TEXT BOOK

OF

VERTEBRATE ZOOLOGY

BY

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PREFACE.

WITHIN recent years the laboratory method has become the basis of instruction in every science. The student is expected to find out a certain number of fundamental facts directly from nature, but while this has in itself great value as a training in observation, the fullest benefit of the study is not obtained unless there be a comprehension of the bearings of the facts observed. Observation and uncorrellated facts do not make a science. Attention can be directed to the relations and significance of the facts ascertained in the laboratory by means of lectures, but a somewhat extended experience has shown that the average student needs something more than his lecture notes, at least when beginning any subject. The present volume is intended to supplement both lectures and laboratory work, and to place in concise form the more important facts and generalizations concerning the vertebrates. It is also hoped that it may have some value for students of medicine in explaining many peculiarities of the structure of man which seem meaningless unless viewed in the light of comparative morphology. When once their meaning is comprehended it is easy to remember them.

The first part of the volume is devoted to an outline of the morphology of vertebrates based upon embryology. This treatment has been adopted, since the author believes that in this way the bearings of the facts can be most clearly shown and most easily remembered. The remainder of the volume presents an outline of the classification of vertebrates, a subject which, in recent years, has been too much ignored in college work. Here the fossils are included as well as the recent forms, since the existing fauna must be studied in the light of the past. Numerous generic names have been mentioned without characterization; they have been inserted in order that the student may be able to ascertain the relationships of the forms he may find mentioned in collateral reading.

In this second part the author has ventured to differ in some points from the majority of American students. Thus he has been unable to recognise in the so called orders of ornithologists groups of birds of more than family rank, while their families are equivalent to genera in the other classes of vertebrates. Again in the matter of nomenclature well-known generic names have been retained, in spite of the law of priority. These are the names of morphological literature, and to have used *Triturus*, *Molge*, *Myctophium*, *Zaglossus;* to have mixed up *Esox* and *Belone* would have served no useful end.

A fair proportion of the illustrations are original; as many more have been engraved for the volume. These latter as well as those borrowed have been credited as far as possible, to the original source. The author would here return his sincere thanks to Professor Robert Wiedersheim, Professor A. S. Packard, and Dr. Bashford Dean for clichés from their works. He would also acknowledge his indebtedness to Professor C. S. Minot, Dr. G. H. Parker, and Mr. F. A. Lucas for assistance in connection with the manuscript. While many hundreds of special articles have been read in the preparation of the work, acknowledgement must be made to the aid received from Wiedersheim's Anatomy, the Embryologies of Minot and Hertwig, Zittel's Paleontologie, Jordan and Evermann's Fishes, Woodward's Fossil Fishes, and Flower and Lyddeker's Mammals. Woodward's Vertebrate Paleontology appeared in time to be of assistance in the correction of the proofs.

A work of this character must be largely a compilation. It is impossible to settle all disputed questions by personal investigation, and one can only take those statements which seem the most reasonable, and which appear to have the most support. That the volume will be found free from error is more than can be hoped. The only apology the author can offer for mistakes of judgment or of fact is based upon the large field, the enormous literature, and the conflicting statements upon many points.

TUFTS COLLEGE, May 14, 1899.

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TEXT BOOK OF VERTEBRATE ZOOLOGY.

PART I.

MORPHOLOGY OF VERTEBRATES.

INTRODUCTION.

NATURALISTS divide all animals into two great groups, — the Protozoa, in which all the functions of life are performed by a single cell which constitutes the whole animal, and the Metazoa, in which the body is composed of many cells, and these cells are arranged into layers and organs with a corresponding differentiation of functions between the many-celled organs.

The metazoa in turn are subdivided into several groups or phyla, the highest of which is called Chordata, while the others are frequently spoken of collectively as Invertebrata. The phylum chordata is characterized by the possession of at least three features which occur in no invertebrate, — a skeletal axis or notochord arising from the inner germ-layer or entoderm ; the possession of paired gill slits connecting the anterior part of the alimentary canal with the exterior ; and a central nervous system which is entirely on one side of the alimentary canal. Details concerning each of these features will be given on subsequent pages.

The chordata embrace at least three subphyla, — the Urochordia or Tunicata, the Cephalochordia or Leptocardii, and the Vertebrata, the subject of the present book. It is possible that a fourth phylum, the Hemichordia or Enteropneusti, is to be included here, but as yet there is not agreement upon this point.

The tunicates include a large number of marine animals which show their chordate features most plainly in the young, the adults being remarkably degenerate. These young have tadpole-shaped bodies, with a central nervous system dorsal in position, a notochord which occurs only in the caudal region, while the gill slits occur on the side of the pharyngeal region. In the course of development in all except the Copelatæ (*Appendicularia*, etc.), the tail becomes absorbed, the notochord being lost, while the body becomes so twisted that both gill slits and vent empty into a common atrial chamber. The body is usually fixed, and is covered by an outer coat or tunic.

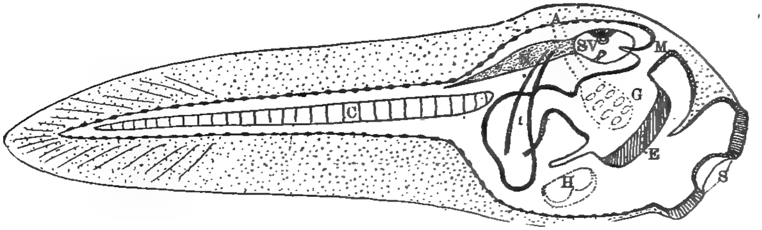

FIG. 1. Diagram of a larval tunicate, after Seeliger. *A*, atrial opening; *C*, notochord; *E*, endostyle; *G*, gill slits; *H*, heart; *M*, mouth; *N*, nervous system; *S*, adhesive disks; *SV*, sensory vesicle.

