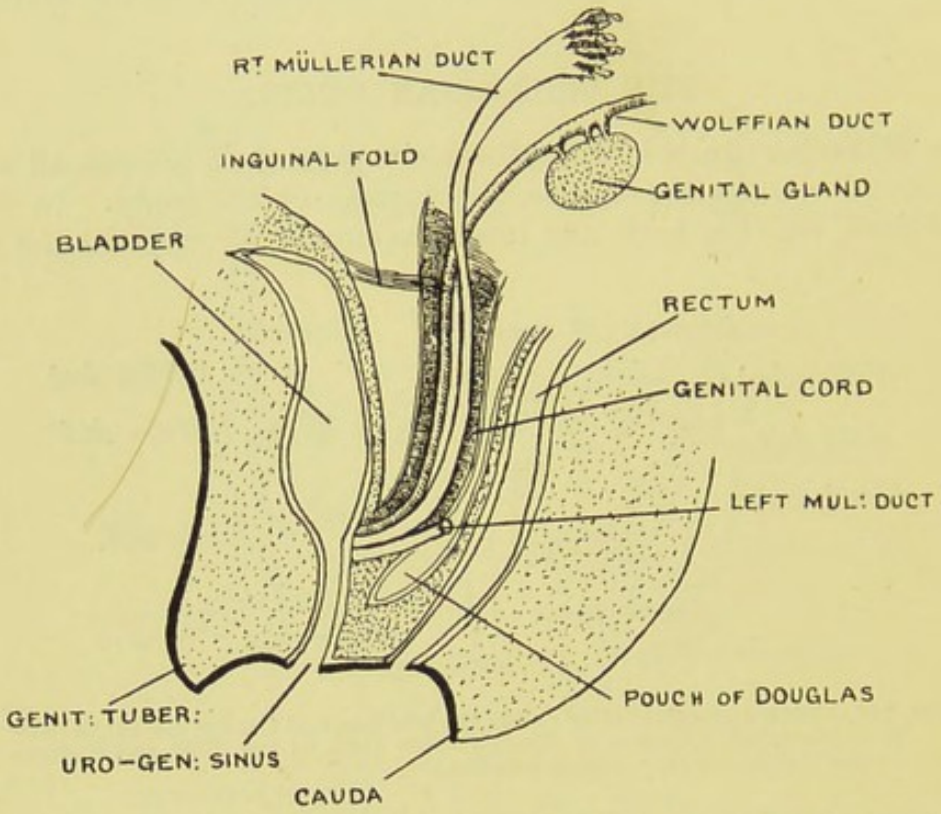


FIG. 347.—Diagram of the Genital Ducts at the commencement of the 3rd month of Foetal Life. Lateral view.

The Genital Cord.—During the 3rd month the Müllerian ducts show two distinct stages in their course:

(1) **Lumbar,** which lies in the Wolffian ridge and is suspended from the posterior abdominal wall by the Wolffian mesentery. This stage afterwards forms the Fallopian tube (Fig. 348).

(2) **A Pelvic stage,** where it lies in the genital cord. The posterior ends of the Wolffian ridges, with their contents, the Wolffian and Müllerian ducts fuse in the pelvis, and thus form the **genital cord.** With their fusion the peritoneal space of the pelvis is separated into a deep posterior part—the pouch of Douglas and a shallow anterior depression—the utero-vesical (Fig. 347). The parts of the Müllerian ducts within the cord form the uterus and vagina. The ureter is also developed within the mesoblastic tissue of the genital cord, but afterwards becomes separated from it.

The genital cord of the foetus at the second month shows the two Müllerian and two Wolffian ducts—in the male as well as in the female (Fig. 347).

The Round Ligament of the Uterus, which is apparent early in the 3rd month, is attached to the Müllerian duct on each side (Fig. 348). The point of attachment marks the junction of the uterine and Fallopian segments of the Müllerian ducts. The round ligament corresponds to the **gubernaculum testis** in the male and its development is similar. Both are developed in the following manner :

Part of the Wolffian ridge is continued backwards as a peritoneal fold to the groin, this part forming the **inguinal fold** (Fig. 348). Within

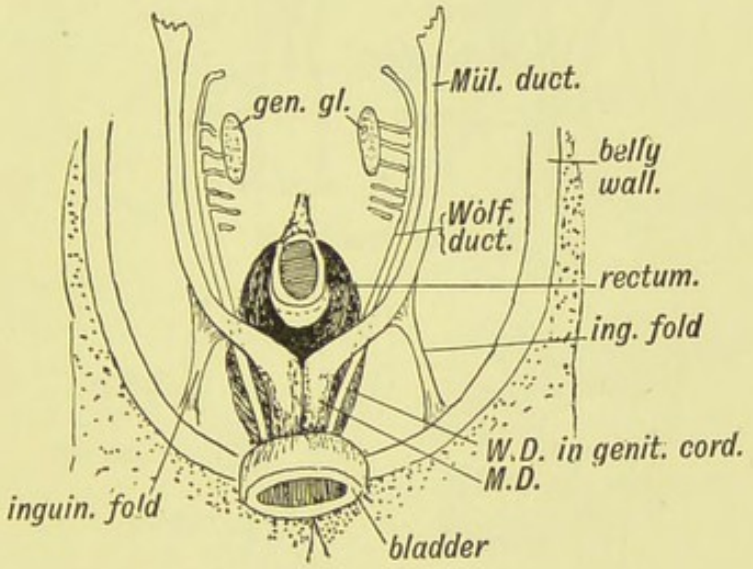


FIG. 348.—Diagram of the Müllerian Ducts at the commencement of the 3rd month. Ventral view.

the inguinal fold, in the mesenteries of the Wolffian body and genital gland and in the subperitoneal tissue of the genital cord a stratum of non-striated muscular tissue is developed. The mesoblastic tissue, in the lower end of the inguinal fold, begins to pierce the abdominal wall external to the deep epigastric artery in the 3rd month, the piercing force being obtained purely from the inertia of its own growth. The growing end, at first merely represented by fine strands of tissue, in later months increases in mass, and carries over it and in front of it, into the scrotum or labium majus, a process of the peritoneum and attenuated representatives of each stratum of the belly wall (Fig. 377, p. 385). The inguinal canal, the round ligament of the uterus and the gubernaculum testis are thus formed by the extension of the substance of the inguinal fold. From the same subperitoneal stratum of muscular tissue are formed the round ligament of the ovary, the muscular tissue in the utero-rectal (utero-sacral) ligaments and in the broad ligaments, and also the outer muscular coat of the uterus.

Formation of Uterus and Vagina.[1]—The parts of the Müllerian ducts lying side by side in the genital cord (Fig. 348) begin to unite in the 3rd month, and by their fusion the uterus and vagina are formed. In all the members of the vertebrate series below and including the Monotremes, the Müllerian ducts remain separate and open in the cloaca (Fig. 349, *A*). The process of fusion begins in the 3rd month.

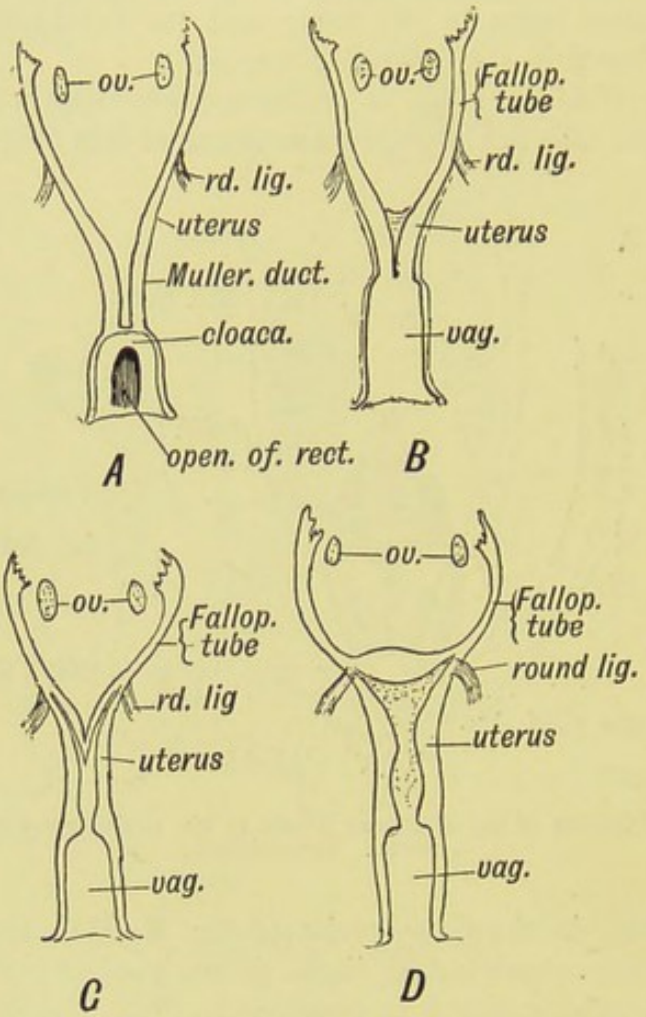


FIG. 349.—Evolution of the Human Form of Uterus.

A, form seen in lowest mammals, reptiles, amphibians, fishes, and in the 2nd month human foetus; *B*, form of Müllerian ducts in rodents; *C*, form in carnivora, etc., and in the 4th month human foetus; *D*, form found in man and higher primates.

The septum formed by the fused mesial walls (Fig. 350) disappears first below the region of the uterine cervix; the process may be arrested at this stage—a stage shown by some adult marsupials. Next, the lower or cervical part of the septum disappears; the human uterus then (3½ months) resembles that of higher mammals (carnivora, etc., Fig. 349, *C*). It may be arrested at this stage (uterus bicornis). Lastly the upper part of the septum disappears (4½ months, Fig. 350). The

[1] H. R. Clarke, *Journ. Obstet. and Gynaec.* 1911, Sept., p. 85 (Origin of Musculature).

fundus, which is the last part to be developed and is only found in the highest primates, is quite well marked in the child at birth.

The musculature appears in the wall of the uterus, vagina and tubes during the 4th month, the inner or circular layer appearing before the outer or longitudinal. Sometimes after birth additions are made to the musculature of the uterus, and the distinction between the two primary layers becomes obliterated. The cervix of the uterus is differentiated from the vagina during the 4th month. At the same date of foetal life the ovarian extremity of the Fallopian tube becomes widened and trumpet-shaped ; the mucous membrane within it becomes

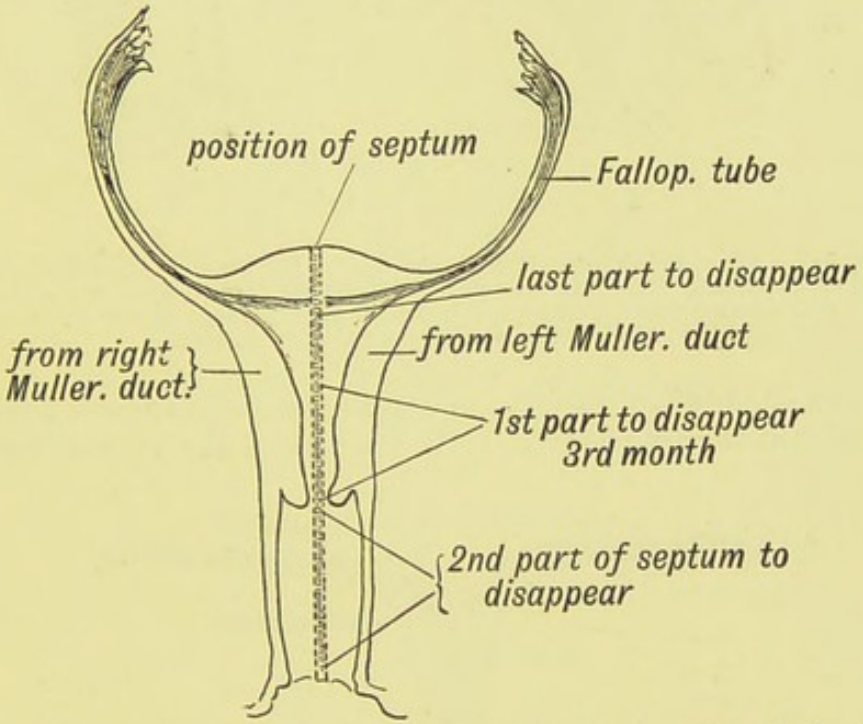


FIG. 350.—Showing the manner in which the Müllerian Ducts fuse to form the Uterus and Vagina.

plicated. The fimbriae are then formed by the extremities of the plicae growing out at the ostium abdominale. Secondary or accessory ostia may also be produced.

Metamorphosis of the Vagina.—About the middle of the 3rd month the lower ends of the Müllerian ducts of the human embryo undergo a remarkable metamorphosis, first fully described by Berry Hart and lately reinvestigated by F. Wood Jones.[1] The mesoblastic tissue in the lower end of the genital cord, which surrounds the terminal segments of the Müllerian and Wolffian ducts, undergoes a rapid growth, pushing downwards that part of the cloaca in which they end—the urogenital sinus (Figs. 351, 352). The epithelial lining of the Müllerian ducts form solid cords lying side by side, with arrow-shaped tips (Fig. 352). The **vaginal cords** proliferate into the tissue of the genital cord

[1] *Brit. Med. Journ.* 1904, Dec. 17th.

and fuse together, the vagina being formed by the breaking down of their epithelial core. **Atresia** of the vagina results from a failure of

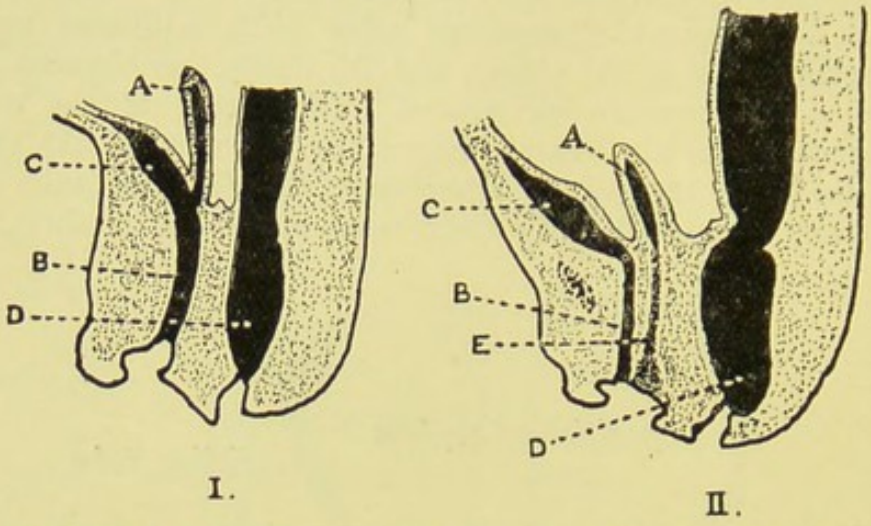


FIG. 351.—Diagrams showing the Termination of the Vagina about the seventh week (I.) and about the thirteenth week (II.). (After Dr. F. Wood Jones.) *A*, Müllerian ducts (vagina and uterus); *B*, urogenital sinus; *C*, bladder; *D*, rectum; *E*, vagina represented by a rod of epithelium.

the process of canaliculization. Septa in the vagina result from incomplete fusion of the two cords. Only the tips of the vaginal cords reach

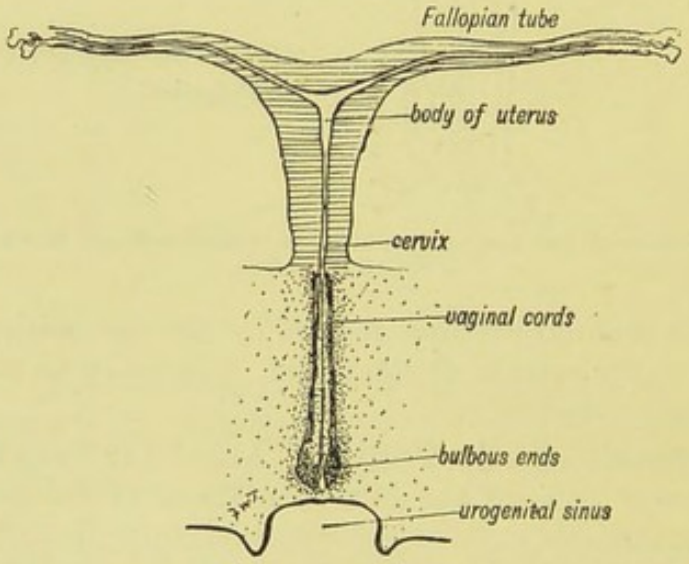


FIG. 352.—Diagram illustrating the manner in which the Vagina is formed by the Fusion of two solid Processes or Cords. (F. Wood Jones.) Berry Hart regards these cords as derived, not from the Müllerian, but from the Wolffian ducts.

the uro-genital sinus; hence a partial septum—**the hymen** [1]—marks the opening of the vagina into the uro-genital sinus. The extent to

[1] For recent papers on development of hymen: D. Berry Hart, *Edin. Med. Journ.* 1911, June; F. S. Taussig, *Amer. Journ. Anat.* 1908, vol. 8, p. 89.

which the terminal septum breaks down varies widely; hence the numerous forms assumed by the hymen.

An explanation of this remarkable change may be found in the formation of a new vagina in lower marsupials which was discovered by J. P. Hill.[1]

In lower marsupials the vaginal segment of the Müllerian ducts are separable into two parts—upper, which lie side by side, and reach towards the cloaca (Fig. 353); lower, which form lateral loops before terminating in the cloaca. Hill found that the young were born by passing from the upper or median segments into the cloaca by the formation of a new passage (Fig. 353). In higher marsupials he found

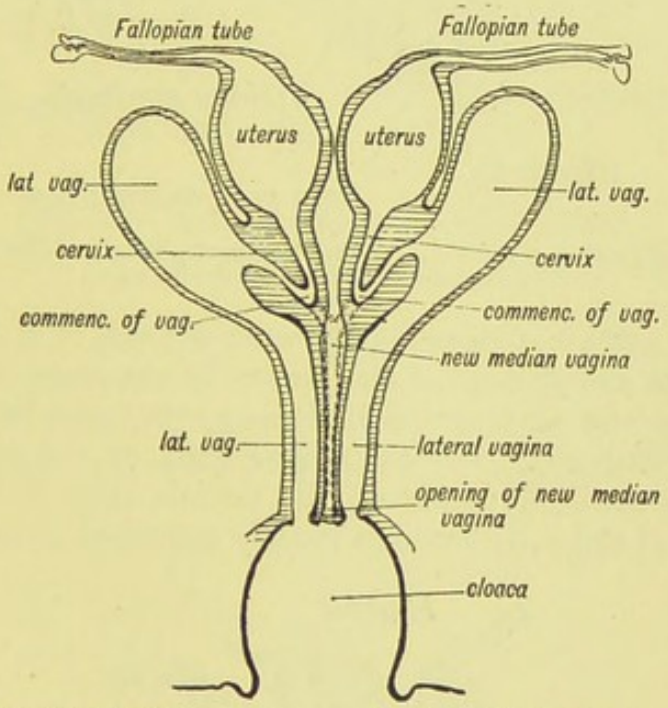


FIG. 353.—Diagram showing the arrangement of the Müllerian Duct in a Marsupial Mammal and the manner in which a New Vagina is formed for the Passage of the Young at Birth. (F. Wood Jones after J. P. Hill.)

that the upper parts of the vaginal segments became fused to form a median vagina, and that the new passage to the cloaca was not temporary as in lower marsupials, but permanent. In monotremes, the Müllerian ducts have to serve only for the passage of unhatched ova, but with the evolution of gestation in the marsupials the ducts, which could convey ova, were unfitted for the transmission of young, and a new passage or median vagina was formed. The evidence is conclusive that there was a cloacal phase in human evolution, and the metamorphosis which takes place in the lower ends of the Müllerian ducts of the human embryo is evidently an abbreviated recapitulation of the formation of the median vagina of marsupials.

[1] *Proc. Linnean Soc. New South Wales*, 1899, March 29th, p. 42; 1900, Aug. 29th, p. 519.

The Müllerian Ducts in the Male.—In the male foetus of the 3rd month the Müllerian ducts are undergoing atrophy, the distinction between the testis and ovary being quite marked by that time, and the process of sexual differentiation already to be seen on close examination. All that remain of the Müllerian ducts in the adult male are their fused terminal segments forming the sinus pocularis or uterus masculinus in the prostate (Figs. 341 and 354). Its depth is commonly

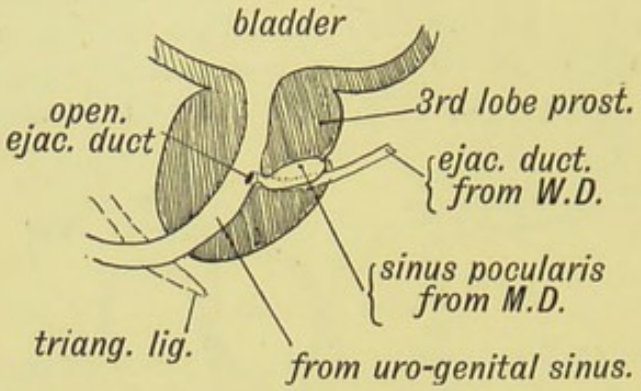


FIG. 354.—A Section of the Prostate showing the Remnants of the Lower Ends of the Müllerian Ducts in the Male.

about 3 or 4 mm., but occasionally such a form as is represented in Fig. 355 occurs and shows the real nature of the sinus pocularis. The vagina, uterus and part of the Fallopian tubes can be recognized in such cases (Primrose). The fimbriated ends of the Müllerian ducts persist as the sessile hydatids on the testicle (Fig. 341). The intermediate part of the tube becomes greatly stretched during the descent

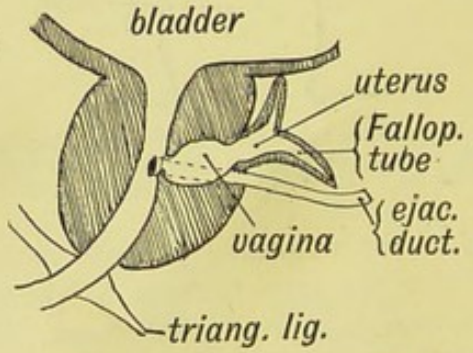


FIG. 355.—A Section of a Prostate showing an unusually developed Uterus Masculinus. (After Primrose.)

of the testicle and disappears, but a remnant of its upper end can be found in the sharp anterior border of the epididymis until quite a late period in foetal life (J. H. Watson [1]). The mesosalpinx shrinks and completely disappears in the anterior border of the epididymis.

The Urogenital Sinus or Canal.—The Müllerian ducts open into the cloaca of the embryo side by side, between and below the openings

[1] *Journal of Anat. and Physiol.* 1902, vol. 36, p. 147.

of the Wolffian ducts (Fig. 347). That part of the cloaca which serves as a common channel for bladder, Müllerian and Wolffian ducts is the urogenital sinus (Figs. 359, *A* and *B*). In the female foetus at the

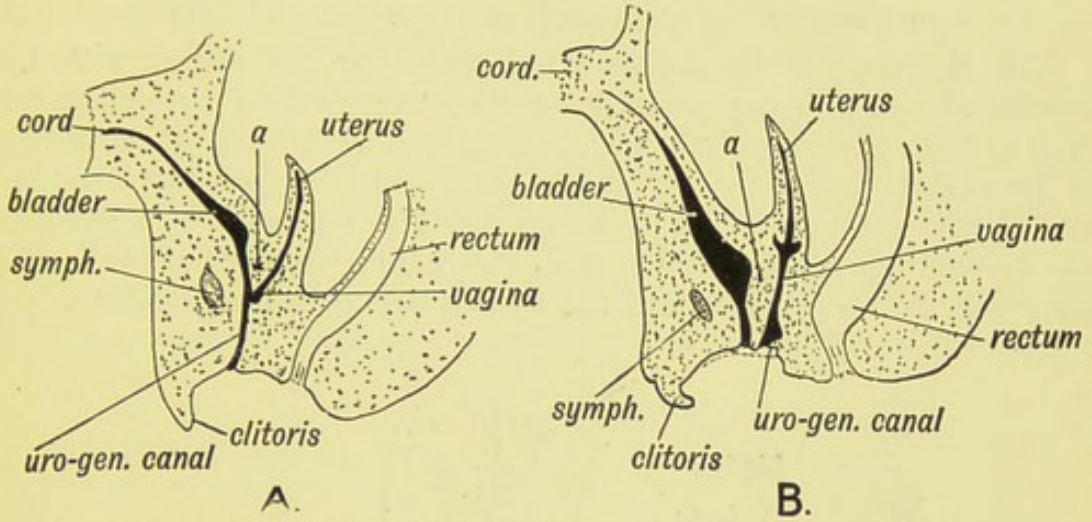


FIG. 356.—Section showing the Urogenital Sinus.
A, in the 3rd month female human foetus; *B*, in the 5th month female human foetus; *a*, the vesico-vaginal septum.

3rd month it is still well marked (Fig. 356, *A*). In all mammals except man it retains this form. By the beginning of the 6th month in the female foetus (Fig. 356, *B*) it will be seen that the urogenital sinus has become shortened and opened out to form the floor of the pudendal

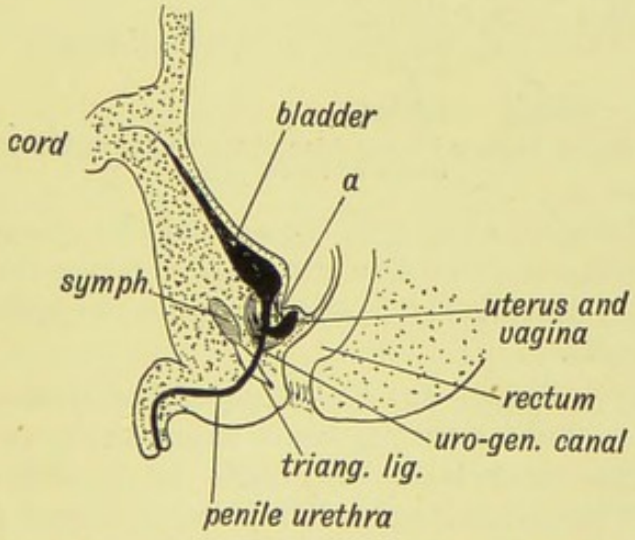


FIG. 357.—Section showing the Urogenital Sinus in the Male Foetus.
a indicates the part corresponding to the vesico-vaginal septum of the female. It is occupied by the 3rd lobe of the prostate.

cleft from the glans clitoris in front to the fossa navicularis behind, and thus the end of the Müllerian ducts (vagina) and urethra come to open separately. The metamorphosis in the genital cord which leads to the formation of the vagina plays a large part in the transformation

(Fig. 351). In the male (Fig. 357) the early foetal form is retained, and the urogenital sinus becomes that part of the male urethra between the sinus pocularis and the fossa navicularis in the glans penis. The female urethra corresponds to the prostatic part above the opening of the sinus pocularis of the male urethra (Figs. 356 and 357).

The Hymen[1] is formed at the junction of the vagina with the urogenital sinus, being covered on its outer surface by epithelium derived from the urogenital sinus, and on its deep surface by epithelium of the vaginal cord. Usually at one point on the hymen, but occasionally at more, the epithelial coverings fuse and break down, leading to one or more perforations. On the other hand, the vaginal cords may not reach the urogenital sinus, the hymen being then imperforate. In

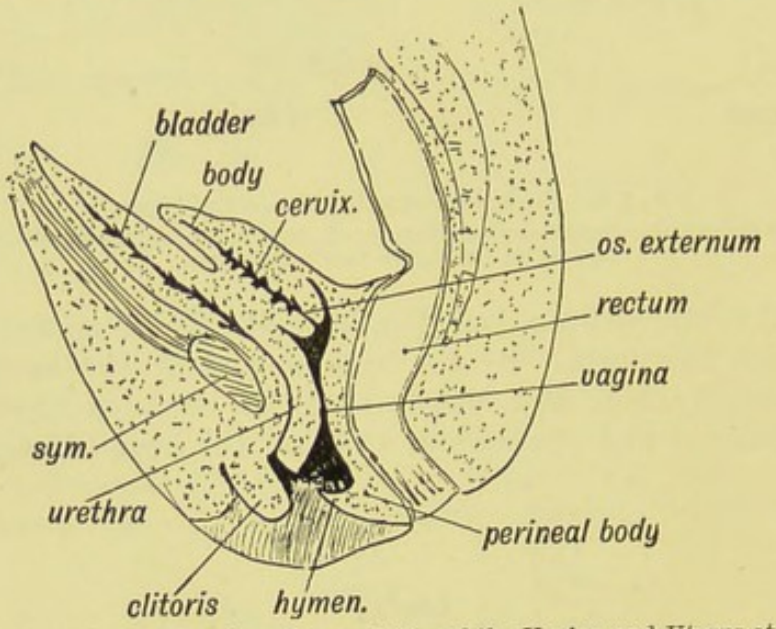


FIG. 358.—A Section to show the condition of the Vagina and Uterus at the 7th month of Foetal Life.

reptiles, as in the human embryo, the part of the urogenital sinus into which the Müllerian and Wolffian ducts open, forms the trigone of the bladder. In such animals the hymen prevents the reflux of urine into the Müllerian ducts.

The Uterus is formed by the fusion of the Müllerian ducts; its muscular walls and thickened mucous lining begin to appear in the 4th month. The outer layer of muscle is derived from the sub-peritoneal layer mentioned on p. 359; it developed at a later date than the inner circular coat. By the 7th month (Fig. 358) the foetal uterus is divided into two parts, the cervix or lower segment and body or upper segment. The lower segment or cervix forms then two-thirds of the uterus; its walls are thick and its upper part is lined by columnar non-ciliated epithelium, containing racemous mucous glands. Its mucous membrane is arranged in palmate folds. The

[1] See references, p. 360.

upper or uterine segment proper composes only a third of the uterus. It is lined by columnar epithelium, which becomes ciliated at the end of foetal life. Uterine glands are developed in it after birth between the 1st and 7th years. At puberty the body of the uterus, instead of being half the size of the foetal cervix, becomes larger than it. The cervix takes no part in menstruation nor in containing the foetus; its true function is unknown. The external os is formed at the junction of the vaginal cords with the uterine segment of the Müllerian ducts; it becomes demarcated at the end of the 4th month. For some time after birth the body of the uterus actually undergoes a reduction in size (Bayer); growth does not become marked until the 7th year.

The Cloaca of the Embryo.[1]—Having thus traced the origin and fate of the genital ducts, it is now necessary to follow the changes which

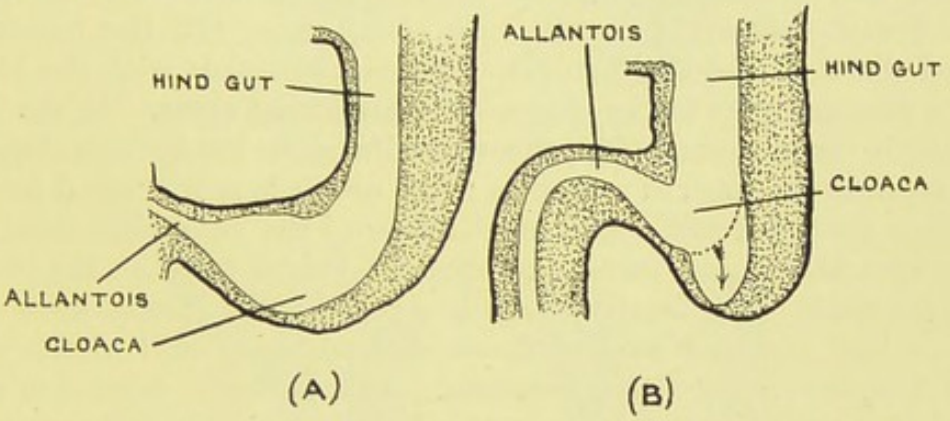


FIG. 359.—The Formation of the Cloaca from the Hind-gut during the 3rd week. (F. Wood Jones.) *A*, section of the posterior end of a human embryo early in the 3rd week; *B*, later in the 3rd week when the hind fold is more produced and the cloaca assuming its triangular form.

are undergone by the cloaca—the common vent for the rectum and genital passages. We have already seen that the cloaca appears early in the 3rd week (Fig. 236, p. 249); its precocious origin being undoubtedly due to the fact that it gives origin to the allantois, by means of which the chorionic circulation is established. Thus in the 3rd week (Fig. 362, *A*) the cloaca forms a relatively large cavity, into which open the rectum and allantois, while the Wolffian duct is also establishing a communication with its more ventral part. At this time the outline of the cloaca, as seen on making a median section of the embryo, is triangular in outline; its dorsal wall follows the curve of the notochord to the point of the tail; a large part of its ventral wall is formed by the cloacal membrane—which is composed of only the two primitive layers—the hypoblast or entoderm which lines the cloaca, and the epiblast or ectoderm which covers the embryo. It will be remembered (see p. 31) that the hinder end of the embryonic body is produced on each side of the primitive streak. Apparently the cloacal membrane occupies the site of a part of the primitive streak, thrust into a ventral

[1] A. G. Pohlmann, *Amer. Journ. Anat.* 1911, vol. 12, p. 1 (Dev. of Cloaca).

position by the outgrowth of the tail (Fig. 259). The hinder apex of the cloaca extends beneath the tail and behind the cloacal membrane and forms that transitory structure known as the **tail gut**. In the 3rd week the cloaca has no perineal opening ; that opening is first established near the end of the 2nd month by an absorption of the cloacal membrane.

Evolution of Cloacal Structures.—To understand the significance of the changes undergone by the cloaca in the human embryo, one must have first a clear conception of the various evolutionary stages known to the comparative anatomist. We have already seen that some of these changes are related to the differentiation of an external penis (p. 343) ; it is now necessary to see how the cloaca becomes modified to assume its mammalian and human form. The essential stages are represented in Fig. 360 ; in the frog (*A*) the cloaca receives the bladder, rectum and Wolffian duct, the duct opening distal to—nearer the cloacal vent—than the rectum. In the tortoise (*B*) the rectum has passed distal to the Wolffian duct, which now opens with the bladder into a common part of the cloaca—the **urogenital sinus.** In the lowest mammals—monotremes (*C*)—the urogenital sinus has become elongated, and assumes the form of a urethra ; the ureter is now severed from the Wolffian duct, but still opens on the floor of the urogenital sinus ; the urine thus has to pass across the urogenital sinus to reach the bladder. In marsupials (*D*) a further stage is reached ; the cloacal anus of the rectum has migrated backwards on the posterior wall of the cloaca until it almost reaches the perineum. This posterior migration of the rectal opening (anus) is already seen in Echidna (*C*), where the urogenital sinus—which represents the proximal part of the cloaca—has already assumed a considerable length. Thus in the evolution of mammals we see that the rectum migrates backwards until its vent or anus almost reaches the surface of the perineum, leaving the greater part of the cloaca as the urogenital sinus.

Ectodermal Cloaca.—The forms of cloaca depicted in Fig. 360 are not entirely derived from the gut or entodermal cloaca, which is seen in the human embryo. The terminal or superficial part is derived from a **cloacal depression** or pit formed on the perineum, and lined by epithelium derived from the ectoderm. The glans of the penis and also of the clitoris are formed in the ectodermal part : the rest of the penis and clitoris is developed in the entodermal part (Fig. 337). We have already seen how the urethral groove on cloacal penis becomes closed off as a separate channel by the union of two **lateral perineal folds**, thus forming a penile urethra. In Echidna (Fig. 337, *B*) one sees that the urethra is made up of two parts—an upper derived from the urogenital sinus, and a lower or penile from the channel enclosed by the lateral perineal folds. These two parts of the urethra are still separated by the communication between urogenital sinus and rectum (recto-urethral passage) (Fig. 337, *C*). In marsupials the primary urethra (urogenital sinus) and secondary or penile urethra have united

by the closure of the recto-urethral passage, and thus the cloaca is separated into two passages—the urogenital in front, the rectal behind. The actual step which brings about the separation is the formation

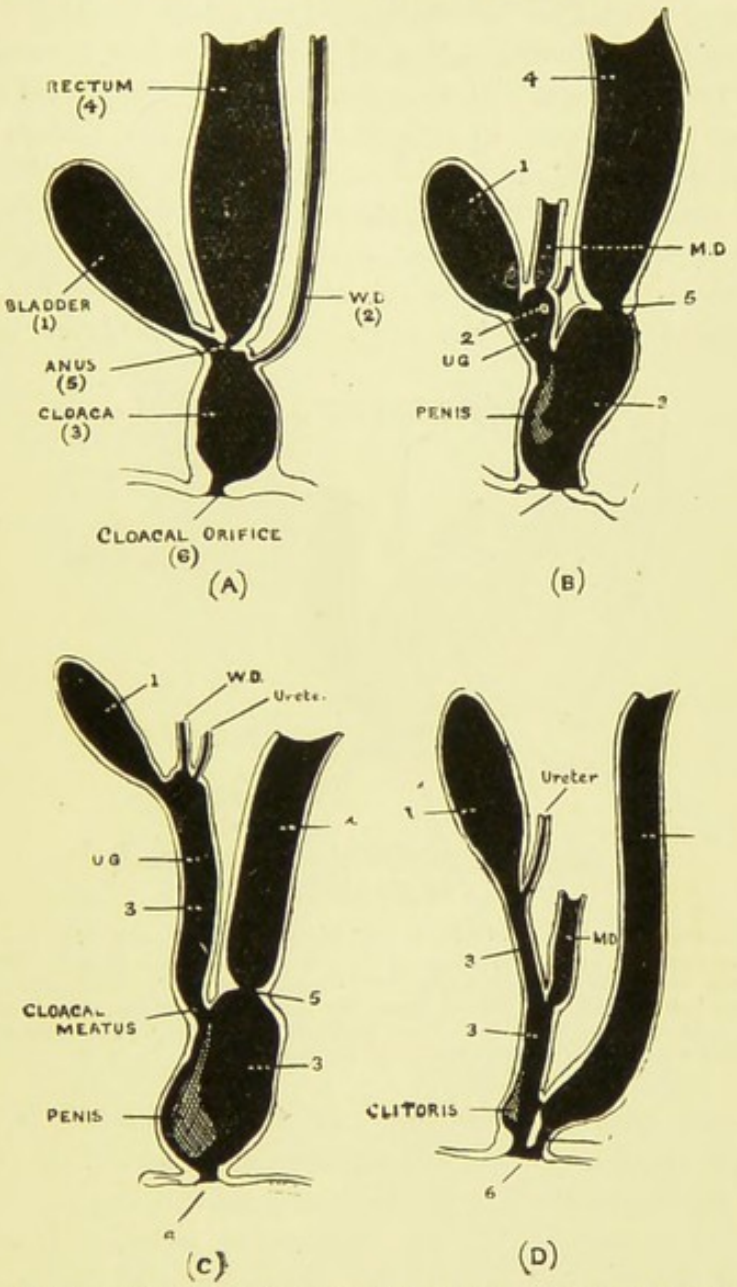


FIG. 360.—Diagrams to show the manner in which the Cloaca is modified and the Termination of the Rectum transferred from the Cloaca to the Perineum in Higher Vertebrates. *A*, the amphibian form; 1, bladder; 2, Wolffian duct (ureter and vas); 3, cloaca; 4, rectum; 5, intra-cloacal anus; 6, cloacal orifice; *M.D.*, Müllerian duct; *B*, form found in the tortoise; *C*, form in monotremes; *D*, form found in female marsupial; *X*, floor of urethra.

in the cloaca (entodermal) of a urethra. We shall see that the recto-urethral communication[1] seen in the cloaca of Echidna is one of the commoner of abnormalities in the human body (Fig. 361).

[1] On developmental grounds Dr. Wood Jones gives a different interpretation. He regards the recto-urethral opening as the former termination of the rectum (cloacal anus); the terminal part of the rectum he regards as a backward growth from the primitive rectum (*Brit. Med. Journ.* 1904, Dec. 14th).

Differentiation of the Human Cloaca.—We are now in a position to interpret the changes which occur in the human cloaca during the 1st and 2nd months (Fig. 362, *A*, *B*, *C*, *D*). In the 3rd week (*A*) the rectum ends proximal to the Wolffian duct as in the frog (Fig. 360, *A*); in the 5th week the cloacal orifice of the rectum has moved backwards, leaving the proximal part of the cloaca as the urogenital sinus, a condition similar to that seen in Echidna (Fig. 360, *C*). As in that animal, the Wolffian ducts and ureters open close together in the sinus. The appearance presented by the backward migration of the rectum is exactly the same as if the cloaca had been divided into rectal and urogenital cavities by the septum marked "*A*" in Fig. 362, *B*, *C*. It is convenient to apply the term given by Retterer to this septal

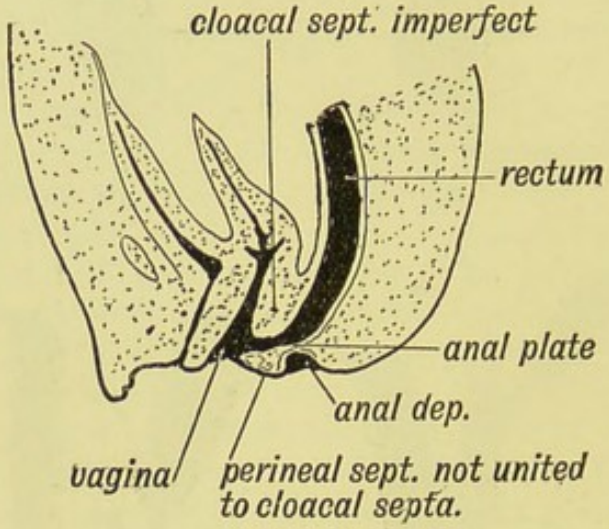


FIG. 361.—Case of a Female Child in which the Rectum opened on the Vestibule while the Normal Anus remains closed by the Anal Plate. The opening on the vestibule represents the recto-urethral opening. The perineal septum below the opening is formed from the union of the lateral perineal folds; the part marked cloacal septum represents the septum between the urogenital sinus and rectum (urorectal septum).

formation—the **urorectal septum.** In the 6th week (*C*) the orifice of the rectum reaches the cloacal depression (ectodermal cloaca) on the perineum; the lower border of the urorectal septum meets the cloacal membrane, thus separating the urogenital passage from the rectal passage. In the 5th and 6th weeks the urogenital cloaca sends a prolongation into the genital eminence situated at the pubic fornix of the perineal depression. The cloacal membrane on the floor of this penile extension of the cloaca breaks down, and the urogenital sinus opens on the perineum (6th week). The groove then seen in the roof of the terminal part of the urogenital passage corresponds to the penile groove of the tortoise. Towards the end of the 2nd month (Fig. 362, *D*) a perineal fold or septum is formed by an outgrowth on each side of the perineal depression—outgrowths which clearly correspond to the lateral perineal folds which enclosed the penile urethra in the cloaca of Echidna. The perineal folds, as they appear, become united with

the lower margin of the urorectal septum, and thus the urogenital passage is separated from the rectal (Fig. 363). Occasionally the union of the perineal and urorectal septa is not complete, a urorectal passage marking the site of their imperfect union (see Figs. 361, 364). It will

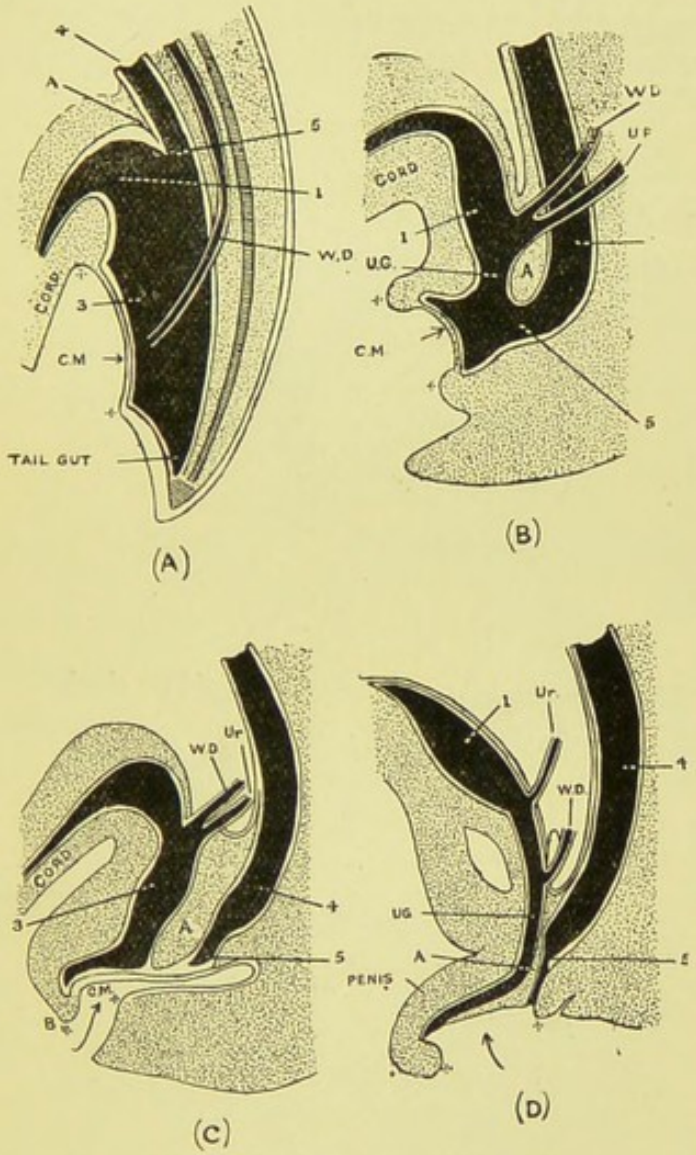


FIG. 362.—Showing the manner in which the Rectum becomes separated from the Urogenital Sinus (entodermal cloaca) during development of the Human Embryo. *A*, From human embryo, 4 mm. long (about twenty days); after Keibel. *B*, From human embryo, 11 mm. long (about thirty-five days); after Keibel. *C* and *D*, Later stages of development; 1, bladder; 2, Wolffian duct (ureter and vas); 3, entodermal cloaca; 4, rectum; 5, anus; *C.M.*, cloacal membrane; *U.G.* urogenital sinus; *A*, mesoblast at junction of rectum and entodermal cloaca; *B*, penis; *XX*, the limits of the perineal depression (ectodermal cloaca).

thus be seen that in the human embryo the rectal orifice migrates backwards until it opens in the posterior part of the perineal depression (ectodermal cloaca), leaving the whole of the entodermal cloaca of the embryo as a urogenital passage or urethra. All those changes take place in the space of the 2nd month.