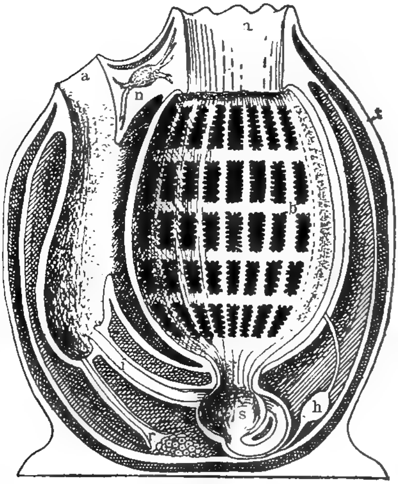

FIG. 2. Diagrammatic section of adult tunicate. *a*, atrial opening; *b*, branchial chamber; *h*, heart; *i*, intestine; *m*, mouth; *n*, nerve centre; *r*, reproductive organ and duct; *t*, tunic; *v*, vent.

The Cephalochordia are represented by *Amphioxus*, and one or two other allied genera which are decidedly fish-like in their general appearance. The body is distinctly segmented; the gill slits are very numerous, extending back along the alimentary canal to the liver ducts, the stomach thus being entirely absent. The notochord extends along the whole length of the animal. These forms, however, differ from the vertebrates in the absence of vertebræ, in the peculiarities of the central nervous system and the nerves which arise from it, in the total absence of a heart, of paired eyes, etc., as well as in the relations of excretory organs, etc. The species are few in number, and are all marine, being found in the warmer seas of all parts of the world; on our coasts as far north as the mouth of the Chesapeake.

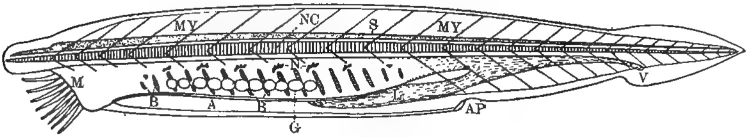

Fig. 3. Diagram of *Amphioxus*, chiefly after Boveri. *A*, atrium; *AP*, atriopore; *B*, branchial clefts; *G*, gonads; *L*, liver; *M*, mouth surrounded by cirri; *MY*, myotomes; *N*, nephridia; *NC*, notochord; *S*, spinal cord; *V*, vent.

The Enteropneusti are decidedly worm-like in appearance, and their pertinence to the chordate phylum is denied by many. The so-called notochord is but a small diverticulum from the alimentary tract without skeletal character, while it is not found that the segmentation of the body is the same as that in the other chordates. The best-known form — *Balanoglossus* — was long considered a worm. It lives in the sand of the seashore in many parts of the world. Other allies are so different in appearance (*Rhabdopleura, Cephalodiscus*) that they were long regarded as Polyzoa.

For further details concerning these forms reference must be made to works upon invertebrates, and to the special papers dealing with them. With this brief reference they must be dismissed here; for the purpose of the present work is to deal with the single subphylum, Vertebrata.

In the second or systematic portion of this volume, the different subdivisions of the group of vertebrates will be defined;

but as it is necessary to use the names of several of the major divisions in the general account of the vertebrates, a tabular statement of classification with familiar examples is given here. Details can be found by reference to the index.

VERTEBRATA.

- **Cyclostomata** (without true jaws).
  - **Myxinoidei** (hag-fishes, borers, — *Myxine*).
  - **Petromyzontes** (lampreys).
- **Gnathostomata** (with jaws).
  - **Ichthyopsida** (with gills in adult or young).
    - **Pisces** (with paired fins).
      - **Elasmobranchii** (sharks and skates).
        - **Holocephali** (elephant-fish, — *Chimæra*).
      - **Ganoidea** (sturgeon, garpike, etc.).
      - **Dipnoi** (lung-fishes).
      - **Teleostei** (ordinary bony fishes).
    - **Amphibia** (frogs, toads, salamanders, etc.).
  - **Sauropsida.**
    - **Reptilia** (lizards, snakes, turtles, alligators).
    - **Aves** (birds).
  - **Mammalia** (rats, cats, elephants, whales, man, etc.).

INTRODUCTORY EMBRYOLOGY.

IN order to understand clearly the structure of a vertebrate, it is well to begin with a short account of some of the phenomena of development, since a knowledge of the history of the parts will make their relations, one to another, more comprehensible. The following outline is given in the briefest manner and in the most generalized form, the various modifications which are found in the different vertebrate groups being ignored.

All vertebrates reproduce by means of eggs. These **eggs** are specialized cells, produced by the female, which have the capacity, after impregnation, of developing into an animal like that which produced them. The **impregnation** consists in the union with the egg of a still more specialized reproductive cell, the **spermatozoan,** produced by the male; and it is only after this union (called also **fertilization**) that development is possible.

The fertilized egg divides (**segments**) again and again, the result being that the egg is converted into a many-celled embryo. At first the cells of this embryo are arranged in a single layer, surrounding a central **segmentation cavity** (Fig. 4). Next, those cells upon one side of the embryo become pushed inside of the others (**invaginated**) much in the same way that one might push in one side of a hollow rubber ball, the result being partially to obliterate the segmentation cavity, and to differentiate the previous single layer into two. This two-layered embryo is known as a **gastrula** (Fig. 5).