Malformations of the Rectum and Anus.—When the rectum reaches the perineal depression, it is in contact with and closed by the cloacal membrane (Fig. 362, *C*). The growth of the perineal septum separates the posterior or anal part of the cloacal membrane from the anterior or urogenital part (Fig. 363, *B*). The posterior part of the membrane proliferates, and forms the anal plug. The plug breaks down at the commencement of the 3rd month, and the permanent anus is thus

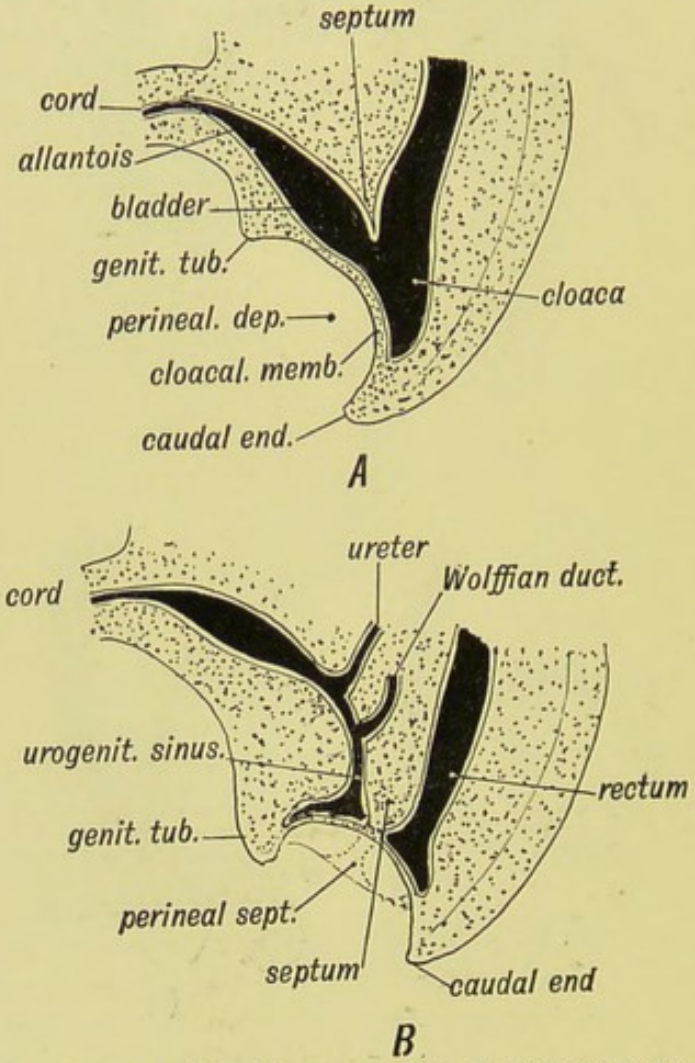


FIG. 363.—*A*, Diagram of the Cloaca and Perineal Depression of an Embryo at the 3rd week. *B*, Illustrating the manner in which the formation of the Perineal Septum separates the Urogenital Passage. The urorectal septum is indicated merely by "septum."

formed. The plug may become invaded by mesoblast, become persistent and give rise to the condition of **imperforate anus.** It is tissue from the perineal septum which probably invades the plug, for in many cases of imperforate anus the urorectal passage is present, showing that the perineal septa had developed abnormally and failed to effect a union with the urorectal septum. In Fig. 364 is shown such a case. The rectum terminates in the prostatic part of the urethra by a small urorectal aperture. In this case the backward migration of the rectum

to reach the perineum has been arrested at a stage seen early in the 2nd month. It opens at the upper margin of the parts formed in the perineal septum. The anal depression—representing the posterior part

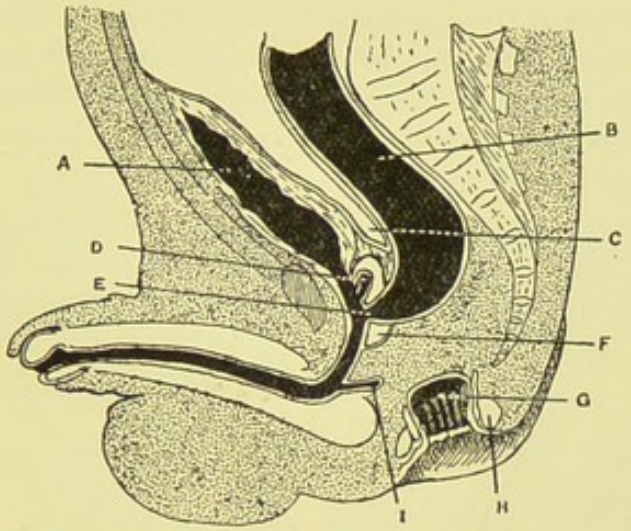


FIG. 364.—Section of Pelvis of a Male Child, showing the Rectum communicating with the Prostatic Part of the Urethra by means of the Urorectal Aperture. *A*, bladder; *B*, rectum; *C*, recto-vesical pouch; *D*, uterus masculinus; *E*, intra-cloacal anus; *F*, prostate; *G*, proctodaeum (ectodermal); *H*, external and internal sphincters; *I*, Cowper's gland.

of the ectodermal cloaca—has been duly developed. In Fig. 365 an exactly similar condition is represented in a female infant. The rectum opens in the male below the orifice of the uterus masculinus, in the

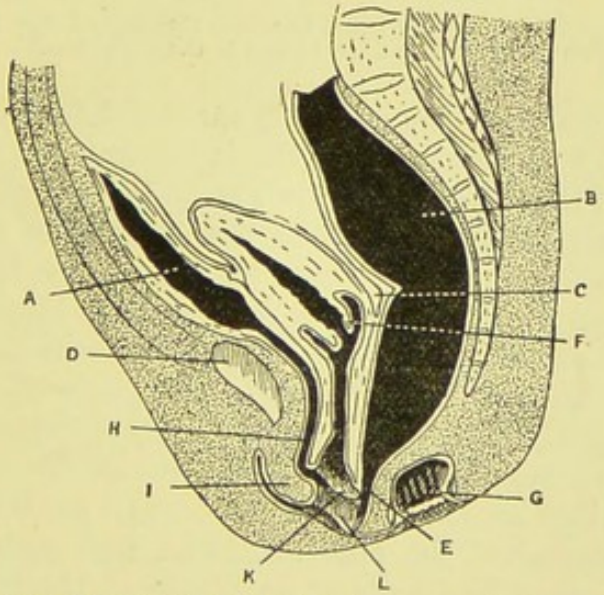


FIG. 365.—Section of Pelvis of Female Infant, showing the Rectum opening into the Navicular Fossa of the Vulva by means of the Urorectal Passage. *A*, bladder; *B*, rectum; *C*, recto-uterine fold; *D*, symphysis; *E*, vulval anus; *F*, cervix; *G*, proctodaeum (rarely present if rectum opens in vulva); *H*, urethra; *I*, clitoris; *K*, hymen.

female at a corresponding point below the orifice of the vagina. The perineal septum in the female forms merely the perineal body, which

separates the terminal part of the rectum from the vulva ; in the male it forms the floor of the urethra and perineum from the sinus pocularis to the lacuna magna in the glans penis. The terminal part of the male urethra, as we shall see presently, has a separate origin. The downward migration of the vaginal orifice in women brings the abnormal urorectal communication into the vulva—the vulva being a derivative of the urogenital sinus. In many cases of imperforate anus (Fig. 366) the urorectal passage is closed, and the rectum terminates an inch or more from the anal depression.

External Genital Organs and Perineum.—That the interpretation just given of the embryological parts entering into the formation of the rectum and urethra is right is seen when the development of the external

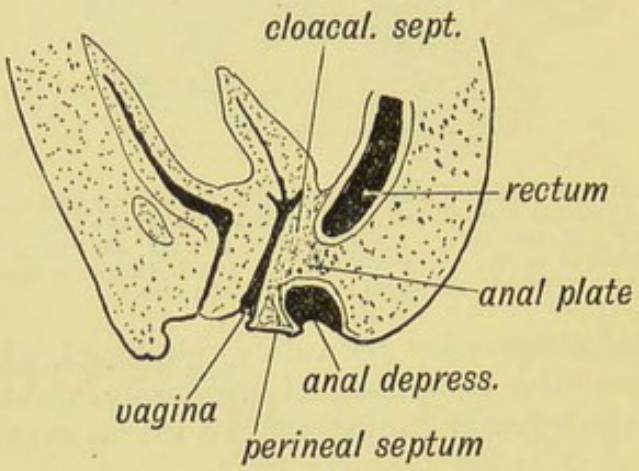


FIG. 366.—A Case of Imperforate Anus in which the Rectum has been arrested in its migration from the Cloaca to the Perineum.

genital organs is traced. The stages in the development of the human urethra, penis and scrotum during the latter part of the 2nd month and earlier part of the 3rd are shown in Fig. 367. Stage I. represents the condition seen in the perineum about the end of the 7th week. The circular fold *A*—cloacal fold [1] it may be named, for it represents the opening or margin of the primitive (ectodermal) cloaca. Within its anterior or pubic fornix is rising up the genital eminence to form the penis or clitoris—according to sex, for at this time the external parts of both sexes are alike, although the ovary is differentiated by then from the testicle. There is a groove or furrow on the under or cloacal aspect of the genital eminence, as on the cloacal penis of the tortoise ; it represents the roof of the penile urethra, and leads backwards to the urogenital sinus. The folds at each side of the furrow (*a*, *a*) are the lateral perineal folds which formed the penile urethra in Echidna. In Stage II. (Fig. 367), reached at the end of the 2nd month, two further changes are seen in progress. The lateral perineal folds (*a*, *a*) have now united behind the genital or urethral furrow, and by so doing

[1] Usually named the outer genital fold.

have separated the anal part of the ectodermal cloaca (perineal depression), in which the rectum now terminates, from the anterior urogenital part. By the union of the posterior ends of those lateral perineal folds the perineal body is formed. The cloacal fold (*A*, *A*) is still well marked, but it is apparent that the genital eminence and its attached folds are being extruded from the cloaca. In Stage III., reached at the commencement of the 3rd month, a condition is represented which

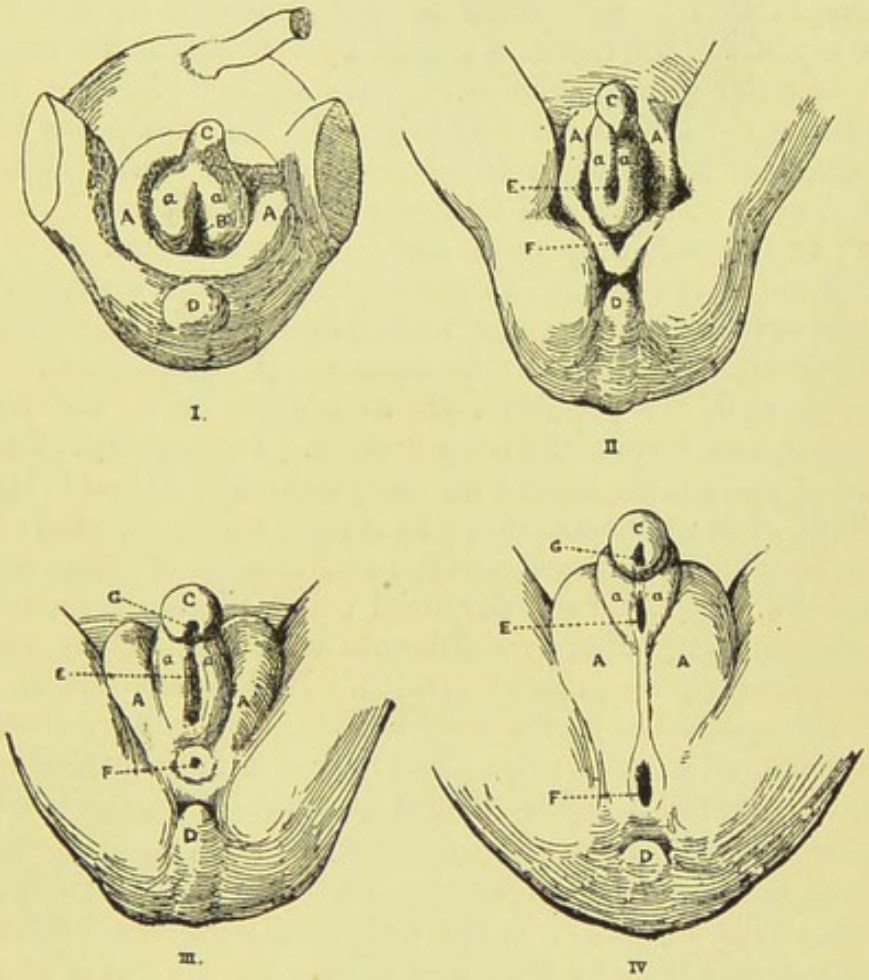


FIG. 367.—Stages in the development of the Human Penis and Perineum. (Drawings by Dr. Stanley Beale after figures given by Kollmann, Keibel and Hertzog.) I. human embryo 25 mm. long (about seventh week); II. 29 mm. long (about eighth week); III. 31 mm. long (about ninth week); IV. 45 mm. long (about tenth week). *A*, lips of cloaca (labia majora); *B*, urogenital orifice being carried to the surface between labia minora (*a*, *a*); *C*, penis becoming extra-cloacal; *D*, tail; *E*, urogenital orifice; *F*, anus; *G*, meatus.

is common to both male and female foetuses. The anus is now extruded from its depression, and lies within the flattened posterior fornix of the cloacal fold. The lateral perineal folds meet behind in the perineal body, where their free margin forms a semilunar fold—the primitive fourchette. Anteriorly the folds unite on the perineal aspect of the glans. Between the folds opens the penile urethra; the opening between the folds forms the primitive meatus. On the under or

perineal aspect of the glans a depression (the phallic groove) packed with an ectodermal plug is also present; it forms the part of the urethra within the glans, and also the secondary or permanent meatus. Stage IV. represents a condition peculiar to the male. A raphe or suture is now seen extending from the anus behind to terminate in front in the two perineal folds—perhaps it would be well to name their anterior parts, which are confined purely to the urethra of the male and vestibule of the female—urethral or inner genital folds. The primitive urethra is now small in size and well advanced towards the glans penis. The raphe is caused by a fusion of the tissues of the cloacal or outer genital folds within the septum primarily formed by the union of the lateral perineal folds. In the female this union does not occur, and hence there is no raphe on the female perineal body (Wood Jones). The cloacal folds remain separate, and form the labia majora; in the male they unite, and form the scrotum.

By the end of the 3rd month the process of union which gives rise to the raphe extends to the glans, and obliterates the primitive meatus, and at the same time forms the fraenum of the prepuce. Thus the anterior parts of the perineal folds unite right up to the fraenum of the prepuce, and enclose the male urethra. In Stage IV. (Fig. 367) the margins of the phallic groove on the glans have united; the plug of epithelium within it breaks down as it unites with the cloacal urethra, and the permanent terminal urethra and meatus are thus established. In Stage IV. (Fig. 367) the preputial collar of skin is seen in process of formation. It is directly continuous with the anterior ends of the folds surrounding the primary meatus. It does not rise up as a free fold;[1] the epithelium on the deep surface of the collar adheres to that on the glans, and hence when the prepuce is fully formed in the 4th month, the prepuce is tightly bound to it until the period of birth.

Hypospadias.—It is not unusual to see cases in which the process of urethral development has been arrested. In the female its complete arrest is normal; in individuals with imperfect differentiation of sexual glands (usually imperfect males) the process is also arrested at an early stage. Fig. 368 represents three conditions of hypospadias due to arrest of development at the terminal stage. In *A* the phallic groove is unclosed; the urethra opens at the primary meatus; the folds bounding the meatus represent the anterior ends of the urethral or perineal folds. In *B* the primitive meatus is unclosed, but the phallic groove is converted into a canal; in *C*, the commonest type, the primitive meatus is open and the phallic groove has remained uncanaliculized.

Perineal Muscles.—From what has been said regarding the cloaca, the evolution of the muscles of perineum from the sphincter

[1] Dr. Berry Hart (*Journ. Anat. and Physiol.* 1907, vol. 42, p. 50) and Dr. Wood Jones (*Brit. Med. Journ.* 1910, Jan. 15th) give another interpretation of the manner in which the prepuce is formed.

of the cloaca will be readily understood. The sphincter in cloacal vertebrates surrounds the part of the cloaca (perineal depression) formed from ectoderm; it is a striated muscle. At the end of the 2nd month this muscle is apparent in the cloacal fold of the human foetus (Fig. 369, *A*). At the beginning of the 3rd month, when the

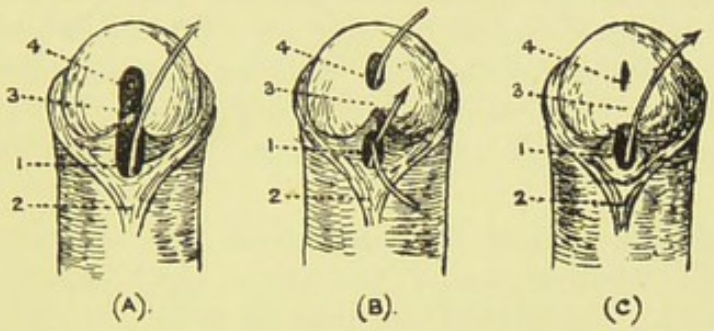


FIG. 368.—Three types of Hypospadias—*A*, in which the Groove in the Glans (phallic groove) is open, and Urine passes by the Urogenital Orifice; *B*, in which the floor of the Phallic Groove is formed, but the Urogenital Orifice is unclosed; *C*, in which the Phallic Groove is unformed or obliterated and the Urogenital Orifice serves as a Meatus. 1, urogenital orifice; 2, fraenum praeputii; 3, phallic groove and canal; 4, permanent meatus.

perineal body is formed, the sphincter of the cloaca becomes divided into urogenital and anal parts[1] (Fig. 369, *B*). The sphincter of the urogenital passage and anus fuse in the perineal body. A part of the urogenital sphincter obtains an attachment to the ischium and forms

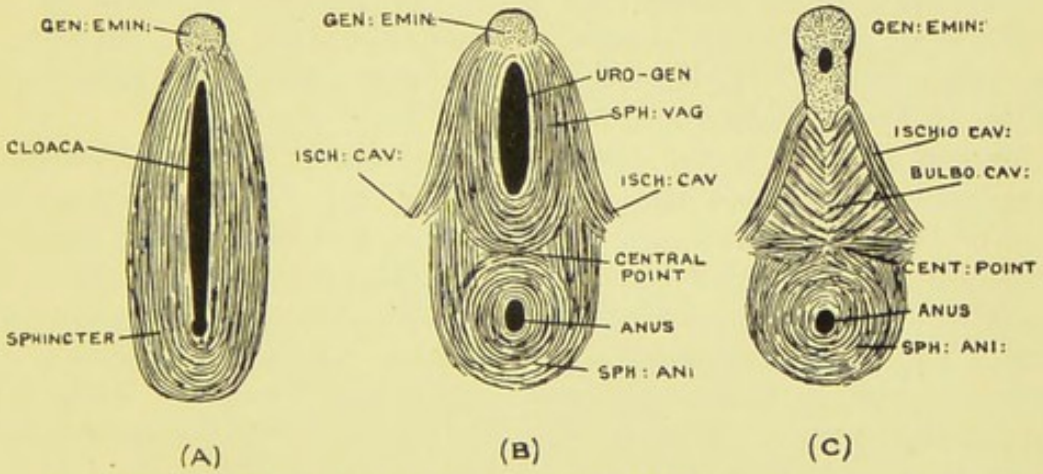


FIG. 369.—Stages in the Evolution of the Perineal Musculature. (After Popowsky.) *A*, sphincter of the cloaca in the 2nd month; *B*, its division at the beginning of the 3rd month; *C*, its condition in the male foetus at the end of the 3rd month.

the ischio-cavernosus (erector penis); another strand, the transversus perinei. With the formation of the urethra in the male, the sphincter of the urogenital passage is carried forwards on the bulb and forms the bulbo-cavernosus; in the female it remains as the sphincter vaginae.

[1] W. J. Otis, *Anat Hefte*, 1906, vol. 30, p. 199 (Dev. of Anus and External Sphincter).

A deeper and older part surrounds the upper part of the urogenital sinus, and becomes the constrictor urethrae.

Origin of the Bladder.—In amphibians the bladder is a diverticulum of the cloaca. In the embryos of reptiles, birds and mammals it becomes modified, to form the allantois; part lies outside the body and is lost at birth, part remains within the body to form the urachus and all the bladder except the trigone. By a downward migration of the orifices of the Wolffian and Müllerian ducts, the upper part of the urogenital sinus, containing the insertion of the ureters, remains to form the trigone of the bladder and supra-genital part of the urethra (Fig. 362).

The Urachus.—When the body stalk becomes elongated in the formation of the umbilical cord, the part of the allantoic cavity within it is obliterated. The part of the allantois within the abdomen, stretching from the umbilicus to the apex of the bladder, becomes the urachus, a fibrous cord, in which all trace of the allantoic cavity is lost (Fig. 372). Occasionally traces of the cavity may remain and form **urachal cysts,**[1] or it may remain open throughout, so that urine escapes from the bladder by a fistula at the umbilicus. The urachus lies behind the linea alba, embedded in the subperitoneal tissue, and flanked on each side by the umbilical artery. In the 7th month the apical part of the bladder is attached by a mesentery to the anterior wall of the abdomen; later the mesentery disappears (Broman).

The Bladder at Birth.—At birth the bladder is elongated and fusiform in shape, with a small trigone (Fig. 372). The capacity of the pelvis is relatively less than in the adult; hence the greater part of the bladder is supra-pubic in position.

Ectopia vesicae [2] is not easily explained on an embryological basis. The condition is shown diagrammatically in Fig. 370, *A*. The anterior wall of the bladder and roof of the urethra and the parts of the belly wall in front of these are absent; the trigone, floor of the urethra, and posterior wall of the bladder are flush and continuous with the belly wall. The symphysis pubis is not formed. Certain chambers in the embryo, such as the neural canal and pericardium, are liable to a dropsy and rupture. Were the cloaca of the embryo to become ruptured along its ventral wall (Fig. 370, *B*) the condition of ectopia would be produced. Further, it is to be remembered, as Berry Hart has pointed out, that the part of the embryo on which the primitive streak is situated comes to form the post-umbilical part of the ventral wall of the abdomen. It is therefore possible that the condition may be due to an unclosed condition of the primitive streak.

[1] For recent literature see Alban Doran, *Proc. Roy. Soc. Med.* April, 1908.

[2] For current theories see Wood Jones, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 193; Keith, *Brit. Med. Journ.* 1908, Dec. 26th; A. M. Paterson and Emrys Roberts, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 332.

Musculature of the Bladder, Urethra and Rectum.—Seeing that the rectum, allantois and cloaca are continuous in the embryo one would expect that the musculature of the parts should show traces of this continuity. Mr. F. Wood Jones found (1) that the band of musculature which passes from the front of the rectum to be lost in the tissue behind the membranous urethra is a remnant of the recto-cloacal communication in the embryo (Fig. 364); (2) that the circular muscular coat of the urethra is continuous above with the sphincter and circular coat of the bladder, and below it becomes continuous with the striated fibres (constrictor urethrae) surrounding the membranous urethra, which, however, are not developed from the

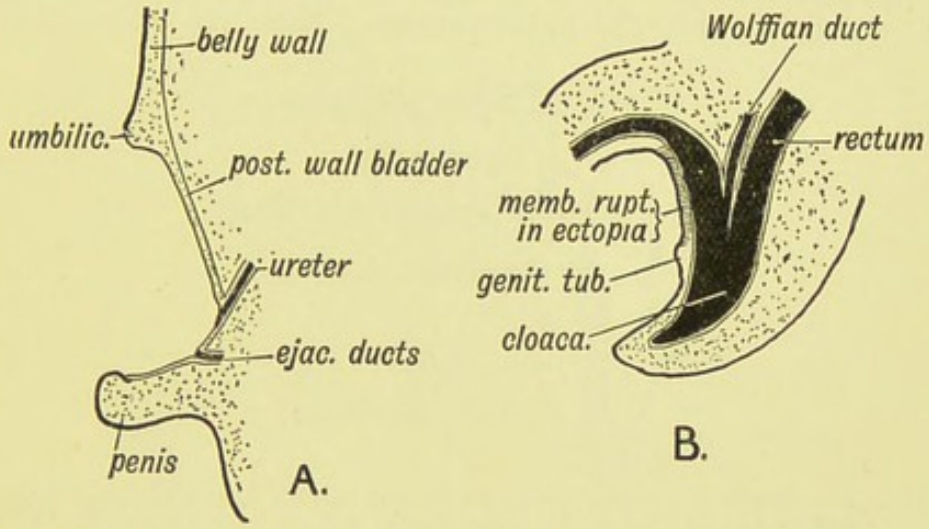


FIG. 370, *A*.—A Section to show the condition of parts of Ectopia Vesicae.
B.—Section of the Pelvis of an Embryo (4th week) to show how the condition is probably produced.

musculature of the urogenital sinus, but from the sphincter cloacae (Fig. 369).

The Neurenteric Canal.—Ano-coccygeal tumours are believed to arise from remnants of the neurenteric canal as well as from the post-anal gut. The neurenteric canal, or blastopore, it will be remembered (p. 16, Figs. 18 and 39), is a communication of the cavity of the hypoblast with the surface of the epiblast. It probably represents the point at which the invagination of the hypoblast took place. As it opens at the anterior end of the primitive streak, which afterwards is included in the posterior end of the neural groove, such a canal might be represented by a remnant passing from the rectum to sacral region of the spinal canal. A vestigeal structure, which is certainly of this nature, has not so far been recognized. The part of the hind-gut which is developed under the tail of the embryo (post-anal gut) disappears in the 2nd month of development, but certain congenital tumours which arise between the sacrum and coccyx may spring from remnants of the **post-anal gut** (p. 366).

External Genitals of the Female.—In the female the parts retain closely the early foetal form represented in Fig. 371. The genital tubercle becomes the glans clitoris. In the genital eminence—of which the tubercle is merely the summit—the corpora cavernosa develop. The inner genital folds form the **labia minora,** the prepuce and fraenum. By the junction of the inner genital folds within the urogenital depression behind, the **fourchette** is formed. Thus the opening into the urogenital sinus (primitive meatus) is bounded by the fourchette, labia minora and fraenum of the prepuce. In the lateral folds, or labia minora, are developed the bulbs of the vestibule. After the third month the external genital folds become prominent around the urogenital depression and form the labia majora. By their anterior union they give rise to the mons veneris. Their posterior extremities

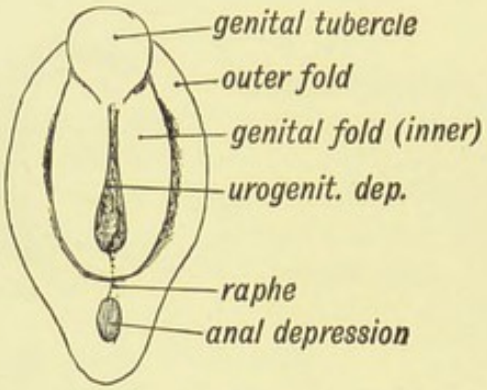


FIG. 371.—Diagram showing the terms usually applied to the External Genital Parts of the Embryo. The outer genital fold represents the cloacal fold; the inner genital folds the anterior parts of the perineal folds; the urogenital depression or cleft, the primary meatus (see Fig. 367).

unite to form the posterior commissure. After the 3rd month the external genital parts undergo a change directly opposite to that which takes place in the male. The primary meatus and penile urethra open up and form the vestibule, into which open urethra and vagina. This change is due to the influence of the ovarian germinal tissue.

External Genitals of the Male.—In the male, at the end of the 3rd month, the inner genital folds corresponding to the fourchette and labia minora, grow forwards as a crescentic shelf, thus closing the urogenital cleft and forming the floor of the penile urethra. While the floor of the penile urethra is formed thus, its roof, corresponding to the vestibule of the female, is derived from the genital or forward prolongation of the cloaca (see Fig. 363, *B*). The erectile tissue in the inner genital folds, which forms the bulbs of the vestibule in the female, form the corpus spongiosum in the male. The corpora cavernosa are formed in the genital eminence. The anterior part of the corpus spongiosum is formed separately in the apical part (glans) of the genital eminence. The corpora cavernosa are developed by the enlargement of capillary vessels of the body of the genital eminence during the

4th month. The part of the urethra within the glans is the last part to be formed, and its development is peculiar. It is formed by a solid rod-like ingrowth of epiblast within the glans which burrows backwards until it reaches the part formed out of the urogenital cleft. The part of the urethra within the glans becomes canaliculized a short time

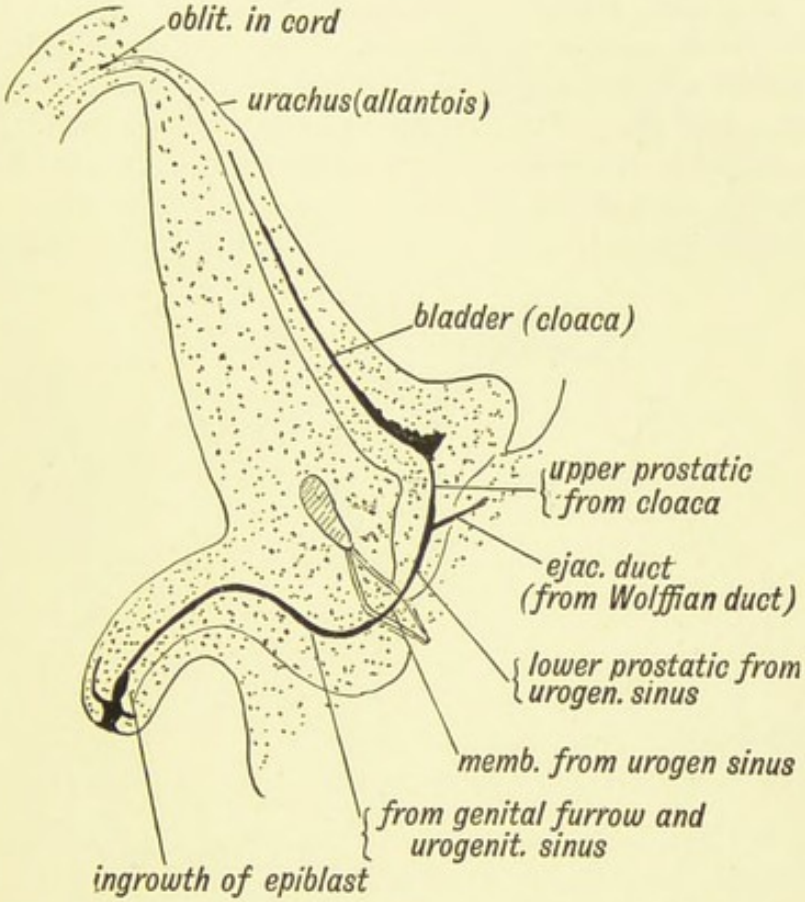


FIG. 372.—A Section of the Male Bladder and Urethra at Birth, showing the Structures derived from the Intra-abdominal part of the Allantois and from the Cloaca.

before birth. The fossa navicularis and lacuna magna occur at the junction of the part of the urethra formed in the glans and the part formed from the urogenital sinus.[1]

The **scrotum** is formed during the fourth month by the union of the external genital folds (labia majora of the female), the raphe formed by their union extending from the fraenum of the prepuce in front to the anterior margin of the anus behind (see p. 374).

[1] For literature on development of urethra see A. Lichtenberg, *Anat. Hefte*, 1906, vol. 31, p. 69 ; J. E. Spicer, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 195.

THE PROSTATE.

The **prostate** [1] is developed by outgrowths of the epithelium (entodermal) lining the upper part of the urogenital sinus and from the mesoblastic tissue surrounding the sinus. It consists of glandular tissue and stroma.

(1) The **glandular tissue** is composed of tubular glands which open into the prostatic part of the urethra. They are developed in the 4th month, as series of solid buds, about 60 in number, from the epithelium lining the upper part of the urogenital sinus (Fig. 373). The buds, which soon become tubular in form, arise from a right and left longitudinal furrow or fold of the wall of the sinus between which the Wolffian ducts open (Pallin). The prostatic furrows reach upwards

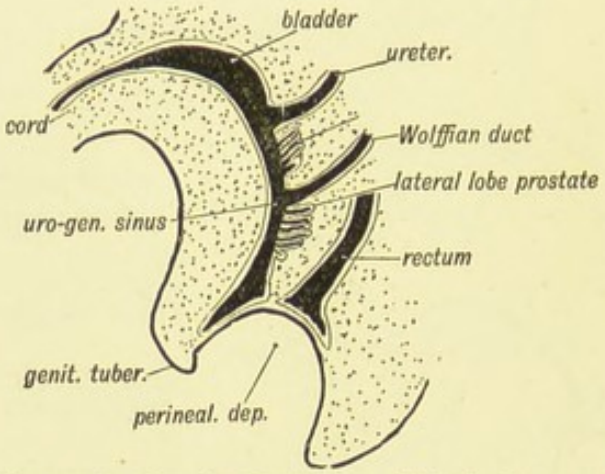


FIG. 373.—A Diagram to show the Position at which the Prostatic Tubules arise.

above the Wolffian openings into the purely urinary part of the sinus and downwards into the part which serves as a common passage for the semen and urine. These segments of the sinus become the **upper** and **lower parts** of the prostatic urethra. The buds from the right and left furrows form two lateral masses or lobes. At first the two lateral lobes, as in mammals generally, lie separately behind the urethra. Other outgrowths also arise from the anterior or pubic side of the sinus —some of these afterwards undergo atrophy—from the side or lateral aspect of the sinus (Fig. 374). The lateral prostatic masses fuse behind the urethra ; in man only do they meet to form an anterior or pubic commissure over it. The tubules of the median or third part arise from the middle line of the floor of the sinus above the openings of the Wolffian ducts (ejaculatory ducts) (Evatt), but the lateral lobes also fuse with this median element, and help to form it. It may be small or even absent.[2]

[1] For recent papers on the development of the prostate see E. J. Evatt, *Journ. Anat. and Physiol.* 1908, vol. 43, p. 314 ; 1911, vol. 45, p. 122.

[2] Thompson Walker, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 189 ; O. S. Lowsley, *Amer. Journ. Anat.* 1912, vol. 13, p. 299.

Skene's tubules, which may be found opening into the urethra of the female, represent prostatic tubules. A reference to Figs. 364 and 365 will show that the female urethra corresponds to the upper prostatic urethra of the male, and that the floor of the vestibule—in which rudiments of prostatic tubules may be formed—represents the lower prostatic urethra.

(2) **The Stroma of the Prostate.**—While the glandular tubes arise in linear groups from the epithelium lining the urogenital sinus—the muscular and fibrous elements arise from the mesoblastic tissue of the genital cord in which the terminal parts of the Wolffian and Müllerian ducts are situated and from the circular musculature of the urogenital

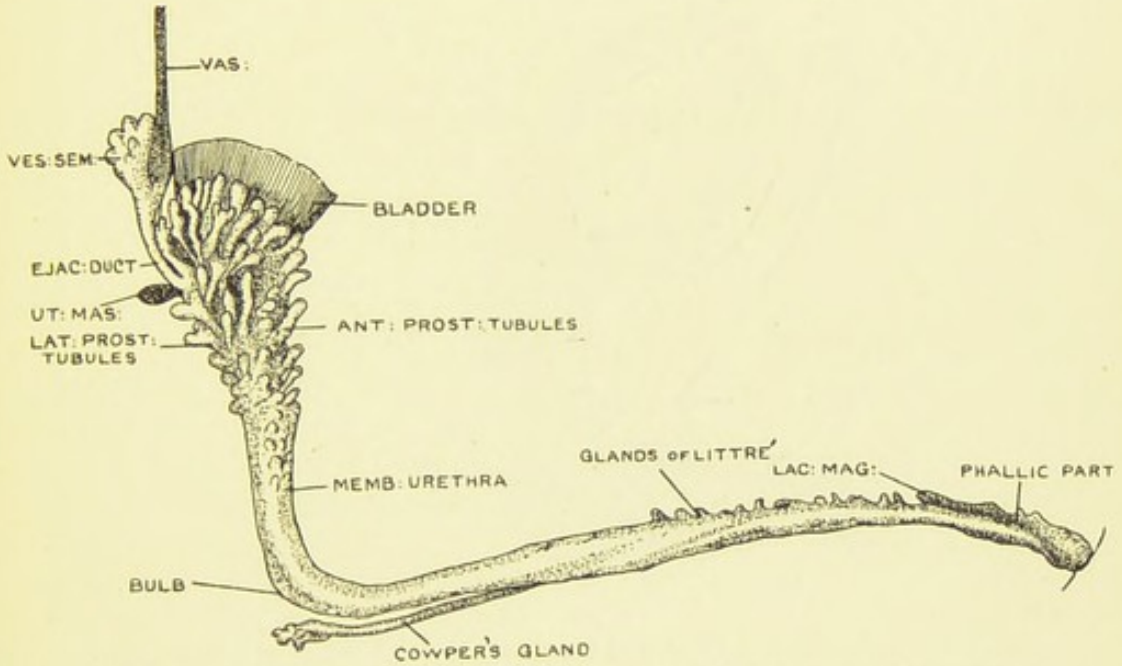


FIG. 374.—The Prostate and Urethra towards the end of the 4th month. (After Broman and Evatt.) The phallic part of the urethra ends posteriorly at the lacuna magna. It is developed in the glans. The uterus masculinus (ut. mas.) is indicated diagrammatically to show its relationship to the common ejaculatory duct.

sinus (see Fig. 375). When the glandular elements grow out they become embedded in and carry before them the circular musculature of the urogenital sinus which thus forms the muscular cortex or inner capsule of the prostate. Probably the stroma of the genital cord also contributes to the musculature of the prostate. The musculature of the uterus, which is also developed from the genital cord, like that of the prostate, is liable to become the seat of fibromyomatous growths in the later years of adult life.

As regards **the nature of the prostate :**

(1) It is purely genital, and develops only in the rutting season in such mammals as manifest a seasonal sexual life. Its development in the female is arrested at a very early stage—probably the result of an ovarian influence.

(2) It remains comparatively undeveloped until puberty. At the age of seven it weighs only 30 grains; after sexual life is established it weighs about 300 grains.

(3) It atrophies on castration, a fact which was utilized by the surgeon in cases of prostatic hypertrophy.[1] Castration performed on old men may lead to insanity. In one man out of three over 55 years of age the prostate hypertrophies, both the glandular and fibro-muscular

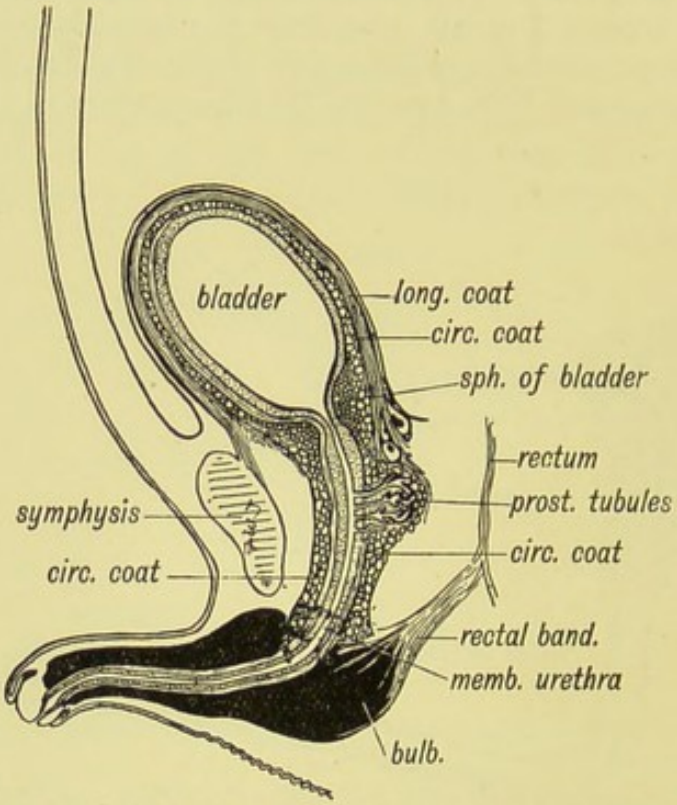


FIG. 375.—Diagrammatic Section of the Bladder and Urethra of a 6th month Foetus to show (1) the development of the Prostate, (2) the relationship of the Prostatic Musculature to that of the Urethra and Bladder. (F. Wood Jones.)

elements participating. Hypertrophy of the median part causes a valvular elevation behind the vesical opening of the urethra.

The Glands of Cowper and Bartholin are produced as solid buds from the hypoblastic lining of the penile extension of the urogenital sinus (Fig. 374). Hence in the female the ducts of Bartholin's glands open outside the hymen at each side of the vagina, for the hymen marks the junction of the Müllerian ducts with the urogenital sinus. In the male the ducts of Cowper's glands open in the bulbous part of the urethra (Fig. 374). Their function is unknown, but they are certainly sexual in nature. The numerous **glands of Littré,** like

[1] E. Pittard, *Compt. Rend. Acad. Sc.* 1911, vol. 152, p. 1617 (Effect of Castration); Cuthbert S. Wallace, *Trans. Path. Soc. Lond.* 1905, vol. 56, p. 80; W. L. H. Duckworth, *Journ. Anat. and Physiol.* 1906, vol. 41, p. 30 (Eunuchoid Man); R. H. Whitehead, *Anat. Rec.* 1908, vol. 11, p. 177, *Amer. Journ. Anat.* 1904, vol. 4, p. 193 (Dev. and Nature of Interstitial Cells).

Cowper's and Bartholin's glands, are produced by tubular outgrowths during the fourth month (Fig. 374). In the male the glands of Littré are produced most numerously along the dorsal aspect of the urethra.

Round the anus, and especially in the furrow between the labium minus and majus, groups of large peculiar sebaceous glands are produced in the 4th and 5th months, corresponding to the **anal** and **preputial** glands of mammals. Occasionally two groups of sebaceous glands occur on the prepuce of the male, especially if hypospadias be present (Shillitoe). Glands round the corona of the glans penis (**Tyson's glands**) are only very exceptionally present.

THE TESTES.

Descent and Development of the Testicle.—The origin of the testis on the inner or mesial side of the Wolffian ridge, and its attachment to the dorsal wall of the coelom by a mesentery common to it and the Wolffian body have been already described (p. 19). The position of the testicle in a foetus of the third month is shown in Fig. 376. It is situated in the iliac fossa. The mesorchium, a fold of peritoneum, binds its attached border to the iliac fossa. At its outer side lies the genital part of the Wolffian body which forms the epididymis. It, also, is suspended by a mesentery—the Wolffian mesentery. The two mesenteries have a common base—the common urogenital mesentery (see Fig. 339, p. 347). The upper part of the urogenital mesentery forms the diaphragmatic fold, with which the peritoneal fold containing the spermatic artery becomes joined; to the combined fold is given the name of **plica vascularis** (compare Figs. 377, 380). This in the female becomes the ovario-pelvic ligament (Fig. 5, p. 4). A fold of peritoneum, the inguinal fold of **plica gubernatrix,** continues the common urogenital mesentery to the groin (Fig. 376). The gubernaculum testis is developed in the plica gubernatrix; in the corresponding fold in the female the round ligament of the uterus appears (see p. 357). The vas deferens (Wolffian duct) turns into the pelvis from the lower end of the epididymis (Wolffian body), and within the pelvis lies in the genital cord (Fig. 348, p. 357). A remnant of the Müllerian duct lies along the inner and ventral aspect of the epididymis.

The Development of the Testis.[1]—Its blood supply comes from the level of the 12th dorsal vertebra; its nerve supply from the 10th dorsal segment of the spinal cord. The testis is therefore developed in the genital ridge between the 10th and 12th dorsal segments. The development of the testis is similar to that of the ovary (Fig. 21, p. 20).

[1] See Eben. C. Hill, *Amer. Journ. Anat.* 1907, vol. 6, p. 439 (Dev. of Blood Supply); D. T. Barry, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 137 (Differentiation of Tubules).

The columnar cells of the germinal epithelium which covers the genital ridge contain between them larger genital cells—the primordial ova. Tubular buds of germinal epithelium grow into the tissue of the genital ridge and form the epithelial lining of the seminiferous tubules instead of, as in the female, the Graafian follicles. Primordial ova are carried down within the tubes of enclosing cells and these produce the spermatogonia (see p. 11). The tunica albuginea is formed from the mesoblastic covering of the genital ridge. The visceral layer of the tunica vaginalis on the testicle is the covering of flattened epithelium which remains after the ingrowth of the genital cells. The vasa efferentia and coni vasculosi are formed from the **genital** Wolffian tubules; the rete testes and vasa recti from the junctional cords (p. 350). Into the

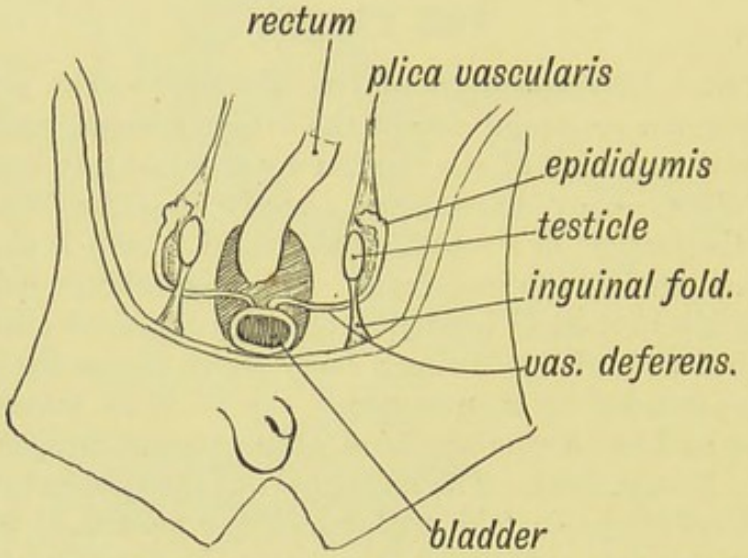


FIG. 376.—The Position of the Testis in a Foetus of 2½ months.

rete open the tubuli seminiferi formed in the testicle. The epididymis is the elongated upper segment of the Wolffian duct (Fig. 341). The Wolffian elements are produced within the Wolffian ridge (Fig. 21).

Formation of the Gubernaculum Testis.[1]—As shown in Fig. 376 there is no trace of the inguinal canal in the 3rd month of foetal life; the various layers of abdominal wall are unbroken, except for a fine strand of tissue which leads towards the site of the scrotum, and evidently serves as a guide for the gubernacular outgrowth. In the fourth month the subperitoneal layer of non-striated muscular tissue in the plica gubernatrix and in the mesorchium takes on a rapid growth (Fig. 377). At the same time the tissues in the whole thickness of the abdominal wall undergo a localized evagination towards the scrotum. They are probably carried down by the growth of the gubernacular bud which pushes its way to the scrotum. The gubernaculum grows

[1] See John Hunter's classical account, Palmer's Edition of his Works, vol. 4, 1837. Also recent paper by Dr. Berry Hart, *Trans. Edin. Obstet. Soc.* 1908-9, vol. 4, p. 4.

downwards as a solid fibro-muscular mass, until it reaches the subcutaneous tissue which at that time completely fills the scrotum. Its attachment to the scrotum is slight and easily broken (Fig. 377). The gubernaculum, as it grows through the abdominal wall, carries with it :

(1) A process of peritoneum (the processus vaginalis) ;

(2) The transversalis fascia (the infundibuliform fascia) ;

(3) The internal oblique and transversalis muscles to form the cremaster ;

(4) The spermatic fascia from the external oblique ;

(5) The deep layer (Scarpa's) of the superficial fascia of the groin.

All these layers are added to the primitive coverings of the scrotum,

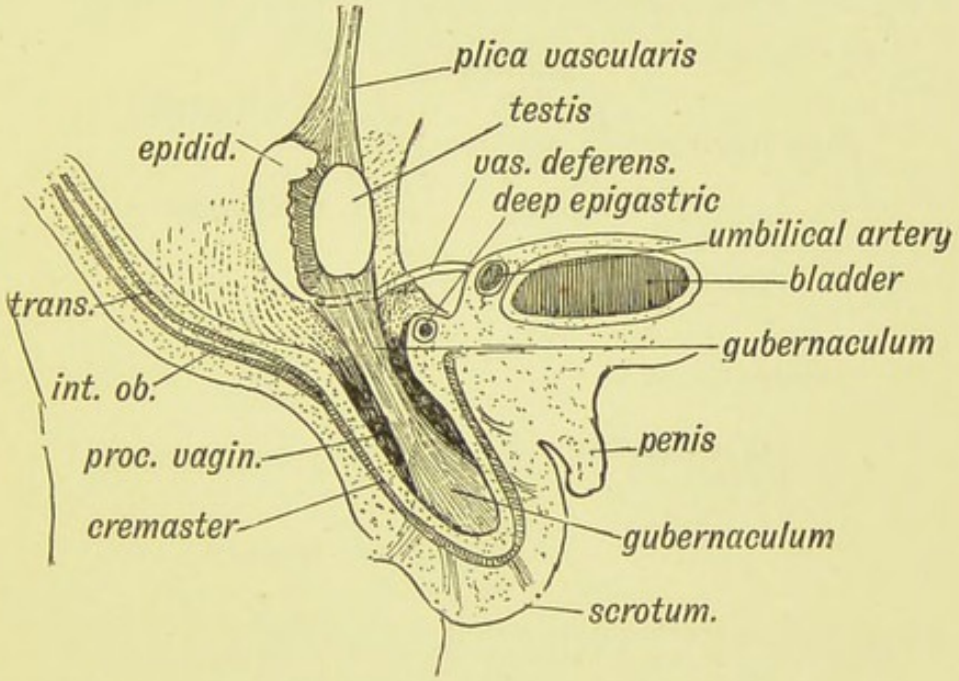


FIG. 377.—Showing the Position of the Testis at the 6th month, and the Formation of the Gubernaculum Testis.

which until then is made up simply of skin and superficial fascia (Fig. 378).

It will be thus seen that the gubernaculum testis is an actively growing mass of fibro-muscular tissue, which, starting from the muscular stratum in the mesorchium and plica gubernatrix in the iliac fossa, invades the abdominal wall, every layer of which it carries as a prolongation within the scrotum. It is an invading army of cells. It draws with it into the scrotum the peritoneum in the iliac fossa, on which the testis is dragged like a log on a sledge.

The testis descends from the loins to the iliac fossa in the 3rd month ; from the 4th to the 7th month it rests at the site of the internal ring ; it spends the 7th month of foetal life in its exodus through the abdominal wall. In the 8th month it leaves the inguinal canal and lies at the external abdominal ring. After birth it reaches the fundus

of the scrotum. The atrophy of the gubernaculum pulls it down. A remnant of the gubernaculum can always be found in the adult behind the epididymis and testicle, within the mesorchium (Fig. 379).

The Processus Vaginalis.—The processus vaginalis becomes occluded at two points soon after birth, but in a considerable proportion of individuals the process of closure is delayed (Fig. 379). The upper point of occlusion takes place at the internal abdominal ring; the lower a short distance above the testicle. The part of the processus vaginalis between the points of occlusion is known as the **funicular process**; the part surrounding the testicle becomes the tunica vaginalis. In quite 30 % of children the occlusion takes place at the internal abdominal ring some considerable time after birth or it fails to appear

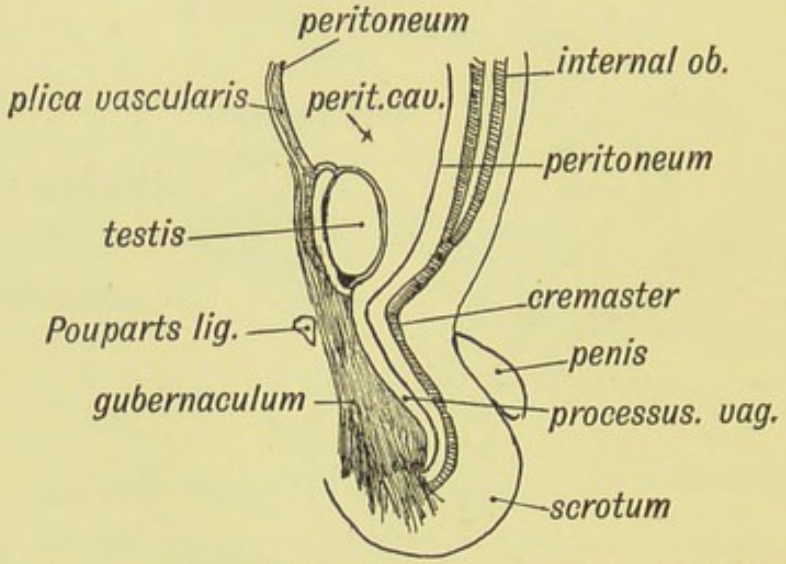


FIG. 378.—The manner in which the Structures in the Wall of the Abdomen are carried out so as to form the Inguinal Canal and Coverings of the Testis.

altogether. Occlusion may fail at the upper point, at the lower point, or at both. Or it may close at both points, but the funicular process, instead of disappearing, may remain open and form a cyst.

Descent of the testicle [1] may be arrested at any stage; often in the inguinal canal; more frequently at the external abdominal ring. Arrest of descent is commonly regarded as a symptom of arrest of testicular development. John Hunter regarded arrested descent of the testicle as due to an imperfection in its development; all recent observations support his opinion. There can be no doubt that in all those mammals [2] in which the testis leaves the abdomen it does so to escape the intra-abdominal pressure to which the abdominal viscera are subjected. Its descent is correlated with the formation of the diaphragm and exclusion of the lungs from the abdominal cavity.

[1] D. Berry Hart, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 4; D. Berry Hart, *Journ Anat. and Physiol.* 1909, vol. 43, p. 244.

[2] See Woodland, *Proc. Zool. Soc. London*, 1903, p. 319.

Violent respiration and movements of the trunk give rise to very high degrees of tension within the abdomen; from some cause at present not understood, a testicle atrophies when subjected to this pressure. On the other hand, the testicle may assume an **ectopic** position. The gubernaculum, as it makes its way towards the scrotum, may take an eccentric course, and bring the testicle to rest in the groin, root of the penis, or over the pubis.

Mesentery of the Testicle.[1]—A not unusual anomaly of the testicle is represented in Fig. 381. It will be observed that the common mesentery, in place of becoming shortened, and thus fixing the testicle

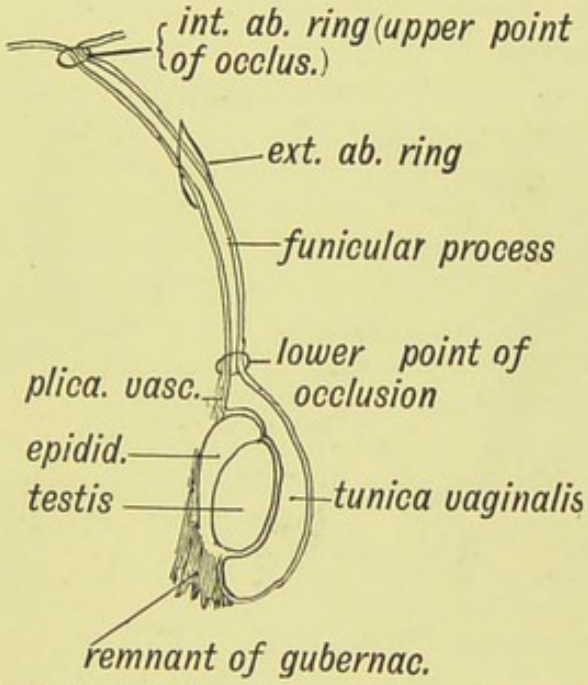


FIG. 379.—A Diagram of the Processus Vaginalis.

and epididymis widely to the peritoneum, becomes narrow and elongated. Such testicles are usually arrested in their descent, and are apt to twist and become strangulated. It will also be observed that a gubernaculum is present, but it has seized and drawn downwards only a loop of the vas deferens. The explanation is shown in Fig. 380. The inguinal fold is made up of two parts, **a lower,** ending on the vas deferens and corresponding to the round ligament of the female; **an upper,** which continues the fold to the epididymis and testicle, and which corresponds to the round ligament of the ovary. In such cases, then, the gubernaculum has not extended to the upper part of the inguinal fold.

The Mesorchium.—The testis and epididymis were suspended within the abdomen by the common urogenital mesentery. In the course of the descent of the testis this becomes shortened by the development of the gubernaculum and binds the testis and epididymis firmly

[1] See Rigby and Howard, *Lancet*, 1907, May 25th.

by their posterior borders to the tunica vaginalis. The digital fossa is situated between the mesorchium and mesentery of the Wolffian body. The mesorchium—the true mesentery of the testicle—may also assume the form of an elongated fold, attaching the testicle to the epididymis (Corner).

Hermaphrodites.[1]—A hermaphrodite—a human individual in which both testis and ovary are present—has never been seen. Dr Bulloch found only five cases on record in which, within the same genital gland, there were present representations of imperfect testicular

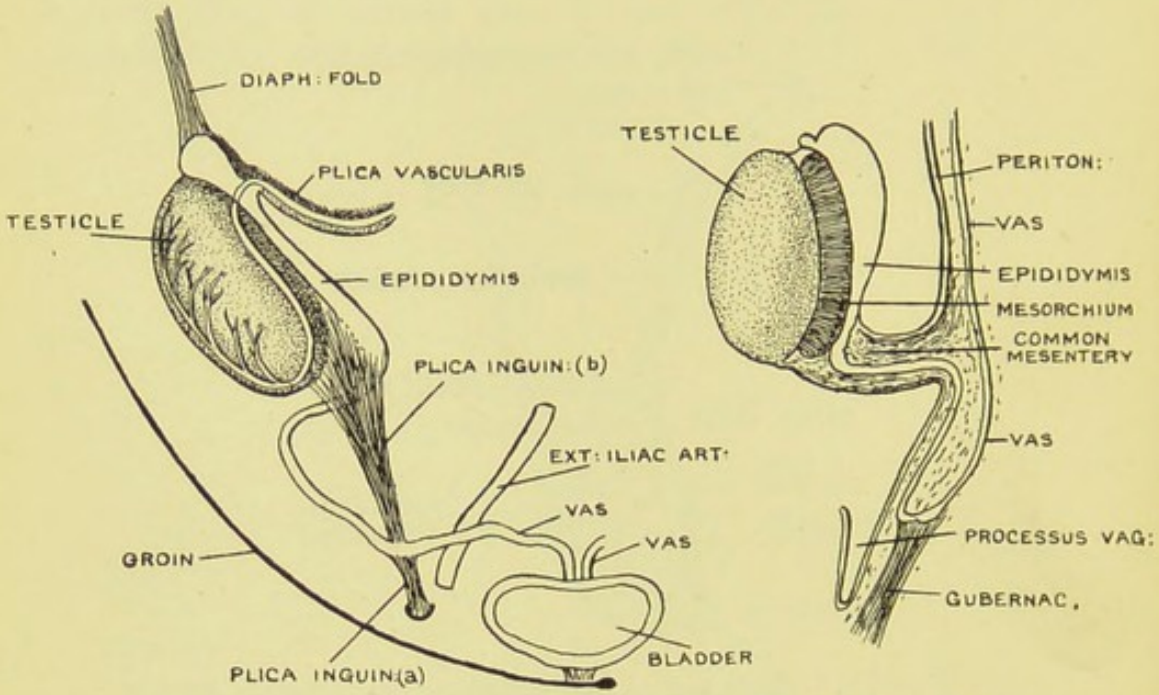


FIG. 380.—To show the Diaphragmatic Fold (upper part of the common genital mesentery), Vascular Fold, and the two parts of the Inguinal Fold in a Foetal Pig. (Eben. C. Hill.)

FIG. 381.—Elongated Common Mesentery of a Testicle arrested in the course of its descent.

and ovarian tissues (ovario-testis); spermatozoa and ova were not present. The term is usually applied to individuals in whom the genital glands are imperfectly developed. Usually they are imperfect males. It is clear that sexual differentiation commences in the 6th week (although no doubt the sex is determined at or before the time of fertilization); by some means—probably by a secretion—the ovarian and testicular tissues exercise a direct and opposite influence on the development of genital structures. Hence, if the gland is imperfect, development of the genital parts is uncontrolled and represents a condition which may best be described as neutral. There is

[1] See Bulloch, *Treasury of Human Inheritance*, London, 1909, Part 3, Section Xa; Berry Hart. *Proc. Roy. Soc. Edin.* 1909, vol. 29, p. 607, 1910, vol. 30, p. 230; J. F. Gudernatsch, *Amer. Journ. Anat.* 1911, vol. 11, p. 267.

evidence to support the opinion that the embryonic genital gland is composite ; the testicle develops within the medullary or central part of the gland ; the ovary from its cortical or more superficial parts.

Development of the Supra-renal Bodies.—In spite of much research there is still a difference of opinion as to the origin and nature of these bodies. They arise within the anterior part of the Wolffian ridge, immediately behind the pleuro-peritoneal passage of the septum transversum, their bases becoming apparent at that site towards the end of the first month of development. The cortex and medulla are certainly of different origin. In Elasmobranchs (sharks, etc.) these two elements are separate, the cortical part forming an inter-renal, unpaired body : the medullary part a body situated above the Wolffian kidney (supra-renal) on each side, and closely connected with a ganglion of the sympathetic system, in connection with which they are developed. In vertebrates above fishes the cortical and medullary parts are combined in one body. The **medulla** arises from the groups of cells which form the sympathetic ganglia ; probably from the primitive cell basis of the semilunar ganglion, which is developed in the dorsal mesentery, close to the pleuro-peritoneal opening. Hence the great plexus of nerves which passes from the solar plexus to the medulla of the supra-renals. The medullary cells begin to migrate into the cortex at the beginning of the 2nd month ; the process of invasion is continued through the greater part of foetal life. The cells, when stationed in the cortex, give rise to true nerve cells, and also to broods of chromogenic cells. By the beginning of the 3rd month they are arranged as recticulating columns set on the walls of branching venous sinuses. Probably the carotid and coccygeal bodies are similar to the medulla in origin and nature (Swale Vincent).

The **cortical part** is of quite different origin. It arises from the endothelium covering the Wolffian ridge—that part of the ridge which lies near the pleuro-peritoneal opening. The endothelium proliferates within the Wolffian ridge and comes in contact with the medullary element derived from the sympathetic. These endothelial cells probably represent the funnel-shaped openings of segmental tubules within the coelom, and are therefore nephric or renal in origin. The cortical cells range themselves in rows between radiating blood sinuses. As the kidneys ascend in the 3rd month they come in contact with the supra-renal bodies. The supra-renal is at first larger than the kidney, even at birth they are nearly equal in size. The nerves and arteries enter the bodies on their renal surface ; the veins emerge on their anterior surface. Aichel[1] still maintains that both cortical and medullary parts arise from mesothelial cells over the Wolffian ridge.

Until the 3rd month the supra-renal bodies are in contact with the upper pole of the testis or ovary. As the genital glands descend, the diaphragmatic fold is drawn from the supra-renal region and frequently

[1] Aichel, *Anat. Anz.* Bd. 17, No. 1, 1900.

carries with it buds of supra-renal tissue. It is therefore readily understood how isolated parts of the supra-renal body (accessory supra-renals) may occur in the broad ligament or in the spermatic cord above the testicle. Such accessory bodies are probably derived from the cortical element which is developed within the Wolffian ridge and body. With the descent of the ovary and testicle, which bring with them the Wolffian body, adjacent accessory supra-renals, if such be present, are also brought down, and may occasionally give rise to peculiar tumours. Supra-renal "rests" may be included in the kidneys, and become sources of tumour-formation. There is usually one or more small accessory supra-renals stationed in front of the aorta between the kidneys, near the origin of the inferior mesenteric artery.

Chromaffin Cells.[1]—The medullary part of the supra-renals belongs to a segmental series of organs. In such fishes as the shark and lamprey, a group of cells (a paraganglion) is thrown off from each ganglion of the sympathetic chain and comes into close contact with the tributaries of the cardinal veins. These cells stain brown with salts of chromium—hence their name; some of these cells remain within the sympathetic ganglia. Although they arise from the same group of cells which give origin to the sympathetic ganglia, they are secretory in nature. The cells are surrounded by a rich plexus of capillary blood channels and are of an orange colour when seen in mass. Chromaffin cells are found in the medulla of the supra-renal, in the carotid body and in the accessory supra-renal which was discovered by Zuckerkandl in the mesentery of the human foetus, at each side of the root of the inferior mesenteric artery. They have outwardly the appearance of small lymphatic glands.

Coccygeal Body [2] is a small mass of chromaffinic tissue, with rich blood supply situated on the ventral aspect of coccyx.

[1] For an account of chromaffin tissue, see an article by Swale Vincent, *Journ. Anat. and Physiol.* Oct. 1903, vol. 38, p. 34.

[2] J. Thompson Walker, *Archiv. für Mik. Anat. und Entwickl.* 1904, vol. 64, p. 121 (Coccygeal Body).

CHAPTER XX.

BODY WALL AND PELVIC FLOOR.

Stages in the Evolution of the Body Wall.[1]—Behind the apparently simple arrangement of structures in the body wall of man lies a long history, only some of the later stages being known to us. Even in the lowest vertebrates the wall surrounding the pericardial and abdominal cavities is already muscular. We presume, however, there was a stage in which they were devoid of muscle, for in all vertebrates the musculature which enters the somatopleure, the embryonic lamina forming the body wall, arises from the muscle plates of the somites placed along each side of the dorsal median axis of the embryo (see p. 60). In fishes the musculature of each side of the body wall is arranged in two systems: (1) a ventral longitudinal (rectus) system, which passes from the pharynx to the tail; (2) a lateral or oblique layer, in which ribs are embedded. Both longitudinal and oblique systems are differentiated from one stratum. It is from a simple system of this nature that the musculature of the human body wall has been evolved (see Fig. 398, p. 412).

Respiratory Stage.—With the evolution of lungs the musculature of the body wall assumed a respiratory function.[2] In fishes its chief use—if one excepts the part it plays in body movements—is to assist in the circulation of the blood within the body cavity—to drive it on towards the heart, and to expand or contract the cavity as the alimentary canal fills or empties. By means of ribs embedded in the septa of the lateral wall, the musculature of the body cavity became capable not only of compressing or diminishing the body cavity, but also of expanding it, and thus could fill the lungs with air. In this manner the body musculature entered into the service of the lungs, and the nerve centres (respiratory centres) in the hind-brain, which formerly regulated the movements of the gills and pharynx, came to have an automatic dominion over musculature of the body

[1] See R. H. Paramore's "Hunterian Lectures," *Lancet*, 1910, May 21st and 28th.

[2] F. Tourneux, *Compt. Rend. Assoc. Anat.* 1902 (Dev. of Walls of Thorax).

wall. The ribs, which served in the simple economy of the fish's body, became strengthened and firmly jointed to the vertebrae; at the ventral ends of those encircling the lungs a supporting bar—the sternum—was evolved; the primitive sheets of musculature became differentiated to act on the ribs. As the lungs begin to expand in the latter part of the 2nd month, respiratory transformations, similar in nature to those just mentioned, are taking place in the human embryo.

Mammalian Stage.—We have already seen that the lungs of mammals develop within special cavities, which ultimately surround the heart; and with the development of the pleural cavities a muscular partition is dislocated from the neck and completely separates the body cavity into thorax and abdomen. With the evolution of the diaphragm, and the disappearance of the lungs from the abdominal cavity, the body wall musculature became further modified, so that it can control the thoracic as well as the abdominal pressure. The evolution of pleural cavities effected a transformation in the thoracic part of the body wall. Their expansion and the differentiation of the thoracic wall are taking place during the 2nd and 3rd months of human development.

Orthograde Stage.—It is believed by many that the upright or orthograde posture is confined to man, and that it represents one of the more recently acquired human characters. This is certainly not the case; man shares the orthograde posture with the group of primates with which he has so many structural affinities—namely, the anthropoid apes. Like man, they carry their bodies in an upright posture during progression. The smallest and most primitive of the anthropoid apes—the gibbon—is of ancient origin; the orthograde posture is therefore an adaptation which has been long established in the higher group of primates. With a change of posture the action and fixation of the musculature of the body wall became again transformed; the mechanism of respiration was necessarily altered. The chest became wide or barrel-shaped, the sternum broad; the heart came to rest on the diaphragm. The muscles of the abdominal wall had not only to carry on their respiratory function; they had also to support the abdominal viscera. The mesenteric adhesions which take place during the 4th, 5th and 6th months of foetal life (see p. 276) are designed to give additional fixation to the viscera. The lower abdominal viscera came to rest on the pelvic floor; the muscles of the tail, which rise within the pelvis of pronograde mammals, were modified to form a muscular hammock for the support of the viscera and the tail disappeared. The caudal or coccygeal vertebrae are more reduced in the anthropoid apes than even in man. The spinal musculature and spinal column were altered to meet the new postural conditions.

Plantigrade Stage.—If man shares the orthograde posture with a group of higher primates, the power of plantigrade progression

is peculiarly his own. Everyone recognizes that the foot, the leg, the thigh of man have undergone extensive structural alterations, but the fact is often overlooked that the process of adaptation has also led to marked structural changes in the body wall. The inguinal region especially has been modified. The great development and complete extension of the thigh have altered the musculature of the groin; Poupart's ligament has been evolved. These structural adaptations have weakened the human groin, and made it a favourite site of hernia. In the normal human upright posture the trunk is balanced on the pelvis; the crest of the ilium and the external oblique have become

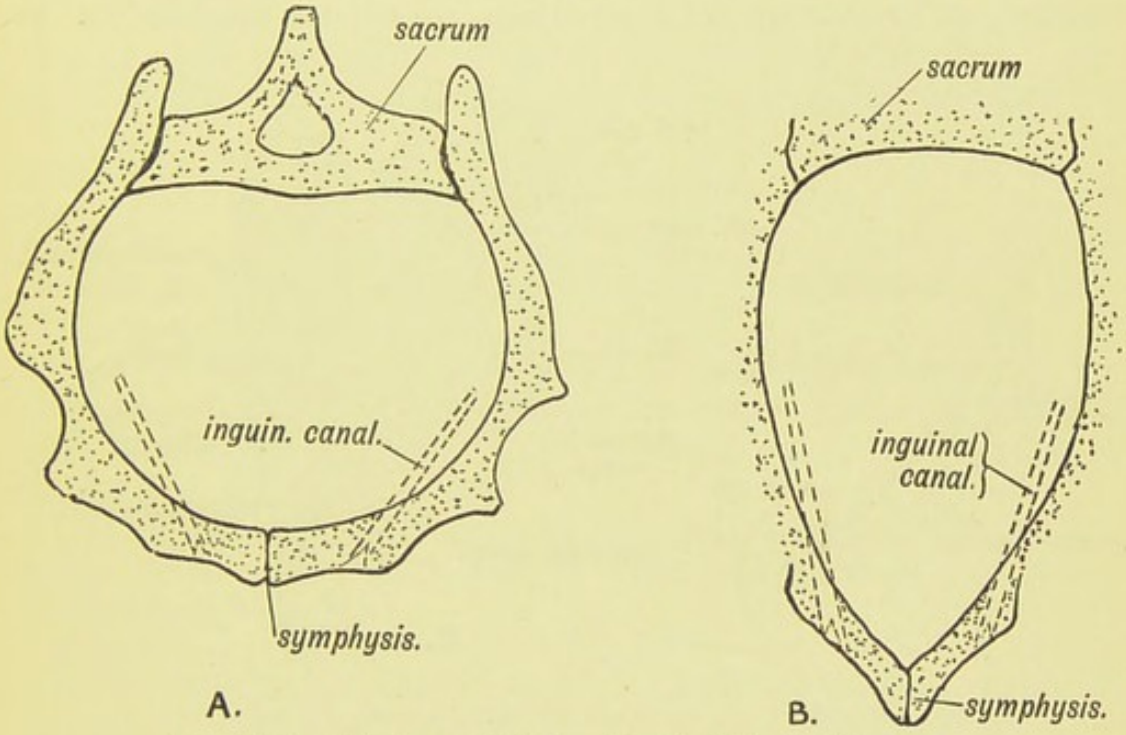


FIG. 382, *A*.—The Form of Pelvis and Inguinal Canal in Man.
B.—The corresponding forms in the Lower Primates.

modified for that purpose. The muscles of the abdominal wall not only support the abdominal viscera, and maintain their respiratory function, but also take a part in producing and regulating the movements of the body. Their functional value is often impaired in man, and hence he is the subject of those forms of slipping or dropping of the viscera which are grouped under the name of **visceroptosis.** He is also liable to many other varieties of static disablements.

Inguinal and **femoral hernia** occur so rarely amongst mammals generally that they may be considered human peculiarities. Their frequency in man is due to certain structural changes in his pubo-femoral region, changes which have resulted mainly from his adaptation to upright progression. His susceptibility to hernia is due to:

(1) The unique form of Poupart's ligament in man. It is scarcely developed in any other animal (Fig. 383). In the orang, for instance,

also an upright primate, the external oblique has no attachment to the crest of the ilium, and takes no part in forming the outer part of Poupart's ligament (Fig. 383), the aponeurosis from the lower muscular digitations terminating directly in the pillars of the external abdominal ring, thus strengthening the region of the inguinal canal. This is the usual termination in the mammalia. In man the anterior part of the iliac crest has grown into the lower digitations of the external oblique and severed them from their tendinous fibres, which now form the main constituent of Poupart's ligament. The digitations thus inserted to the iliac crest help in balancing the body.

(2) The internal oblique and transversalis (conjoined parts) in the orang, and in all primates except man, arise from the firm tubular

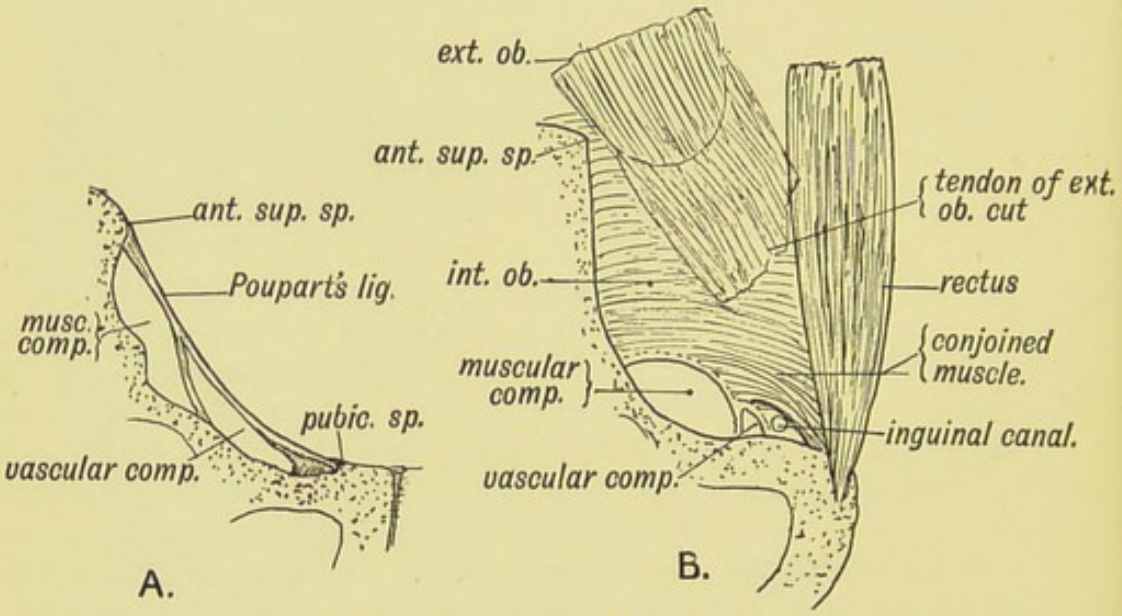


FIG. 383, *A*.—Poupart's Ligament and the Crural Passage of Man.
B.—Poupart's Ligament, Crural Passage, and Sphincter-like Conjoined Muscle of the Orang.

sheath of the ilio-psoas, also from the extensive anterior border of the ilium, and, arching over the spermatic cord, end in a long insertion on the ilio-pectineal line. They act as a powerful compressor or sphincter of the inguinal canal, and thus prevent hernia (Fig. 383, *B*).

(3) The human manner of walking and the great head of the human child at birth require a wide pelvis. All mammals adapted to the pronograde posture have a narrow pelvis, and hence a narrow anterior abdominal wall (Figs. 382 *A* and *B*) through which the inguinal canal passes very obliquely. The course of the canal is more direct in man, and therefore offers a greater facility to the escape of the abdominal contents.

(4) Owing to the width of his anterior abdominal wall, the size of the space between the edge of the pelvis and Poupart's ligament (the crural passage) is very much greater in man than in any other animal

(Figs. 383, *A* and *B*). In him, the most internal part of the passage is left unfilled, and this unfilled space forms the femoral or crural canal through which femoral hernia may escape. The formation of the femoral canal has, therefore, no embryological basis; it is not like the inguinal canal the site of an embryological outgrowth of peritoneum. The crural passage is relatively larger in women than in men, owing to the greater size of the female pelvis, and hence femoral hernia are much more common in women than in men. Some hint as to the method of treatment of hernia in man may be obtained from a consideration of the arrangement of structures which prevent them in other animals.

(5) Perhaps the most important factor in the causation of hernia in man is the compression to which the abdominal contents are subjected by the contraction of the musculature of the abdominal parietes.

THE PELVIC FLOOR.

The Coccyx.—It is necessary to consider the coccyx here, because the changes which it has undergone in the evolution of the human body are intimately connected with the formation of the pelvic floor. The coccyx in man is commonly composed of four vertebrae, more or less vestigial in nature, which represent the basal caudal vertebrae of tailed mammals. Evidence of their vestigial or retrograde nature is to be found in:

(1) Only their centra are developed—with the exception of the first, which shows partial formation of transverse processes and neural arches (superior cornua);

(2) Delay in the appearance of the centres of ossification. These, instead of beginning in the 7th week as in a typical vertebra, commence after birth. The centre for the 1st coccygeal vertebra appears in the 1st year, that for the 4th vertebra about the 25th year; the 2nd and 3rd at intermediate periods. All four are fused into one piece about the 30th year.

(3) Late in life, between the 40th and 60th year, the coccyx unites with the sacrum.

The number of coccygeal vertebrae varies; four is the normal number, but there may be three or five. In the young foetus (2nd month) as many as eleven coccygeal vertebrae have been counted. The first coccygeal vertebra may join the sacrum, making six sacral vertebrae. The coccygeal vertebrae in anthropoids are more reduced as regards the development of their parts than in man.

The evidence of the former existence of a **true tail** in the ancestral human stock consists of:

(1) From the 4th to the 8th week the coccygeal region of the spine protrudes (Fig. 384), and the vertebrae number from 8 to 11; the notochord is traceable beyond the vertebral segments.

(2) Vestiges of the extensor and flexor muscles of the tail are frequently found (10 % of bodies) on the dorsal and ventral aspects of the sacrum and coccyx. Occasionally small nodules of bone are found in front of the human coccyx, spanning the continuation of the middle sacral (caudal) artery; these nodules represent the chevron bones or haemal arches of tailed mammals. The depressors of the tail are attached to the chevron bones (see Fig. 385).

(3) True tails, consisting of external prolongations of the coccyx, commonly fibrous, rarely containing vertebrae, occasionally occur.

(4) The post-anal pit, always to be seen in the newly-born child, marks the point at which the coccyx disappears below the surface early in the 3rd month; its disappearance being correlated with the

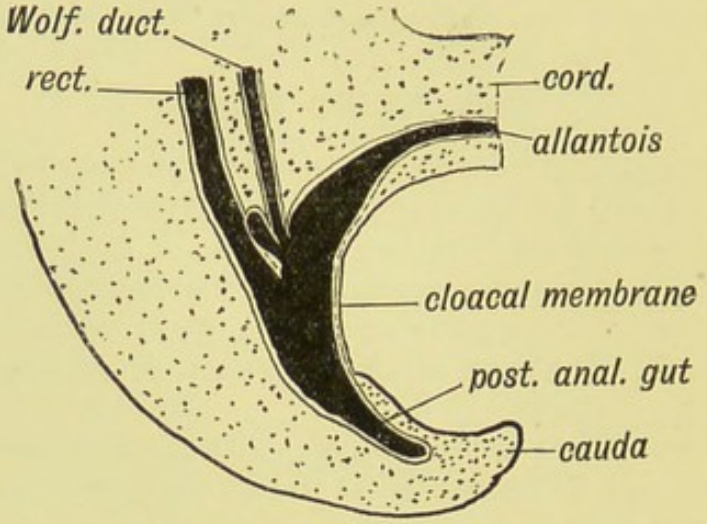


FIG. 384.—The Caudal End of the Body in a Human Embryo of the 3rd week.

division of the cloaca and the establishment of the permanent anus. In man the coccyx forms part of the perineal floor. Instead of projecting far beyond the gut, as in tailed mammals, it terminates $1\frac{1}{4}$ inches above the commencement of the anal canal.

The Pelvic Floor is peculiarly extensive in man, an adaptation to his upright posture. The floor is formed by the following structures:

(1) The levator ani and its sheath (recto-vesical and anal fasciae) on each side;

(2) The coccyx and coccygeus muscles;

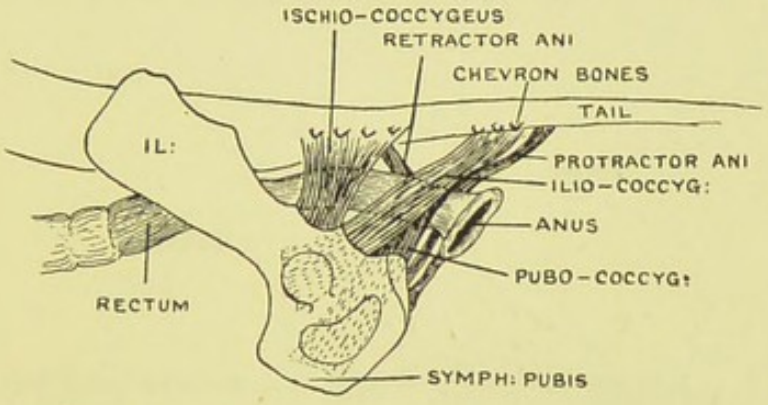
(3) The constrictor urethrae and triangular ligament;

(4) The pyriformis and its sheath may also be included.

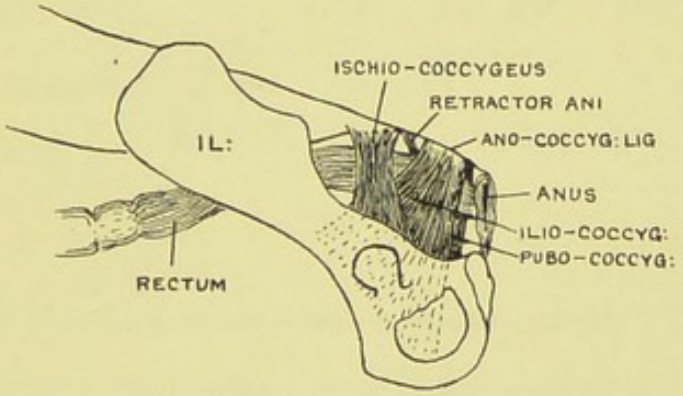
Development of the Pelvic Floor.[1]—The pelvic floor has been evolved in man by a transformation of the tail and the caudal muscles.

[1] The following are some of the more recent British papers dealing with this subject: P. Thompson, *Myology of the Pelvic Floor*, Manchester, 1899; R. H. Paramore, *Lancet*, 1910, May 21st and 28th. In the *Journal of Anatomy and Physiology* the following papers have appeared: P. Thompson, 1901, vol. 35, p. 127; A. M. Paterson, 1907, vol. 41, p. 93; D. Berry, 1907, vol. 42, p. 97; G. Elliot Smith, 1908, vol. 42, p. 198 *et seq.*; P. Cameron, 1908, vol. 42, p. 438.

The arrangement of tail muscles in a four-footed mammal, such as the monkey or dog, is shown in Fig. 385, *A*, and the modification of this form in anthropoids and man in Fig. 385, *B*. In mammals, two muscles, the pubo-coccygeus and ilio-coccygeus act as depressors of the tail, which in four-footed animals plays the part of a perineal shutter. They are attached to the small V-shaped chevron bones on the under surface of the basal caudal vertebrae. Another muscle, the ischio- or spino-coccygeus, acts as a lateral flexor of the tail. It



A PRONOGRADE FORM.



B. ORTHOGRADE FORM.

FIG. 385.—Diagram to show the Pelvic Muscles of a Pronograde Ape (*A*) and of an Orthograde Ape (*B*).

is attached to the transverse processes of the caudal vertebrae, and rises from the dorsal border of the ischium. In man the pubo-coccygeus and ilio-coccygeus are blended into one sheet and form the levator ani. The shrinkage of the tail leaves the muscle partly stranded on the ano-coccygeal ligament (Fig. 385, *B*). Other fibres of the pubo-coccygeus loose their primary insertion to the coccyx, and become attached to the prostate, central point of the perineum, and to the anal canal. Both muscles, especially the ilio-coccygeus, retain in part their primitive attachment to the coccyx (cauda). The spino-coccygeus, or coccygeus muscle, is partly fibrous in man, its outer laminae forming

the small sacro-sciatic ligament; its inner laminae remain muscular and form the coccygeus. In man, too, the origin of the ilio-coccygeus has sunk from the pelvic brim of the ilium on to the obturator fascia (P. Thompson); traces of the primitive origin from the pelvic brim can often be detected (Fig. 387). The white line, a structure peculiar to man, marks the new point of origin of the levator ani from the obturator fascia.

In fishes (selachians) the levator ani is represented by a backward continuation of the rectus abdominis (Paramore). The pelvic part of

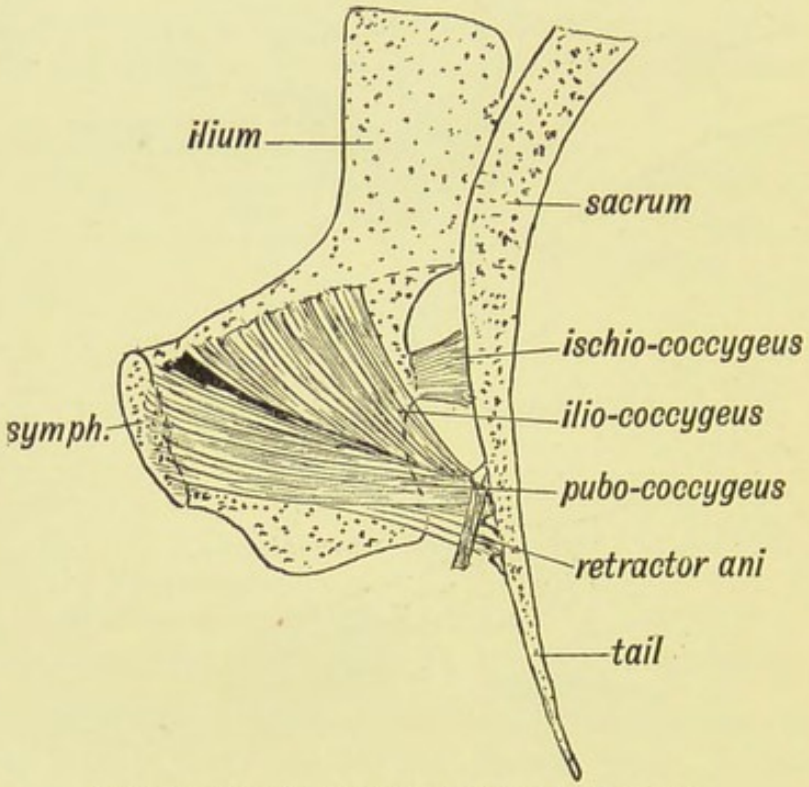


FIG. 386.—The Pelvic-caudal Muscles of a Monkey.

the rectus is attached behind to the tail; anteriorly it is attached to the movable pelvic girdle. The cloaca of the dog-fish passes out between the right and left primitive representatives of the levator ani, which can act on the cloaca, not by depressing the tail as in mammals, but by pulling the pelvis backwards.

On the dorsal and ventral aspects of the sacrum and coccyx, fibrous or muscular vestiges of the anterior and posterior sacro-coccygeal muscles (elevators and flexors of the tail) are commonly to be found in man.

The Pelvic Fascia and Fasciae in General.—It has been customary to regard fasciae as separate structures forming distinct sheets with devious and complex courses. It is possible by dissection to prepare and display them according to accepted descriptions, but the structures so displayed are artificial and not the true structures which the surgeon or physician has to deal with in actual practice.

Embryology is the best guide to their nature. Take, for example, the development of the fasciae seen on making a section of the upper arm. When the limb bud has appeared, which it begins to do about the end of the 3rd week of development, a section through it reveals a uniform composition of more or less rounded mesoblastic cells with a covering of epiblast (Fig. 388, *A*). Very soon the central cells near the axis of the bud are densely grouped and form the basis of the humerus. Others, derived from the muscle plates of the paraxial segments, arrange themselves to form the biceps, triceps and muscles of the arm ; others form the walls of vessels and the sheaths of nerves.

After these various groups of cells have become differentiated, there

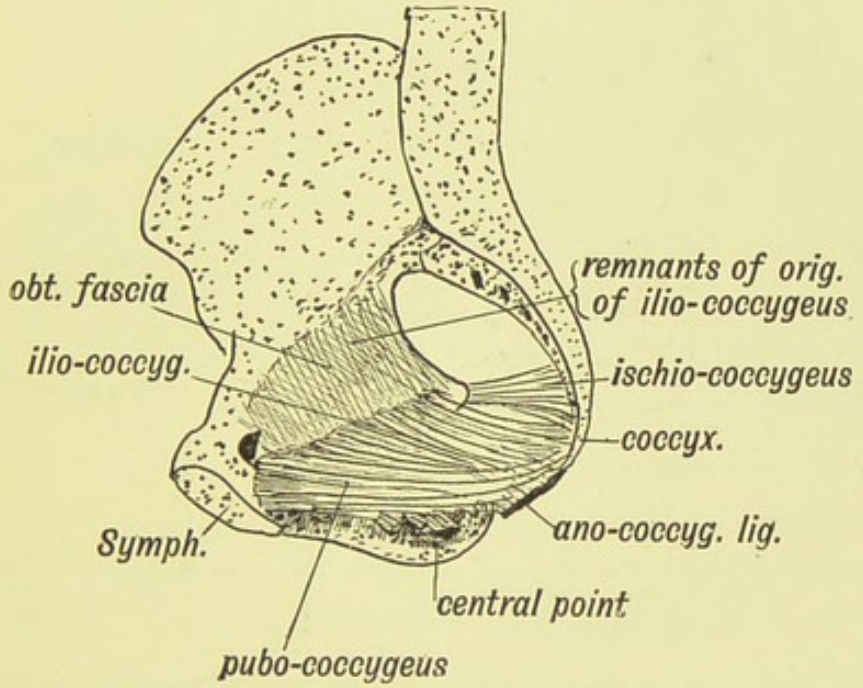


FIG. 387.—The Pelvic Muscles of Man—corresponding to those shown in Fig. 386.

are numerous cells left over which form a basis in which the specialized cells and groups of cells are packed and ensheathed. The undifferentiated mesoblast forms the connective tissue or fascial system of the part. From the manner of its origin it is evident that the connective tissue system—the fasciae and septa—must form a continuous spongework of sheaths, each being in continuity with that of every surrounding structure. The sheaths of the biceps, triceps and brachialis anticus, the periosteum of the humerus, the deep fascia, internal and external intermuscular septa, the sheaths of the vessels and nerves of the arm, represent the mesoblastic tissue which was left over after the individual structures of the brachium were differentiated, and are, from the manner of their origin, necessarily in continuity. They can only be artificially separated from each other. It is more accurate and easier to describe fasciae, then, not as separate structures, but as adjuncts of the structures which they surround or ensheath. As to the manner in which

connective tissue is developed, there are two opinions: (1) that the substance of the cell body elongates and forms a fibre; (2) the more probable, that fibres are formed in a substance which lies outside the cell body, but is under the influence of the cell.[1]

The Pelvic Fascia, which strengthens the pelvic floor, is composed of the sheaths of four muscles:

(1) The Levator Ani;
(2) The Obturator Internus;
(3) The Pyriformis;
(4) The Constrictor Urethrae and deep Transversus Perinei.

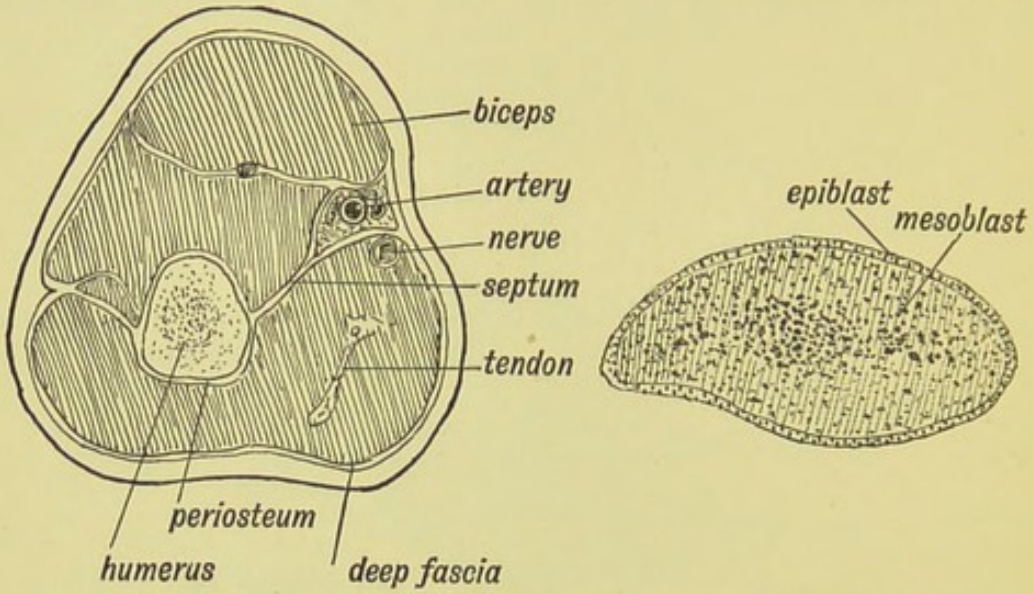


FIG. 388, *A*.—Diagrammatic Section of the Arm Bud of an Embryo at the commencement of the 4th week.
B.—Corresponding Section of the Adult Arm.

The fibrous capsules of the following viscera also form part of it:

(1) Prostate and Vesiculae Seminales in the male;
(2) Vagina and Uterus in the female;
(3) The Bladder;
(4) The Rectum. Under the title of pelvic fascia these eight elements are combined.

To these must be added the important sheaths of the vessels—especially of the vesical, uterine and perineal arteries.[2]

I. **The Obturator Fascia** is the sheath on the inner or pelvic aspect of the obturator internus; the sheath on the outer side of the muscle is formed by the periosteum and obturator membrane. The obturator fascia is attached at the circumference of the muscle. There it becomes

[1] For recent literature see F. P. Mall, *Amer. Journ. Anat.* 1901, vol. 1, p. 329; A. von Szily, *Anat. Hefte*, 1907, vol. 33, p. 225; J. G. Ferguson, *Amer. Journ. Anat.* 1912, vol. 13, p. 129; Korff, *Ergebnisse der Anat.* 1907, vol. 17, p. 247.

[2] See references on p. 396 under the names of Professor Paterson and Professor Elliot Smith.

continuous with the periosteum of the os innominatum. The part above the white line (supra-linear) is intra-pelvic; the part below (infra-linear) is perineal and situated on the outer wall of the ischio-rectal fossa.