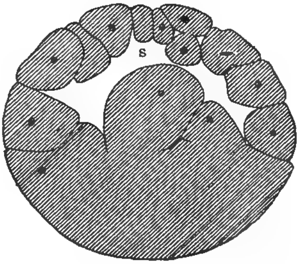

FIG. 4. Section of an early stage of the egg of *Amblystoma* showing the smaller cells at one pole, the larger at the other, and at *S* the segmentation cavity.

The outer of the two layers of the gastrula is called the **ectoderm**, the inner the **entoderm.**[1] The cavity bounded by the entoderm is the **archenteron** (stomach), and the opening where ectoderm and entoderm meet, and where the archenteron communicates with the external world, is the **blastopore.** Usually the blastopore is an elongate slit, its major diameter coinciding with the longitudinal axis of the future animal. Soon after invagination, the blastopore begins to close, the opposite lips

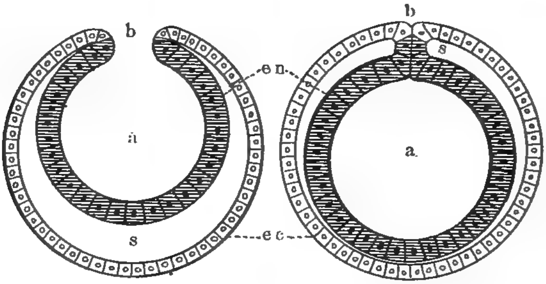

FIG. 5. Diagram of a gastrula and of the later closure of the blastopore. *a*, archenteron; *b*, blastopore; *ec*, ectoderm; *en*, entoderm; *S*, segmentation cavity.

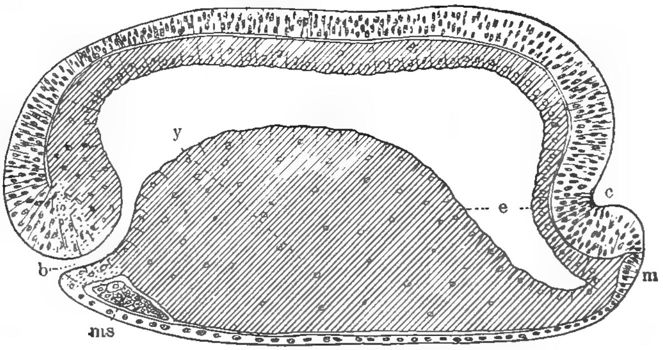

FIG. 6. Sagtital section of early embryo (late gastrula) of *Amblystoma*. *b*, blastopore; *c*, beginning of infolding of brain; *e*, entoderm; *m*, thickening of ectoderm for mouth, hypophysis, and nose; *ms*, mesoderm; *y*, yolk-mass.

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[1] In many English works these two layers are called respectively **epiblast** and **hypoblast**, while the mesoderm, to be mentioned later, is called **mesoblast**. There is no longer necessity for using these terms.

uniting in the median line. This process of closure begins at one end and proceeds towards the other, the end where the first union takes place being the anterior. In some forms the blastopore never closes completely, but persists in part as the anus of the adult. In those forms where it closes completely the anus later appears in the line of fusion. Another landmark may be noted here, — the blastopore closes along the median line of the back; and the region of this closure is known as the **primitive streak,** the line of closure being the **primitive groove.**

From the region of the blastoporal lips (primitive streak) there next grows into the segmentation cavity, on either side, a third layer, — the **mesoderm.** In several forms (Fig. 7) this mesoderm clearly arises as an outgrowth from the entoderm in the shape of a double fold, its walls bounding a cavity (**cœlom**) which at first is connected with the archenteron. Later the connection between these cœlomic pouches and the archenteron is lost, the lips of the outgrowth fusing, and then the mesoderm completely separates from the entoderm. In other cases the mesoderm appears as a solid outgrowth from the same point, and later it splits so as to form a cœlom comparable to that first described.[1] The result in either case is that the segmentation cavity is still farther reduced by the extension into it, on either side of the embryo, of a flattened, mesodermic sac. In this sac two walls can be

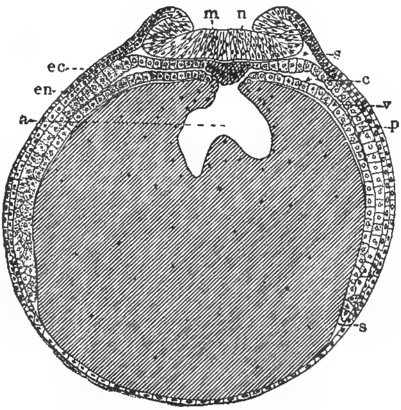

FIG. 7. Transverse section of *Amblystoma* embryo showing formation of mesoderm (mesothelium). *a*, archenteron; *c*, cœlom; *ec*, ectoderm (outer layer); *en*, ectoderm (nervous layer); *m*, medullary plate; *n*, notochordal cells; *p*, parietal layer of mesothelium; *s*, remains of segmentation cavity; *v*, visceral (splanchnic) layer of mesothelium.

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[1] The type of cœlom in the first case is called an **enterocœle**; in the second a **schizocœle.**

distinguished: the one turned towards the ectoderm is called the **somatic** or **parietal layer**; the one facing the entoderm is the **splanchnic** or **visceral layer.**

Besides this mesoderm arising thus as a continuous outgrowth, another type of mesoderm also invades the segmentation cavity. This arises by the migration or inwandering into this space of single cells, which may separate themselves from either entoderm or mesoderm; or in some instances, as recent investigations tend to show, from the ectoderm as well. Since these two types of mesoderm differ in their origin, and, as will be seen later, in their character and fate, they have been given different names. That mesoderm which bounds the cœlomic cavities and all parts formed from it is called **mesothelium**; that which arises from the scattered immigrant cells is **mesenchyme.**

At this point, where the four **germ-layers** of the embryo are differentiated from each other, it will be interesting to state what portions of the adult vertebrate are derived from each.

The ectoderm gives rise to the outer portion (epidermis) of the skin, the outer layer of scales, hair, feathers, the enamel of the teeth, nails, claws, true horn, and the essential parts of all sensory and nervous structures.

The entoderm develops into the lining of the alimentary canal and the various cavities — gills, lungs, liver, pancreas — connected with it; also to the notochord, and possibly to the lining of the blood-vessels.

From the mesothelium arises the lining of the body cavity, reproductive and excretory organs, and the voluntary muscles (including the muscles of the heart).

The mesenchyme produces the deeper layers of the skin, the lower portions of scales, and the dentine of the teeth; involuntary muscles, connective tissue, fat, cartilage, bone, blood, and lymph corpuscles.

From the point where the germ-layers are outlined the development must be traced in two different directions. One line follows out the differentiation of the cells and their grouping into tissues; the other traces the development of the various organs of the adult.

HISTOLOGY.

Histology deals with the minute structure, and especially with the characters of the cells and the tissues arising from them. In the adult occur cells varying in shape and size, and adapted for various functions; those cells which are alike grouped together into tissues. A **tissue,** then, may be defined as an aggregate of similar cells, together with a varying amount of intercellular substances, usually produced by the cells themselves. The cells themselves are the living portions of the tissue; the intercellular substance, by its amount and character, being directly influential in determining the nature of the tissue. Tissues may be solid or fluid; may form thin sheets or thick masses. All tissues can be grouped under four heads, — epithelial, nervous, muscular, and connective.

Epithelial tissues are the primitive tissues. An **epithelium** is a layer of cells covering any free surface on or in the body. Thus in the gastrula both ectoderm and entoderm are epithelia, since the one covers the outside, while the other lines the archenteron. The mesothelium is also epithelial[1] since it lines the cavity of the cœlom. Epithelia are classified according to shape, arrangement, or character of the cells. In **cubical** or **columnar epithelium** the cells have shapes corresponding to their names; in **pavement** epithelium the cells are greatly flattened, so that each one, while very thin, covers, comparatively, a large amount of surface. Epithelia are **simple** when the cells are arranged in a single layer; **stratified** when they form several layers. In some cases the epithelial cells may bear on their free sur-

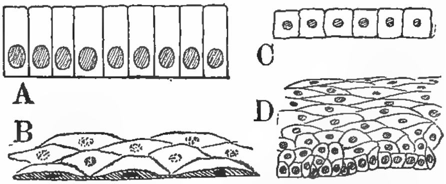

FIG. 8. Epithelia; *A*, columnar; *B*, pavement, in perspective; *C*, cubical; *D*, stratified.

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[1] The term epithelium is sometimes restricted to those layers on the outer surface of the body, or, like the epithelium of the lungs and stomach, connected with the exterior. The similar cells in the closed cavities, like the body cavity or the blood-vessels, are then called **endothelia.** The distinction is of little importance.

faces minute vibratile hair-like processes (**cilia**), whence this type is called **ciliated epithelium.** Again, epithelia may be grouped according to function, and then cuticular, sensory, and glandular epithelia may be recognized. Epithelia may give rise to important structures, such as hair, feathers, scales, enamel of the teeth, etc., which will be mentioned in the proper places.

Nervous tissue arises from the ectoderm, and hence from epithelium. It has for its purpose the recognition and transferrence of impulses, the perception of sensations, and the production of other impulses which shall affect nervous or other tissues. It has for its essential constituent nerve cells, to which are usually added other cells of a supportive nature. **Nerve cells** (or **ganglion cells**) consist of a central nucleated body from which radiate one or more protoplasmic processes which, after a longer or shorter course, break up into minute branches or **fibrillations.** It must, however, be kept in mind that these processes are really parts of the cell, although the term cell is frequently restricted to the central mass, while the processes are called nerve fibres, etc. When a nerve cell has two protoplasmic processes it is spoken of as bipolar; when more than two as multipolar.[1] One of these processes is of considerable

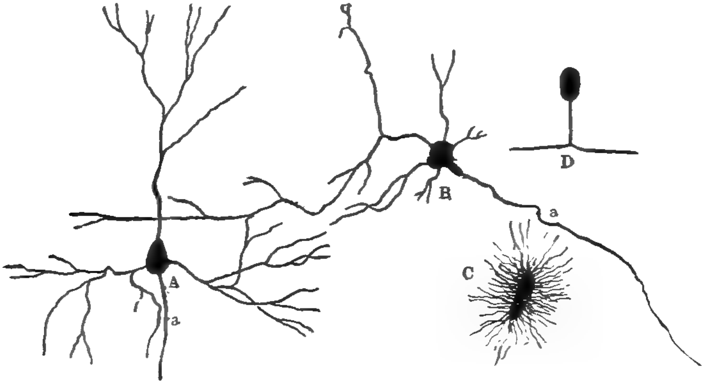

FIG. 9. Different forms of nerve cells from cat. *A*, pyramid cell from cerebrum; *B*, cell from spinal cord; *D*, unipolar cell from spinal ganglion; *C*, glia cell from spinal cord; *a*, axis cylinder.