II. **The Recto-vesical and Anal Fasciae.**—The levatores ani form a muscular floor for the pelvis, stretching from the white line of one side to the white line of the other. The sheath on their under surface —on the inner wall of the ischio-rectal fossa—forms the anal fascia. On the upper surface, their sheath forms the greater part of the recto-vesical fascia. The pelvic viscera rest on the upper surface of the levatores ani and the capsules of the viscera are continuous with the sheath on the upper surface of the muscles. The combined visceral

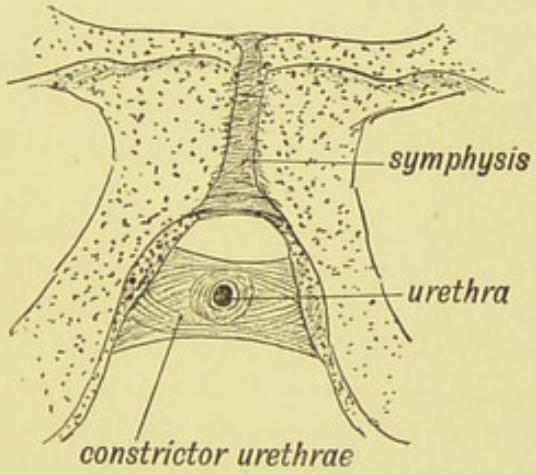


FIG. 389.—The Constrictor Urethrae Muscle.

capsules and upper sheath of the levatores ani form the recto-vesical fascia.

III. **The Triangular Ligament** is situated in the neighbourhood of the constrictor urethrae muscle (Fig. 389), but it can scarcely be regarded as its sheath. It is rather a fibrous septum for giving attachment to the prostate on its deep or pelvic surface and to the bulb and root of the penis on its lower or perineal aspect (Delbet, Elliot Smith). The inferior transverse fibres of the constrictor form really a separate muscle —the deep transverse perineal. The apex of the prostate rests on the muscle, its fibrous capsule being continuous with the posterior layer of the muscle sheath—the deep layer of the triangular ligament.

IV. The inner sheath of the pyriformis forms the **pyriform fascia.** The coccygeus is continuous with the levator ani and its sheath forms part of the recto-vesical fascia. The loose perirectal sheath is also continuous with the tissue of the fascia pyriformis.

The pubo-prostatic ligaments and the lateral vesical ligaments are strengthened parts of the fibrous capsule of the prostate, which provide the bladder with a pubic fixation. The vesical musculature, in emptying the bladder, acts from the pubic fixation thus obtained. The great

strains to which the pelvic vessels are exposed when the pelvic floor and viscera are depressed in forced muscular efforts renders a strong fibrous protective sheath necessary. Hence the tough fibrous coating round the uterine and vesical vessels. Alcock's canal is formed from the fibrous sheath round the pudic artery and nerve (Elliot Smith).

The Cervical Fascia.[1]—From what has been said of the pelvic fascia, the nature and arrangement of the cervical fascia will be readily understood. It is composed of (1) the sheaths of the cervical muscles (sterno-mastoid, etc.); (2) of the sheaths of vessels (carotid sheath, etc.); (3) the sheaths of nerves (axillary sheath, etc.); (4) the fascial capsules of viscera, such as the thyroid body, salivary glands, and pharynx. The carotid sheath and sheaths of the great vessels from the base of the skull to the pericardium within the thorax are formed to a great extent from mesoblastic tissue which was developed within the visceral arches of the pharynx. At first the pericardium lies beneath the mouth and pharynx. With the development of the neck at the end of the 2nd month of foetal life, the cervical structures and their sheaths become stretched.

The muscular sheaths on the inner aspect of the transversalis, iliacus and psoas also have been regarded as forming distinct fasciae.

On the other hand, some fasciae are quite discrete structures. The palmar fascia is part of the palmaris longus muscle; the plantar, part of the plantaris muscle; the vertebral aponeurosis or fascia, part of the layer of muscle to which the serratus posticus superior and inferior belong; the epicranial aponeurosis is part of the platysma sheet. The middle layer of the lumbar fascia represents a primary septum developed between the dorsal and ventro-lateral groups of musculature (see p. 60).

Fascial structures have also a distinct relationship to the **lymphatic system**. Loose alveolar tissue really represents tissue broken up by lymph spaces. Lymphatics follow the septa and capsules of glands and muscles; the lymphatics of the lung collect in the connective tissue separating its lobules. The most remarkable of all the capsular tissues of the body are those represented by the membranes of the central nervous system; there the lymphatic spaces, or clefts which correspond to lymphatic spaces, have separated the cerebral capsule into three layers—the pia mater, arachnoid and dura mater.

Leonard Hill has also drawn attention to the part which ensheathing fasciae play in assisting the circulation of the blood. Every contraction of the muscles of the thigh tends to force the venous blood within the sleeve formed by the fascia lata on towards the heart.

The Body Wall.—Having thus traced the evolution of the pelvic floor and discussed the nature of fasciae generally in connection with the pelvic fascia, we pass on to consider the development and nature of the abdominal and thoracic walls.

[1] See Parsons, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 153.

Bilateral Symmetry of the Body.—From a developmental point of view the body is made up of two symmetrical halves ; each half of the embryonic plate, taking the medullary groove as the line of division, contributes equally to the formation of the body. Each produces a half of the nervous system, each a half of the vascular, muscular and alimentary systems, so that each individual is in reality made up of two identical halves, right and left.

The Ventral Line of the Body.—The two halves are united along the **ventral line** from the mouth to the anus (see Fig. 390). The

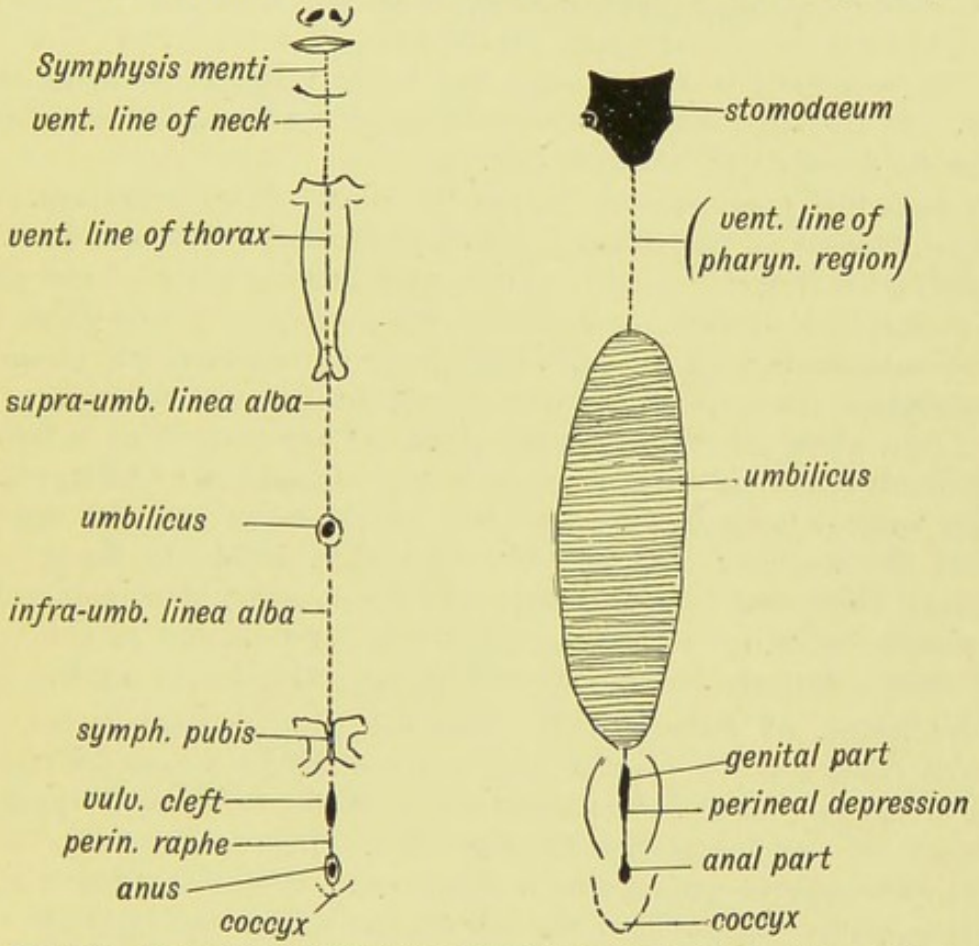


FIG. 390.—Diagram of the Structures formed in the Median Ventral Line of the Body.
FIG. 391.—The Median Ventral Line in an Embryo of three weeks, to contrast with the Corresponding Line in the Adult.

mesoblast, muscle plates, dermatomes, nerves and cartilaginous outgrowths, which are produced on each side of the median dorsal line of the body, meet on each side of the median ventral line. In this line are developed the symphysis of the lower jaw, the body of the hyoid bone (copula), the white line of the neck and angle of the thyroid cartilage, the sternum, the supra-umbilical part of the linea alba, umbilicus, infra-umbilical part of the linea alba, symphysis pubis, the septum of the penis, and of the scrotum and perineal raphe. The ventral line is continued forwards on the face between the parts derived from the mesial nasal processes.

The idea was at one time prevalent that the whole of this line was formed by the fusion of one somatopleure with the other; the median ventral line was the suture formed by the union. Such is not the case. The blastoderm, which lies at first like a cap on the yolk sac (Fig. 18, p. 16), is produced or folded anteriorly to form the fore-gut and the part of the body above the umbilicus; it is produced posteriorly to form the hind-gut and the part of the body below the umbilicus. The blastoderm grows out from the umbilicus to form the embryo in much the same way as a soap-bubble is blown from the bowl of a pipe. In an embryo, at the commencement of the 3rd week, the greater part of the ventral line is occupied by the umbilicus (Fig. 391). At that time the umbilicus is 3 mm. long, the entire ventral line being about 4 mm. At the 6th week the ventral line measures 15 mm., the umbilicus retains its former size, about 3 mm.

At first the somatopleure shows no trace of segmentation. The paraxial masses of mesoblast become segmented early and form the muscle plates (Fig. 57, p. 59). From each muscle plate of the primitive segments a process grows down into the somatopleure (Fig. 392). The somatopleure thus becomes segmented secondarily, the process of segmentation spreading from the dorsal to the ventral side of the plate, but, along the median ventral line of the body wall, a band of the primitive mesoblastic tissue remains unchanged and undifferentiated. In the ventral band between the left somatopleure and the right are formed the sternum and the linea alba (Fig. 390). In lower vertebrates, in fishes, and to a less marked extent in amphibians and reptiles, the somatopleure becomes segmented from end to end of the trunk, each muscle segment being distinctly recognizable in the adult.

Formation of Ribs.[1]—Ribs, like all true skeletal bones, pass through three stages: (1) They are represented by a mesenchymatous or membranous basis in the fibrous tissue (septa) between the muscular segments of the somatopleure (Fig. 392). The condensation of the costal mesenchyma appears as a direct outgrowth from the primitive vertebra at the beginning of the 4th week. Ribs were originally vertebral processes. (2) The mesenchymatous basis or **blastema** of the rib becomes cartilaginous. (3) Ossification of the cartilage begins in the 8th week, but the process of ossification leaves the ventral parts of the costal segments untouched; they form the costal cartilages; in lower forms they become ossified and form sternal ribs. The process of chondrification begins at the dorsal end of the ribs in the 6th week, and spreads ventrally, thus repeating the order in which the blastema was laid down. There is this difference, however, between the two stages—the centre for the chondrification of the rib appears independ-

[1] For development and differentiation of ribs see Charles R. Bardeen, *Amer. Journ. Anat.* 1905, vol. 4, p. 163; also p. 265; Geddes, *Journ. Anat. and Physiol.* 1912, vol. 47, p. 18. For ossification of ribs: Franklin P. Mall, *Amer. Journ. Anat.* 1906, vol. 5, pp. 433.

ently of that for the neural arch, whereas the blastema is a direct extension from the arch. The ribs from the 1st to the 7th are developed in the somatopleure over the pericardium (Fig. 392). In lower vertebrates, such as reptiles, each rib articulates with the neural arch of a vertebra by two heads, dorsal and ventral (Fig. 53, *A*, p. 55). The tuberosity of a rib represents its dorsal head. In man, with the exception of the first and last rib, or in some cases, the two last ribs, the costal head is placed opposite an intervertebral disc, for in position the disc represents the ventral or chordal part of a primitive vertebra. In the case of the first rib the head has shifted backwards to the body

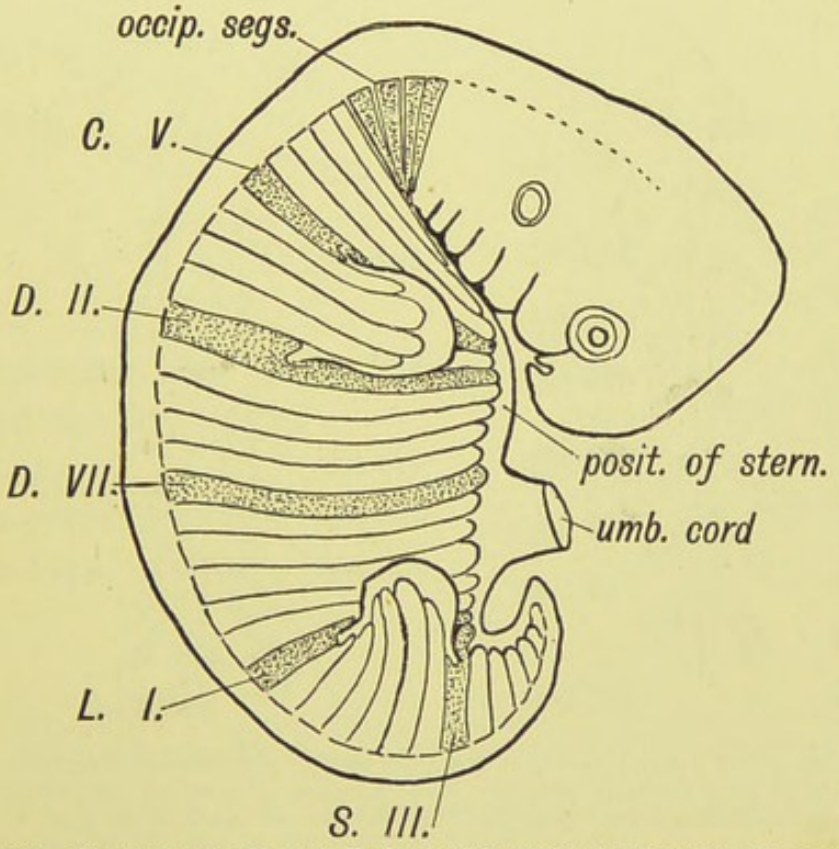


FIG. 392.—Diagram of a Human Embryo (5th week) showing the Arrangement and Extension of the Mesoblastic Segments. (After A. M. Paterson.) The first and last of each segment entering into the formation of the limbs is stippled. The position is indicated in which the sternum is formed.

of the first vertebra, while in the 12th and sometimes the 11th, the head and tuberosity are fused, and both articulate with the part of the vertebra which represents a transverse process.

The Sternum.—In man and anthropoids the sternum has become flat and highly modified with the alterations in the shape of the thorax (Fig. 329, p. 334). With the adaptation to the upright posture the thorax becomes flattened from back to front; its transverse diameter is as great, or greater, than the antero-posterior. The type of respiration is greatly altered. The sternum also becomes wider and shorter. To understand the nature of this change, it is necessary to note the

characters of the sternum of a pronograde mammal, such as the dog or ape (Fig. 393). In such, the sternum is typically made up of seven segments :

1. A modified anterior segment, the **pre-sternum** ;

2. Five narrow, cylindrical segments or **sternabrae,** forming the body of the sternum ;

3. The **ensiform process,** a hind segment, complex in nature and ending in the middle ventral line. The ensiform process frequently bifurcates and is never segmented.

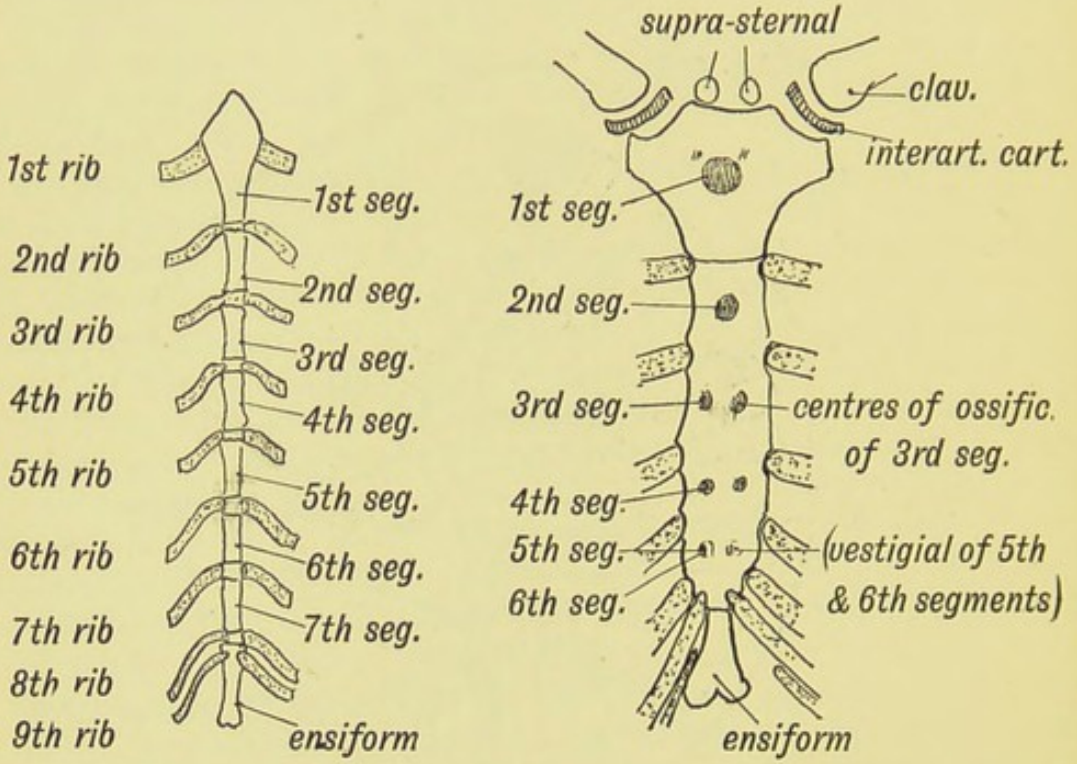


FIG. 393.—The Form of Sternum in a Pronograde (quadrupedal) Mammal.
FIG. 394.—The Form of Sternum in a Mammal adapted to the Orthograde (upright) Posture. The Points of Ossification are also shown.

The chief changes in the human sternum are :

1. Each segment has become flat and wide ;

2. The segments of the body fuse together during the years of adolescence, the fusion beginning behind and passing forwards ;

3. The 4th sternabra of the body is usually vestigial and is probably made up of two or more fused segments.

In low primates 8 or 9 pairs of ribs may reach the sternum, six or more sternabrae being then present. In man the number has been reduced to 7 pairs, the sternal ends of the 7th pair lying in front of the fourth sternabra. It is not uncommon to find the 8th rib reaching the sternum, especially on the right side ; it is rare to find the 7th pair fail to reach the sternum. The more frequent presence of an 8th sternal rib on the right side is due to right-handedness (Cun-

ningham), or, as seems more probable, to give a more secure origin to the right costal fibres of the diaphragm, which have a greater resistance to overcome during inspiration, than those of the left side. In man and the anthropoid apes a new feature appears in the lower costal cartilages. The 5th, 6th and sometimes the 7th throw out processes which articulate with the cartilage below. When, during inspiration, the diaphragm raises the chest, these articulations permit it to act on the 5th and 6th pairs of ribs as well as on the 7th pair.

Morphology of the Sternum.[1]—In amphibia the ventral parts of the shoulder and pelvic girdles develop towards the ventral median

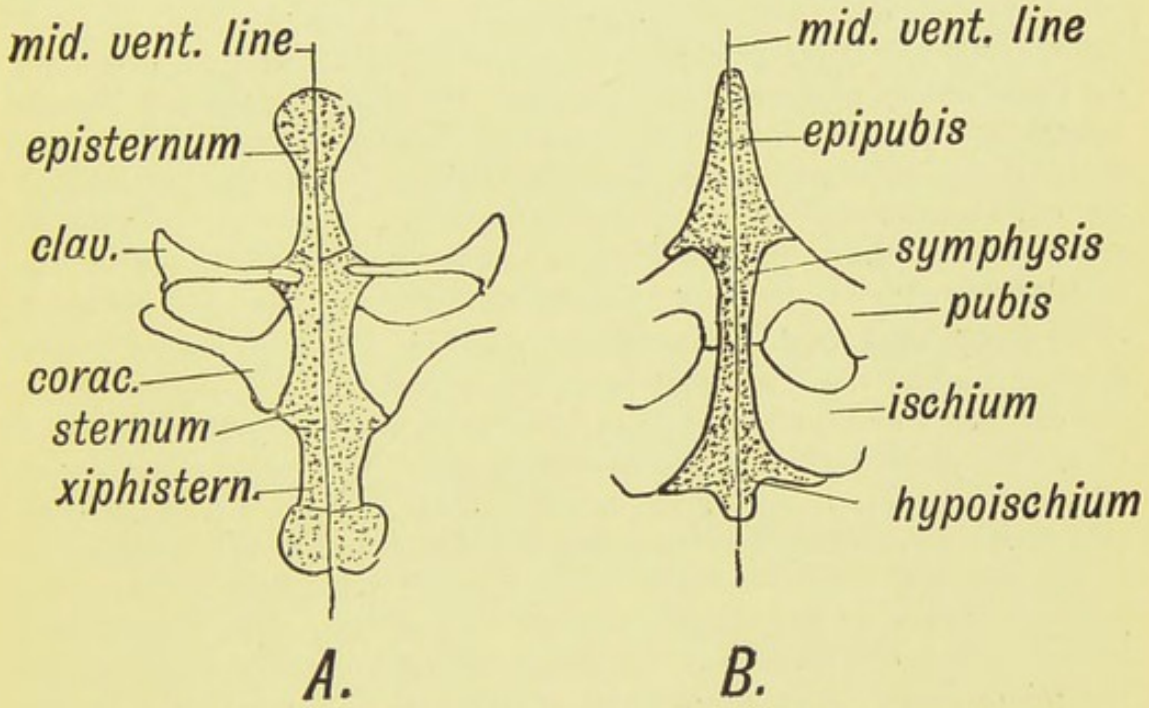


FIG. 395.—The Cartilages developed on each side of the Median Line between the Shoulder and Pelvic Girdles. *A*, the shoulder girdle of the frog; *B*, the pelvic girdle of sphenodon. (The term "epi-sternum" is wrongly applied in Fig. *A*; it should be omo-sternum or supra-sternum. There is now a general agreement that the term episternum should be applied to the membrane bone formed between the clavicles.)

line. In the median line a rod of cartilage is formed between them (Fig. 359). The median rod is differentiated as right and left bars from the ventral parts of the limb girdles. The right and left bars fuse to form the median cartilages. The median rod between the shoulder girdles becomes the sternum; it is divided into three parts—anterior, which projects in front of the girdle (omo-sternum or supra-sternum); posterior, behind the girdle; and the middle, with which the shoulder girdle articulates (Fig. 395, *A*). The sternum affords a basis from which muscles act on the shoulder girdle, and also a ventral

[1] The account given by Paterson (Hunterian Lectures, 1903) has been followed with some modifications. For an introduction to the more recent literature see Whitehead and Waddell, *Amer. Journ. Anat.* 1912, vol. 12, p. 89.

basis for the articulation of the shoulder girdle. In all classes of vertebrates, the sternum is developed over and shields the heart. The median cartilage of the pelvic girdle is similarly divided into anterior, middle and posterior parts (Fig. 395, *B*).

The evolution of a costal type of respiration in reptiles leads to a further stage of development. Some of the costal processes of the vertebrae grow towards the median ventral line, some of them reaching and articulating with the middle part of the bar between the shoulder girdles; this part now serves as a fulcrum or sternum for both ribs and girdle. Such a condition is also seen in birds and monotremes (Fig. 417). In the higher mammals, the ventral part of the shoulder girdle retains only its ventral connection with the sternum through the clavicle; it still serves as the basis of origin for muscles which act on the shoulder girdle and on the arm. Its chief purpose has become respiratory. In the human sternum the three parts of the primitive sternum can be recognized: the supra-sternal bones (Fig. 394) which are only rarely separated from the presternum, represent the anterior part (omosternum); the manubrium and body, the middle part of the shoulder girdle sternum; and the ensiform process, the posterior part.

Development of the Sternum.—In Fig. 396 four stages in the development of the human sternum are represented. Stage *A* shows the extent to which the ribs have become chondrified towards the end of the 6th week; the cellular costal blastema, into which the process of chondrification is spreading, is not shown. In the following week (Stage *B*) the process of chondrification has reached the middle line in the region of the presternum. The ventral ends of the ribs are now joined together by a ventral or lateral sternal bar. The sternal bars in the region of the presternum have begun to fuse together across the middle line. At their anterior extremities they are joined by the ventral cartilaginous end of the clavicle. In the presternum there is thus an element apparently derived from the ventral end of the clavicle. In Stage *C*, about the 8th week, the process of fusion is advanced, but the projection of the foetal heart and liver at this time (see Fig. 39, p. 40) tends to keep them apart. Each sternal bar has now 7 ribs continuous with it, and its posterior end is free. Early in the 3rd month (Stage *D*) the process of fusion is complete, the cartilaginous basis of the sternum has been formed by the fusion of right and left bars. The diaphragm is descending at this time to its final position, the pleural cavities are rapidly forming, and the liver is assuming a more abdominal position. Charlotte Müller,[1] whose illustrations are represented here, found that the mesenchymal sternal bars were chondrified as direct extensions from the ribs.

The sternum is thus developed in the median ventral line over the pericardium and between the mandible in front and the umbilicus

[1] *Morph. Jahrb.* 1906, vol. 35, p. 591.

behind (Figs. 390, 392). The mesoblast condenses during the 4th week on each side of this part of the median line to form the right and left mesenchymal halves of the sternum, which anteriorly are continuous with the bases of the ventral part of the shoulder girdle (Fig. 397). These two halves, the right and left **mesenchymal sternal bars,** fuse gradually in the middle line, the process of fusion commencing at the presternum and spreading backwards.

The sternum is regarded by Paterson as a structure rising independently of the ribs on each side of the median ventral line. This,

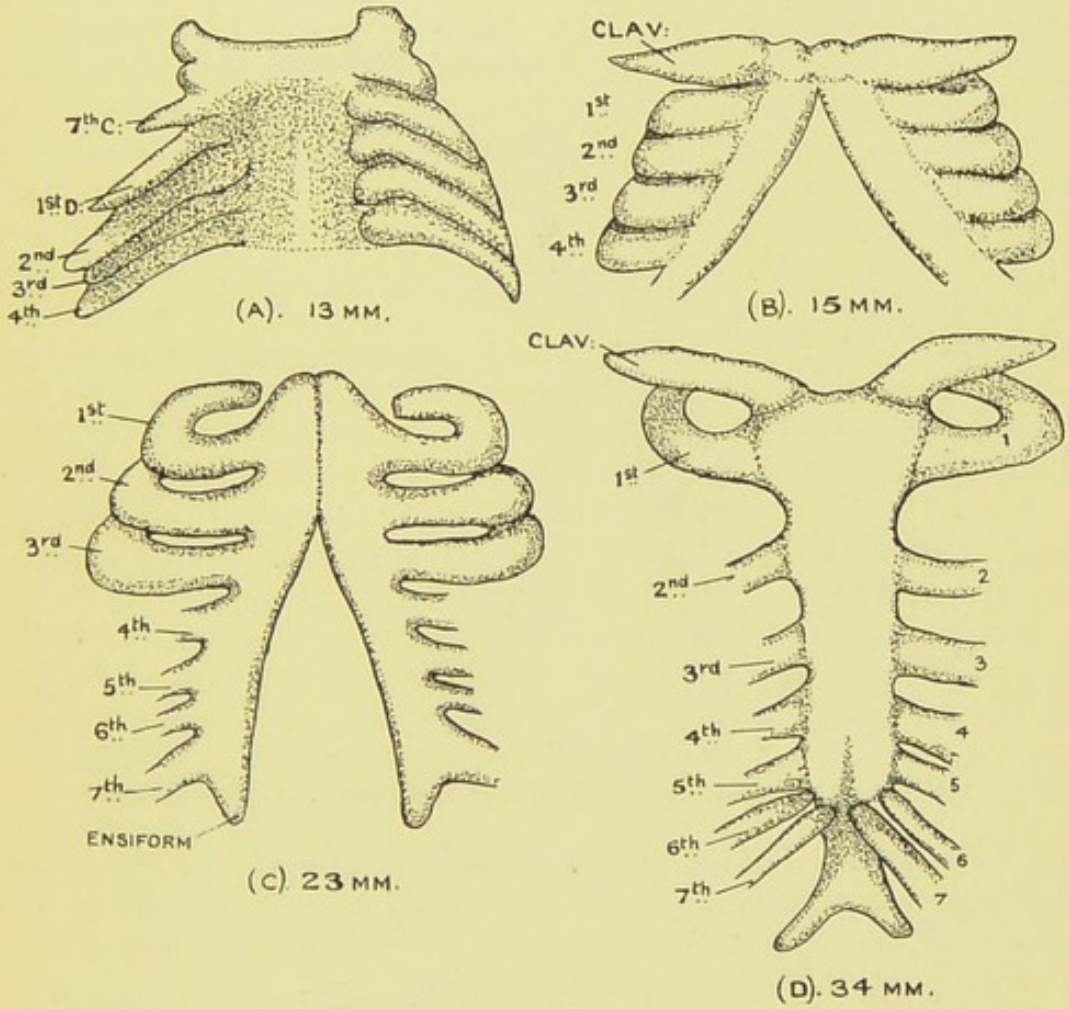


FIG. 396.—Four Stages in the Chondrification of the Human Ribs and Sternum and showing the Fusion of the Sternal Bars. (After Charlotte Müller.) *A*, 6th week ; *B*, 7th week ; *C*, 8th week ; *D*, early in 3rd month.

however, is not the commonly accepted view. Ruge's researches led him to the conclusion that the segments of the sternal bars were produced as buds from the ventral ends of the ribs. The evidence of comparative anatomy and the difference in the type of the cartilage cells in the costal and sternal elements negative Ruge's interpretation.

In its development the sternum passes through three stages—fibrous, cartilaginous and bony.

1. **Fibrous** or **mesenchymal Stage.**—At the 6th week (Fig. 397) the

costal cartilages are already chondrified. The mesoblast on each side of the median line, in which they end, has become condensed, and forms the membranous basis of the two sternal bars (Paterson). The bars begin to fuse together anteriorly.

2. **Cartilaginous Stage.**—The blastema of each sternal bar begins to chondrify in the intervals between the ends of the costal cartilages. The process of chondrification and fusion proceed apace, and by the commencement of the third month the segments of each side have united to form the **cartilaginous** sternal bars (Paterson). Fibrous joints are subsequently formed between the presternum and mesosternum

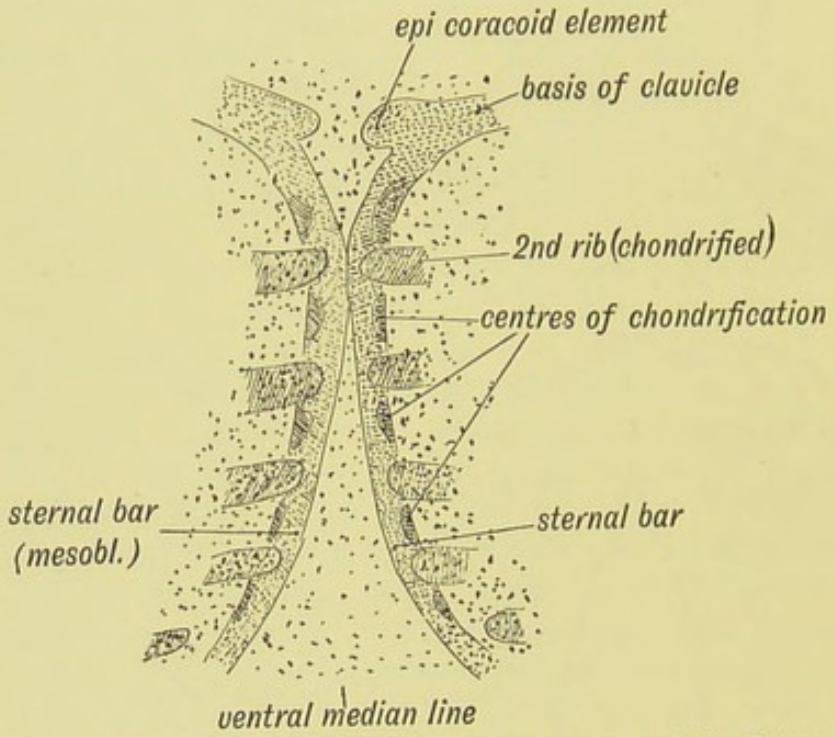


FIG. 397.—The Sternal Bars in an Embryo of six weeks. (After Paterson.)

and between the mesosternum and ensiform process. A fibrous, and then synovial joint, is also developed at the union of the costal cartilages with the sternum, except in the case of the first pair, where a synovial joint is only occasionally present.

3. **Ossification.**—A centre appears for each sternabra ; those for the third and fourth of the mesosternum are frequently double, one being placed on each side. The centres for the 4th mesosternal segment are frequently absent. The centre for the presternum (there may be two or even more) appears about the 4th month ; the centres behind appear in the 6th and 7th month ; that for the 4th sternabra of the mesosternum appearing about the time of birth ; that for the ensiform four or five years after birth. The process of fusion of segments begins behind about puberty ; the segments of the mesosternum are united together by the 25th year. Occasionally a median foramen may be seen in the sternum ; it is due to imperfect union of the sternal bars.

The Sterno-Manubrial Joint [1] becomes of great functional importance in man and those primates adapted to the upright posture. Even in old age this joint is rarely ossified (8 per cent., Paterson). In man a considerable respiratory movement occurs between the manubrium and body of the sternum. The manubrium moves in continuity with the ventral ends of the first pair of ribs; the body of the sternum follows the excursion of the 3rd to the 7th pairs of sternal ribs. As a rare abnormality (commoner in black than in white races) this joint is formed between the first and second segments of the mesosternum.

Presternum.—Clear evidence of the origin of the sternum from the shoulder girdle is to be seen in the presternum. In the earlier developmental phases, it is continuous with the precoracoid element in the ventral end of the clavicle (Figs. 395, 396, 397). It is separated from this element by the development of the sterno-clavicular joints and meniscus. In over 80 per cent. of bodies the upper border of the human manubrium sterni shows traces of the supra-sternal bones which represent the anterior parts (omosternum, epicoracoids) of the primitive sternum. Very rarely these bones are separate (Fig. 394); commonly they are present as elevations or nodules on each side of the suprasternal notch (Paterson). The interclavicular ligament, which represents the interclavicle of birds (episternum), reptiles and monotremes (Fig. 417), is attached to the presternum.

Linea Alba.—The separation of the sternal bars is not the reproduction of an ancestral phase, but is simply due to the embryological disturbance caused by the large yolk sac and the large embryonic liver. In Fig. 398 is shown the early condition of the linea alba—from the classical research by Bardeen and Lewis.[2] The umbilical cord is still distended by a loop of intestine, and the two recti are wide apart, separated by the mesial ventral membrane—the **primitive linea alba.** The two sternal bars are also held apart by the condition of the umbilical structures; indeed, the primitive linea alba is not only wide, but also extends from the neck to the perineum. In the 3rd month the umbilical structures become reduced, the chest wall expands before the growing lungs and the mesial ventral line becomes gradually closed.

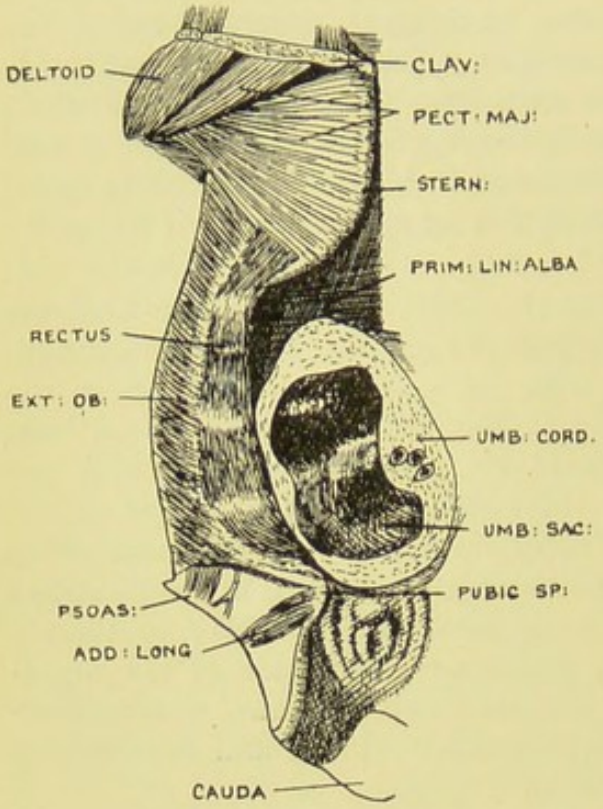
In Fig. 399 a transverse section is shown of the muscular layers in the anterior or thoracic body cavity of a lizard.[3] It will be seen that there are three layers: an outer represented by the rectus and external oblique; an inner by the transversalis, and a middle double layer—the internal and external intercostals. In the abdomen they are

[1] Keith, *Further Advances in Physiology*, edited by Leonard Hill, 1909 (Arnold); *Journ. Anat. and Physiol.* 1896, vol. 30, p. 275.

[2] C. R. Bardeen and W. H. Lewis, *Amer. Journ. Anat.* 1901, vol. 1, p. 1; *Amer. Journ. Anat.* 1901, vol. 1, p. 123 (Nerves of Abdominal Wall).

[3] Keith, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 243; Kazzander, *Anat. Hefte*, 1904, vol. 23, p. 541 (Dev. of Rectus Abdominis).

combined in one layer—the internal oblique. The three layers are functionally different ; the transversalis is a constrictor of the body cavity ;



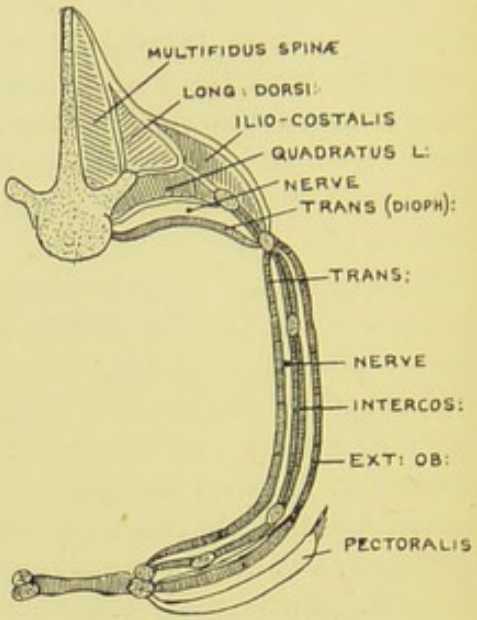


FIG. 398.—The Primitive Linea Alba in a Human Foetus in the 7th week—20 mm. long. (After Bardeen and Lewis.) Only the right half of the body is shown ; the rectus abdominus is lateral in position, it and the sternal bars being kept from the mesial ventral line by the structures in the neighbourhood of the umbilicus.

FIG. 399.—Transverse Section of the Thoracic Wall of a Lizard to show the Primitive Arrangement of the Muscular Strata of the Body Wall.

the middle layer is mainly respiratory in its action ; the outer is also respiratory, but chiefly concerned in body movements.

CHAPTER XXI.

THE LIMBS.

Evolution of the Limbs.[1]—The nature of the primitive structures from which limbs were evolved is still a much debated question. The manner of their development in vertebrate embryos makes it certain that they were not outgrowths from the vertebral system; in every case they sprout out from the somatopleure, which encloses the body cavity, and are always supplied by the nerves of that lamina—the ventral branches of the spinal nerves. We are also certain that the limbs correspond to the pectoral and pelvic fins of fishes. It is clear that when pulmonary forms of vertebrates were evolved, the slight structures which were equal to the balancing and finer movements of an animal suspended in water, had to undergo great modifications in order to become capable of moving and supporting the body on land. It was with the evolution of pulmoniferous land-living vertebrates that a very definite type of limb made its appearance. In all cases it is the same; it is made up of a basal segment or girdle, with a free part divided into proximal, middle and distal segments. The distal segment carried 5 digits.

Although man has departed greatly from the primitive mammalian type in the structure of his brain and trunk, yet in the elements which enter into the formation of his limbs he has retained more of the ancestral mammalian features than many other mammals. He retains the original number of digits; the bones of his hand and foot are much less specialized than those of the horse. It is true that the skeleton of his lower extremity has been extensively modified for his plantigrade posture, yet under all the adaptational features one can see very clearly the outlines of a most primitive form.

[1] The following papers will give those interested a clue to the extensive literature on this subject: Geddes, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 350; Osborn, *Amer. Journ. Anat.* 1907, vol. 7, p. 171; Goodrich, *Quart. Journ. Mic. Science*, 1906, vol. 50, pts. 1, 11; E. Müller, *Anat. Hefte*, 1909, vol. 39, p. 469.

Embryonic Limbs.[1]—The limbs begin to appear at the end of the 3rd week. A slight elevation or ridge is then seen to run along the dorsal border of the somatopleure, at some distance from the row of primitive segments formed in the paraxial mesoblast (Fig. 400). The limb buds spring from this ridge as flat processes with an upper, dorsal or extensor surface, and a lower, ventral or flexor surface. The two borders are anterior or cephalic and posterior or caudal. It is generally held that the lateral ridge, of which the limb buds are specialized parts, represents a continuous row of lateral fins. If this

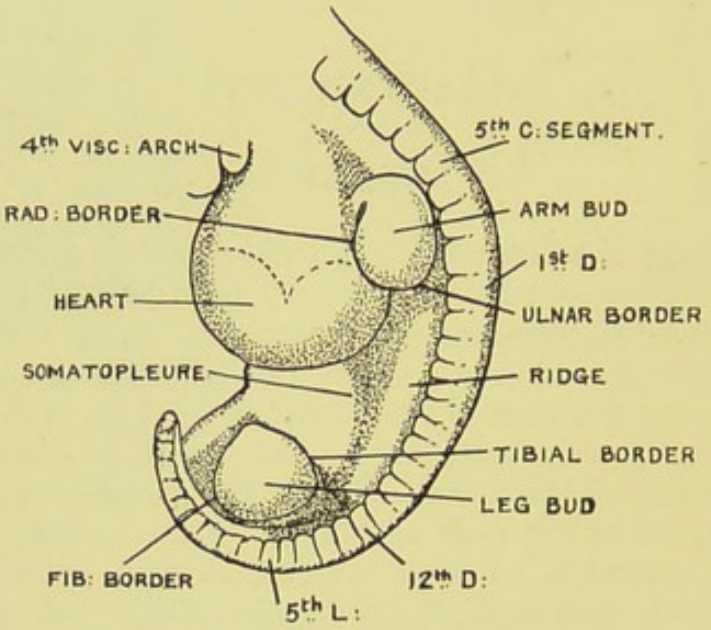


FIG. 400.—Lateral View of a Human Embryo at the 28th day, showing the Limb Buds, Lateral Ridges, and Primitive Segments.

view is right, then the fore and hind limbs represent highly specialized fin-rays.[2]

A section shows each bud to be composed of undifferentiated mesoblast, with a covering of epiblast (Figs. 388, *A*, *B*, pp. 400 and 420). It represents in structure a process of the undifferentiated mesoblast of the somatopleure or body wall; hence the limbs are to be regarded, not as structures developed from the axis of the embryo, but as *processes of the body wall*. Extensions grow into each limb bud from the muscle-plate and skin-plate (dermatome) of the segments which are situated opposite the origin of the bud. Each corresponding segment of the spinal cord also sends to the limb bud a nerve process. At least seven body segments contribute to the formation of each limb (Fig. 392). Outgrowths from the myotomes into the limbs have been observed only in the embryos of lower vertebrates; their occurrence in higher

[1] Development and Differentiation, see Bardeen's Monographs, *Amer. Journ. Anat.* 1904, vol. 4, pp. 163, 265; vol. 6, p. 259 (muscles and nerves of lower extremity); also Bardeen and Lewis, 1901, vol. 1, p. 1.

[2] See references on p. 413.

vertebrates is inferred. When the arm musculature becomes apparent as a mass in the 5th week, it shows no signs of a multiple origin.

Changes in External Conformation.—In the 4th week (Fig. 401) the limb buds are unsegmented; in the 5th a constriction marks the hand off; the position of the elbow being indicated in the same week. In the 7th week the fingers appear as thickenings in the *webbed* hand, the middle digit being indicated first. They become free early in the 3rd month; occasionally they remain attached, the child being born with

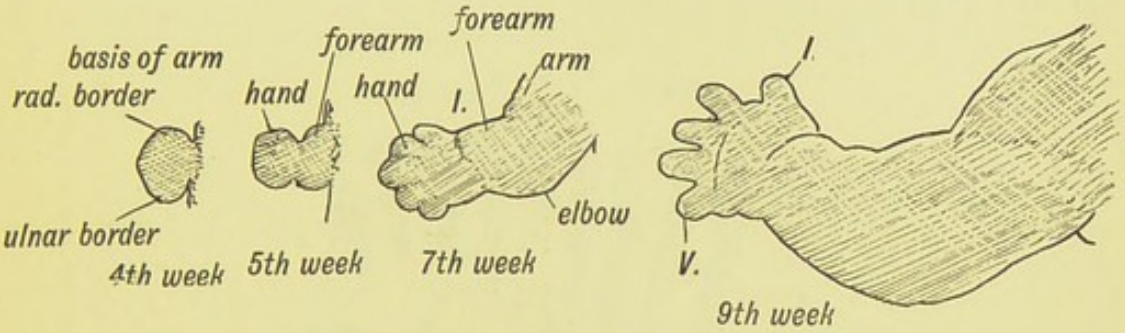


FIG. 401.—Development of the Upper Limb. (After His.)

its fingers in a **syndactylous** condition. The shoulder remains buried in the body wall; the skeletal structures of the arm and thigh are the first to be differentiated; those of the forearm and leg precede the cartilaginous differentiation of the shoulder and pelvic girdle. In all the embryological changes the upper extremity is nearly a week ahead of the lower.

The Internal Differentiation of Tissues begins at the basal part of the limb and spreads towards the digits, the terminal phalanges being the

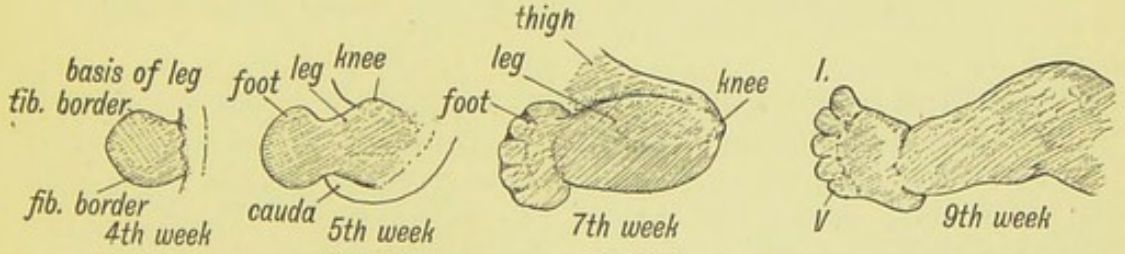


FIG. 402.—Development of the Lower Limb.

last of the skeletal parts to become differentiated (8th week). The mesoblast or mesenchyme becomes condensed in the axis of the bud and forms the cellular basis, or **blastema,** of the limb bones. The skeletal basis of mesoblast is continuous, but where joints are to be formed there occur opener formations in the arrangement of the cells. Centres of chondrification appear in the skeletal blastema of the arm in the 5th week (shaft of humerus) and the leg in the 6th week (shaft of femur). The condition of the skeletal blastema of the arm of a human foetus

at the end of the 1st month is shown in Fig. 403.[1] The centres of chondrification have appeared for the humerus, radius, ulna and certain of the carpal bones; the centres for the phalanges have not yet begun. The scapula, acromion and clavicle (outer part) are continuous; a common centre appears for scapula and acromion, the outer clavicular blastema is chondrified separately. Before the end of the 2nd month the cartilaginous bases of all the arm bones have been differentiated, the terminal phalanges being the last to form. Centres of ossification begin to appear in the latter part of the 2nd month, and correspond generally to the centres of chondrification.