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[1] In some cases 'unipolar' nerve cells are found; but the process in these is soon found to divide, its halves going off at right angles to the previous course, thus showing that these cells are really bipolar.

length, and is known as an **axis cylinder** or **axon**; the others are shorter, and as they soon break up into minute branches, they are called **dendrites.** In most cases the axis cylinders have a similar method of termination. Recent investigations show that the only connection between nerve cells consists in an interlacing of these fibrillæ; two nerve cells never join.

The axis cylinder is the essential part of a nerve fibre. Of these fibres two kinds are to be recognized. In the **medullated fibres** the axis cylinder is surrounded by a **medullary sheath** of a peculiar substance (myelin) rich in fat. This sheath, it is to be noted, usually stops before the end of the axis cylinder, and in most cases it is not continued to the central mass of the cell. In the non-medullated fibres the sheath is lacking, and only the axis cylinder is found. Both medullated and non-medullated fibres may have a second sheath (the **neurilemma** or **sheath of Schwann**) derived from the connective tissue (see below), and containing scattered nuclei.

Nervous tissue is made up of these nerve cells. In a nerve proper we have but a bundle of nerve fibres (axis cylinders, medullated or non-medullated) bound together by connective tissue, while the bodies of the cells are absent. These nerves are but conducting trunks, bearing impulses to or from the central portion of the cell. From their color, those parts which are formed entirely of nerve fibres are called the **white matter.** The cell bodies, together with fibres, dendrites, etc., unite to form the **gray matter,** which may be aggregated in smaller centres (**ganglia**) or in larger continuous tracts, as in the brain and spinal cord. In these parts occur certain supporting cells

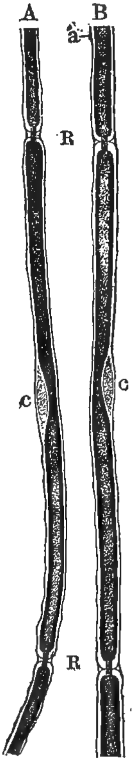

FIG. 10. Portions of medullated nerve fibres (from Martin). The medullary sheath, stained black by osmic acid, is interrupted at *R*, the nodes of Ranvier, across which the axis cylinder extends. Outside the medullary sheath is the (mesenchyme) sheath of Schwann, the nuclei of which are seen at *c*.

(neuroglia) derived from the ectoderm, but lacking entirely in nervous properties. These **glia cells** are extensively branched, their branches running between fibres and cell bodies (Fig. 9, *C*).

Muscular tissue is the special contractile element in the body. It is of two kinds, different in origin, structure, and action. The mesenchyme gives rise to the **smooth muscle.** This consists of long spindle-shaped cells, each usually containing a single nucleus, and being marked with fine longitudinal lines. These cells may occur singly, or may be arranged in small bundles or thin sheets; and in all cases they are not under control of the will, a fact that gives rise to the name, **involuntary muscles,** often applied to them. Smooth muscular tissue is slow in its action.

FIG. 11. Smooth muscle fibres.

Striped muscular tissue, on the other hand, is derived from the mesothelium by modification from the muscle plates, to be described later. It occurs usually in larger masses than does the mesenchymatous muscular tissue, and is (except in the case of the heart) under control of the will. This striped tissue consists either of separate cells (heart muscles) or of usually long cylindrical, so-called **primitive fibres, each** of which contains several nuclei; i.e., is syncytial. In these primitive fibres the bulk of the protoplasm has been altered into a strongly contractile substance marked with fine transverse lines. Around each fibre is a structureless envelope, the **sarcolemma;** while the fibres are bound together into muscle bundles by means of connective tissue envelopes **(perimysium)** bearing nerves and blood-vessels, and continuous with the tendons and fascia by which the muscles are attached to other structures. The nuclei are oval, with their long axes parallel to the direction of

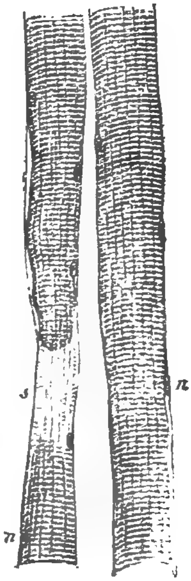

FIG. 12. Cross striped muscle fibres showing the nuclei (*n*) and the sarcolemma, *s*, where the muscle fibre is torn. From Hertwig, after Gegenbaur.

the fibres. In the mammals they are placed upon the periphery of the fibres (Fig. 12, *n*), in the lower vertebrates near the centre. The muscles of the heart agree in origin and cross-banding with the voluntary muscles, but differ in being cellular rather than syncytial, and in being removed from the control of the will. All cross-banded muscles are capable of rapid contractions.

The connective tissues are all of mesenchymatous origin, and are characterized by a great development of the intercellular substance, which is usually a product of the cells. They are the supporting tissues of the body, and vary accordingly as this intercellular substance varies, and may correspondingly be grouped under several subheads, the principal ones being enumerated below.

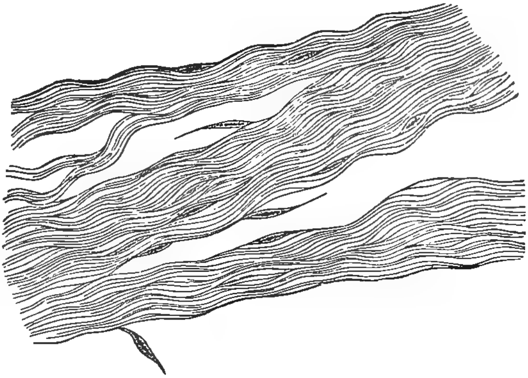

FIG. 13. Fibrous non-elastic connective tissue (from Martin).

In **fibrous connective tissue** (**white** or **non-elastic tissue**) the cells are branched or spindle-shaped, and the intercellular substance is more or less fibrous, the fibres being parallel, interlaced, or in a network, so that there result sheets, membranes, or bundles, accordingly as the part to be played varies. In some cases this tissue is loose (**areolar tissue**), such as is found between the skin and deeper parts; at other times it is much firmer, as in the case of tendons. This type of tissue also gives rise to

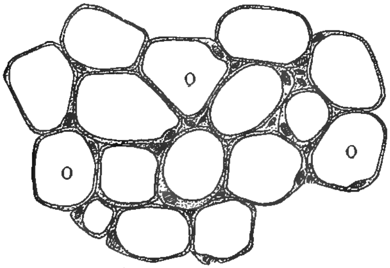

FIG. 14. Fat. *o*, oil globules in the connective tissue cells.

fat (**adipose tissue**) by the deposition of oil *in* the protoplasm of the cells. In **elastic tissue (yellow connective tissue)** the intercellular fibres are larger, and elastic in character.

FIG. 15. Elastic tissue (from Martin).

In **cartilage** the intercellular substance (here called the **matrix**) is more solid and firmer. It varies considerably in abundance, and in proportion to its amount the cartilage gains as a supporting tissue. When the matrix is homogeneous, the result is **hyaline cartilage;** but it may be traversed by fibres of white or yellow connective tissue, thus producing **fibrous** or **elastic cartilage.** The cells of cartilage are circular, oval, or fusiform in outline; but they send out very fine protoplasmic processes which traverse the matrix, thus connecting all parts. Cartilage increases in size in three ways, — by addition of new cells to the outside, by increase in the amount of the matrix, and by division of the cells in the cartilage itself. In almost every section of cartilage several generations of cells may be readily traced by observing the capsules surrounding them. Cartilage is very closely related to bone, and is frequently converted into that more solid substance by a change (**ossification**) in its matrix. Cartilage may also be calcified by the deposition of lime upon its surface. Calcified cartilage and bone are entirely distinct.

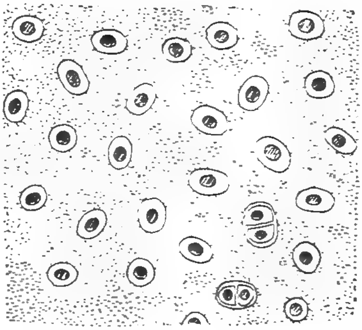

FIG. 16. Hyaline cartilage, the matrix dotted.

In **bone** this matrix consists of an organic basis combined with salts of lime (chiefly carbonate and phosphate); while cartilage is usually solid, bone is traversed by tubes (**Haversian**

canals) bearing nutrient vessels, etc. Arranged in layers concentric to these canals or parallel to the surface of the bone are the cells, each occupying a space (**lacuna**) in the dense matrix. These cells are connected by fine, branching, protoplasmic processes, which run in minute tubules (**canaliculi**) through the layers (**lamellæ**) of the matrix. Both cartilage and bone are enveloped in a layer of fibrous connective tissue, called respectively **perichondrium** and **periosteum.**

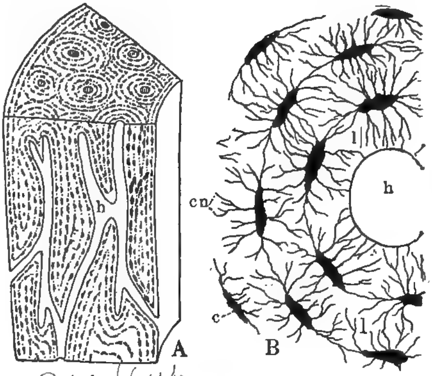

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FIG. 17. Bone. *A*, piece of a long bone showing the appearance under low power in longitudinal and cross sections; *B*, a transverse section of three lamellæ surrounding an Haversian canal, from a slice of dried bone; *c*, bone corpuscles; *cn*, canaliculi; *h*, Haversian canal; *l*, lamellæ.

Many bones, as has just been said, pass through a cartilage stage in their history, the general outlines being built up in that more yielding substance. Later the matrix is dissolved little by little, and is replaced by the lime salts, the cells (**osteoblasts**) becoming enclosed in the hardened substance. Such bones are called **cartilage bones.** Other bones, however, have no cartilage stage, but arise from the calcification of the intercellular substance of membranes, and these are called **membrane bones.** In either case the process of ossification proceeds from fixed spots (**centres of ossification**)

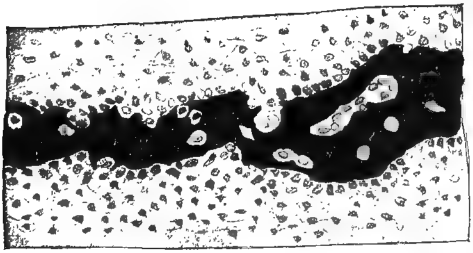

FIG. 18. Development of membrane bone (mandible of pig). Around the (black) bone are numerous osteoblasts, some of which are included in the bony substance.

extending gradually in all directions until the final result is much the same. In structure cartilage bones and membrane bones are very similar, but the differences in the history is very important, as will be seen later in dealing with the skeleton.