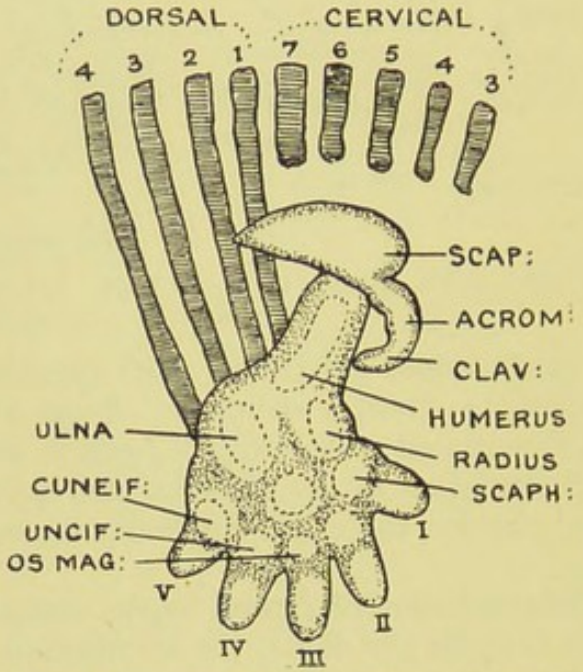


FIG. 403.—The Skeletal Blastema of the Upper Extremity of a Human Embryo at the close of the 1st month—10 mm. long, showing the Cartilaginous Centres for the Formation of Bones. (W. H. Lewis.)

The mesoblast between the chondrified bases of the bones, by a process of vacuolation within and between the cells, opens out into a cavity and forms the synovial membranes of the joints (Fig. 424). The joints are all formed before the end of the 3rd month. During the 2nd month muscles, vessels and nerves are differentiated; the tissue left over, not included in these structures, forms their sheaths, and the fasciae and connective tissue of the limb. The processes of the nerve cells to form the nerves, and of the muscle plates to form the muscles, grow in very early (see Fig. 407). The blood vessels appear first as a capillary plexus surrounding the ingrowing nerve buds; in some mammals (the lemur, etc.) this embryonic plexus persists and forms the **plexus mirabile.** The limb vessels spread outwards from the segmental vessels.

[1] W. H. Lewis, "Development of the Arm," *Amer. Journ. of Anat.* 1901, vol. 1, p. 145; E. Gräfenberg, *Anat. Hefte*, 1906, vol. 30, p. 1.

Skeletal Blastema of Lower Extremity.—About the beginning of the 7th week the blastema of the ilium becomes joined to the costal masses of the 1st, 2nd and 3rd sacral vertebrae (Fig. 404). The scapula, which at the beginning of the 2nd month lies opposite the 4th, 5th, 6th, 7th cervical vertebrae, retains its freedom (Fig. 403). By the middle of the 7th week the cartilage centres have appeared for the majority of the bones of the lower extremity (Fig. 404). The centres for some of the tarsal and for the phalanges are formed before the end of the 2nd month, the terminal phalanges being the last. The acetabulum develops at the site of union of the iliac, ischial and pubic cartilages

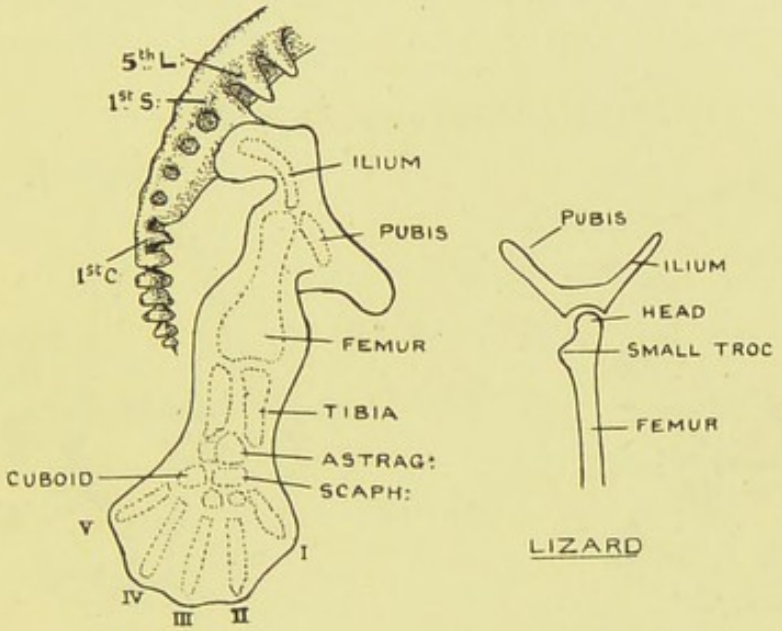


FIG. 404.—The Skeletal Blastema of the Lower Extremity of a Human Embryo in the 7th week—14 mm. long. (Bardeen.) Inset is the outline of the upper part of the lower extremity of a lizard. (Parsons.)

at the end of the 2nd month. At that time the femur has no neck—a condition seen in reptiles (Fig. 404). The neck begins to form early in the 3rd month. In the 3rd month the symphysis pubis is formed.

Torsion and Rotation of the Limbs.—As the limbs are developed, the extensor surfaces of the knee and elbow are directed upwards. If the body of an adult were placed in the prone position, it would be necessary, in order the restore the limbs to their embryonic position, (1) to draw them out at right angles to the axis of the body, (2) to rotate the leg **outwards** so that the extensor surface of the knee is directed upwards, with the great toe in front and the little toe behind. (3) The arm, on the other hand, would require to be rotated **inwards** to bring the elbow (extensor surface) into the dorsal position. The rotation which brings the embryonic limbs into the adult position appears to occur at the junction of the limb girdle with the trunk.

Rotation at the Limb Girdle.—To understand the extent of this rotation it is best to compare the scapula and ilium and pick out

their corresponding points. The extensors of the thigh and arm may be taken as guides. The long head of the triceps and rectus femoris of the quadriceps manifestly correspond; their points of origin—the anterior border of the ilium and axillary border of the scapula—may be regarded as homologous points. The other corresponding points are shown in Fig. 405. The sacral articular surface of the ilium corresponds to part of the supra-spinous fossa. To restore the limb girdles to their primitive and corresponding positions, the scapula has to be rotated so that its axillary or posterior border comes to occupy the position of its spine, while the ilium has to be placed at right angles to the spine and its anterior border rotated outwards until it occupies a position corresponding to the axillary border of the scapula. The

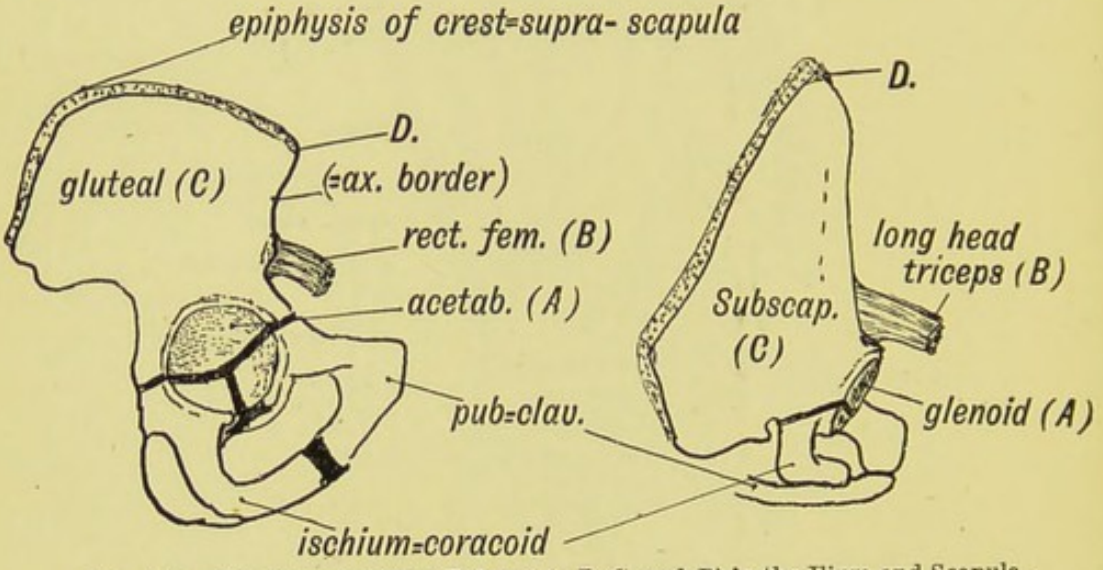


FIG. 405.—The Corresponding Points (*A*, *B*, *C*, and *D*) in the Ilium and Scapula.

free edge of the spine represents a former border of the scapula; the supra-spinous blade of the scapula appears first in mammals.

There is a manifestly spiral twist in the humerus, but it is doubtful if this be in any way due to the torsion which the limb undergoes.

Lately Professor Parsons [1] and Professor Geddes [2] have shown that although there is a direct correspondence in the elements of the upper and lower extremity, the correspondence is a reversed one—the right ilium representing a "mirror-image" of the right scapula. Clearly they are right. There is no evidence of a rotation of the elements of the limb-girdles during development. A reference to Fig. 406 will show that there is a correspondence between the structures on the distal border of the fore-limb and on the proximal border of the hind-limb. The subscapularis, teres major and latissimus dorsi (*A*), derivatives of a common flexor mass, correspond to the ilio-psoas—also the derivative of a common flexor mass (A^1). The triceps and quadriceps (*C*, C^1)

[1] F. G. Parsons, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 388.

[2] A. C. Geddes, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 350.

also agree; so do the olecranon and ulna with the patella and tibia. The specialization of the proximal digit of the hand to form a pollex, and of the first of the foot to form a hallux, occurs only in primates, and are comparatively late modifications in the evolution of vertebrates. The mirror-image theory particularly applies to the distribution of nerves. To explain this peculiar relationship, which exists between the fore and hind limbs of the same side in vertebrates, one is tempted to suppose that they represent anterior and posterior

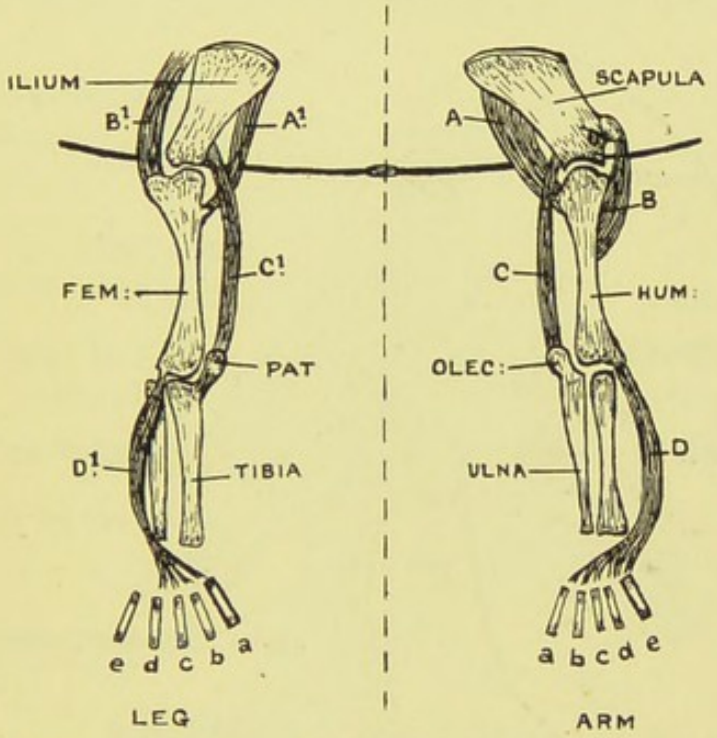


FIG. 406.—Diagram of the Fore and Hind Limbs of the same side to show the "Mirror-image" Relationship between their Constituent Parts. The vertical line passing through the umbilicus is regarded as the centre from which the two limbs have become differentiated. (After Parsons and Geddes.)

halves of a single primitive locomotory appendage; the line of separation is represented by the adjacent borders of the limbs. On such a theory the adjacent borders should be constituted alike.

Segmental Nature of the Limbs.—The nerves of the limbs, probably also the muscles, vessels and skin, are derived from a number of the primitive body segments. The 4th cervical to the 2nd dorsal contribute to the formation of the upper extremity; the 1st lumbar to the 3rd sacral to the lower, but even in man the extent to which the most anterior and most posterior of each of these contributes to the limb varies considerably in extent. Since the processes of the skin and muscle plates of these segments retain in the limbs (so we infer from the study of lower vertebrate limbs) their original nerve supply, it is evident that the muscles and skin of the human limbs may be assigned to their original body segments by a study of the distribution

of the nerves. Such a study has been carried out by a great number of men during the two last decades.[1] The primitive simple arrangement of muscle segments may be seen in the fins of certain fishes, but in man these segments have been divided and combined and special muscles formed from them; yet the primitive arrangement can be recognized.

Nerve Supply of the Limbs. The Arm.—It is important to note that the limb buds arise from the ventro-lateral aspect of the trunk (Fig. 407) near the junction of the somatopleure with the paraxial

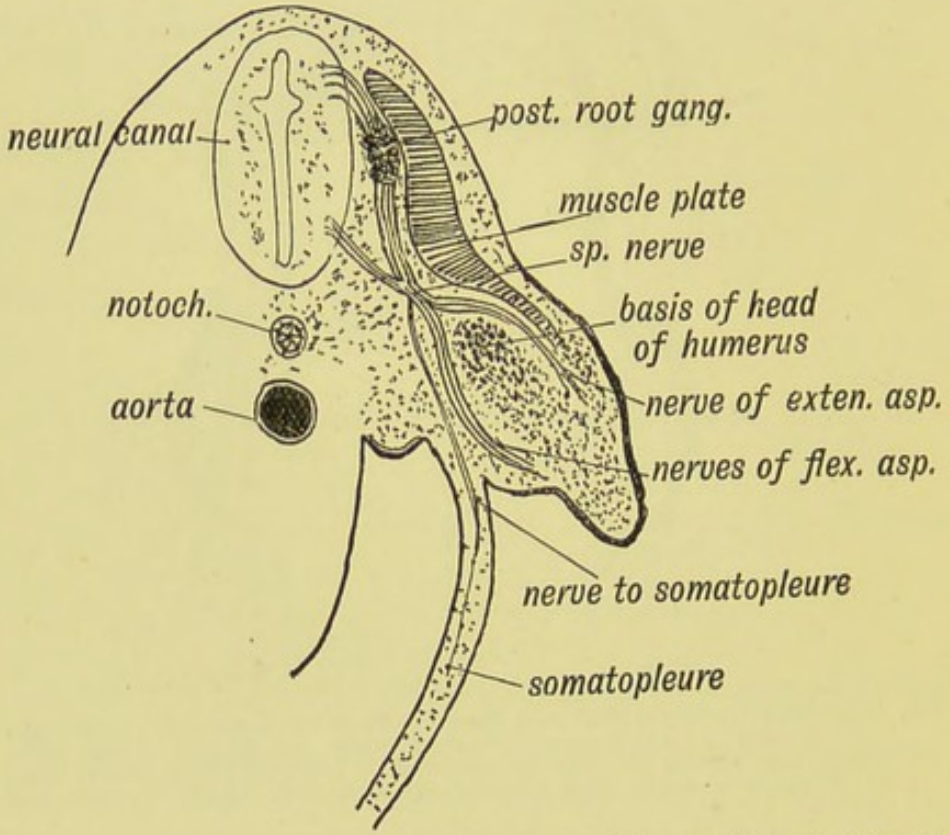


FIG. 407.—Section of the Arm Bud of a Human Embryo at the end of the 4th week. (Alex. Low.)

mesoblast. Therefore the nerves of the limbs are the nerves of the ventro-lateral zone—the lateral cutaneous branches of the typical segmental nerves (Fig. 408). The muscles are derived from the ventro-lateral sheet, which gives rise to all the muscles of the body wall. As soon as the limb buds appear, bundles of fibres from the anterior and posterior nerve roots of the corresponding body segments enter them and keep time with their growth. The limb nerves are at first so large in comparison with the size of the limb bud that they are crowded together and already form a plexus (Figs. 409, 410). As they enter the bud, the nerves encounter the condensed skeletal mesoblast at its

[1] For references to recent papers see Geddes, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 350; also the researches of Bolk, *Morph. Jahrb.* from 1894 to 1898.

base and divide into a dorsal or extensor set and a ventral or flexor set (Figs. 407 and 408).

The relationship of the segmental nerves to the arm bud at the end of the first month of development is shown in Fig. 409—a drawing taken from Professor Streeter's research.[1] The base of the arm is then situated in the cervical region; the hypoglossal nerve issues almost at its anterior border. The arm descends during the 2nd month, the nerves consequently undergoing an elongation. The ventral divisions of the spinal nerves from the 5th cervical to the 1st dorsal have entered the bud, and already the chief nerves can be traced. The brachial

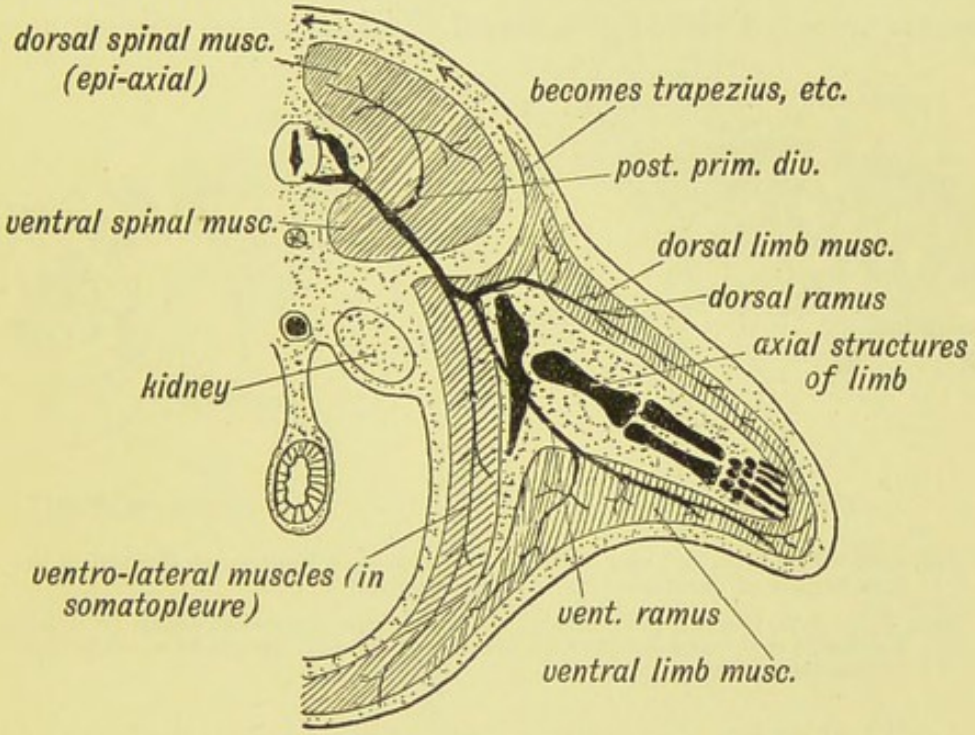


FIG. 408.—Schematic Section showing the Origin and Arrangement of the Muscles and Nerves of the Limbs. (After Kollmann.)

plexus is formed; it is not due to a compression of the nerves due to a lack of room, but represents a physiological or functional adaptation. Professor Goodrich [2] found that in fishes only the posterior root or sensory fibres entered into the plexiform arrangement—the motor or ventral fibres proceed into the limb without exchanging fibres. By the beginning of the 3rd month all the muscles and nerves are differentiated. In Fig. 409 the distinction between the nerves of the extensor and flexor aspects of the limb is shown.

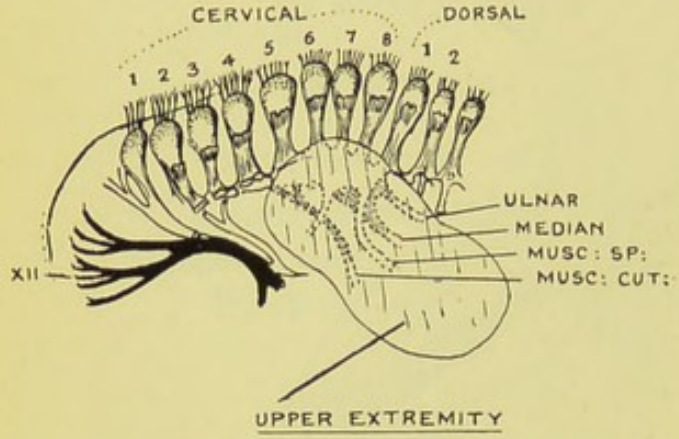
In Fig. 410 the bud of the hind limb of the same embryo is represented. It will be seen that the stage of development is less advanced than in the arm. The crescentic base of the limb is in relationship with the spinal nerves from the 1st lumbar to the 3rd sacral. The

[1] Geo. L. Streeter, *Amer. Journ. Anat.* 1908, vol. 8, p. 285.

[2] See reference on p. 413.

crural and sciatic plexuses are continuous; their separation occurs in the middle of the 2nd month, when the ilium becomes attached to the costal processes of the sacrum.

The nerve supply assists to indicate the body segments from which the arm is developed (Fig. 411). The 4th cervical is the most anterior, the 2nd dorsal, sometimes it is the 3rd, is the most posterior segment. Hence the arm is produced from seven, or more commonly eight, segments in all. Each segment contributes from its nerve, its muscle plate and probably also its artery (see p. 231). The typical distribution of a segmental nerve to the limb bud is shown diagrammatically in Fig. 408. Each segmental nerve, as is the case with the typical lateral cutaneous nerves, divides into a **dorsal** division for the extensor muscles,



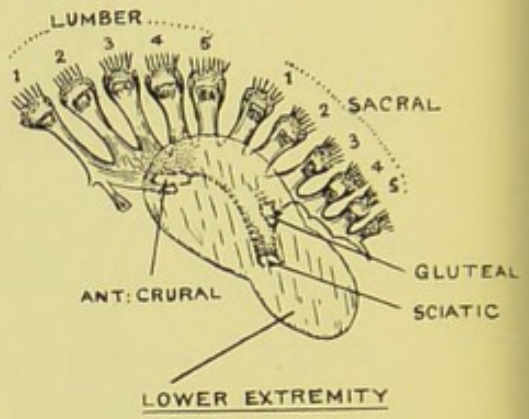


FIG. 409.—The Arm Bud and its Nerves in a Human Embryo at the end of the first month of development. (After Streeter.)

FIG. 410.—The Bud of the Lower Extremity with its Relationship to Spinal Nerves in a Human Embryo at the end of the first month of development. (After Streeter.)

and **ventral** for the flexor muscles. The nerves to the extensor muscles form the posterior divisions and posterior cord of the brachial plexus; the nerves to the flexor muscles form the anterior divisions and the outer and inner cords. The processes to the limbs from the skin plates and muscle plates are also divided into dorsal and ventral sets; the one set making up the extensor aspect of the limb; the other, the flexor aspect.

Clinical and experimental research has shown that each of the seven or eight segments contributes to the cutaneous supply of the limb. The classical investigations of Sherrington [1] in the segmental distribution of the sensory nerves in the limbs of apes, showed that they are arranged in a definite and orderly manner (Fig. 412). The sensory distribution of the spinal nerves in the human arm is shown diagrammatically in Fig. 411. The distribution of the motor nerves of each segment is fully described in anatomical text-books.

[1] Sherrington, *Journ. of Physiol.* 1892, p. 639.

Only three anomalous points in the arrangement of nerves in the upper limb require attention: (1) The segments which supply nerves for the arm are nearly constant. The extent, to which the 4th cervical and 3rd dorsal contribute, varies; the degree of variation is markedly less than in the lower limb. (2) A part of the musculo-cutaneous nerve frequently joins the median below the insertion of the coraco-brachialis;

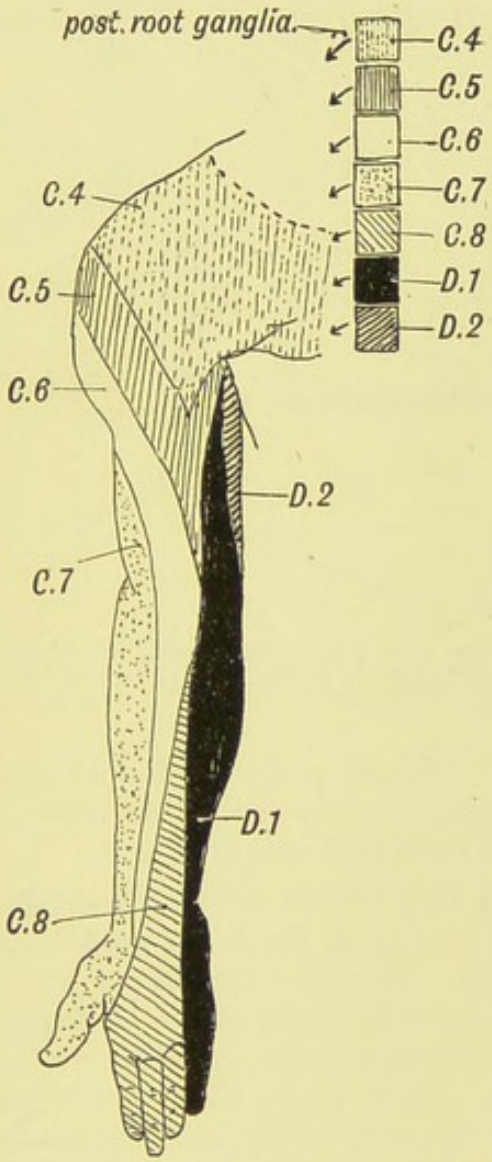


FIG. 411.—The Distribution of the Posterior Roots of the Spinal Nerves on the Flexor Aspect of the Arm.

this communication is frequently seen in lower primates; its meaning is not known. (3) A communication between median and ulnar in the forearm is also common and is seen constantly in some primates. The communicating branch passes with the deep branch of the ulnar nerve to the palm. It is also manifest that there is a correspondence between the musculo-spiral nerve on the proximal border of the arm and the sciatic on the distal border of the leg.

The Formation of Nerve Plexuses[1] depends on the following factors: (1) Each skin segment is supplied not only by its own nerve, but by the nerve of the segment in front of it and behind it. (2) A muscle segment, such as may be seen in the rectus abdominis, is supplied by its own and the two adjacent nerves, the fibres forming a plexus before entering the muscle. (3) Each muscle is formed by the combination of parts of two or more segments, and therefore its nerve rises from two or more spinal nerves. (4) The muscles of the limbs have

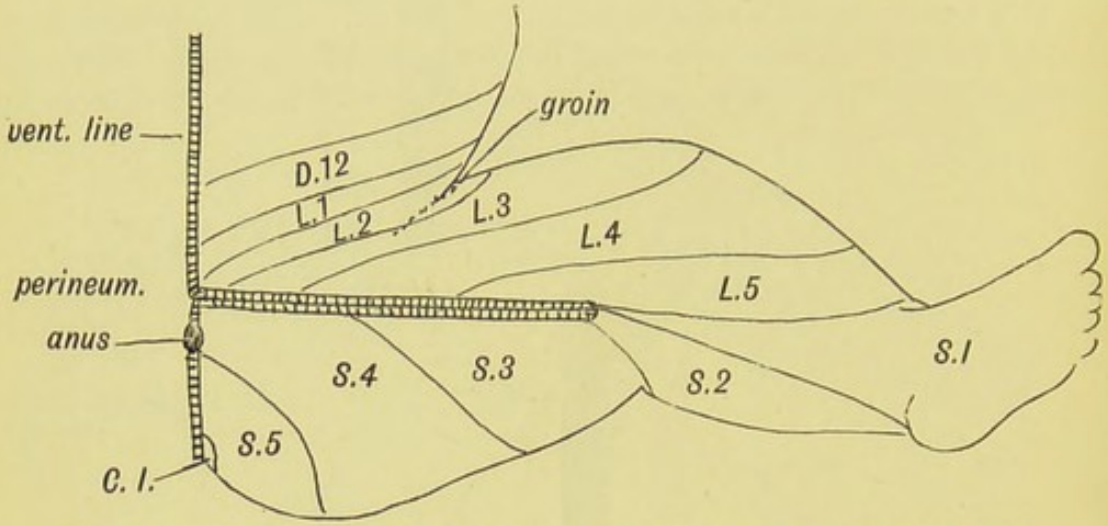


FIG. 412.—Diagram to show the typical manner in which the Posterior Nerve Roots are distributed in the Lower Limb (based on Sherrington's researches into the Sensory Distribution of the Limb Nerves of Apes).

migrated from their original positions and carried their nerves with them. All these influences have led to the nerve fibres being assorted into definite cords at their first outgrowth.

Nerve Supply of the Lower Limb.—Usually ten segments contribute to the nerve supply of the lower limb—the 12th dorsal to the 4th sacral (Fig. 413). The sensory nerves are derived from these segments; the motor nerves begin at the 1st lumbar segment and end at the 3rd sacral. There is a considerable variation in the number of body segments or vertebrae to which the lower limb is attached; usually it is the 25th vertebra which becomes the 1st sacral, but it may be the 26th or 24th (p. 46). Of these three forms, the first is the normal type (25th); the second the post-fixed type (26th); the third the pre-fixed type (24th). There is even a greater variation in the segments which contribute nerves to the limb; the **normal** motor segments are the 1st lumbar to the 3rd sacral; in the **post-fixed type** (more common than the next) the motor segments commence at the 2nd lumbar and cease at the 4th sacral; in the **pre-fixed type** the motor segments commence at the 12th dorsal and end at the 2nd sacral. The spinal

[1] H. Braus, *Verhand. Anat. Gesellsch.* 1910, p. 14 (Origin of Nerve-Plexuses).

nerve which bifurcates and joins both lumbar and sacral plexuses is known as the **nervus furcalis.** In the normal type it is the 4th lumbar ; in the pre-fixed type it is the 3rd lumbar ; in the post-fixed type the 5th lumbar.

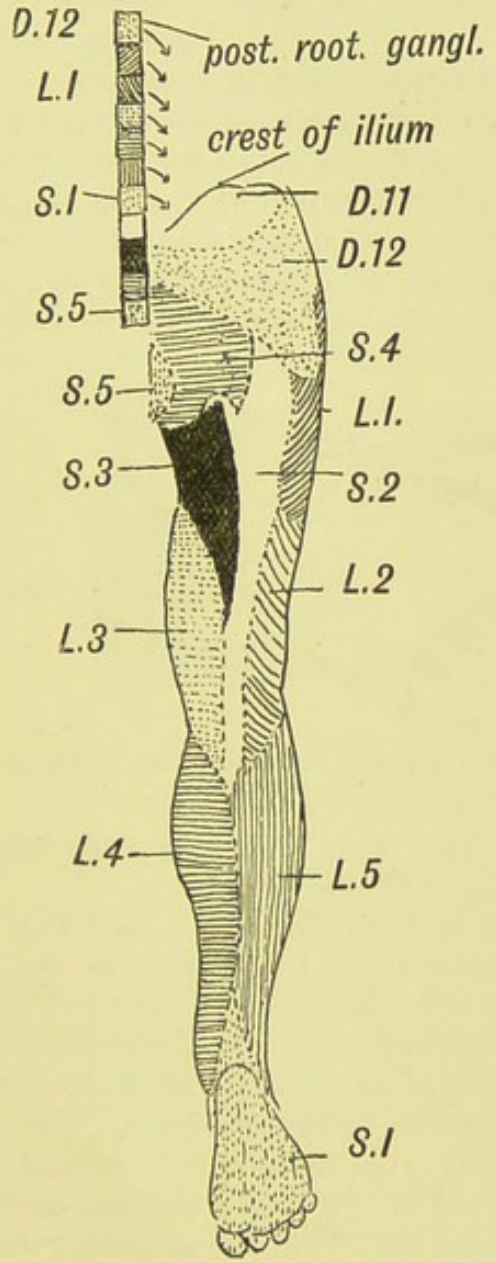


FIG. 413.—Flexor Aspect of the Lower Limb, showing the Sensory Distribution of the Segmental or Spinal Nerves.

The **nervus bigeminus,** normally the 4th sacral, may also vary in a corresponding manner.

The nerves to the extensor surface of the lower limb, the anterior crural, external popliteal, etc., represent the **dorsal divisions** of lateral cutaneous nerves (Fig. 408). The nerves to the adductor and flexor aspects, the obturator and internal popliteal, represent the **ventral divisions.** In a considerable number of individuals, the dorsal division

(external popliteal) and ventral (internal popliteal) of the great sciatic separate in the pelvis, the external popliteal perforating the pyriformis.

The segmental distribution of the motor nerves in the lower extremities is given at length in text-books on anatomy. The muscular segments correspond approximately in their distribution with those of the skin.

It will be remembered that the perineal region is developed behind the limb buds of the lower extremities (Fig. 392); hence its nerve supply from the most posterior nerve segments (3rd and 4th sacral).

Sherrington found that the posterior roots of the limb nerves were distributed in a regular and simple manner in apes. His results are applied to the lower limb of a human foetus in Fig. 412. The actual distribution in man, which has been partially worked out by clinicians,

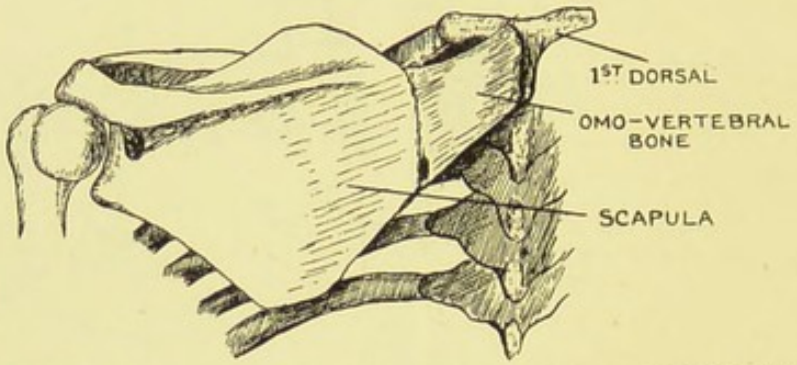


FIG. 414.—The Omo-vertebral Bone in a Case of Congenital Elevation of the Shoulder.

varies considerably from what might be expected from Sherrington's results (compare Figs. 412 and 413).

In the human leg and foot there is a tendency for the nerve fibres destined for the outer digits to proceed in the external saphenous nerve instead of by the musculo-cutaneous. The **external saphenous** nerve may supply the 4th and 5th digits (the ancestral form) in a manner similar to the ulnar nerve in the hand; more frequently it is confined to the outer side of the 5th digit. The outgrowing fibres of the obturator nerve may be divided into ventral and dorsal parts by the blastema of the pubis. In such a case the more ventral fibres cross the ramus of the pubis and form the **accessory obturator** nerve.

Congenital Elevation of the Shoulder.[1]—We have already seen that the arm of the human embryo is cervical in position—in this respect resembling the pectoral fins of fishes. It descends during the 2nd month, reaching its final position over the ribs in the 3rd month. Its descent is not only accompanied by an elongation of the brachial nerves, but also by a downward migration of certain muscles—originally placed in the neck—the trapezius, the serratus magnus, and the latissimus

[1] The condition is often spoken of as *Sprengel's* shoulder. See H. A. T. Fairbank, *Brit. Med. Journ.* 1911, ii. p. 1533. For recent literature see D. M. Greig, *Edin. Med. Journ.* Sept. 1910; March 1911.

dorsi. The descent may be arrested. The condition, which is not rare in children, is often accompanied by irregularities in the formation of the cervical vertebrae—for the elongation of the cervical region to form a neck is related to the descent of the shoulder, of the heart, and of the diaphragm—and with the appearance of a skeletal element of the shoulder girdle which is present in certain fishes (dipnoi and selachians). This omo-vertebral element is represented in Fig. 414—from the classical case of Willet and Walsham (1880). In fishes this bone joins the supra-scapula to the occiput; when it appears in man it is usually fixed to, or articulates with, the spinous processes of the lower cervical vertebrae. Man's upright posture has thrown the duty of constantly supporting the shoulder on the trapezius. Under certain

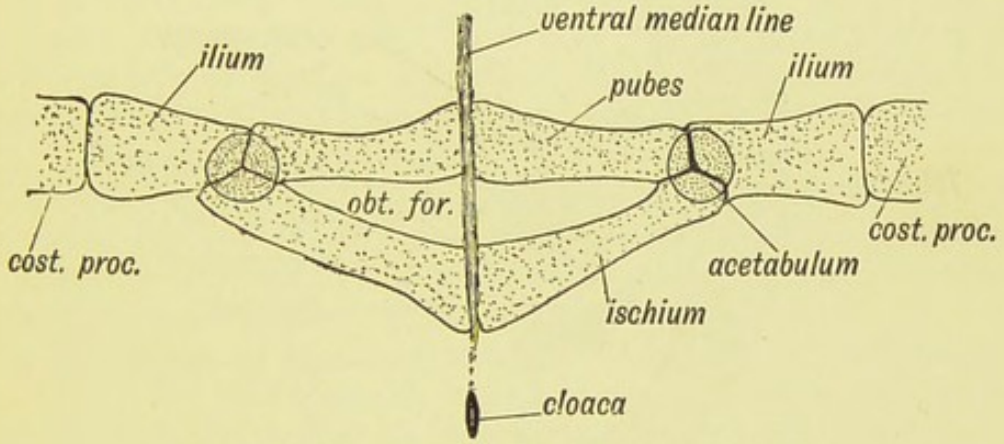


FIG. 415.—Diagram of the Pelvic Girdle of a Lizard.

circumstances it gives way, the shoulders then drooping. Symptoms may then arise from pressure of the nerves against the 1st rib—or a cervical rib.[1]

Pelvic and Shoulder Girdles.—In the basal part of each limb bud a cartilaginous arch is developed. It consists of a **dorsal** and **ventral** part, the joint cavity for the articulation of the limb being situated at the junction of the two parts. Fishes retain this simple primitive form of girdle.

The **pelvic girdle** has undergone less modification from the primitive type than the shoulder girdle. The primitive type of pelvic girdle, such as is seen in the crocodile or lizard, and of which the mammalian type is a derivative, is shown diagrammatically in Fig. 415. For comparison the human girdle in the 5th week foetus is shown in Fig. 416.

The dorsal element consists of the **ilium**; it is attached by ligaments to the costal process of one or more sacral vertebrae. In the ventral portion of the mesenchymal arch are developed two cartilaginous elements, the **pubes** and **ischium**, both of which take part in the formation of the acetabulum (Fig. 415). Both reach the ventral median line in which a median bar of cartilage is developed (see Fig. 395).

[1] T. W. Todd, *Anat. Anz.* 1912, vol. 41, p. 385.

In man the following changes may be noted: (1) The costal processes of the sacral vertebrae (2½ usually) have fused together to form the lateral sacral mass; with these the ilium articulates (Fig. 404); (2) the vertebral border (crest) has become enormously elongated and gives attachment to abdominal muscles, cutting off the fibres of insertion of the external oblique which form the chief part of Poupart's ligament; (3) the ischium does not reach the ventral line. In most birds, neither ischium nor pubes reach the ventral line. The pubes fail to meet in cases of ectopia vesicae, just as the sternum is cleft in cases of ectopia cordis. The symphysis pubis is formed in the ventral line in the 3rd month. The cotyloid bone—os acetabuli—is formed

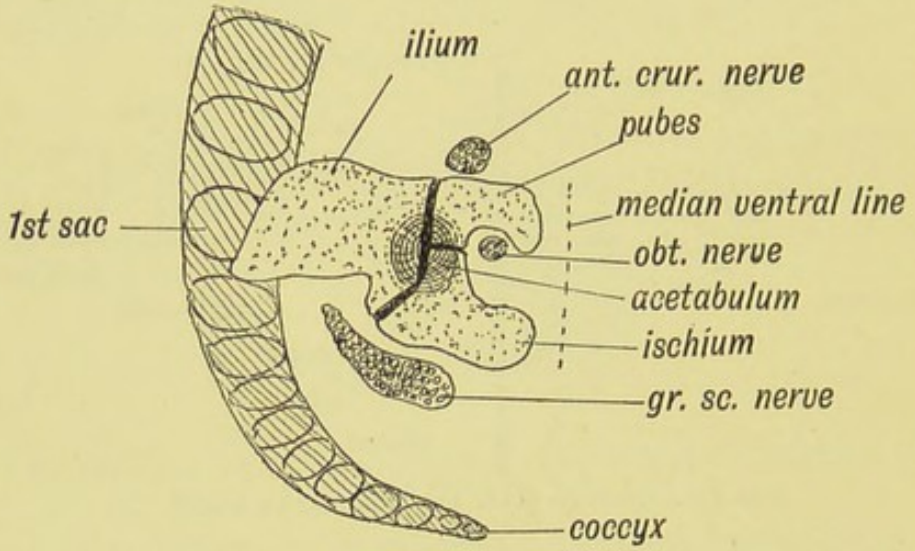


FIG. 416.—The Pelvic Girdle of a Human Foetus at the 7th week. (After Kollmann.)

in the Y-shaped cartilage between the three elements. It ossifies in the 13th year. Professor Howes has pointed out that it is this ossification which forms the pubic part of the acetabulum, and that it is really part of the pubes.

The **median pelvic bar** corresponds to the sternum, and like it is of bilateral origin. In reptiles (Fig. 395, p. 407) it is divided into anterior, middle and posterior parts. The anterior parts form the cartilaginous epiphysis of the pubic crest, which represent the marsupial bones, and correspond to the supra-sternal ossifications; the middle parts form the cartilaginous surfaces of the symphysis; the posterior parts (the hypoischium of reptiles) form the epiphyses on the pubic arch and ischial tuberosity (Parsons).

Congenital Dislocation of the Hip Joint.—Under this title two quite different groups of cases are included: (1) cases in which there has been an arrest of development of the parts entering into the formation of the hip joint; (2) cases which are produced during the act of birth. It is only the first group which is referred to here. In

the 7th week—when the foetus is about 20 mm. in length, the three cartilaginous elements—ilium, ischium and pubis—meet in a Y-shaped acetabular suture, the pubic element being later in chondrifying than the other two. In the later part of the 2nd month the hip joint is formed by (1) cartilaginous outgrowths from all three elements, but especially from the iliac—to form the acetabular cup ; (2) the separation of the head from the shaft of the femur by the formation of the neck (see p. 417). The joint is completely formed early in the 3rd month. The synovial lining of the joint arises from an ingrowth of mesoblast into the blastemal tissue between the acetabulum and head of the femur (Jenkins[1]). The outgrowth of the acetabular brim may be arrested at the reptilian stage reached in the 2nd month ; congenital dislocation of the femoral head, which is fully formed, results. In the cases of cleft palate and imperforate anus (and this is a similar case) human development is arrested at a reptilian stage. The condition has an obscure relation to the development of the female sexual characters ; 90 % of cases occur in female infants.

Shoulder Girdle.—The duckbill (ornithorhynchus) shows the most generalized type of mammalian shoulder girdle ; it resembles closely the primitive reptilian type ; from such a form the various types of mammalian shoulder girdle were probably evolved.

The dorsal part of the arch consists of (1) **scapula**, (2) **supra-scapula** (Fig. 417). The supra-scapula is represented in man by the cartilage along the vertebral border ; it ossifies in the early years of manhood. The supra-spinous part of the scapula appears first in higher mammals ; it is produced late in the development of the scapula (in the 3rd month of foetal life) by the upgrowth of the supra-spinous blade of the scapula ; it is not represented in the pelvic girdle. The dorsal segment of the pelvic girdle becomes fixed to the costal processes ; the corresponding part of the scapula remains free.

In the typical reptilian shoulder girdle, as in the pelvic (Fig. 415), two elements are formed in the ventral part of the arch—a posterior part—the **coracoid**, corresponding to the ischium, and an anterior—the **precoracoid**, corresponding to the pubes.[2] Both elements reach the ventral median line in which the sternum is developed (p. 407). In ornithorhynchus the coracoid element is represented by two bones—the coracoid and epicoracoid—the second of which is formed from the

[1] G. T. Jenkins, *Brit. Med. Journ.* Dec. 15, 1906. For recent paper on congenital dislocation see G. C. Simpson, *Lancet*, 1911, vol. 11, p. 1129 ; Bridge, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 57 (Congenital Dislocation in Bandicoot).

[2] I have repeated the statement made in the last edition, but the reader will perceive if the mirror-image correspondence is true (p. 418) ; there the ischium on the distal side of the pelvic girdle corresponds with the coracoid on the proximal side of the shoulder girdle—as stated above—but the representative of the pubis should be on the distal—not on the proximal side of the shoulder girdle as the clavicle is placed. I am convinced that there is no pubic representative in the shoulder. Developmental phenomena show that the clavicle is a new formation.

anterior end of the sternal bar and therefore corresponds to the supra-sternal ossification of man. The dorsal extremity of the coracoid helps to form the glenoid cavity ; its ventral articulates with the presternum. In man and all higher mammals, in which mobility of the fore limb is of advantage for speed and free movement, the coracoid element is much reduced. It forms merely a process on the scapula, which it joins in man about the 15th year. It still enters into the formation of the glenoid cavity, the articular part (supra-glenoid) having a separate centre of ossification which appears in the 12th year. It is possible that the costo-coracoid ligament may be derived from the ventral part of the coracoid element—the part which articulates with the sternum in the duckbill. The **precoracoid** in the shoulder girdle of the lizard corresponds to the pubic element in the pelvis. The precoracoid, which,

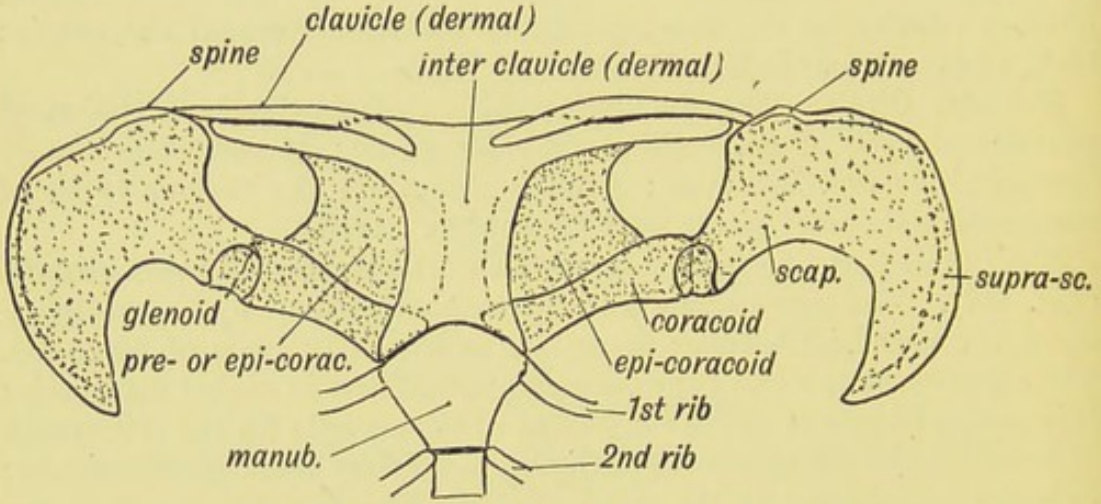


FIG. 417.—The Shoulder Girdle of Ornithorhynchus.

like all the primitive elements of the pelvic and shoulder girdle, is formed in cartilage, has been partly or entirely replaced in all mammals by the development over it of the clavicle, a dermal or membrane-formed bone, the first of all the bones to ossify. There is thus no true representative of the clavicle in the pelvis. The interclavicle so strongly developed in the ornithorhynchus and in the " merry-thought " of the fowl is also a dermal bone. It is represented in man by the inter-clavicular ligament. It is highly probable that the clavicle does not completely replace the precoracoid. Its inner or ventral part becomes (1) the cartilaginous inner end of the clavicle ; (2) the interarticular cartilage (Fig. 418).

In order to give greater mobility and speed to some four-footed mammals, the clavicle has been reduced to a ligamentous band, except at its extremities (rabbit, dog, etc.). In climbing animals, and those in which the power of grasping or embracing is highly developed, the clavicles are fully developed.

Maldevelopment of the Clavicle.—There is a malformation of the clavicle, which throws light on its double nature. In the congenital disease known by the cumbersome name of **cleido-cranial dysostosis,**[1] the clavicle is made up of two parts—an outer and inner, united by a fibrous band which may form only a short ligament, or may even represent the middle two-thirds of the bone. In such cases all the bones of the skeleton which are formed in membrane—especially those of the cranial vault—are imperfectly ossified. The condition in this disease suggests that the clavicle is a compound bone made up of outer and inner elements, and that arrest has occurred before the two elements have become joined by a third or membrane-formed bone. The clavicle is represented in the 5th week by a mesoblastic basis, which is

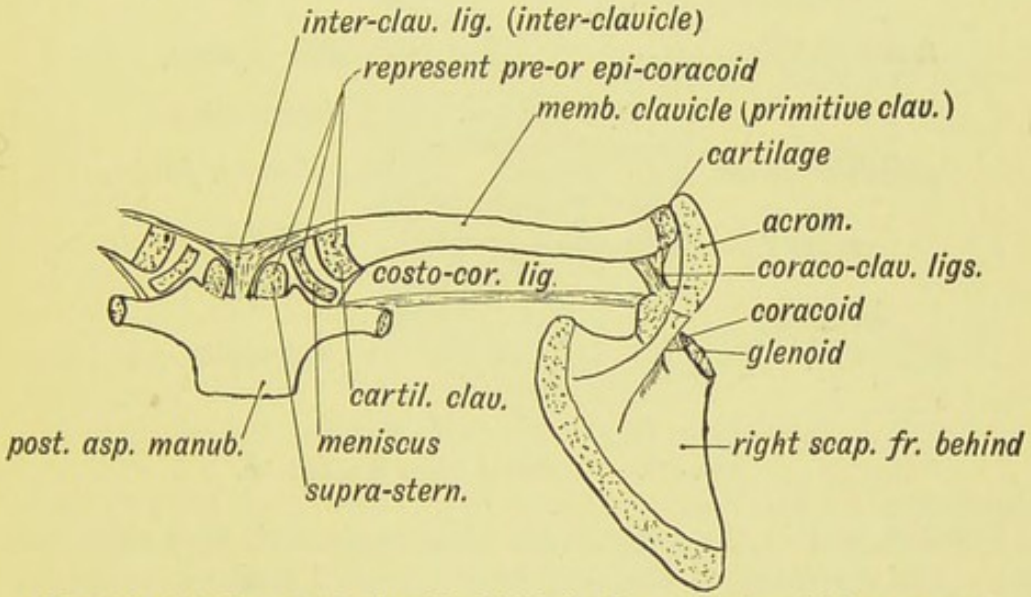


FIG. 418.—The Parts in the Shoulder Girdle of a Human Foetus which correspond with those of Ornithorhynchus.

continuous with the acromion at one end, and with the anterior end of the sternal bar at the other (W. H. Lewis [2]). Two centres of chondrification appear early in the 6th week—one at the outer, the other at the inner end—the inner one, which we suppose to represent the epicoracoid, fusing with the cartilaginous sternal bar. Ossification occurs at the end of the 6th week—before the two cartilage centres have met. Professor Mall [2] observed that two centres of ossification appear, but fuse into one in the 8th week. Professor Fawcett has also observed double centres in the clavicle. In cleido-cranial dysostosis some condition occurs which arrests the formation of the membranous ossification between the parts formed in cartilage; ossification in cartilage proceeds normally in such cases.

The **acromion process** is ossified from several centres which appear in the years of adolescence; the epiphysis so formed may be united

[1] For recent paper see D. Fitzwilliams, *Lancet*, 1910, vol. 2, p. 1466.

[2] See reference, p. 416.

to the spine by fibrous tissue only. This occurs in over 8 % of subjects (Symington), and may be mistaken for a fracture of the process. The coraco-clavicular ligaments may be derived from the precoracoid element.

The Hand and Foot.—The hand and foot of man, as is the case in all primates, retain the primitive arrangement of elements much more closely than do most other mammalian orders. The primitive type of hand or foot, out of which the various forms found in mammals have been modified, are seen in such reptiles as the lizard or tortoise (Fig. 419). In the hand of man the same bones are to be seen as in

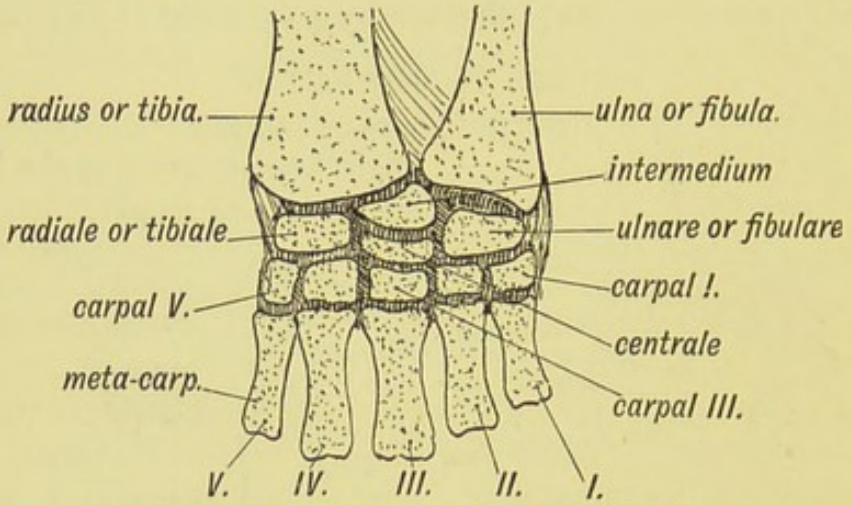


FIG. 419.—The Carpal Bones of a Tortoise.

the tortoise, and in the same order of arrangement, with some exceptions. The elements in the foot of a typical lizard resemble closely the arrangement seen in its hand ; the same elements are present even in the highly modified human foot. The hand and foot bones have undergone great specialization in most mammals. In the evolution of the horse, for instance, one lateral digit after another has become vestigial, leaving the central digit enormously enlarged and specialized to form the lower part of the extremities. In ruminants the 3rd and 4th digits have become specialized ; the rest of the digits have become reduced until only traces of them are left ; in rodents the hallux is vestigial. The hallux and pollex are the mammalian digits most liable to undergo retrogression. In man, on the other hand, the hallux and pollex find their greatest development.

Comparison of the Tarsus and Carpus.[1]—Both are the derivatives of such a typical form as is shown in Fig. 419. In the typical tarsus or carpus there occur the following bones :

[1] See note on p. 429, and Fig. 406. Recent papers on carpal and tarsal bones : see R. B. S. Sewell. *Journ. Anat. and Physiol.* 1906, vol. 40, p 152 (Astragalus) ; T. Manners Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 255 (Navicular of Foot) ; H. M. Johnston, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 59 (Scaphoid of Hand).

1. **Radiale or Tibiale** forms the scaphoid in the hand and astragalus in the foot.

2. **Intermedium** forms the semilunar in the hand; in the foot it is much reduced and usually unites with the astragalus to form the external tubercle of that bone. It may remain separate and form the **os trigonum** (Fig. 420).

3. **Ulnare** becomes the cuneiform in the hand, the os calcis in the foot. During the cellular and early cartilaginous stages in the development of the human tarsus, the os calcis is in contact with the fibula. In the hand the ulnare and intermedium are bound by fibrous bands to the ulna (Fig. 419); these bands assist to form the triangular fibro-

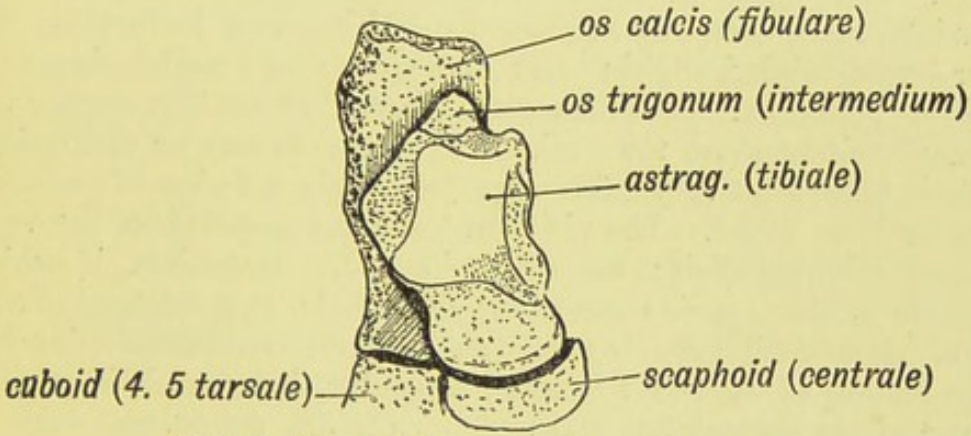


FIG. 420.—The Os Trigonum and Bones of the Tarsus.

cartilage; in the ankle the corresponding bands form the middle and posterior fasciculi of the external lateral ligament.

4. **Carpale or Tarsale I.** becomes the trapezium in the hand, the internal cuneiform in the foot. In the prehensile foot of apes, the hallucial articular surface is directed inwards for the movable big toe. This is also the case during the foetal development of the human foot (Leboucq). At no period of development is the hallux of man directed inwards and separated from the other toes. In man the great toe resumes a primitive position, and its metatarsal lies parallel nearly with the metatarsal series.

5. **Carpale or Tarsale II.** forms the trapezoid in the hand, the middle cuneiform in the foot.

6. **Carpale or Tarsale III.** forms the os magnum in the hand, the external cuneiform in the foot.

7. **Carpale or Tarsale IV. and V.** have united in both hand and foot to form the unciform and cuboid. This union is seen in mammals generally. The unciform process has a separate centre of chondrification (Lewis). In the cat and carnivores the scaphoid and semilunar unite together, a union which may occur in man.

The Os Centrale is situated between the first and second rows of the carpal or tarsal bones (Fig. 419). In the foot it forms the scaphoid

—a bone which plays an important part in the formation of the plantar arch—but is yet remarkably late in beginning to ossify, viz. about the 3rd year. It appears in the membranous stage of the human carpus, but at the end of the 2nd month it has joined the dorsal and distal aspect of the scaphoid of the hand. It may be occasionally detected as a tubercle on the dorsal aspect of the scaphoid, or even as a separate bone. It is a separate bone in the carpus of all primates except the gorilla, chimpanzee and man. There are two centralia in lower vertebrate forms. The styloid process at the base of the 3rd metacarpal bone may occur as a separate ossification (*os styloideum*).

The Pisiform (ulnare laterale of Forsyth Major) is of doubtful nature. It is possible that in a very early stage of the evolution of mammals there were more than five digits—one behind the little finger—post minimi digiti; and another on the radial side of the hand—a prehallux. Supernumerary digits, when they appear, are commonly situated on the radial side of the thumb or ulnar side of the little finger, but they may represent merely a fission of the normal pollex or little finger. The pisiform has been regarded as the vestige of a post-minimal digit; the sesamoid on the trapezium, in which a slip of the extensor ossis matacarpi pollicis ends, as a remnant of a prehallux. It is possible also to regard the pisiform as a sesamoid developed in the tendon of the flexor carpi ulnaris—for that muscle is originally a flexor of the metacarpus and ends on the 5th metacarpal—the pisi-metacarpal ligament representing the terminal part of the tendon. The pisiform, however, is developed with the rest of the carpal bones and before the tendon of the flexor carpi ulnaris. In mammals generally, but not in man, the pisiform articulates with the ulna as well as the cuneiform, and its synovial facet opens into the wrist joint. It may be represented in the foot by the heel epiphysis of the os calcis. The gastrocnemius, which represents the flexor carpi ulnaris in the leg, is also primitively a flexor of the metatarsus; the long plantar ligament, from which it is separated by the growth of the heel, represents the continuation of its tendon.

The Eversion of the Foot and Development of the Arch.—The human foot has been highly modified for upright progression. The chief modifications are:

(1) Gradual **eversion** of the foot, so that the sole can be applied to the ground. Even at birth—and for some time after—and always up to and before the 7th month of foetal life, the soles of the feet are inverted, so that when the foetal limbs are in their natural position they are directed towards the belly of the child. In club foot the natural process of eversion does not take place. The ape's foot is kept normally in the inverted position, an adaptation for prehension. The following factors assist in producing eversion:

(*a*) The neck of the astragalus (Fig. 421), which in the foetal foot is long and directed downwards and inwards at an angle to the

axis of its body, becomes relatively shorter and directed more in line with the axis of the articular surface of its body (Fig. 421). Further, the outer border of the tibial articular surface of the astragalus is prominent in the foetus ; the inner border is much the lower ; a growth upwards of the inner border causes the astragalus and foot to rotate outwards (Lazarus).

(*b*) The bones on the inner side of the foot, particularly the scaphoid and internal cuneiform, grow more rapidly than those on the outer side of the foot—especially after birth. This tends to evert the foot and also to produce the longitudinal arch.

(*c*) A special evertor of the foot is produced—the peroneus tertius —a muscle peculiar to man. It is developed from the outer and lower fibular fibres of the extensor longus digitorum and represents part of the tendon of that muscle to the 5th toe. The peroneus brevis and longus may also assist, especially the latter,

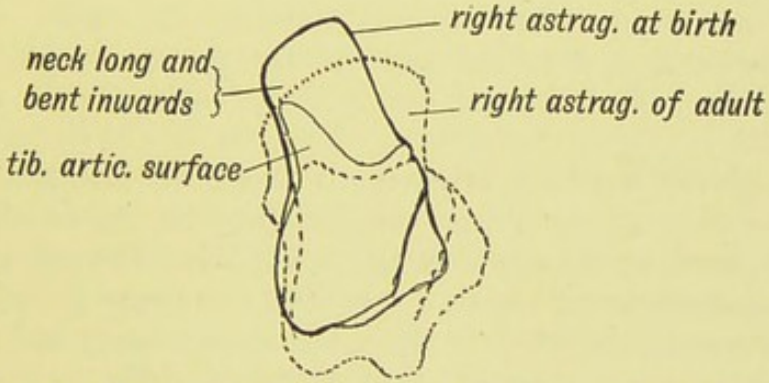


FIG. 421.—The Foetal and Adult (in dotted outline) Forms of the Astragalus contrasted.

which in apes is a grasping muscle, acting as a flexor of the metatarsal bone of the hallux.

(2) The tarsal bones of the human foot—especially the astragalus and os calcis—are of great size when compared with the tarsal bones of other primates ; while the digital or phalangeal elements, except in the case of the great toe, which is relatively of great size, have undergone retrogression. This is especially the case in the human little toe ; some of its muscles are not infrequently fibrous, and the terminal phalanx may not be separated from the middle phalanx. The terminal phalanx is the last to be differentiated in development of the fingers and toes (in 3rd month).

(3) The plantar arches, both longitudinal and transverse, are produced. The arch of the foot is a human character. At birth the child is flat-footed when the weight of the body rests on its feet ; the head of the astragalus touches the ground. When the muscles are removed by dissection the foot of the newly born child shows a well-developed arch (Russell Howard). The arch becomes stable as the child learns to walk. The chief factor in its production is the growth of the tarsal

bones—especially of the scaphoid and internal cuneiform—and 1st metatarsal and the co-ordinated action of the muscles. Hence in rickets, where the normal tarsal growth is disturbed, the occurrence of flat foot. Amongst the structures which help to maintain the arch are :

(*a*) The growth of the os calcis into the heel separates the tendon of the plantaris from its prolongation in the sole—the middle part of the plantar fascia, which assists in maintaining the arch. In lower primates the two parts are continuous, the tendon of the plantaris plying across the os calcis in a cartilage-lined groove.

(*b*) The internal lateral ligament of the ankle (anterior part) and the inferior calcaneo-scaphoid ligaments undergo great development in man.

(*c*) The flexor brevis digitorum which in lower primates arises principally from the long flexor tendons in the sole, has its origin completely transferred to the os calcis in man. It can thus act more powerfully in maintaining the arch. The flexor accessorius, a detached part of the flexor longus hallucis, is specially well developed and helps to maintain the arch of the foot.

(*d*) The tibialis posticus, originally a flexor of the metatarsus, corresponding to the flexor carpi radialis in the hand, obtains a secondary attachment to the scaphoid. The tibialis anticus, which answers to the extensor ossis metacarpi pollicis, becomes permanently inserted to the internal cuneiform and metatarsal. Both of these muscles, thus modified, help to maintain the arch of the foot. So does the tarsal part of the tendon of the tibialis posticus.

(*e*) The long plantar ligament, originally a part of the tendon of insertion of the gastrocnemius—also assists to maintain the arch.

(4) The development of the great toe and the peculiar arrangement of its muscles must also be regarded as adaptations in the foot to upright posture and progression.

Comparison of the Muscles of the Upper and Lower Extremities.—As a mental exercise it may be worth the student's while to briefly review the corresponding muscles in the two limbs. He has already seen that the arm and leg buds are similar in origin and made up of similar elements. Each is subsequently modified for its special function. In this comparison the theory of the "reversed image"[1] must be kept in mind, and especially the relationship of the muscles to nerves and to digits.

Pollex and Hallux.—The extensor ossis metacarpi pollicis corresponds to the tibialis anticus. The thumb muscle has commonly a

[1] See note, p. 429.

carpal insertion as well as metacarpal. The extensor brevis or primi internodii pollicis is constant in man only; it is a segment of the extensor ossis metacarpi pollicis.

The extensor brevis hallucis is not represented in the thumb.

Second Digit.—In the lower primates each finger has two extensors—a deep and superficial. The deep in the second digit becomes the extensor indicis; in the little finger it forms the extensor minimi digiti. The deep extensor muscles have disappeared in man from the 3rd and 4th digits, but occasionally reappear. In the leg the deep extensors have migrated to the foot, and form the extensor brevis digitorum. That for the little toe, however, has not descended; it is always vestigial, if present. It runs beneath or with the peroneus brevis, and is known as the peroneus quartus or **peroneus quinti digiti.** If the mirror image theory is true it represents the extensor brevis pollicis.

Flexors and Extensors of the Metacarpus.[1]—These have retained their primitive insertions in the hand; their modifications in the foot have been already mentioned. Both at the knee and elbow joint the origins of these muscles have undergone much shifting and migration.

The comparison already made between the scapula and ilium (p. 419), will help the student to understand the correspondence between the muscles of the thigh and arm.

Migration of Muscular Attachments.—Many of the human muscles acquire during development attachments to segments at a distance from those from which they are developed. The serratus magnus arises from 5th, 6th, 7th cervical segments; its attachment has extended backwards from the 1st rib until, in man, it reaches the 8th rib; the trapezius, originally situated in the neck, migrates backwards, and in the beginning of the 2nd month obtains an insertion to the shoulder-girdle, and before the end of the 3rd month its origin has reached as far backwards as the 12th dorsal spine along the median dorsal line. The latissimus dorsi migrates to the median dorsal line over the spinal musculature and reaches the spines and crest of the ilium. The diaphragm, which arises in the neck (4th and 5th segments) comes to be attached in the floor of the thorax. The facial musculature takes its origin in the hyoid arch. The subvertebral (hypaxial) musculature is a migrated part of the transversalis sheet. The omohyoid is attached at first to the sternum; it migrates along the clavicle and reaches (often it fails to reach) the upper border of the scapula. The migration of the subclavius has been in an opposite direction; originally it reached to the humerus. The case of the extensor brevis digitorum of the foot has just been mentioned. The flexor accessorius is a part

[1] J. P. M'Murrich, *Amer. Journ. Anat.* 1906, vol. 6, p. 407 (Plantar Musculature); J. P. M'Murrich, *Amer. Journ. Anat.* 1904, vol. 4, p. 33 (Musculature of Thigh).

of the flexor longus hallucis which has migrated to the sole of the foot. The opponens of the thumb and of the little finger is a separated part of the short flexor muscles of these digits. These are only a few of the more striking examples of the migration of the attachment of muscles.

Vestigial and Abnormal Muscles of the Limbs and Trunk.—(1) The muscles of the human **ear and scalp** may be described as vestigial when compared to the development in other mammals. Although their action on the ear and scalp is feeble, yet they serve as most important bases into which certain psychological states are reflected.

(2) The **levator claviculae** (omo-trachelian) is a muscle which passes from the upper transverse cervical processes to the outer end of the

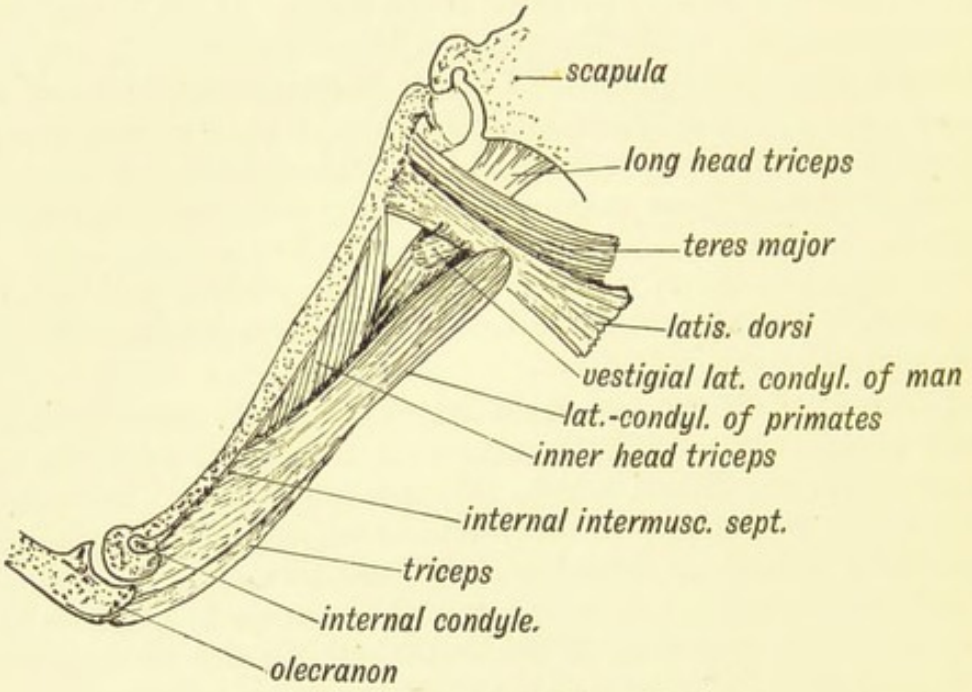


FIG. 422.—Latissimo-condyloideus Muscle.

clavicle or acromion process. It is well developed in climbing primates. It is not a common muscle in man. It can be recognized during life in the posterior triangle of the neck.

(3) The **latissimo-condyloideus** (dorsal epitrochlearis), a climbing muscle, is always represented in man, commonly by a fibrous bundle between the tendon of the latissimus dorsi and the long head of the triceps (Fig. 422). It may be occasionally muscular. In apes it passes from the latissimus dorsi at the axilla to the inner aspect of the elbow and arm, which it retracts in climbing. It belongs to the same sheet as the coraco-brachialis. The **ligament of Struthers**—a strip of fibrous tissue over the internal intermuscular septum, above the internal condyle—represents part of the tendon of this muscle. The muscular slips occasionally found crossing the brachial or axillary artery from the latissimus dorsi to the coraco-brachialis or biceps are derivates.

Other slips found crossing the floor of the axilla, between the adjacent borders of the pectoralis major and latissimus dorsi, are parts of the muscular sheet out of which these two muscles are developed.

(4) The **pectoralis externus** arises from the 4-5-6 ribs and costal cartilages, beneath the axillary border of the pectoralis major. This is its normal condition in most mammals, but in man it is commonly fused with, and forms part of, the pectoralis major.

(5) The **sternalis** is a new muscle. The pectoralis major is formed from the same ventral longitudinal sheet as the rectus abdominis and sterno-mastoid. The fibres of the sternalis, which lie along the sides of the sternum, superficial to the origin of the pectoralis major, represent a persistent part of the primitive longitudinal sheet. The sternalis is a derivative of the *sphincter colli*, part of the platysma sheet (Parsons).

(6) In the **sterno-mastoid** four elements are recognized: sterno-mastoid, sterno-occipital, cleido-mastoid, cleido-occipital. The cleido-occipital fibres, which form part of the same sheet as the trapezius, are often absent. On the other hand, the cleido-occipital fibres may be continuous with the trapezius.

(7) The **pectoralis minor** is sometimes inserted to the capsule of the shoulder and great tuberosity of the humerus. This is the primitive insertion of the muscle. The coracoid insertion is a secondary attachment seen only in man and some of the higher primates. When the pectoralis minor is inserted to the coracoid, the former fibres of insertion become fused with, and form part of, the coraco-humeral ligament, which, however, is a distinct structure, and represents a specialized part of the capsule of the shoulder joint.

(8) In some apes (such as the Gibbons) the **biceps** has four heads—the two usual, the long and short, and two others, one from the inner border of the humerus and one from the bicipital groove. These two extra heads appear frequently in man.

(9) The **epitrochleo-anconeus** is frequently present. It crosses the ulnar nerve from the internal condyle to the olecranon.

(10) The **palmaris longus** and its homologue in the leg, the **plantaris,** are vestigial, aberrant in form, and often absent. The plantar and palmar fasciae represent their divorced tendons. The plantaris and palmaris undergo retrograde changes in the primates with the transformation of claws to nails.

(11) Each digit (fingers and toes) in lower primates, such as monkeys, is provided with three short muscles which arise from the carpus or tarsus. The three muscles are (Fig. 423): (1) a short flexor on the radial side of the digit; (2) a short flexor on the ulnar side; (3) a **contrahens** or adductor muscle (always absent in the middle digit). The ten short flexor muscles form a deeper sheet than the four contrahentes. Of this form the arrangement of the short muscles in the human hand is a derivative. The remnants in the human hand and foot of the contrahentes are: (1) The adductors of the 1st digit (pollex

or hallux); (2) fibrous remnants of the others occur over the deep plantar or carpal arch (Fig. 423). The short flexors in man have become (1) the seven interossei; (2) the flexores breves (ulnar and radial) and opponens of the first digit; the flexor brevis and opponens of the fifth digit (see Fig. 423). The ulnar flexors of the thumb and great toe are absent or fibrous.

(12) The **pyramidalis** is often absent in man or vestigial. It is the tensor of the linea alba.

(13) Remnants of the **extensors and flexors of the tail** may occur between the sacrum and the coccyx (p. 396).

(14) The **coccygeus** is vestigial; its superficial part forms the small sacro-sciatic ligament.

(15) Fibres of the biceps of the thigh may be followed into the **great sacro-sciatic ligament.** This ligament, which is almost peculiar to

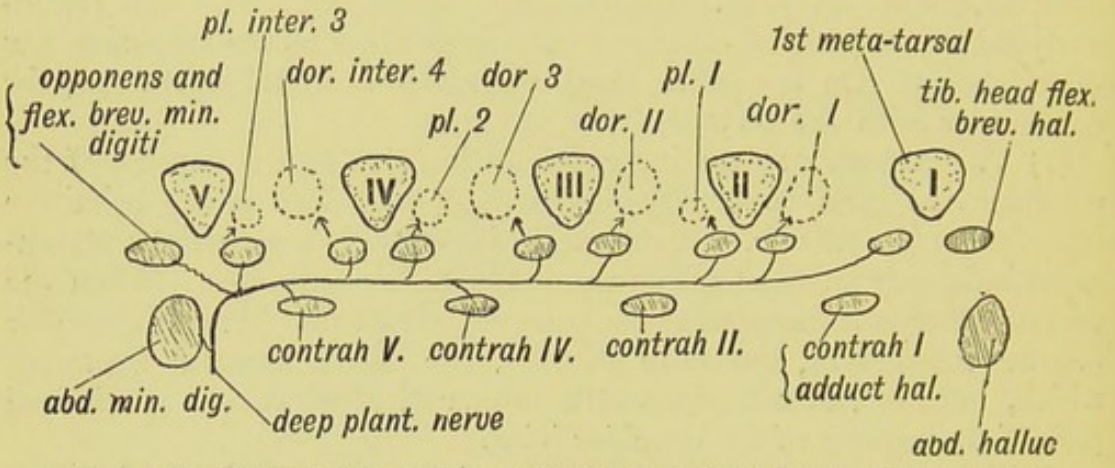


FIG. 423.—The Morphology of the Short Muscles of the Digits. The muscles shaded are those of the ape's hand or foot; the positions of the corresponding muscles in the human hand or foot are indicated by dotted outlines.

man—in other primates it is quite thin and slender—may contain fibres derived from the caudo-femoral group of muscles, such as the tenuissimus, a long strap-like muscle which passes from the coccyx to the femur and leg in lower mammals. The sacro-sciatic ligament is mainly derived from the great median sheet, out of which the middle layer of the lumbar fascia is also formed. Parsons regards the **short head of the biceps** as a derivative of the tenuissimus, while others regard it as part of the muscular sheet which forms the peroneal muscles. Amongst primates, it is found only in man, the anthropoids, and some South American apes. The short head of the biceps corresponds to the brachialis anticus in the arm, and is supplied by the external popliteal nerve.

(16) The **psoas parvus** is also vestigial. It acts primarily as a flexor of the pelvis on the spine. It begins to disappear in those primates which assume the erect posture.

(17) The **scansorius** is a separated segment of the gluteus medius and minimus. It rises from the anterior border of the ilium and passes

to the great trochanter. It corresponds to the teres minor. It is not constant in any animal. Bland-Sutton is certainly in error in regarding part of the ilio-femoral ligament as a derivative of this muscle.

(18) The **flexor brevis digitorum** to the little toe and the adductor transversus of the great toe are often fibrous.

Vessels of the Limbs.[1]—When the limbs appear at the end of the 3rd week, they contain a rich capillary network supplied by two superficial arteries—and corresponding veins—one situated on the proximal, the other on the distal border. When the nerves shoot out in the limb buds in the 4th week, arteries accompany them, and thus at an early stage the nerve paths also become the arterial paths (Bertha de Vriese). The main artery of the arm accompanies and lies deep to the median nerve, but a chain of arterial anastomoses is also formed superficial to the nerve—the first artery of the chain passing between its two heads. The chief artery of the arm appears to be derived from the vessel to the 6th cervical segment, that for the leg arising from the iliac part of the umbilical artery.

The Vas Aberrans.—This vessel rises in the circum-neural plexus of the arm bud and gives origin to a number of anomalous arrangements of the brachial artery. If a newly-born child be well injected, a number of branches derived from the axillary, brachial and main arteries of the forearm will be found to form an anastomotic chain along the superficial aspect of the median nerve. The upper end of the chain is formed by a branch from the axillary ; the lower end is completed by a branch of the ulnar or radial at the elbow. In South American apes this anastomosis always opens up to form a supplemental brachial artery—the vas aberrans—ending usually as the radial. From the manner of its origin and disposition in front of the median nerve, it will be seen that the vas may arise from the axillary or upper part of the brachial, and terminate in the radial, ulnar or brachial, according to the branches which participate. It may be so large as to simulate a large branch of the axillary or a division of the brachial. Such a condition is spoken of as high division of the brachial. The vas may supplant the brachial artery altogether, which is then represented by a trunk which ends high up in the arm by giving off the superior and inferior profunda arteries. The brachial vessel formed from the vas is recognized by its position superficial to the median nerve. In lower apes the brachial artery commonly divides a little above the elbow. This position of division is rare in man. In cases of high division the radial, or even the ulnar, may be superficially placed in the forearm.

Internal Saphenous Artery.—The main artery of the lower

[1] For development of arteries see Erik Müller, *Anat. Hefte*, 1903, vol. 22, p. 377. For comparative anatomy of vessels in limbs of primates see articles by Dr. Manners Smith, *Journ. Anat. and Physiol.* 1910, 1911, 1912, vols. 44, 45, 46 ; E. Goeppert, *Ergebnisse der Anat.* 1904, vol. 14, p. 170.

limb during the 2nd month is the internal iliac artery and its continuation—the sciatic branch of the inferior gluteal. In the 2nd month an anastomosis opens up along the anterior crural nerve, which joins the primitive sciatic artery in the popliteal space, and ultimately (3rd month) forms the external iliac and femoral arteries (Bertha de Vriese). The primitive sciatic is continued as the peroneal artery, and ends on the dorsum of the foot (dorsal pedis). In most mammals —in all primates except man—the anastomotica magna of the femoral artery is as large as the popliteal and passes over the inner side of the tibia with the internal saphenous vein to reach the dorsum of the foot, where it forms the dorsalis pedis artery. This vessel is known in them as the internal saphenous artery, and corresponds to the radial artery in the forearm and wrist. It is well developed in the human foetus in the 3rd month—exactly as in the ape. The superficial branch of the anastomotica magna rarely assumes such a development in man after foetal life ; but the course taken by the internal saphenous artery explains the position of its accompanying vein, the internal saphenous, in front of the internal malleolus. In man only is the internal saphenous vein continued up the thigh to a saphenous opening in the groin. Its primitive termination is in the femoral vein at the lower end of Hunter's canal. The saphenous opening is peculiar to man.

The Superficial Plantar Arch, formed from the internal plantar artery, is seldom complete in man. The pressure to which it is subjected in the standing posture has led to its partial obliteration. It corresponds to the superficial palmar arch.

The Supra-condylar Process [1] is well developed in lemurs, the lowest primates, and in mammals of many orders. Its function is unknown. It occasionally appears in man. It is developed from the humerus about two inches above the internal condyle as a hook-like process of bone. It lies in front of the internal intermuscular septum, and when well developed the brachial artery and median nerve may pass beneath it, as they do in such animals as the squirrel and cat.

Development of Joints.—Each limb bone is formed from a centre of chondrification which appears early in the 2nd month within the unjointed skeletal blastema of the limb bud. At these centres the mesoblastic cells assume the characters of cartilage cells ; growth proceeds most rapidly at the periphery of the cartilage centres ; as the growing centres approach each other, part of the original blastema is left between them. This tissue, which may be named the **interchondral disc,** forms the first basis of a joint (Fig. 424). The cells in the peripheral part of the blastema condense and form a **perichondrium** round the growing cartilage. Through the interchondral discs the perichondrium is continuous from cartilage to cartilage, and is the basis out of which the **capsule** of a joint is formed. Between the growing

[1] T. Dwight, *Amer. Journ. Anat.* 1904, vol. 3, p. 221.

ends of the cartilages, the central part of the interchondral disc is absorbed, the joint cavity being thus formed; the peripheral part lines the capsule and forms the **synovial membrane,** the cells of which, even in the adult, show by their structure that they are cartilaginous in nature. In certain pathological conditions, the synovial villi give rise to cartilaginous nodules.

Interarticular Fibro-cartilages.—In every developing joint fringes of synovial membrane, representing the interchondral disc, project in the gap between the articular margins of bones (Fig. 424). In the elbow joint they are present, even in the adult; in the hip and shoulder joint they form the cotyloid and glenoid ligaments. In the knee joint they are much better marked; at no time were these ever parts of a tendon. At the wrist joint the interchondral disc forms the **triangular fibro-cartilage,** but here it is possible that certain other

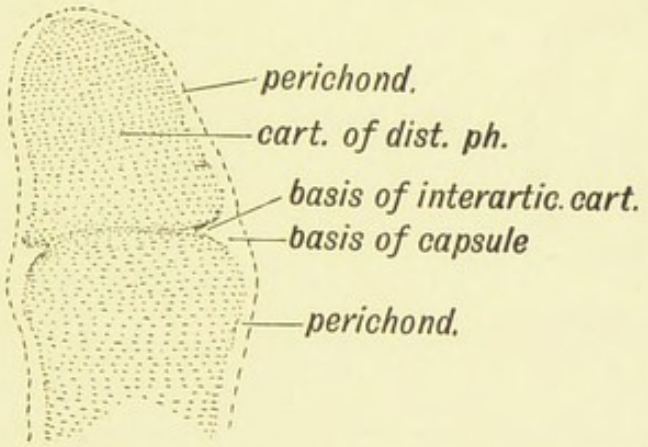
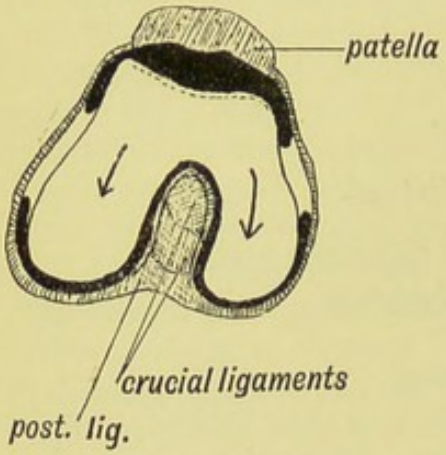


FIG. 424.—Diagram of the Interphalangeal Joint of the Great Toe of a Foetus in the 3rd month of development. The perichondrium is continued from one phalanx to the other. Out of the interphalangeal part is formed the capsule of the joint. (After Nicolas.)

elements are included. A nodule of cartilage, which may ossify, is present; within it certain ligaments which united the radius and ulna, and these two bones with the semilunar and cuneiform, have been included (Parsons and Corner). The complete evolution of this cartilage appears in man only; it plays a part in the mechanism of pronation and supination. In the **sterno-clavicular joint** two synovial cavities are formed, one on either side of the interchondral disc. In this case the disc may contain an element derived from the precoracoid, but it is to be remembered that it is only in the higher primates that a complete interarticular disc is present. Two synovial cavities are also formed in the **temporo-maxillary joint,** the meniscus separating two joints, which are functionally different. The upper is for gliding movements, the lower for hinge-like movements.

Capsular Ligaments.—Certain parts of the capsule of every joint become thickened and specialized according to the strains to which the

joint is subjected. Parsons found that it is the middle gleno-humeral ligament of the shoulder joint which becomes enlarged and projects within the joint of pronograde mammals. In man, the coraco-humeral ligament is by far the strongest. The anterior part of the capsule of the hip joint in man has to withstand the strain of the body when the thigh is extended in the upright posture. Part of it becomes specialized to form the ilio-femoral or Y-shaped ligament. In the knee joint the posterior part of the capsule is strengthened to prevent over-extension. The development of the condyles of the femur isolates a posterior part of the capsule which projects within the joint and forms the crucial ligaments (Fig. 425). The ligamentum teres, the best example of an **interarticular ligament,** appears in the human foetus, as it is permanently in the reptilia, as part of the capsule of the joint.



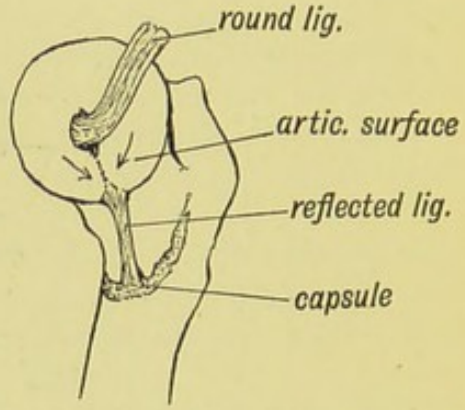


FIG. 425.—Showing the Origin of the Crucial Ligaments of the Knee.
FIG. 426.—Showing the Origin of the Ligamentum Teres and Reflected Bundle of the Capsular Ligament.

It is isolated by the development of the head of the femur, which expands as a wing on each side of the ligamentum teres, and by the fusion of the wings isolates it from the capsule (Fig. 426). The **reflected ligament,** on the under surface of the neck of the femur, is the part of the capsule with which the ligamentum teres was continuous.

Knee Joint.—In Fig. 427 is given a diagrammatic representation of the posterior aspect of the knee joint as seen in a primitive mammalian type. Three interarticular discs are shown ; an internal tibio-femoral, an external tibio-femoral and a fibulo-femoral. When the fibula became excluded from the knee joint, the fibulo-femoral disc, from which fibres of the popliteus took origin, was included in the tendon of that muscle (Carl Fürst). The **popliteus** originally passes from the fibula to the tibia like the pronator quadratus in the forearm. The upper fibres migrate to the capsule and to the fibulo-femoral disc, and through the disc and its ligaments gain an attachment to the femur. Thus, instead of rotating the tibia on the fibula, the popliteus muscle now rotates the tibia on the femur. Occasionally the cavity of

the human knee joint communicates with the superior tibio-fibular joint through the synovial diverticulum beneath the tendon of the popliteus. The upper end of the fibula becomes excluded from the knee joints after the 7th week. There are five separate synovial cavities developed in this joint—one between the patella and femur, two between the femoral condyles and the primitive semilunar cartilages, and two between the cartilages and the upper extremity of the tibia. The five joints become continuous in the 4th month, the crucial and alar ligaments being derived from the primary septa between the cavities (Bardeen).[1] The external semilunar cartilage is circular in form and continuous with the posterior crucial ligament in primates, in which the power of rotation of the knee is highly developed ; in man the circular form of the cartilage is lost and it only retains part of its

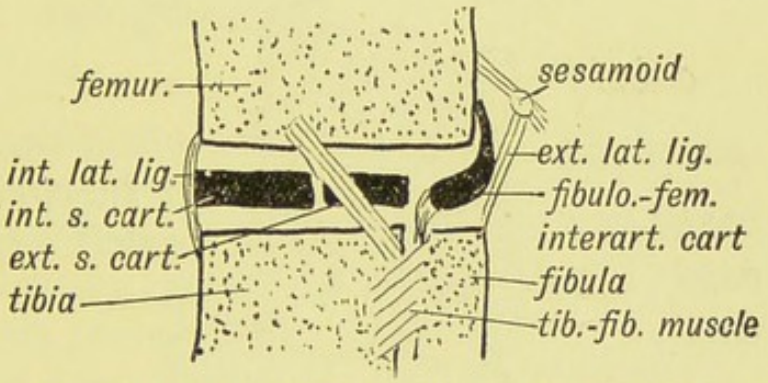


FIG. 427.—Scheme of a Primitive Mammalian Knee-joint to show (1) the Articulation of the Fibula with the Femur ; (2) the Fibulo-femoral Interarticular Cartilage which becomes included in the Tendon of the Popliteus ; (3) the Tibio-fibular Muscle out of which the Popliteus is evolved ; (4) the division of the Tibio-femoral Interarticular Cartilage into external and internal Semilunar Cartilages. (Carl Fürst.)

continuity with the posterior crucial ligament (Parsons). The ligamentum mucosum, which in many mammals separates the knee joint into three compartments—two condylar and a patellar—is much reduced in man.

Ossification of Bones.—The simplest and most primitive manner in which bones pass from the cartilaginous to the osseous stage is seen in the carpus and tarsus (Fig. 428). The bone is entirely deposited within the cartilage by a process of **endochondral ossification.** The various stages in this process may be grouped as follows : (1) calcification of the intercellular matrix in the centre of the bone—a temporary phase in human ossification, but a permanent one in some fishes ; (2) an invasion of vasoformative and osteoblastic cells which, commencing at a point beneath the perichondrium, reach the middle of the central area of calcification and form a centre of ossification (Fig. 428). The osteoblasts and their accompanying vessels, when the cartilage cells are absorbed, deposit bone in the spaces of the calcified matrix. A

[1] See reference, p. 414.

section through an ossifying and growing carpal bone shows (1) a centre of ossification ; (2) a surrounding narrow area of calcification ; (3) a peripheral area of actively growing cartilage ; (4) a covering membrane or perichondrium. The processes of growth and ossification cease when the cartilage beneath the perichondrium is completely transformed to bone. Not only are the tarsal and carpal bones formed thus, but so are the epiphyseal ends of all long bones.

In the shafts of long bones, to the process of endochondral ossification, another—the **ectochondral**—is added (Fig. 429, *A*, *B*, *C*, *D*). An endochondral centre is formed as in the tarsal bones, and from this centre the process extends rapidly in every direction. Some of the osteoblasts, instead of invading the cartilage, form a layer beneath

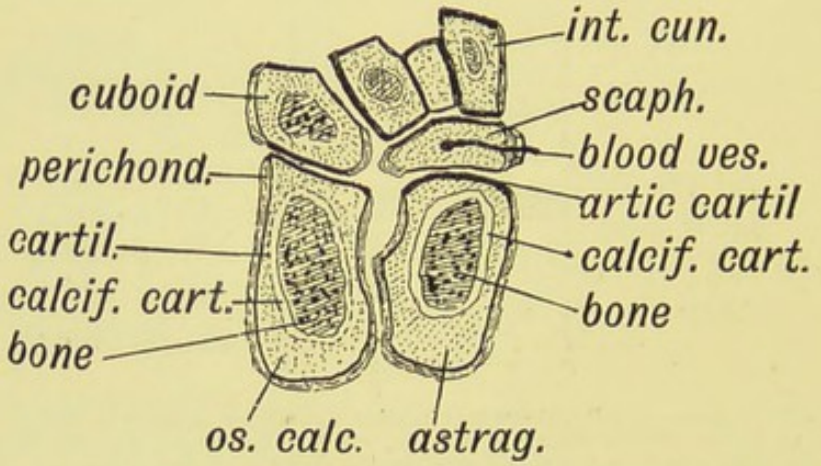


FIG. 428.—Section of the Tarsus at the 3rd year of development to show pure Endochondral Formation of Bone.

the perichondrium, which surrounds the endochondral centre. The perichondrium now becomes periosteum ; the deposit of periosteal bone leads to an increase in the thickness of the shaft (Fig. 429, *C*); the extension of the endochondral ossification into the growing cartilaginous ends of the bone leads to an increase in the length of the shaft. As the periosteal bone is deposited, the endochondral bone within it is absorbed and a medullary cavity is formed, in which red marrow begins to appear in the 6th month (Fig. 429, *D*). The cartilaginous parts of the bone, at each extremity of the shaft, form the epiphyses. When the endochondral centres appear and grow within the epiphyses, a line of growing cartilage is gradually isolated between them and the endochondral centre of the shaft (Fig. 429, *D*). At the **epiphyseal line** the bone grows in length. By the formation of epiphyses at the ends of long bones, the growing line of cartilage is sheltered from the friction and stress to which it would be exposed on the articular ends of the bones. All the cartilage of a bone, except that on the articular surfaces, is ossified when the body is fully grown. The evidence at our disposal points to the absorption of the cartilage and the deposition of bone

points as being regulated by secretions derived from the thyroid, pituitary and other glands of internal secretion.[1]

The Nature of Epiphyses.[2]—Epiphyses are of three kinds: (1) pressure epiphyses, forming the articular extremities of long bones

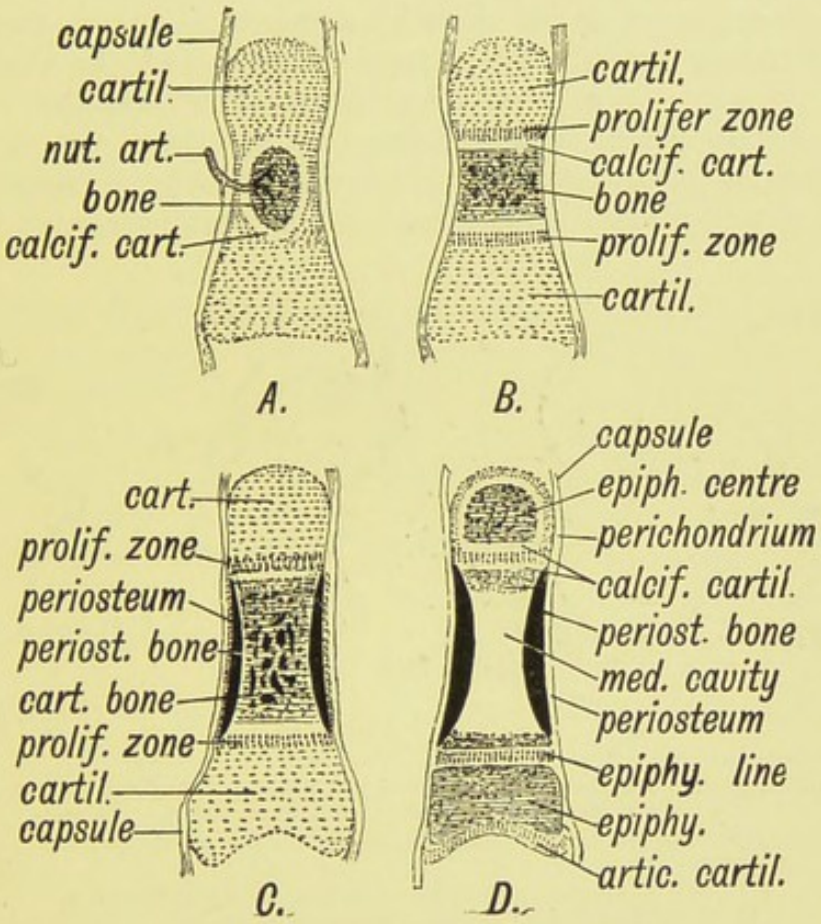


FIG. 429.—Ossification of a Long Bone by Endochondral and Ectochondral Ossification. (After Nicolas.)