Closely allied to bone is the **dentine** of teeth and scales, the chief differences lying in the greater density of the intercellular substance, and in the fact that the dentine-producing cells (**odontoblasts**) do not become included in the solid structure. The same fine protoplasmic processes of the cells exist, lying in **dentinal canals** which pursue a nearly parallel course.

Blood and **lymph** are connective tissues, with a fluid intercellular substance (**plasma**) in which float the cells. In lymph the cells are all of one type, known as **leucocytes,** white in color, and possessed of marked amœboid powers. In blood, besides the leucocytes (**white corpuscles**), there are also numerous **red corpuscles,** the source of color of the blood. These red corpuscles have no amœboid powers, but are merely the means of transferrence of oxygen and carbon dioxide[1] to and from the tissues. In the lower vertebrates the red corpuscles are oval and nucleated; in the mammals the nuclei are lost, and the corpuscles are usually biconcave, circular disks. The **blood plaques** may also be mentioned.

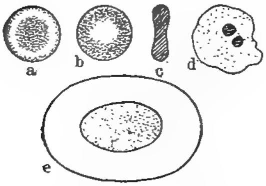

FIG. 19. *a*, *b*, *c*, red blood corpuscle of man; *d*, white corpuscle of man; *e*, red corpuscle of frog.

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[1] Carbon dioxide is also carried by the plasma.

MORPHOLOGY OF THE ORGANS OF VERTEBRATES.

FROM the point where the four germ-layers are clearly differentiated from each other, we have now to trace the various derivatives of each; but it must be kept in mind not only that various organs are in the process of development at the same time, while the necessities of treatment demand that they be arranged in sequence, but that two or more layers not infrequently contribute to the same organ. In such cases the organ is described in connection with that layer which is most prominent or most important in its structure. In the following account the stages of development are traced only with such detail as is necessary for a clear interpretation of the adult structure. For more extended accounts the student must go to the embryological manuals and special memoirs.

ENTODERMAL ORGANS.

The differentiation of the entoderm by invagination has been described (p. 5). By this process of gastrulation a layer of entoderm cells comes to lie inside the other or ectoderm cells, and by the closure of the blastopore (usually complete) it assumes the form of a sac, the cavity of which is the archenteron. As the embryo elongates, the sac forms an elongate tube. In the middle line of its dorsal wall a cord of cells, lying between the outgrowing cœlomic pouches (Fig. 7, *n*), becomes constricted off from the rest,[1] and occupies a position between the other entodermal structures and the nervous system (Figs. 7 and 20). This rod is the **notochord,** the subsequent history of which is given in connection with the skeleton.

The rest of the entoderm, after the formation of the noto-

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[1] In a few forms (e.g., *Amblystoma*) this cord is at first tubular; later its lumen is lost.

chord, gives rise to the lining (epithelium) of the digestive canal (alimentary tract) and its appendages, and of the respiratory organs (gills and lungs).

The first step in the differentiation of the alimentary structures is the formation of an outpocketing on the ventral side, the beginning of the liver (Fig. 20, *l*). This occurs some distance in front of the middle of the body, and divides the alimentary canal into pre- and post-hepatic portions. The post-hepatic portion gives rise to the intestine and its various divisions, including the pancreas; from the pre-hepatic region are developed the pharynx, with the respiratory structures, the gullet, and the stomach.

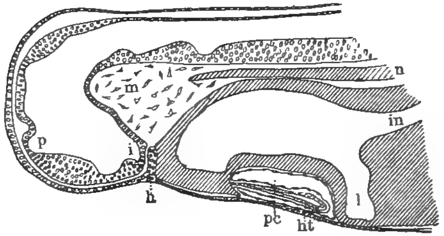

FIG. 20. Longitudinal section of *Amblystoma* embryo. *h*, hypophysis; *ht*, heart, its endothelial walls not shown; *i*, infundibulum; *in*, intestine; *l*, liver; *m*, mesenchyme; *n*, notochord; *p*, pineal outgrowth; *pc*, pericardial cavity.

The Mouth. — Besides these entodermal structures, the alimentary tract, as usually considered, embraces as well the cavity of the mouth, the lining of which is ectodermal in origin. The mouth arises as an inpushing or involution of the ectoderm[1] at the anterior end of the ventral surface of the body. The inpushing usually takes the form of a cup, the blind end of which impinges directly upon the closed anterior end of the alimentary canal proper, thus forming a double partition between the two (Fig. 55). These two membranes, one ectodermal the other entodermal in origin, fuse, and then an opening breaks through, thus placing the whole in communication. From this ectodermal oral invagination or **stomodæum** are developed the lips, teeth, tongue, and glands.

The lips bound the opening of the mouth. In all the lower vertebrates they are merely folds of epithelium, or, as in turtles

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[1] In some forms this inpushing is plainly a paired structure, a fact which adds no little weight to the view which regards the vertebrate mouth as having arisen from the coalescence of a pair of gill slits.

and birds, they may be entirely absent. In the mammals fleshy lips moved by muscles first occur, and even here they are lacking in monotremes and cetaceans. In turtles and birds the edges of the jaws, and to a greater or less extent the roof of the mouth, is covered with a cornified epithelium forming the so-called beak, and the same is true of the adult monotremes. The surface of this may be thrown into folds for the purpose of crushing the food, but these structures are not to be compared with true teeth.