A, Ossification within the cartilage of the shaft.

B, Complete ossification of the middle part of the shaft.

C, Formation of bone in the shaft outside the cartilage by osteoblasts beneath the perichondrium (now named periosteum).

D, Complete absorption of the endochondral bone of the shaft; formation of a medullary cavity; appearance of endochondral centres in the epiphyses; formation of the epiphyseal lines.

(Fig. 430, *B*); (2) traction epiphyses, which form processes for the insertions of muscles (Fig. 430, *B*); (3) atavistic epiphyses, formed by the union of an element which formerly existed as a separate bone (Fig. 430, *A*).

[1] Keith, *Lancet*, April 15th, 1911; *Journ. Anat. and Physiol.* 1913, vol. 47, Jan.

[2] The account given by Parsons has been followed. See *Journ. Anat. and Physiol.* vol. 37, p. 315; vol. 38, p. 248; vol. 42, p. 388. R. L. Moodie, *Amer. Journ. Anat.* 1907, vol. 7, p. 443 (Reptilian Epiphyses). A. Kirchner, *Anat. Hefte*, 1907, vol. 33, p. 513 (Epiphyses of Os Calcis and 5th Metatarsal).

The upper extremity of the femur affords typical examples of pressure and traction epiphyses. By the extension of the ossification of the shaft within the cartilage of the upper extremity of the femur, the pressure and traction epiphyses become widely separated to form the head and trochanters. **Pressure epiphyses** are the first to ossify, their centres appearing in the order of their functional importance; they are always fitted to the shaft by a species of dovetailing to withstand dislocating forces. The upper extremity of the shaft of the humerus projects as a three-sided pyramid within the epiphysis; Professor Arthur Thomson has shown that the lower end of the shaft of the femur is fitted within its lower epiphysis by a number of projections not well marked in the human bone but pronounced in those

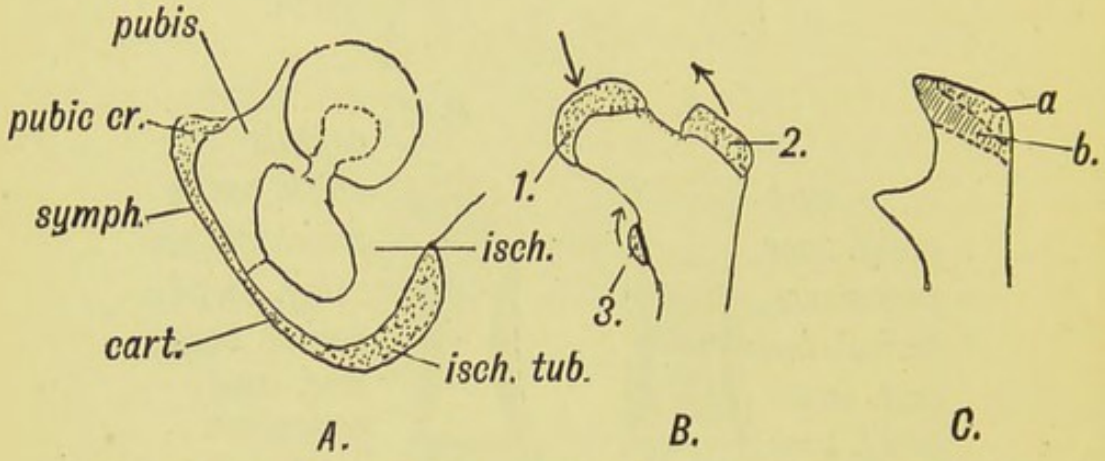


FIG. 430, *A*.—The Epiphyseal Cartilage of the Pubis and Ischium, which arises from the Median Cartilage of the Pelvic Girdle. (Parsons.)

B.—Traction and Pressure Epiphyses on the upper extremity of the Femur.

C.—The Epiphyses of the Olecranon: *a*, the usual Epiphyses; *b*, occasional Epiphyses: both *a* and *b* may be present. (Fawcett.)

animals which maintain the knee in a flexed position. Epiphyses are mammalian characters; their rudiments are to be seen in reptilia.

The great trochanter is the **traction epiphysis** of the gluteus medius and minimus; the small trochanter, of the psoas and iliacus; the third trochanter, in which a centre appears in the 20th year (Dixon), that of the gluteus maximus.

As examples of **atavistic epiphyses,** Parsons cites the following: those of the ischium and pubis (Fig. 430, *A*) from the median pelvic bar (Fig. 395, p. 407); the coracoid process; the epiphysis on the os calcis, the scale-like epiphysis of the olecranon (Fig. 430, *C*), the internal and external condyles of the humerus may be derived from **sesamoid ossifications,** such as are now seen in the patellae, in the tendons of the popliteus, outer head of gastrocnemius (occasional), peroneus longus, tibialis posticus and at the metacarpo-phalangeal joints of the thumb and great toe. The **patella** is usually regarded as a sesamoid, but

recently Mlle. Bertha Vriese has collected evidence to show that it is really a true morphological skeletal element.[1]

Lines of Pressure and Tension of Bones.—The trabeculae, in which the bony matter is deposited by the osteoblasts, are arranged so as to withstand the forces to which the body is subjected. When a bone, such as the astragalus, rib or neck of the femur, is laid open by a section, the trabeculae appear to form straight lines or septa which converge and meet at various angles; when, however, such bones are examined stereoscopically with the X-rays, the trabeculae are seen to be arranged in a double spiral—one system twisting from right to left, the other from left to right (Haughton and Dixon).[2] By this means, the greatest strength is obtained with the least expenditure of material.

Split Hand and Foot.—The extremities are subject to a remarkable series of malformations, which apparently represent arrests of their development. The digits may be abnormally short (brachydactyly), owing to an arrest in the differentiation of the blastema of the phalanges, the terminal phalanx being unseparated from the middle.[3] This is of frequent occurrence in the fifth digit of the foot. In another series of cases the hand or foot appears as if cleft—an appearance due to the fact that three or more of the digits on the ulnar side of the hand or fibular side of the foot have remained joined or webbed, as in the embryo of the 2nd month (Fig. 403). The condition is hereditary.[4] In more extreme cases the digits on the radial, or more rarely, those on the ulnar side of the hand, may be absent; the corresponding bone of the forearm or leg is also undeveloped. Such cases lead one to suppose that the two distal segments of the limbs are developed from a radial and ulnar or tibial and fibular buds, and in such cases only one of these has been affected. Both may be arrested, the extremities terminating with the proximal segment. In extreme cases the limb buds are undeveloped.

[1] Bertha de Vriese, *Bull. de l'Acad. Roy. de Sc. Belgique*, 1909, March 27th.

[2] Dixon, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 223.

[3] A. Fischel, *Anat. Hefte*, 1910, vol. 40, p. 1; J. D. Fiddes, *Anat. Anz.* 1912, vol. 40, p. 544 (Supernumerary Hallux); J. Symington, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 100 (Hyper-phalangism in Cetacea).

[4] See T. Lewis, *Biometrika*, 1907, vol. 6, p. 25.

CHAPTER XXII.

SKIN AND ITS APPENDAGES.

Stages in the Evolution of the Skin.—We have already seen that the structures which are developed in the human embryo can be best explained by supposing that at one stage of evolution the ancestry of mammals lived and breathed in water. The skin of the human embryo until the end of the 2nd month of development is translucent, and has many points in common with that of the lowest gill-bearing vertebrates. In the 3rd month a fine superficial horny stratum appears, a stage representing the evolution into a terrestrial form of life. The appendages

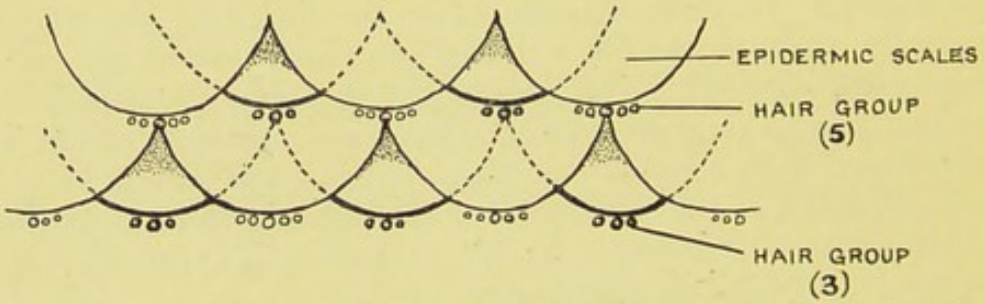


FIG. 431.—Showing the Arrangement of Hair Groups in the Human Foetus and their Relationship to Hypothetical Dermal Scales. (Stöhr.)

of the skin—its hair and glands—appear later; they seem to be modifications of glandular and sensory structures seen in the soft skin of amphibia. The hairs are developed in groups and lines.[1] Their arrangement can be best explained, according to Dr. Max Weber, by supposing that the skin of primitive mammals was covered by scales, and that the hairs sprouted out in groups at their tessellated junctions, as in certain living edentates (see Fig. 431). The human hairs are arranged in irregular series, but in most instances only the chief hair of a group is developed. In later period of foetal life, however, the chief hair has one or two subsidiary hairs planted on either side of it—making one of a group of three or five hairs (Fig. 431).

[1] For recent paper see Stöhr, *Verhand. Anat. Gesellsch.* 1907, p. 153.

The skin of man, compared to other primates, is comparatively hairless. We must regard his nudity as a lately acquired character. At the 7th month of foetal life the chimpanzee and gorilla have hair only on the scalp, eyebrows and lips ; the rest of the body is nude, except for fine hairs or lanugo. This is also the condition in the human foetus at a corresponding period ; in man the development of hair appears to be arrested at a stage reached in foetal life by other primates. The human skin is also more sensitive and more richly supplied with sensory nerves than is the case in other primates. In Professor Elliot Smith's opinion the rich sensory supply to the skin may have been a factor in bringing about the large size of the human brain. In the distribution and " lie " of the hair on his body and limbs man also resembles the hairy anthropoids.

There are on record a number of cases of men and women, in whom the whole surface of the body was covered with a close covering of hair.

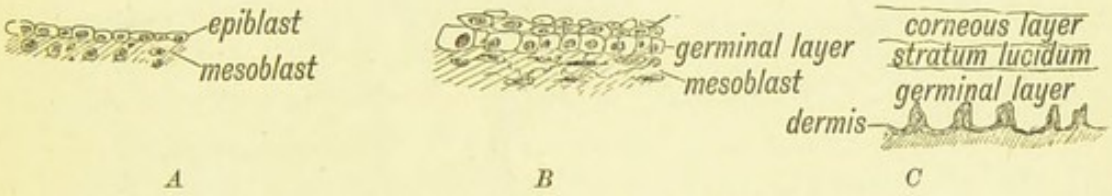


FIG. 432, *A*.—The Strata of the Skin during the first month.
B.—The Strata of the Skin during the second month.
C.—The Strata of the Skin from the sixth month onwards.

The development of hair on the face is certainly regulated by a secretion derived from the sexual organs, for in eunuchs the beard is never developed. It is also well known that the thyroid has a direct influence on the development and growth of hair. Desquamation from the epidermis begins in the 3rd month of foetal life, and never ceases until death. In a certain disease of foetal life, named **Ichthyosis,** desquamation does not take place ; the unshed epidermis is seen to be caked and cracked on the surface of the child at birth.

Development of the Skin.—Considerable assistance in the understanding of the diseases to which the skin is liable and of the nature of the growths which arise from the epidermis, such as corns, bunions, and cancer, is to be obtained by studying the manner in which the skin is developed. At first (see Fig. 432) the human embryo is covered by a single layer of epithelium (**epiblast or ectoderm**), as is the case in the adult amphioxus. By the end of the 1st month there are two layers, the lower representing the **germinal** layer ; the upper the **epitrichium** (Fig. 433), so named because the hairs are developed beneath it, and when they grow out in the sixth month this surface layer of flat epithelium is shed.

In the 3rd month the germinal layer is differentiated into two strata —a basal layer of columnar cells resting on the dermis, and a mucous

layer (Fig. 433, *B*). In the 4th month the corneous or protecting layer is developed from the superficial mucous cells; in the 5th appears the stratum lucidum between the corneous and the mucous[1] (Fig. 432, *C*).

The epidermis rests at first on undifferentiated **mesoblast or mesoderm,** consisting of small round cells closely imbedded in a mucoid matrix. This is the normal structure of undifferentiated mesoblast. The superficial mesoblastic cells are condensed beneath the epidermis to form a corium towards the end of the 3rd month; an areolar or subcutaneous stratum of tissue is differentiated at the same time. The mesoblastic cells become fibrillated and by the fifth month the mucoid substance has almost disappeared, but even in adult life, when the thyroid body is diseased or removed, a mucoid substance may reappear, and a condition resembling the foetal state be thus produced. In the

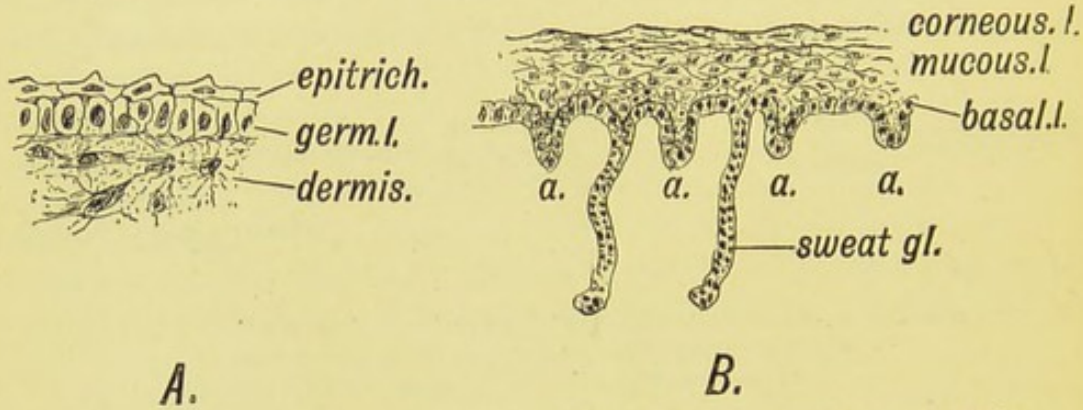


FIG. 433, *A*.—Diagrammatic Section of the Skin at the commencement of the second month.

B.—Diagrammatic Section of the Skin at the commencement of the fifth month. *a. a. a.* Infoldings of the epidermis between the primary ridges.

mucous membranes of the lips, anus and vulva, the superficial layer of epithelium does not become cornified.

Formation of Dermal Papillae.[2]—Up to the end of the 3rd month the epidermis is easily detached from the corium as a flat membrane, but early in the 4th month they become more closely united by ridges of epidermis becoming folded within corresponding furrows on the corium. About the 4th month, the dermal papillae, which are grouped in lines and ridges as is well seen in the palm, are formed in the following manner:

Long, linear furrows of epidermis grow down into the dermis (corium) and divide its surface into narrow ridges (Fig. 433, *B*). These ridges

[1] Comparative anatomy of epidermis: see F. K. Studnička, *Anat. Hefte*, 1909, vol. 39, p. 1.

[2] For recent paper and literature see E. J. Evatt, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 66. Also paper by Walter Kidd, same volume, p. 35. M. Heidenhain, *Anat. Hefte*, 1906, vol. 30, p. 419, O. Schlaginhaufen, *Ergebnisse der Anat.* 1905, vol. 15, p. 628. H. H. Wilder, *Amer. Journ. Anat.* 1901, vol. 1, p. 423. W. Kidd, *The Sense of Touch in Mammals and Birds*, London, 1907.

are subsequently subdivided into papillae. The down-growing nature of the epiblastic (epidermal) cells which is here exemplified, is of the greatest clinical importance. The enamel organs, we have seen, arose by a species of downgrowth of the epidermis ; so do hairs, sweat glands and sebaceous follicles. Prolonged pressure and friction welds the corneous cells into a solid plate, such as the callosities seen on the palms



FIG. 434.—The more common patterns formed by the Dermal Papillae on the tips of the Fingers.
A, The Loop Pattern. *B*, The Triangle Pattern. *C*, The Whorl Pattern.

of manual labourers. Normal desquamation is arrested ; the cells produced in the deeper layers, unable to grow to the surface, grow inwards and produce corns. In cancer, the epithelial cells of the skin renew their youth and invade the dermis and deeper tissues.

Sweat glands arise as buds from the epiblastic troughs (Fig. 433, *B*). Their ducts open on the surface of the skin in lines or rows corresponding

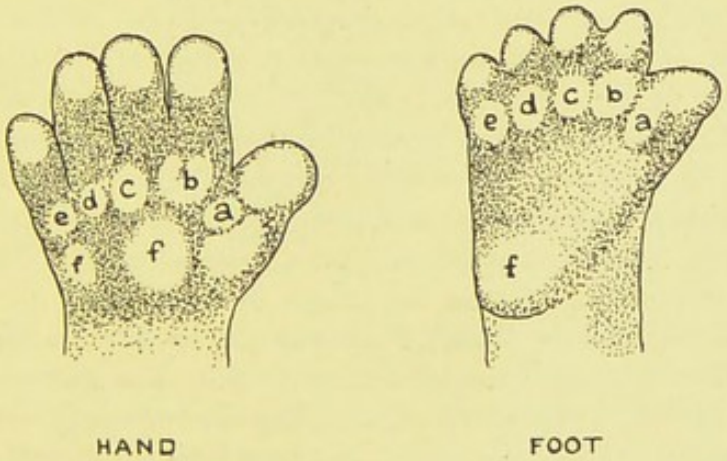


FIG. 435.—The " Pad " Elevations on the Palm and Sole of a Human Embryo at the end of the 2nd month of development. (After Retzius.[1])

to the primary epidermal furrows. In the 5th month the epidermis round their mouths is raised up into ridges, and it is these ridges which give rise to the papillary patterns on the balls of the fingers and elevations of the palm. It will be thus seen that the epidermal ridges correspond not to the lines of **dermal** papillae, but to the furrows of epidermis lying between the papillae.

The papillary lines on the palms and fingers give security of grasp

[1] *Biolog. Untersuch.* vol. 11, 1904, Jena.

(Hepburn). They are arranged in most variable patterns, but the prevailing types in man are those arranged as loops, spirals or whorls (Fig. 434). So variably are the types arranged on the pulps of the digits, that probably no two people show them in the same sequence counting from thumb to little finger in both hands. Hence the impress of the ten finger-tips has been successfully used in the identification of criminals.

These epidermal patterns[1] are formed on elevations which appear on the human hand and foot at the end of the 2nd month, and which certainly correspond to the horny pads found on the feet of quadrupeds. Besides the elevations on the terminal phalanges there are five situated on the palm and sole at the base of the digits. Three others are situated on the proximal part of the palm. In the human foot the elevation corresponding to the hypothenar elevation of the palm undergoes a remarkable enlargement to cover the heel (Fig. 435).

The Hairs.[2]—Hairs begin to develop in the fifth month. Morphologically, a hair may be regarded as a dermal papilla which has become sunk in the subcutaneous tissue, and capped by a process of epidermis. Hairs appear to have been primarily touch organs, and are modifications of the touch bodies found in the skin of reptilia (Gegenbaur). These touch bodies are composed of epithelial cells, having the same shape and arrangement as those which form the taste buds round the circumvallate papillae of the human tongue. The cells which cap the hair papilla evidently represent the primary sensory cells of the touch bodies; they are situated in line, and continuous, with the basal or germinal layer of the skin (Fig. 436). They produce the cells of the medulla of the hair. The tip of the developing hair becomes bent and obliquely embedded in the more superficial layer of the epidermis before it actually reaches the surface. The primary function of the hairs as touch organs is seen in the vibrissae round the mouths of carnivora, but the hair of man no longer is subservient to the sense of touch. Friedenthal has found that certain of the hair-roots in the lips and eyebrows of the human foetus develop the same large sensory bulbs as are found in the roots of the vibrissae of lower mammals.

The first stage in the development of a hair is the ingrowth of epidermis as a solid bud, which pushes in front of it the dermis to form the papilla on which the hair grows. Only the two deeper of the primary layers of the epidermis are carried inwards to form the hair sheath and hair root.

The hairs produced at the 5th month are fine in texture (**lanugo**), and by the 7th month the whole body is covered by them. The hair

[1] See references, p. 452.

[2] See Friedenthal, *Zeitschrift für Ethnol.* 1912 vol. 43, p. 974; K. Backmund, *Anat. Hefte*, 1904, vol. 26, p. 315; P. Stöhr, *Anat. Hefte*, 1904, vol. 23, p. 1; L. Stieda, *Anat. Hefte*, 1910, vol. 40, p. 285.

roots of the eyebrows, eyelids, and of the lips and scalp are the first to appear; their rudiments can be detected in the 4th month. The production of hair buds goes on until birth, the later buds and hairs being thicker and stronger. After birth, new hairs are constantly reproduced within the sheaths to replace the old. Probably the manner in which new hairs are produced resembles that of teeth, viz., from processes of the original bud. Hairs appear first on the head and then on other parts of the body. The fat in the subcutaneous tissue takes the place of hair as a heat conserver. Certain sexual hairgrowths appear on the face, pubes and axilla at puberty. Morphologically, the

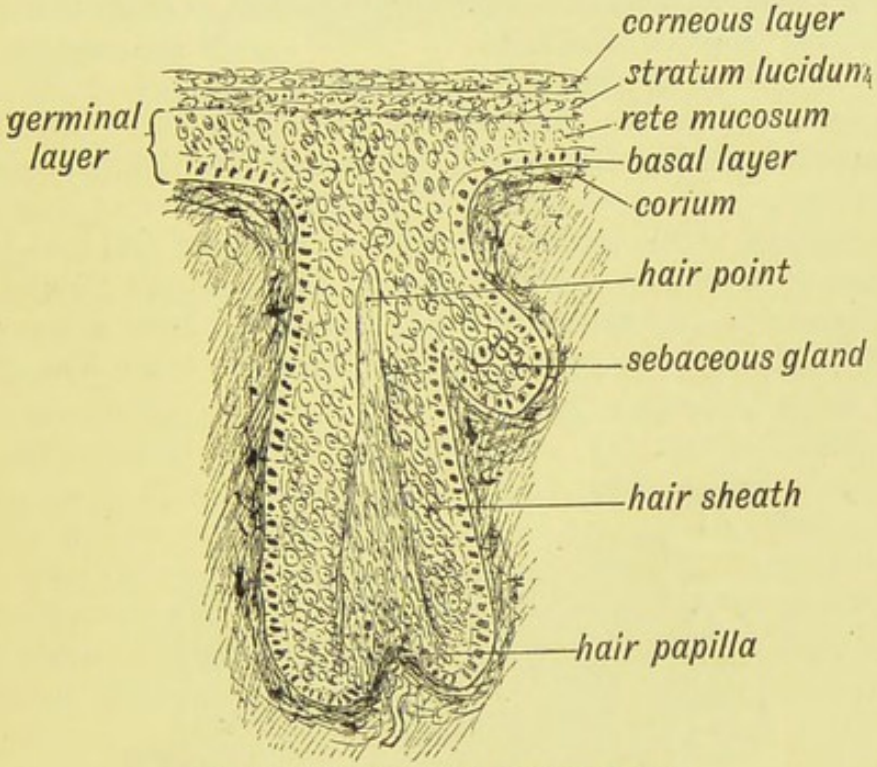


FIG. 436.—Diagram of a Developing Hair.

pubic region represents the separated axillary regions, and probably the explanation of sexual hairs in the axilla is due to this correspondence, for there is a persistent tendency towards symmetry of development in the upper and lower extremities. The primitive mammary ridges, also sexual structures, end at the axilla and groin.

The Nails.—The nails are made up of the basal, stratum mucosum and stratum lucidum layers of the skin (Fig. 437), the corneous layer being lost after the 4th month of foetal life. They appear first in the 3rd month as fields of thickened epidermis on the tips of the digits, but are afterwards shifted dorsally, carrying their palmar nerves with them, so that the terminal phalanx is wholly supplied from the palmar digital branches. The nail of the little toe, a digit in a retrograde phase of development, is frequently shaped like a claw, probably a reversion to a primitive form. The nail is produced on the scattered papillae (the

matrix) at its root. The area of production is marked by the lunule. On the nail bed, in front of the lunule, the papillae are arranged in longitudinal rows. If the nail be pressed, as by the boot, the lateral papillae, under the nail fold (see Fig. 437) are directed downwards, and

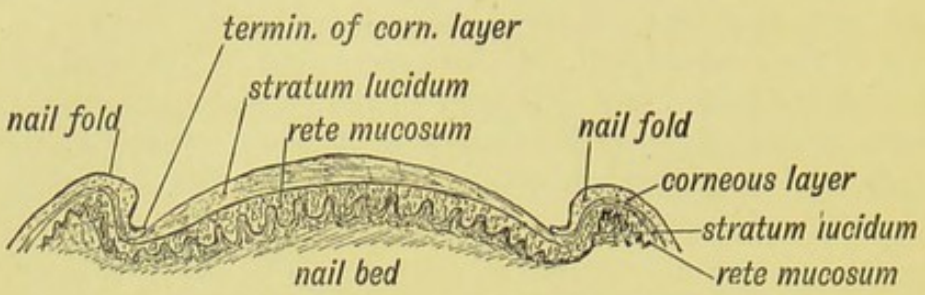


FIG. 437.—Diagrammatic Section across a Nail.

their epithelial outgrowths follow the same direction, thus causing ingrowing nail.

About the end of the 7th month the matrix of the nail root becomes differentiated, active growth sets in and the terminal margin of the nails becomes free; it grows forwards over the corneous layer which covers the terminal row of papillae of the nail bed. The ridge of

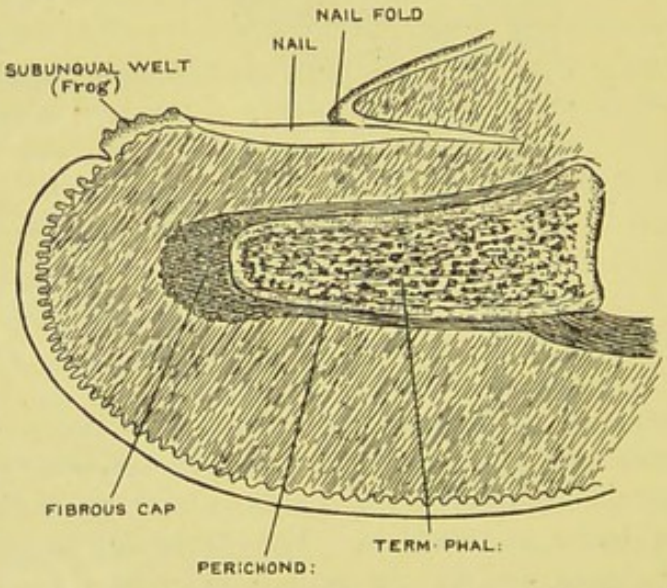


FIG. 438.—Diagrammatic Section of the Terminal Joint of the Digit of a Human Foetus to show the Cap of the Phalanx and the Subungual Welt.

corneous epithelium under the nail-tip represents the central part of the hoof ("frog") of ungulates (Fig. 438).

The nail is carried by the terminal phalanges. Professor Leboucq observed that the tip of the terminal phalanges of the foetus is covered by a special fibrous cap [1] (Fig. 438), which undergoes ossification directly from membrane, while the rest of the phalanx is laid down and ossified

[1] F. A. Dikey, *Journ. Anat. and Physiol.* 1906, vol. 40, January.

in cartilage. The terminal phalanges have thus a special element added to them for the support of the nail and for the fixation of the terminal bulb of the digits. The subungual welt, shown in Fig. 438, comes to lie under the free margin of the nail. In lower mammals it is highly developed ; it forms the " frog " of the horse's hoof.

Sweat Glands.[1]—In the 5th month solid processes of epidermis grow into the dermis and produce sweat glands (Fig. 433, *B*). They arise at the same time and in the same manner as, and often in common with, the buds of hair roots and sebaceous glands. They are produced within the epidermal ridges, and hence the ducts of sweat glands, as may be seen on the palms and fingers, open along the summits of these. The sweat glands in the axilla are peculiar. In section they resemble the acini of the mammary gland, also believed to be highly modified sweat glands. The axillary glands contain much epithelial debris. They appear to be sexual in nature. The wax glands of the external auditory meatus are also modified sweat glands.

Sebaceous Glands.—The sebaceous glands are outgrowths from the more superficial part of hair buds (Fig. 436). Their epithelial lining is derived from the germinal layer. In sheaths which have become occluded from the loss of the hair, or when the mouth of the gland is blocked, the secretion is retained, and a sebaceous cyst or wen, so frequently seen in the scalp, is produced. Round the mouth, on the lips and nose, the sebaceous gland, especially in disorders of the sexual organs, are apt to retain their secretions and become inflamed, small pustules being thus produced. The Meibomian glands in the eyelids are modified sebaceous glands. At birth the child is covered by the **vernix caseosa,** which is composed of desquamated corneous epithelium and the secretion of sebaceous glands.

THE MAMMAE.

The mamma is developed in the same manner in both sexes.[2] At puberty the female breast undergoes a great development, while in the male it retains the infantile form.

The Female Breast.—The mamma of the female is of cutaneous origin, and in its earlier stages of development resembles, and probably corresponds to, a collection of sweat glands arising from a small circular depressed area of skin (Fig. 439, *C*). In the lowest of mammals —the monotremes—the mammary gland is represented by two areas of pubic skin studded with numerous milk glands. The mammary areas are surrounded by a fold or rampart of skin—the mammary area being thus depressed within a cutaneous cup. The surrounding fold,

[1] F. Diem, *Anat. Hefte*, 1907, vol. 34, p. 187 ; C. Schoeppler, *Anat. Hefte*, 1907, vol. 34, p. 429.

[2] E. Bresslau, *Ergebnisse der Anat.* 1909, vol. 19, p. 275.

in the course of evolution, appears to have been transformed into a process or nipple. The manner of development is the key to the anatomy of the mamma. The adult female breast is composed of two elements :

(*a*) Glandular tissue derived from the epiblast by a process of in-budding ;

(*b*) An intricate arrangement of connective tissue derived from the mesoblastic subcutaneous tissue over the pectoralis major.

I. Origin of the Glandular Tissue.

The Mammary Line is a slight ridge of epiblast which stretches along each side of the embryo, from the axilla to the groin, and is the first stage of mammary development in mammalian embryos (Fig. 441). In the sow, for instance, mammae are produced along the whole length of the mammary line. In about 15 % of men a more or less distinct supernumerary mamma or nipple is to be found, and these occur for the greater part in the inguino-axillary line (Fig. 442). Such as occasionally occur on the back or thigh are probably of the nature of dermoid tumours, or it may be that the sweat glands of these regions have by some means become converted to mammary tissue. Supernumerary nipples occur much more frequently in men than in women. This one may expect, because the more vestigial the condition of an organ, the greater is the tendency to the production of ancestral (atavistic) forms.

Developmental Stages.—Seven stages may be recognized in the developmental history of the glandular mammary tissue.

Four of these take place **before birth** :

1st (Fig. 439, *A*). The deeper layer of epiblast thickens over the mammary area ; this thickening represents a part of the mammary ridge or line. This stage is seen in the 2nd month.

2nd (Fig. 439, *B*). The thickening becomes depressed, thus giving rise to a slight pit on the surface.

3rd (Fig. 439, *C*). From the depression arises a number of solid buds, exactly similar to those of sweat gland (5th month). The stalks of these buds form the epithelial lining of the lactiferous ducts.

4th (Fig. 439, *D*). The lobular buds, for each bud develops into a lobe, subdivide at their growing extremities. At first solid, they begin to canaliculize (7th to 9th months). At or about birth the pit or depression, from which the lobular buds originated, is raised, evaginated, and forms the surface of the nipple (Fig. 439, *D*). Thus the ducts come to open on the apex of the nipple. An ampulla is developed in each duct within the base of the nipple. Stage 3 represents the marsupial—the lowest form of mamma. It is normal for the glandular tissue of the newly born child to secrete milk during the two weeks following birth (Roger Williams).

Stages after Birth.—Stage 5 occurs at puberty ; the latent infantile lobular buds again undergo a rapid growth, and give rise to

the minor lobules and acini. Stage 6 occurs towards the end of pregnancy, and consists of a renewed production of glandular tissue. Stage 7 sets in with the menopause, and is characterized by an atrophy of the glandular tissue formed in the later stages of development.

In the process of subdivision, minor buds of adjacent lobes frequently unite together. Hence it is found difficult, during dissection, to separate the gland into its primary lobes. In any of the three later stages a localized and invading hypertrophy of the cells of the glandular tissue may take place. In this manner cancer is produced. The part played

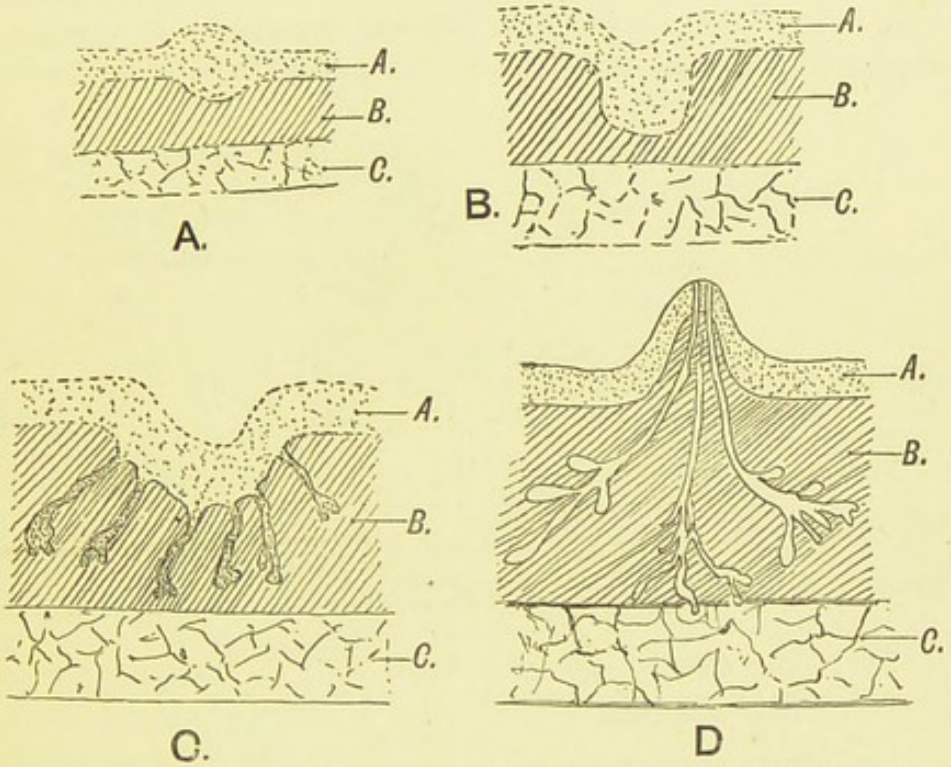


FIG. 439.—Showing the Various Stages in the Development of the Mamma *A*, during the 2nd month; *B*, at the commencement of the 3rd month; *C*, at the 5th month; *D*, at birth.

A=Epiblast; B=Subcutaneous tissue (mesoblast); C=Pectoralis major.

by the lymphatics, which are situated in the mesoblastic tissue of the gland, in the spread of this disease, makes their study important.

II. **Origin of the Capsular or Mesoblastic Part of the Gland.**—As the glandular buds grow out into the subdermal mesoblastic tissue, which reacts and hypertrophies around the invading processes, they divide it (see Fig. 440), into (*a*) superficial, and (*b*) deep layers, these being joined together by (*c*) interstitial septa. The superficial and deep layers are fused in (*d*) the circum-mammary tissue in which the final glandular buds terminate. The processes as they grow outwards also take on (*e*) perilobular and periductal sheaths. The deep and superficial layers are also connected with the anterior sheath of the pectoral muscles and the skin—for they are all parts of the same subdermal or subcutaneous mesoblastic layer.

Lymphatics.—As each part of the capsule carries a network of lymphatic vessels, into which the glandular lymph passes, it will be seen that the arrangement of the parts of the capsule is an important matter in both the physiology and surgery of the gland. The **peri-ductal** and **perilobular** lymphatics communicate through the **septal** or **interstitial** vessels with the **superficial mammary** and deep (**retro-mammary**) lymphatics (Fig. 440). The **superficial** communicate with the **subcutaneous** ; the deep with those in the **pectoral sheath,** and thus it will be seen that mammary cancer may spread to the skin or pectoralis major. The deep and superficial join in the **circum-mammary** lymphatics, and from these pass **efferent vessels** to the **pectoral** and **central** glands of the axilla. The lymph passes from these to the deep

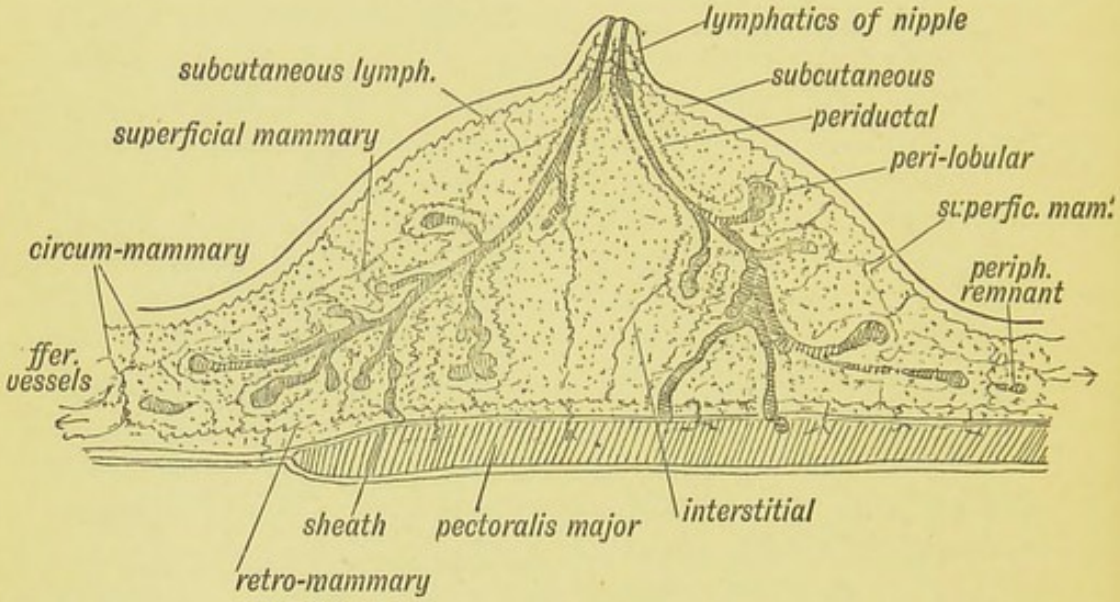


FIG. 440.—Diagrammatic Section of the Breast to show the Arrangement of its Capsule and Lymphatics. The lymphatic vessels are represented by thin wavy lines.

axillary and inferior deep cervical glands—all of which are involved in late stages of cancer of the breast. Other efferent vessels pass from the circum-mammary to the **anterior intercostal** glands of the upper four spaces ; one or two vessels may go to the **cephalic** gland. During the mammary hypertrophy, which takes place at the end of pregnancy, there is a further formation of lymphatic glands in the axilla (Stiles).

Peripheral Remnants.—Isolated or semi-isolated small masses of glandular substance are found situated in the circum-mammary tissue, beyond the body of the gland. Some may pierce the sheath of the pectoralis major, and become a source of recurrent cancer. The presence of glandular remnants is explained by the fact that, when the primary budding takes place, the subdermal mesoblast is shallow and of small extent ; in the subsequent growth of the thorax, the tissue in which the mamma is developed is widely spread out.

The Position of the Mammary Gland is as a rule wrongly described. Quite a third lies on the serratus magnus and beyond the anterior border of the axilla. The axillary lobe reaches upwards in the axilla to the upper border of the third rib, where it is in contact with the **central set** of lymphatic glands (Stiles).

Fat begins to be deposited in the subcutaneous tissue during the 5th month of foetal life. It forms a large element of the mammary gland after puberty. The subcutaneous tissue, out of which the capsule of the gland is formed, normally contains much fat. After lactation, when the glandular tissue atrophies to a considerable extent, a growth of fat replaces it. If no fat is deposited, or if it be absorbed, then the breast loses its plump form and hangs on the chest.

The mammary nerves (secretory) come from the 3rd, 4th and 5th intercostals; the nipple is supplied from the same nerves. The nipple contains non-striated muscle, and is covered with touch papillae, and surrounded by modified sweat and sebaceous glands.

To render the glandular mammary tissue clearly recognizable from the surrounding connective tissue, Stiles adopted the method of immersing the mamma in a 5 % of HNO_3 for two days. The glandular tissue becomes of a dark yellow tint and thus can be detected even in minute quantities from the surrounding tissue of mesoblastic origin.

Dermis and Subcutaneous Tissue.—The subepidermal mesoblast, out of which the dermis and subcutaneous tissues are differentiated, is at first composed of cells of rounded outline embedded in a homogeneous jelly-like matrix. Mall regards the matrix as a living substance in which, quite independently of the cells, connective tissue fibres are differentiated, both white and yellow. Processes are certainly developed from the cells, but it is doubtful if these ever become detached and form independent fibres.

Fat Cells.—Certain granular cells of the connective tissue, especially of the subcutaneous layers, have the property of secreting **fat,** which appears first as diffuse droplets. These ultimately run together and produce the characteristic outline of adipose cells. Fat cells appear first in the subcutaneous tissue during the 5th month of foetal life; later it appears in the subserous tissue of the body wall. It reaches its greatest normal development just before and after birth. Two theories are held regarding the origin of fat cells: (1) that they are cells of the connective tissue differentiated and set aside permanently to form and store fat; (2) they are ordinary connective tissue cells temporarily laden with fat.[1] There is present at birth a sharply differentiated mass of fat and lymphoid tissue in each posterior triangle of the neck and extending on each side beneath the trapezius muscle. Hatai regards this mass as the representative of the **interscapular gland** of hybernating mammals (see p. 323).

[1] See article by Batty Shaw, *Journ. Anat. and Physiol.* Oct. 1901.

Touch Bodies and Sense Organs.—The cells of the ectoderm in the simpler forms of invertebrate animals not only protect the body but many of them become specially sensitive, and thus afford the animal knowledge of its surroundings. In the development of the olfactory mucous membrane, of the auditory cells and of the taste

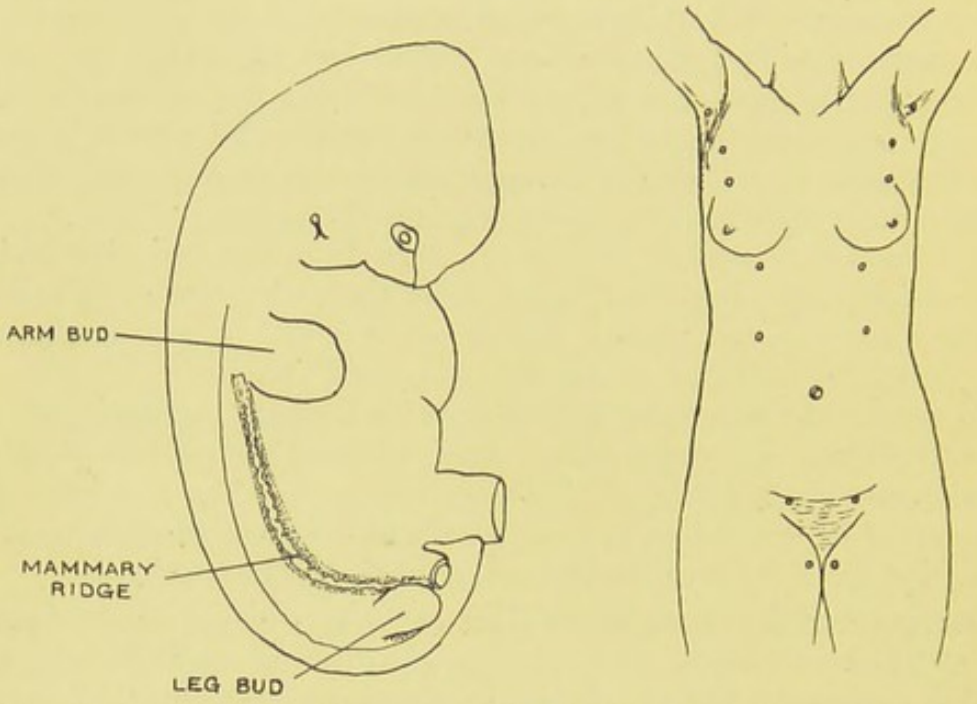


FIG. 441.—Embryo of a Pig—corresponding to the end of the 1st month of human development—showing the Mammary Ridge extending from Axilla to Groin. Only the pectoral part develops in the human embryo. (After Schultze.)

FIG. 442.—Diagram to show the Position in which Supernumerary Mammae are usually found. (After Merkel.)

buds of the human embryo this specialization of areas of the ectoderm is seen. The retina, the brain, spinal cord and nerves are also areas of the ectoderm which have been highly specialized and set aside for the purpose of correlating the organism with its surroundings. Although the various forms of touch bodies, such as the Pacinian corpuscles and those of Krause and Meissner, have not been traced developmentally, there can be little doubt that they arise directly from the epidermis beneath which they are situated.

INDEX.

[*The numbers refer to the pages.*]

A

Abnormalities of development, 30. (See also under each part.)
Accessory obturator nerve, 426.
Accessory processes of vertebrae, 56.
Accessory supra-renals, 390.
Accessory thyroid bodies, 246.
Achromatin, 8.
Acoustic ganglia, 217.
Acromegaly, 132, 157.
Acromion process, 431.
Adloff, P., 168.
Affenspalte, 114.
Agar, W. E., 135.
Age of foetus, Estimation of, 40.
Agger nasi, 181.
Aichel, 389.
Alar cartilages of nose, 143.
Albrecht, 145.
Alimentary tract, 17, 246.
Allantois, 15, 24.
Allantois, Origin of, 34.
Allen, B. M., 350.
Ameloblasts, 164.
Amnion, 28.
Amnion, Origin of, 33.
Anal depression, 373.
Anal fascia, 401.
Anal membrane, 366.
Andrews, H. R., 15.
Anencephaly, 74.
Angular gyrus, 199, 202.
Anterior commissure, 95, 103.
Antrum of Highmore, 153, 178.
Antrum of mastoid, 212.
Anus, Formation of, 372.
Anus, Malformation of, 370.
Anus, Musculature of, 374.
Aorta, arches of, 230, 232.
Aorta, dorsal, 230, 233, 317.
Aortic arches, 229.
Aortic septa, 306.
Aortic stems, 230.
Appendix, 276, 277.
Aqueduct of Sylvius, 84, 199.
Aqueductus cochlea, 216.
Aqueous chamber, 193.
Arai, H., 128.
Archenteron, 12.
Arch of aorta on right side, 232.
Arch of foot, Development of, 434.
Arm, Nerve supply of, 420.
Arteries of body segment, 61.
Ask, F., 197.
Assheton, R., 30, 37.
Asterion, 123.
Astragalus, 434.
Atlas, 54.
Atlas, Joints of, 55.
Atresia vaginae, 360.
Attic of tympanum, 211.
Attraction sphere, 8.
Auditory meatus, external, 206.
Auditory meatus, internal, 219.
Auditory ossicles, 211.
Auricles of heart, 302.
Auricular septa, 304.
Auriculo-ventricular bundle, 300.
Auriculo-ventricular valves, 298, 309.
Axis, 54.
Axis cylinders, 73.
Azygos lobe of lung, 333.
Azygos veins, 287.

B

Backmund, K., 454.
Ballantyne, J. W., 36.
Bardeen, C. R., 51, 58, 123, 404, 411, 414, 444.
Bardeleben, 46.
Bartholin, Glands of, 382.

Bashford, 7.
Basi-hyal, 228.
Basi-ventralia, 51.
Bayer, 365.
Beard, 10, 18, 37, 243.
Bell, E. T., 243.
Berry, R. J. A., 272, 274.
Biceps of arm, 439.
Biceps of leg, 440.
Bicipital rib, 47.
Bilaminar blastocyst, 11.
Bilaminar blastoderm, 11.
Bile ducts, 254.
Binocular vision, 191.
Bladder, 376.
Bladder, Musculature of, 377.
Blair Bell, 6.
Bland-Sutton, 55, 129, 153, 336.
Blastema, 415, 417.
Blastocyst, 11.
Blastodermic vesicle, 11.
Blastopore, 30.
Blastopore, Position of, 16.
Blastula, 11.
Blood, 319.
Blood-islands, 318.
Blood vessels, Formation of, 318.
Body stalk, 16, 25.
Body, Symmetry of, 403.
Body, Ventral line of, 403.
Body wall, 402.
Body wall, Stages in Evolution of, 391.
Bolk, L., 56, 141, 420.
Bolton, J. S., 107.
Bone, Formation of foramina and canals in, 152.
Bone-marrow, 323.
Bones, Development of, 445.
Bones, Lines of pressure and tension in, 449.
Bones, Ossification of, 444.
Bonnot, 323.
Brachet, A., 337.
Brachycephalic skull, 130.
Bradley, O. Charnock, 79, 80, 251.
Brain capsule, 133.
Brain, Commissures of, 95.
Brain, Development of, 77.
Brain, Fissures of, 81, 107, 115.
Brain, Growth of, 118.
Brain, Membranes and Arteries of, 116.
Brain, Secondary sulci and gyri of, 115.
Brain, Significance of convolutions of, 107.
Branchiae, 221.
Branchial arches, 224.
Branchial segments, 135.
Braus, H., 424.
Bregma, 123.
Bregmatic fontanelle, 118.
Breman, J. C., 349.
Bremner, J. L., 38, 334.
Bresslau, E., 457.
Bridge, 429.
Broek, A. J. P. van den, 13.
Broman, 211, 256, 261, 314, 318, 337, 376.
Bronchi, Formation of, 330.
Bronchi, Ramification of, 332.
Bruni, A., 49.
Bryce, T. H., 13, 242.
Bulbus arteriosus, 306.
Bulla ethmoidalis, 180.
Bulloch, W., 388.
Butterfield, 240.

C

Caeco-colic sphincter, 274.
Caecum, Development of, 275.
Caecum, Morphology of, 274.
Calcarine fissure, 113, 201.
Calloso-marginal fissure, 113.
Cameron, J., 75, 94, 106, 188, 217, 287.
Cameron, P., 396.
Canalis cranio-pharyngeus, 161.
Cardiac septa, 304.
Cardiac tube, Flexures of, 297.
Cardiac tubes, Origin of, 294.
Cardinal veins, 287.
Carotid bodies, 246.
Carpale, I., II., III., IV., V., 433.
Carpus, 432.
Carter, J. T., 171.
Cartilages of Jacobson, 143.
Cartilages of visceral arches, 227.
Cartilaginous part of skull, Development of, 119.
Caudate lobe of liver, 259.
Caudopore, 67.
Central canal, 67.
Central fissure, 115.
Centrosome, 8.
Centrum, 51.
Cephalic index, 130.
Cerato-hyal, 228.
Cerebellar tracts, 71.
Cerebellum, 77, 80.
Cerebellum, Fissures of, 81.
Cerebellum, Function of, 84.
Cerebellum, Peduncles of, 82.
Cerebral hemispheres, 97.
Cerebral veins, 286.
Cerebral vesicle, 97.
Cerebro-spinal fluid, 79, 98.
Cerebrum, Origin of, 89.
Cervical fascia, 402.
Cervical rib, 47.
Cervical sinus, Formation of, 225.
Cervico-occipital region, Variations of, 48.
Cheatle, A., 217.

Chevron bones, 396.
Choanoid muscle, 194.
Choroid, 193.
Choroid fissure of eye, 190.
Choroidal fissure of brain, 106.
Chorion, 14, 16, 22, 27.
Chorion, Origin of, 33.
Chromaffin cells, 390.
Chromatin, 8.
Chromosome, 8.
Ciliary muscle, 193.
Ciliary processes, 189, 193.
Circulation at birth, 311.
Circulatory system, Development of, 281.
Clark, E. R., 321.
Clarke, H. R., 358.
Clavicle, 430, 431.
Clavicle, Maldevelopment of, 431.
Cleft palate, 141, 145.
Cleido-cranial dysostosis, 431.
Cloaca, 343, 365, 368.
Cloaca, Ectodermal, 366.
Cloaca, Parts formed from, 368, 372.
Cloaca, Sphincter of, 374.
Cloacal membrane, 368.
Cloacal structures, Evolution of, 366.
Coccygeal body, 390.
Coccygeus, 440.
Coccyx, 395.
Cochlear ganglion, 218.
Coeliac axis, 62, 318.
Coelom, 13, 249, 342.
Coelom, Divisions of, 314.
Coelom, Origin of, 31.
Coelom, Pericardial, 294.
Coelom, Umbilical, 269.
Collateral fissure, 114.
Coloboma iridis, 191.
Colon, Development of, 272, 275.
Commissures, Development of, 103.
Common genital mesentery, 3.
Congenital stenosis, 308.
Congenital pulmonary stenosis, 309.
Conjugal ligament, 55.
Contrahentes, 439.
Conus arteriosus, 306.
Coracoid, 429.
Cornea, 187.
Corpora quadrigemina, 84, 199.
Corpus callosum, 95, 103.
Corpus luteum, 6.
Corpus striatum, 90, 96, 109.
Cortex, Development of, 107.
Costal processes, 55, 404.
Cowper, Glands of, 382.
Crania, Abnormal, 132.
Cranial axis, 133.
Cranial nerves, Nuclei of, 87.
Cranial nerves in visceral arches, 228.
Cranial nerves, Segmental arrangement of, 88.
Cranium, 117.
Cricoid cartilage, 228, 336.
Crusta petrosa, 166.
Cunningham, D. J., 45, 110.
Cushing, H., 92.
Cuticular membrane, 165.
Cuvier, Duct of, 283, 284, 299.

D

Dale, 265.
Dandy, W. E., 16, 319.
Dareste, 36.
Darwin's tubercle, 208.
Decidua, 20.
Decidua reflexa, 21.
Decidua serotina, 21, 27.
Decidua vera, 21.
Decidual cells, 20.
Dedekind, F., 198.
Delbet, 401.
Dendrites, 73.
Dendy, 85.
Dental papilla, 164.
Dental sac, 166.
Dental shelf, 164.
Dentary element, 156.
Dentigerous and other cysts of the jaw, 168.
Dentine, Origin of, 163.
Dentitions, Number of, 168.
Dermal bones, Development of, 120, 150.
Dermal papillae, Formation of, 452.
Dermis, 452.
Derry, D., 396.
Diaphragm, Development of, 337.
Diem, F., 457.
Dikey, F. A., 456.
Diverticula, Congenital, 270.
Dixon, A. F., 217, 351, 449.
Dolichocephalic skull, 130.
Doran, A., 351, 376.
Dorsal aortae, 233, 317.
Dorsal commissure, 105.
Dorso-cervical region, Variations of, 47.
Dorso-epitrochlearis, 438.
Dorso-lumbar region, Variations of, 47.
Double, A. F. Le., 46.
Drummond, W. B., 323.
Duckworth, W., 133, 141, 382.
Duct of Gartner, 349.
Ducts of Cuvier, 283, 299.
Ductus arteriosus, 230.
Ductus endolymphaticus, 214.
Ductus venosus, 291.
Duodeno-jejunal fossa, 279.
Duodeno-jejunal loop, 271.
Duodenum, 278.
Duodenum, Congenital occlusion of, 271.
Dura mater, 116, 122.
Dwight, T., 442.

E

Ear, Development of, 204.
Ear, External, 206.
Ear, Muscles of, 208, 438.
Ear, Nerve centres of, 218.
Ectoderm. See Epiblast.
Ectopia cordis, 317.
Ectopia vesicae, 376.
Ectorhinal fissure, 113.
Edgeworth, F. H., 135, 171, 233.
Elze, C., 38.
Embryo, Differentiation of, 1, 11.
Embryo and membranes, 14.
Embryonic structures, Persistence of, 269.
Enamel, Origin of, 164.
Encephalocele, 75.
Endo-cardial cushions, 304.
Endoderm. See Hypoblast.
Ensiform process, 406.
Epaxial muscles, 60.
Epiblast, 12, 185, 224, 451.
Epicanthic fold, 196.
Epicoracoid, 429.
Epididymis, 349.
Epiglottis, 238.
Epi-hyal, 228.
Epiphyseal lines, 446.
Epiphyses, Nature of, 447.
Epipteric bone, 130.
Epipubis, 427.
Epitrochleo-anconeus, 439.
Epitrichium, 451.
Epoophoron, 349.
Erythroblasts, 319.
Erythrocytes, 320.
Essick, C. R., 78.
Eternod, A. C. F., 22, 30, 50, 168, 292, 319.
Ethmoid, Lateral mass of, 126.
Ethmoid, Vertical plate of, 144.
Ethmoidal sinuses, 180.
Eustachian tube, 208, 227.
Eustachian valve, 301.
Evatt, E. J., 380, 452.
External auditory meatus, 227.
External ear, 206.
External ear, Muscles of, 208, 234.
Eye, 184.
Eyeball, 185, 192, 195.
Eyelids, 195.

F

Face, Development of, 138.
Face, Evolution of, 138.
Face, Malformations of, 141.
Face and scalp, Muscles of, 162, 234.
Facial angle, 133.
Fairbank, H. A. T., 426.
Falciform ligament of liver, 258.
Fallopian tube, 6, 7, 355.
Farmer, J. B., 9.
Fasciae, Nature of, 398.
Fat cells, 461.
Fawcett, E., 53, 56, 123, 127, 145, 305.
Federow, V., 334.
Female pronucleus, 7.
Femoral hernia, 395.
Ferguson, J. G., 400.
Fertilization, Phenomena of, 10.
Fick, R., 7.
Fiddes, J. D., 449.
Filum terminale, 69.
Fimbria, 6, 355.
Fischel, A., 46, 449.
Fischer, G., 170.
Fissure of Sylvius, 108.
Fissures of brain, 81.
Fissures of brain, Formation of, 81, 106.
Fissures, Temporal, 115.
Fissures, Temporary, 106.
Fitzwilliams, D., 431.
Flack, Martin, 302.
Flechsig, 110.
Flexor brevis digitorum, 441.
Flint, J. M., 327, 332.
Floccular fossa, 217.
Flocculus, 82.
Foetal circulation, Remnants of, 312.
Foetus, 40.
Fontanelles, 122.
Foot, 432, 449.
Foot, Eversion of, 434.
Foot, Muscles of, 440.
Foramen caecum, 244.
Foramen ovale, 304.
Foramina in bone, Formation of, 129, 152.
Fore-brain, 68, 89.
Fore-brain in human embryo, 90.
Fore-brain, Roof of, 97.
Fore-gut, 15, 247.
Fornix, 103, 176.
Forssner, H., 271.
Forsyth, 246.
Fossa of Rosenmüller, 227.
Fourchette, 378.
Fourth ventricle, 78.
Fox, H., 226.
Frassi, L., 38.
Frazer, J. E. S., 93, 150, 174, 177, 209, 226, 235, 328, 335.
Friedenthal, 454.
Frontal bone, 120.
Frontal sinus, 179.
Frontal sinus, Infundibulum of, 179.
Fronto-nasal process, 139.
Fundus of stomach, 260.
Funicular process, 386.
Furcula, 327.
Fürst, 190.
Futamura, R., 234.

G

Gadow, H., 51, 151.
Gage, Sussana P., 16.
Gall bladder, 254.
Ganglia, Posterior root, 62.
Ganglia, Sympathetic, 62.
Gartner, Duct of, 349.
Gaskell, W. H., 63, 67, 135, 161, 198.
Gaskell's theory, 137.
Gastro-hepatic omentum, 257.
Gastro-splenic omentum, 262.
Gaupp, E., 127, 135, 145, 155.
Geddes, 413, 418.
Gemmill, 10.
Geniculate bodies, 84.
Geniculate ganglion, 84.
Genital cord, 348, 356.
Genital folds, 372.
Genital organs (external), 372, 378.
Genital ridge, 18.
Genital ridge of male, 383.
Genital tubercle, 378.
Genital Wolffian tubules, 350.
Gennari, Stria of, 201.
Germinal epithelium, 5, 451.
Germinal spot, 7.
Germinal vesicle, 7.
Giraldes, Organ of, 350.
Gladstone, R., 287.
Glaesmer, 48.
Goeppert, E., 441.
Goodrich, E. S., 135, 413, 421.
Gould, E. Pearce, 232.
Graafian follicle, 5.
Grafenberg, 416.
Grail, 135.
Great omentum, 265.
Great sacro-sciatic ligament, 440.
Green, Edridge, 195.
Greig, D. M., 426.
Greil, 306, 327.
Grosser, O., 116, 247.
Gubernaculum dentes, 167, 171.
Gubernaculum testis, 357.
Gubernaculum testis, Formation of, 357, 384.
Gudernatsch, J. F., 388.
Gyrus subcallosus, 176.

H

Haemolymph glands, 323.
Hairs, 454.
Hallux, 436.
Hammar, J. A., 211, 242, 323.
Hamulus of lachrymal, 195.
Hand, 432, 449.
Hand, Muscles of, 439.
Hare lip, 141.
Harrison, R. G., 75, 169.
Hart, D. Berry, 37, 193, 359, 374, 384.
Hassall, Corpuscles of, 243.
Head, Shape of, 131.
Heart, Abnormalities of, 309.
Heart, Changes in position of, 313.
Heart, Demarcation of, into chambers, 296.
Heart, Development of, 294.
Heart, Evolution of, 281.
Heart, Fixation of, 283.
Heart, Valves of, 309.
Heiberg, K. A., 265.
Heidenhain, M., 452.
Heiss, R., 330.
Hepatic veins, 291.
Hepburn, D., 121, 454.
Hermaphrodites, 388.
Hernia, 393.
Herring, P. T., 92.
Hertzog, M., 13.
Hett, Seccombe, 240.
Hiatus semilunaris, 179.
Hill, J. P., 11, 30, 169, 361.
Hill, Leonard, 335, 402.
Hilton, W. A., 271.
Hind-brain, 68, 77.
Hind-gut, 15, 247, 272.
Hip joint, Congenital dislocation of, 428.
Hippocampal commissure, 95, 103.
Hippocampal fissure, 113.
Hippocampal formation, 105.
Hippocampal gyrus, 105.
His, 75, 96, 107, 319.
Hochstetter, 106.
Horse-shoe kidney, 354.
Howard, R., 387.
Howes, 51, 136.
Huber, G. C., 351.
Hubrecht, A. W., 22.
Hunter, John, 384.
Huntingdon, G. S., 320.
Hutchison, 323.
Huxley, 136.
Hyaloid artery, 193.
Hyaloid canal, 193.
Hydatids of genital glands, 349.
Hydrocephaly, 123.
Hymen, 360, 364.
Hyoid, 228.
Hyoid arch, 224.
Hyo-mandibular cartilage, 151.
Hypaxial muscles, 61.
Hypoblast, 12, 224.
Hypochordal bow, 51.
Hypogastric arteries, 312.
Hypoischium, 427, 448.
Hypospadias, 374.
Hypothalamus, 91.

I

Ichthyosis, 451.
Ileo-caecal bloodless fold, 278.

Ileo-caecal fossa, 278.
Ileo-caecal valves, 277.
Ileo-colic fold, 278.
Ileo-colic fossa, 278.
Ileo-colic part of bowel, 274.
Ileo-colic part of bowel, Volvulus of, 280.
Ileo-colic sphincter, 274, 277.
Iliac arteries, 318.
Iliac veins, 288.
Ilium, 417, 427.
Imperforate anus, 370.
Incus, 211.
Inferior medullary velum, 78.
Inferior turbinate bone, 178.
Inferior vena cava, 288.
Infra-cardiac bursa, 257.
Ingalls, N. W., 38.
Inguinal fold, 357.
Inguinal hernia, 393.
Inouye, M., 145.
Inter-articular cartilages, 443.
Interchondral disc, 442.
Intercostal vein, Left superior, 286.
Intermediate cell-mass, 17, 347.
Intermedium, 433.
Internal auditory meatus, 219.
Internal geniculate body, 200.
Internal lateral ligament of ankle, 436.
Internal pterygoid plate, 150.
Internal saphenous artery, 441.
Interparietal bone, 130.
Interscapular gland, 323.
Intersegmental septum, 50.
Intersigmoid fossa, 273.
Interstitial cells, 5.
Interventralia, 51.
Interventricular foramen, 309.
Interventricular septum, 309.
Intestine, Great, 272.
Intestine, Great, Fixation of, 256.
Intestine, Small, 268.
Iris, 193.
Island of Reil, 108, 111.
Isthmus of thyroid, 244.
Iter venosum, 284, 314, 326.

J

Jackson, C. M., 40.
Jacobson's organ, 143, 181.
Jacobson's cartilage, 143.
Jaekel, O., 54.
Jansen, Murk, 132.
Jaw, Cysts of, 168.
Jaw, Growth changes in, 157.
Jenkins, G. T., 429.
Jenkinson, J. W., 30, 211.
Johnson, F. P., 250.
Johnston, L., 191, 261.
Johnston, H. M., 432.
Joints, 442.
Joly, 6.
Jones, F. Wood, 16, 46, 278, 359, 374.
Jordan, H. E., 269.
Jugular vein, 283.
Jugular vein, primitive external, 286.
Junctional ring, 25.

K

Kallius, E., 185, 235, 335.
Karyokinesis, 7, 8.
Kazzander, 411.
Kerr, Graham, 76.
Kidd, W., 452.
Kidney, Origin of, 351.
Kidney, Horse-shoe, 355.
Kirchner, A., 447.
Knowles, 170.
Knee-joint, 444.
Kohlbrugge, J. H. F., 10.
Kölliker, 75, 192.
Korff, 400.
Kuithan, 80.
Kupffer, 75.

L

Labia minora, 378.
Labyrinth, 204.
Lachrymal bone, 195.
Lachrymal gland, 197.
Lack, L. A. H., 274.
Lagena, 216.
Lambda, 123.
Lamina cinerea, 106.
Lamina terminalis, 91, 95, 106.
Langelaan, J. W., 79.
Langerhans Islands, 265.
Langhan's cells, 15.
Lanugo, 454.
Larynx, 335.
Lateral nasal process, 147.
Lateral nasal process, Cartilage of, 147.
Lateral recess of pharynx, 241.
Lateral ventricle, 97.
Latissimo-condyloideus, 438.
Leboucq, 456.
Left innominate vein, 286.
Left superior intercostal vein, 286.
Leg, Nerve supply of, 424.
Lelievre, 320.
Lenhossék, M. von, 189.
Lens, 185.
Lens, Capsule of, 187.
Lens, Vascular capsule of, 192.
Leucoblasts, 320.
Leucocytes, 320.
Lesser sac of peritoneum, 267.
Levator claviculae, 438.
Levator glandulae thyroideae, 245.
Lewis, F. T., 58, 75, 192, 270, 287, 294, 302, 321, 449.

Lewis, W. H., 411, 431.
Lichtenberg, A., 379.
Lieberkuhn, Glands of, 272.
Lieno-renal ligament, 262.
Ligament of Struthers, 438.
Ligaments, 443.
Ligaments, Capsular, 443.
Ligamentum teres, 444.
Limbic bands, 301.
Limbs, 413.
Limbs, Arteries of, 441.
Limbs, Embryonic, 414.
Limbs, Evolution of, 413.
Limbs, Joints of, 442.
Limbs, Ligaments of, 442.
Limbs, Nerve supply of, 420.
Limbs, Segmental nature of, 419.
Limbs, Torsion and rotation of, 417.
Limbs, Veins of, 441.
Limbs, Vessels of, 441.
Limiting sulci of Island of Reil, 109.
Linck, A., 49.
Linea alba, 411.
Lingual papillae, 238.
Lingual tonsil, 242.
Lingula, 82, 128.
Littré, Glands of, 382.
Liver, changes after birth, 259.
Liver, Development of, 251.
Liver, Ligaments of, 257.
Liver, Morphology of, 258.
Liver, Veins of, 253.
Lockwood, 285.
Loeb, 36.
Long plantar ligament, 436.
Low, A., 16, 155, 271, 280.
Lower jaw, Development and ossification of, 155.
Lowsley, O. S., 380.
Lumbar plexus, 422.
Lung, Blood supply of, 334.
Lung buds, 328.
Lungs, Changes at birth, 334.
Lungs, Development of, 327.
Lungs, Evolution of, 324.
Lungs, Lobes of, 332.
Lymphatic glands, 320, 323.
Lymphatic system, 321, 402.
Lymphatic vessels, 321.
Lymphocytes, 320.
Lymphoid tissue, 242.

M

MacCallum, J. B., 344.
Mackenzie, Ivy, 302.
M'Clure, C. F. W., 321.
M'Murrich, J. P., 437.
Macrostoma, 141.
Maggi, 121.
Majendie, Foramen of, 80.
Malar, 153.
Malar, Orbital plate of, 195.
Male pronucleus, 7.
Mall, F. P., 40, 53, 106, 116, 125, 128, 150, 286, 309, 337, 400.
Malleus, 156, 211.
Mamma, Lymphatics of, 460.
Mamma, Origin of glandular tissue, 457.
Mamma, Peripheral remnants of, 460.
Mammae, 457.
Mammary gland, Development of, 458.
Mammary gland, Position of, 461.
Mammary line, 458.
Mammillary processes of vertebrae, 56.
Mandible, Evolution of, 156.
Mandibular processes and arch, 139, 154, 224.
Marshall, Francis H. A., 4.
Marshall, Vein of, 299.
Marrow, 323.
Mastication, Muscles of, 171.
Mastoid, 212, 216.
Masur, A., 164.
Maxilla, Ossification of, 150.
Maxillary process, Nerves and Arteries of, 152.
Maxillary processes, 139, 149.
Maxillo-turbinal, 178.
Mayou, 196.
Mazilier, R., 327, 337.
Measurements of foetus, 40.
Meckel's cartilage, 151, 155.
Meckel's diverticulum, 268.
Meconium, 280.
Medulla, Laminae of, 78.
Medulla oblongata, 76.
Medullary folds, 67.
Medullary plate, 33, 73.
Medullary velum, Inferior, 78.
Medullary velum, Superior, 82.
Meek, A., 68, 135.
Membrana pupillaris, 193.
Membrana, Tympani of, 159, 213, 227.
Membranous labyrinth, Origin of, 213.
Meningocele, 74.
Mesenteric recess, 256.
Mesentery, Common genital, 3.
Mesentery of appendix, 278.
Mesentery of small gut, 279.
Mesentery of small gut, Abnormal fixation of, 280.
Mesial nasal processes, 143.
Mesoblast, 452.
Mesoblast, Divisions of, 59.
Mesoblast, Origin of, 31.
Mesocardium, 294.
Mesocardium, arterial, 315.
Mesocardium, venous, 315.
Mesocephalic skull, 130.
Mesoderm. See Mesoblast.

Mesogastrium, 255.
Mesogastrium, Dorsal, 260.
Mesohepaticum, 256.
Mesonephros, 342, 344.
Mesonephros, Fate of, 348.
Mesorchium, 387.
Mesosalpinx, 3.
Mesovarium, 3.
Metacarpus, Flexors and extensors of, 437.
Metanephros, 342.
Metopic suture, 121.
Microcephaly, 123.
Mid-brain, 68, 77, 84.
Mid-gut, 246, 268.
Milligan, W., 217.
Mitosis, 7, 8.
Mollier, 320.
Monro, Foramen of, 91.
Monro, Sulcus of, 96.
Moodie, R. L., 447.
Morris, H., 45.
Morula, 11.
Müller, Charlotte, 408.
Müller, E., 413, 440.
Müllerian ducts, 355, 362.
Müller's muscle, 199.
Muscle plate, 60.
Muscles, Abnormalities of, 438.
Muscles, Migration of, 437.
Muscles of body segment, 60.
Muscles of extremities, 436.
Muscles, Primary groups of, 60.
Musculature of Trunk, 60.
Muthmann, E., 351.
Myotome. See Muscle plate.

N

Nails, 455.
Nasal air sinuses, Development of, 178.
Nasal cavities, 173, 177.
Nasal duct, 147, 181.
Nasal processes, 142.
Nasal processes, Arteries and nerves of, 148.
Naso-palatine foramen, 146.
Neck, Development of, 221, 250.
Neocranium, 137.
Neopallium, 100, 105.
Nerve cells, Nature of, 73.
Nerve plexuses, Nature of, 424.
Nerves, Development of, 73, 75.
Nerves of body segment, 62.
Nerves of limbs, 420.
Nerves, Somatic, 62.
Nerves, Splanchnic, 62.
Nervous system, Evolution of central, 66.
Nervus bigeminus, 425.
Nervus furcalis, 425.
Neural arch, 51.
Neural canal, 17, 68, 70.
Neural canal, Divisions of, 68.
Neural canal, Malformations of, 74.
Neural canal, Membranes and vessels of, 75.
Neural crest, 62.
Neural flexures, 84.
Neurenteric canal, 16, 69, 377.
Neuroblasts, 70.
Neuroglia, 70.
Neuromere, 87.
Neuron, 74.
Neuropore, 67.
Nicholls, 85.
Norberg, J., 33.
Nose, Malformations of, 183.
Notochord, 17, 32, 48.
Notochord, Fate of, 49.

O

Oblique vein of Marshall, 299.
Obturator fascia, 400.
Occipital bone, 123.
Occipital condyle (median), 54.
Occipital fontanelle, 124.
Occipital joint, 54.
Occipital lobe, 201.
Occipital ridges, 134.
Occipito-atlanto-axial articulations, 54.
Odonto-blasts, 165.
Oesophagus, 250.
Olfactory lobe, 175.
Olfactory nerves, 174.
Olfactory peduncle, 175.
Olfactory pits, 174.
Olfactory plates, 174.
Olfactory sense epithelium, Origin of, 174.
Olfactory structures, 174.
Olfactory tract, Termination of, 176.
Omo-trachelian, 438.
Opercula of Island of Reil, 110, 111.
Oppel, A., 247, 327.
Optic chiasma, 91, 95, 104.
Optic cup, 188.
Optic lobes, 200.
Optic nerve, 188.
Optic radiations, 199.
Optic thalami, 90, 95, 97.
Optic tracts, 199.
Optic vesicle, 187, 191.
Ora serrata, 188.
Oral plate, 160.
Orbit, Formation of, 195.
Orbital muscles, 198.
Organ of Corti, 216.
Organ of Geraldés, 350.
Organ of hearing, Development of, 204.
Organ of Rosenmüller, 349.

Osborn, 413.
Os calcis, 433, 435, 446.
Os centrale, 433.
Os epactal, 130.
Os Japonicum, 153.
Os trigonum, 433.
Ossification of bones, 446. See under Cranium.
Ostium abdominale, 6, 358.
Otis, W. J., 375.
Otocyst, 213.
Ova, Discharge of, 5.
Ova, Origin of, 18.
Ovario-pelvic ligament, 3, 359.
Ovary, Descent of, 2.
Ovary, Position of, 4.
Ovum, 4, 9.
Ovum, Development of, 1.
Ovum, Discharge of, 5.
Ovum, Division of, 7.
Ovum, History of, within the Fallopian tube, 6, 7.
Ovum, Implantation of, 20.
Ovum, Nourishment of, 21.
Owen, Sir R., 119.

P

Palatal rugae, 153.
Palate, 149.
Palate bone, 149, 151.
Palate, Primitive, 138.
Palate, Soft, 150.
Palato-glossus, 150.
Palato-quadrate bar, 151.
Paleocranium, 137.
Palmaris longus, 439.
Pancreas, 263.
Pancreas, Relationship to peritoneum, 265.
Papillae folliatae, 238.
Papillary patterns, 453.
Parachordal cartilages, 124.
Paradidymis, 350.
Paramastoid process, 134.
Paramore, R. H., 391, 396.
Para-occipital process, 134.
Paraterminal body, 105.
Para-thyroids, 246.
Paraxial mesoblast, 17.
Parietal bone, 120.
Parieto-occipital fissure, 201.
Paroophoron, 349.
Parotid gland, 239.
Parovarium, 351.
Pars ciliaris retinae, 189.
Pars membranacea septi, 309.
Pars triangularis, 110.
Parsons, F. G., 134, 158, 228, 274, 277, 313, 402, 418, 444.
Patella, 448.
Paterson, A. M., 46, 376, 396, 407.
Patten, 121.
Paulet, J. L., 235, 239.
Pectoralis externus, 439.
Pectoralis minor, 439.
Pelvic fascia, 398, 400.
Pelvic floor, 395.
Pelvic floor, Development of, 396.
Pelvic girdle, 427.
Pelvic musculature, 396.
Pelvis, Adaptations of, 393.
Penis, Evolution of, 343.
Pensa, A., 254.
Pericardium, 314, 315.
Perichondrium, 442.
Pericranium, 122.
Peridental membrane, 166.
Perineal body, 368.
Perineal septa, 368.
Perineum, 372.
Perineum, Muscles of, 374.
Periotic capsule, 216.
Peritoneal cavity, 315.
Peritoneal fixation, Process of, 267.
Peritoneum, 249.
Peritoneum, Lesser sac, 256.
Permanent teeth, Origin of, 167.
Peroneus brevis, 437.
Peroneus longus, 437.
Peroneus tertius, 436.
Peter, K., 139, 174.
Peters, 13, 23.
Peterson, Otto, 56, 349.
Petro-mastoid, Origin of, 125, 216.
Petro-mastoid, Ossification of, 125, 216.
Peyer's patches, 272.
Pharyngeal recess, 227, 241.
Pharyngeal tonsil, 227, 241.
Pharynx, Development of, 221.
Pharynx, Structures developed from, 235.
Phrenic nerve, 337.
Pineal body, 91, 94.
Pisiform, 434.
Pittard, E., 382.
Pituitary body, Origin of, 91, 92, 128, 161.
Placenta, Formation of, 27.
Placenta, Formation of blood spaces in, 23.
Plantar arches, 434.
Plantar fascia, 436.
Plantar ligaments, 436.
Plantaris, 439.
Plasma, 319.
Platysma myoides, 234.
Platysma sheet, 234.
Pleura, 329.
Pleural cavities, 315.
Pleural passages, 284, 329.
Pleural-peritoneal opening, 337, 340.
Plicae fimbriatae, 238.

Plica gubernatrix, 383.
Plica semilunaris, 196.
Plica triangularis, 241.
Plica vascularis, 383.
Pohlmann, A. G., 365.
Polar body, 7.
Pollex, 436.
Pons Varolii, 77.
Popliteus, 444.
Portal vein, 289.
Post-anal gut, 377.
Posterior cardinal vein, 283.
Posterior commissure, 87.
Posterior root ganglion, 62.
Post-frontal, 130.
Posture, Change in, 43, 268, 332, 392.
Poupart's ligament, 393.
Pre-chorion, 33.
Pre-coracoid, 429, 430.
Premaxillary bones, 144, 145.
Prepuce, 374.
Preputial glands, 374.
Pre-sternum, 411.
Primitive groove, 29.
Primitive jugular vein, 213.
Primitive segments, 50.
Primitive streak, 29.
Primitive utricle, 215.
Primordial ova, 5, 18.
Primrose, 362.
Processus vaginalis, 386.
Proctodaeum, 366.
Pronephros, 342, 348.
Pronuclei, 7, 10.
Prostate, 380.
Prostate, Nature of, 381.
Prostate, Stroma of, 381.
Protovertebrae, 50.
Psoas parvus, 440.
Pterion, 123.
Pterotic, 216.
Pterygo-palatine bar, 150.
Pterygoid plate, Internal, 150.
Pubes, 427.
Pulmonary artery, 334.
Pulmonary artery, Stenosis of, 308.
Pulmonary diverticulum, 328.
Pulmonary system, Development of, 327.
Pulp of teeth, 162, 166.
Pyramidal tracts, 71.
Pyramidalis, 440.
Pyramid of thyroid, 244.
Pyriform fascia, 401.
Pyriform fossa, 238.

R

Rachischisis, Total, 74.
Radiale, 433.
Ramm, M., 141.
Ramstroem, M., 337.
Rathke's pocket, 161, 177.
Rauber's layer, 12.
Reagan, F., 230.
Recto-vesical fascia, 401.
Rectum, 272.
Rectum, Abnormalities of, 370.
Rectum, Malformations of, 370.
Rectum, Musculature of, 377.
Rectum, Separation of, 368, 372.
Reid, D. G., 268, 277.
Reid, R. W., 69.
Renal organs, Succession of, 342.
Renal-portal circulation, 287.
Rennie, 265.
Respiratory system, 324.
Respiratory system, Evolution of, 324.
Respiratory system, Morphological parts of, 327.
Rete testis, 350.
Retina, 190.
Retina, Pigmentary layer of, 188.
Retro-caecal fossa, 278.
Retro-calcarine-fissure, 114.
Retro-pharyngeal diverticulum, 250.
Retterer, 320.
Rhinencephalon, 97, 102, 175.
Ribs, 55.
Ribs, Formation of, 404.
Ribs, vestigial, 55.
Riedel's lobe, 259.
Rigby, H., 387.
Roberts, E. Emrys, 21, 376.
Robinson, A., 22, 50, 124, 294, 318.
Rolando, Fissure of, 115.
Rosenburg, E., 46.
Rosenmüller, Fossa of, 227.
Rosenmüller, Organ of, 349.
Rubashkin, 239.
Rynberk, G. van, 58.

S

Sabin, Florence, 321.
Saccule of larynx, 337.
Sacral plexus, 424.
Sacral vertebrae, 56.
Sacro-coccygeal region, Variations of, 47.
Sacro-lumbar regions, Variations of, 46.
Sacro-sciatic ligaments, 440.
Sagittal fontanelle, 122.
Salivary glands, Origin of, 239.
Sandstrom, 246.
Santorini, Duct of, 263.
Scansorius, 440.
Scaphoid, 432.
Scapula, 429.
Scapula, Congenital elevation of, 65.
Schaeffer, J., 154, 181, 238.

Schlaginhaufen, O., 452.
Schlater, G., 30.
Schoeppler, C., 457.
Schorr, G., 145.
Schumacher, 48, 135.
Sclerotic, 194.
Sclerotome, 49.
Scrotum, 379.
Sebaceous glands, 457.
Seessel's pocket, 239, 241.
Segment, Constitution of, 58.
Segmentation, 35.
Segmentation, Abnormal, 64.
Segmentation of body, 36, 39, 58.
Segmentation of skull, 119.
Selenka, 23.
Sense organs, 462.
Sensori-motor areas of brain, 97, 115.
Septal cartilage, 143.
Septum primum of auricle, 304.
Septum secundum of auricle, 304.
Septum transversum, 250, 255, 284.
Sesamoid ossification, 448.
Sewell, R. B. S., 432.
Shaw, Batty, 461.
Sherrington, 422, 426.
Shillitoe, 383.
Shore, 287.
Shoulder, Congenital elevation of, 426.
Shoulder girdle, 427, 429.
Sigmoid flexure, 272.
Simian fissure, 114.
Simpson, G. C., 429.
Sino-auricular node, 302.
Sinus subpericardiacus, 334.
Sinus venosus, 284, 289, 298.
Sinus venosus, Fate of, 298.
Sinus venosus, Valves of, 299.
Skeleton of body segment, 59.
Skene's tubules, 381.
Skin, 450.
Skin, Development of, 451.
Skin, Sense organs of, 454.
Skull, Development of, 117, 119, 120.
Skull, Evolution of, 117.
Skull, Growth of, 117.
Skull, Primitive membranous, 119.
Skull, Segmentation theory of, 135.
Skull, Segments of, 119.
Skull, Shape of, 131.
Smith, E. Barclay, 46, 258.
Smith, G. Elliot, 65, 78, 80, 90, 97, 106, 107, 110, 111, 113, 176, 201, 376, 451.
Smith, G. M., 278.
Smith, Priestly, 186.
Smith, T. Manners, 46, 432, 441.
Smith, W. Ramsay, 169.
Somatopleure, 17.
Somatic nerves, 62.
Somites, 18.
Spemann, 192.
Spermatocyte, 9.
Spermatozoa, Formation of, 9, 18.
Sphenoid, Development of, 127.
Sphenoidal sinus, 180.
Sphenoidal turbinate bone, 180.
Sphincter colli, 235.
Spicer, J. E., 379.
Spigelian lobe of liver, 256, 267.
Spina-bifida, 75.
Spinal column, 43.
Spinal column, Curves of, 45.
Spinal column, Evolution and Development of, 43.
Spinal column, Unstable regions of, 46.
Spinal cord, 69, 70.
Spinal cord, Development of, 69.
Spine, Pyramids of, 44.
Spinous processes of vertebrae, 57.
Splanchnic nerves, 64.
Splanchnopleure, 17.
Spleen, 261.
Squamosal, 121, 212.
Stapes, 211.
Sternabrae, 406.
Sternalis, 439.
Sterno-clavicular joint, 443.
Sterno-manubrial joint, 411.
Sterno-mastoid, 439.
Sternum, 405.
Sternum, Development of, 408.
Stevens, T. G., 4.
Stieda, L., 454.
Stöhr, P., 242, 450, 454.
Stomach, 260.
Stomach, Coats of, 261.
Stomodaeum, 140, 160.
Streeter, G. L., 76, 78, 88, 204, 215, 229, 421.
Striae terminalis, 100.
Stroud, 80.
Struthers, Ligament of, 438.
Studni, 452.
Stylo-hyal, 228.
Styloid process, 228.
Subclavian arteries, 231.
Subclavian veins, 286.
Subcommissural organ, 85.
Subcutaneous tissue, 461.
Sulcus lunatus, 114.
Sulcus rectus, 115.
Sulcus terminalis, 298.
Sunier, A. L. J., 58.
Superficial plantar arch, 442.
Superior medullary velum, 82.
Superior vena cava, 283.
Supra-condylar process, 442.
Supra-renal bodies, Development of, 389.
Supra-renals, Nature of, 389.
Supra-scapula, 429.

Supra-sternal bones, 406.
Swale-Vincent, 246, 389.
Sweat glands, 457.
Swim-bladder, 324.
Sylvian fissure, 108.
Sylvius, Aqueduct of, 84, 199.
Symington, 55, 336, 449.
Sympathetic nerves of body segment, 63.
Synovial membranes, 442.
Syncytium, 15, 21.
Szily, A. von, 400.

T

Taenia terminalis, 301.
Tail, Muscles of, 440.
Tail, Vestiges of, 395.
Tandler, J., 230, 271, 348.
Tapetum lucidum, 194.
Tarsale, I., II., III., IV., V., 433.
Tarsus, 432.
Taussig, F. S., 360.
Teacher, J. H., 13.
Teeth, Development and morphology of, 163.
Teeth, Eruption of, 170.
Teeth, Effect of civilization on, 171.
Teeth, Morphology of, 168.
Teeth, Neanderthal, 170.
Teeth, Roots of, 170.
Tegmen tympani, 210.
Telencephalon, 90, 91.
Temporal ridges, 134.
Temporary fissures of brain, 106.
Temporo-maxillary articulation, 158, 443.
Tenon, Capsule of, 194.
Testes, 383.
Testicle, Descent and development of 383, 386.
Testicle, Mesentery of, 387.
Thalamencephalon, 90, 91.
Thallus, 37.
Thebesian valve, 301.
Third trochanter, 390.
Thompson, F. D., 246.
Thompson, Peter, 16, 79, 250, 396.
Thomson, A., 131, 258.
Thorax, Diameters of, 333.
Thymus, 240, 242.
Thyng, F. W., 263, 270.
Thyro-glossal duct, 244.
Thyroid, 244.
Thyroid cartilage, 335.
Thyroids, Accessory, 246.
Tibialis posticus, 437.
Tims, Marrett, 169.
Todd, T. W., 46.
Tongue, 235.
Tongue, Muscles of, 237.
Tonsil, 240.
Tooth, Development of, 163.
Tooth, Structure of, 163.
Touch bodies, 462.
Tourneux, F. and J. P., 123, 161, 391.
Trabeculae cranii, 126, 143.
Transverse processes of vertebrae, 57.
Transverse sinus, 316.
Treitz, Band named by, 271.
Triangle, Ovarian, 4.
Triangular fibro-cartilage, 443.
Triangular ligament, 401.
Trigonum olfactorium, 176.
Trophoblast, 12, 15.
Tschassownikow, S., 7.
Tuberculum impar, 235.
Tunica vaginalis, 315.
Turbinate processes, 178.
Twins, 36.
Tympanic bulla, 211.
Tympanic plate and articular eminence, Development of, 159.
Tympanic ring, 159.
Tympano-hyal, 227.
Tympanum, 210, 227.
Tyson's glands, 383.

U

Ulnare, 433.
Umbilical arteries, 25.
Umbilical cord, Formation of, 25.
Umbilical faecal fistula, 270.
Umbilical hernia, 27, 270.
Umbilical urinary fistula, 27.
Umbilical veins, 291.
Umbilical veins, Nature of, 293.
Umbilicus, Formation of, 25, 403, 268.
Urachal cysts, 376.
Urachus, 376.
Ureter, 353.
Ureter, Double, 355.
Urethra, Female, 363, 372.
Urethra, Male, 366 *et seq.*
Urethra, Musculature of, 377.
Urogenital cleft, 372.
Urogenital sinus or canal, 362.
Urogenital system, 342.
Urorectal septum, 368.
Utero-sacral ligaments, 357.
Uterus, Formation of, 358, 364.
Uterus, Round ligament of, 357.
Uvea, 188.

V

Vagina, Atresia of, 360.
Vagina, Formation of, 358.
Vagina, Metamorphosis of, 359.
Vaginal cords, 359.
Valvulae conniventes, 272.
Vasa aberrantia, 350.

Vas aberrans, 441.
Vas deferens, 349.
Vasoformative cells, 318.
Veins of trunk, Development of, 283.
Velum, Inferior medullary, 78.
Velum interpositum, 98.
Venae cavae, 283, 299.
Venous valves, 298.
Ventral aortic stems, 230.
Ventral mesentery, 255.
Ventral mesogastrium, 260.
Ventricles of brain, Third, 91.
Ventricles of brain, Fourth, 78.
Ventricles of brain, Lateral, 91.
Ventricles of heart, 308.
Ventro-lateral muscles, 60.
Vernix caseosa, 457.
Vertebra, Development of, 51.
Vertebra, Morphological parts of, 51.
Vertebrae of mammalia, 53.
Vertebrae, Ossification of, 53.
Vesiculae seminales, 349.
Vestibular ganglion, 217.
Vestibule of left auricle, 303.
Vestigial fold of Marshall, 285.
Vestigial muscles, 438.
Vestigial roots and ganglia, 88.
Vestigial turbinates, 180.
Villi of intestine, 271.
Visceral arches, 221, 223.
Visceral arches, Arteries of, 229.
Visceral arches, Cartilages of, 227.
Visceral arches, Muscles of, 233.
Visceral arches, Nerves of, 221.
Visceral arteries, 318.
Visceral clefts, 224, 226.
Vitelline veins, 289.
Vitelline vessels, 269.
Vitello-intestinal canal, 22, 268.
Vitreous humour, 192.
Vomer, 143.
Vriese, Bertha de, 116, 441, 449.

W

Waddell, 407.
Walker, T., 380, 390.
Walkere, C. E., 7.
Wallace, C. S., 382.
Warner, 123.
Watson, J. H., 362.
Weber, Max, 450.
Weidenreich, F., 320.
Weidersheim, 197.
Weigner, K., 48.
Werry, D. E., 56.
Wharton's jelly, 26.
Whitehead, R. H., 382, 407.
Whitnall, 194.
Wichmann, S. E., 355.
Wijhe, J. W. van, 135.
Wilder, H. H., 452.
Williams, L. W., 49.
Wilson, J. T., 30, 79, 169.
Wirsung, Duct of, 264.
Wolffian body, 287, 342, 344, 351.
Wolffian body, Fate of, 348.
Wolffian ducts, 345, 347.
Wolffian tubules, 346, 347.
Woodland, 386.
Wormian bones, 123, 129.
Wright, W., 37, 135.

Y

Yolk sac, 15, 17, 22, 268, 289.
Yolk sac, Nature of, 33.
Young, A. H., 22, 24, 318.
Young, James, 13.

Z

Zuckerkandl, E., 181, 390.

GLASGOW: PRINTED AT THE UNIVERSITY PRESS BY ROBERT MACLEHOSE AND CO. LTD.

The University Library
Leeds

Staff and Research Students	Other Readers
Date issued	Date due for return
	31 JUL 1946
	2 NOV 1946
	26 NOV 1946
	8 FEB 1947
	5 MAR 1947
	20 MAR 1947
	1 APR 1947
	CANCELLED