Teeth. — In the formation of teeth two layers, ectoderm and mesenchyme, are concerned. The epithelium lining the mouth becomes inpushed into the deeper layers, where teeth are to be formed (Fig. 21). In the lower vertebrates there is a separate inpushing for each tooth, but in the mammals there is a continuous ingrowth,— the **dental ridge.** In other respects the features of development are essentially the same in all. The ingrowth is to be regarded, morphologically, as vesicular; and the deeper wall of the vesicle becomes pushed inside the other, so that there results a two-walled cup, the cavity of which becomes filled with mesenchyme. The cells of the inner layer become columnar and form the **enamel organ**; the immigrant mesenchyme cells constitute a **dental papilla,** the external cells of which are known as **odontoblasts,** from their power of secreting a bone-like substance, the **dentine** or **ivory** of the tooth. The inner surface of the enamel organ likewise secretes a cup of denser substance, **enamel,** upon the outer face of the dentine.

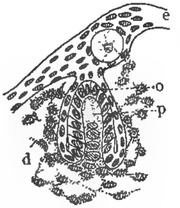

FIG. 21. Tooth germ of *Amblystoma*. *d*, derma; *e*, epidermis; *o*, enamel organ; *p*, dental papilla.

By growth of the deeper portions (dentine) the enamel covered tip or **crown** of the tooth is forced up through the epithelial layers so that it comes into position for use. The deeper portion or **root** contains a central or **pulp cavity,** in which are remains of the mesenchyme, together with nerves and blood-vessels, these together forming the **pulp.** In the mammals the root is covered by a second coat, the **cement,** formed by the surrounding tissues (Fig. 22).

In the lower forms the process of tooth formation may continue for a long time, even through life, new teeth thus arising to make good the loss of others. In the mammals, however, there are at most but two of these sets of teeth, — a temporary **or milk dentition,** and a second or **permanent dentition,** the details of which are given in connection with that group.

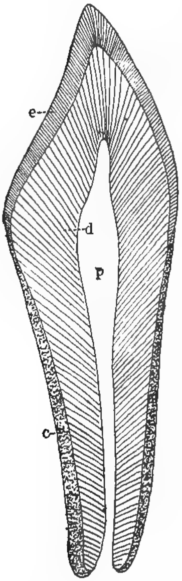

FIG. 22. Diagrammatic section of mammalian incisor tooth. *c*, cement; *d*, dentine; *e*, enamel; *p*, pulp cavity.

In the lower vertebrates teeth may appear in any part of the mouth where there are solid parts (bones or cartilages) to support them. Thus in fishes and amphibia we may find them not only along the edges of the jaws, but upon any of the bones which lie in the walls of the oral cavity. In the higher vertebrates they are confined solely to the edges of the jaws.

Teeth are very variable in shape, a fact largely correlated with differences in food. In the lower vertebrates all of the teeth of an individual are closely similar to each other. This is the **homodont** condition; the **heterodont** dentition appears in the mammals, and occasionally in the lower groups, where the teeth in the different regions of the mouth are of different shapes. Usually in the lower vertebrates each tooth possesses but a single root and a single cusp; while in the mammals, besides these simple teeth, there are others, with two, three, or several roots, the crowns also showing a corresponding duplication of parts.

In the elasmobranchs the teeth rest upon but are not firmly united to the skeletal parts. In the other ichthyopsida they are usually firmly united to the bones of the mouth by continuous growth, and the same is true of many reptiles. In others they may be implanted in sockets (**alveoli**) in the jaws, a condition which is universal in the mammals.

Besides these true or calcified teeth, horny teeth occur here and there, as in the cyclostomes, where the oral hood and the tongue are armed with such structures resting upon epithelial papillæ, or in the larvæ of the anura, where, besides the horny jaws, there are numbers of minute cornified teeth. Mention may also be made here of the œsophageal teeth of the snake *Rhachiodon*, which consist of ventral processes of the cervical vertebræ, each with its cap of enamel. These project through the dorsal wall of the œsophagus, and serve to cut open the eggs upon which these reptiles feed.

Tongue. — The tongue is primitively a fleshy fold of the floor of the mouth, supported to a greater or less extent by some of the elements of the first visceral (hyoid) arch (see skeleton). In the fishes this tongue is without its own muscles, and can be moved only in connection with the branchial arches. In the cyclostomes, on the other hand, lingual muscles — protractors and retractors — of considerable size appear, while in the amphibia and higher groups similar muscles are usually well developed.[1] In the amphibia the tongue is fastened by its ventral surface or its anterior end. In the reptiles, on the other hand, it is fastened behind. In this group, as in the birds, it is usually horny, with few intrinsic muscles, and in these the hyoid becomes more modified as a lingual skeleton. In the mammals the tongue reaches its highest development, with very considerable variations of form. Beneath the tongue, in many mammals, is a small fold, the **sublingua,** which is regarded by Gegenbaur as homologous with the tongue of the lower forms, the mammalian tongue being a structure peculiar to that group.

Oral Glands. — Glands connected with the oral cavity first appear in the amphibia, where in the epithelium occur numerous mucous glands, the secretion of which moistens the lining of the mouth. Besides these, the higher amphibia have a larger **internasal gland** opening in the palate region. In the reptiles glands are more numerous, occurring on and beneath the tongue, and along the margins of the jaws. From these latter are developed the poison glands of snakes; while if the lizard *Heloderma* be poisonous, its poison is secreted from the large sublingual gland. In the birds the glands are not so numerous, those of the tongue, palatal region, and angle of the mouth, being most conspicuous. In the mammals three pairs of glands

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[1] Occasionally (*Pipa*, *Dactylethra*) a tongue is not formed.

occur, — a sublingual, a submaxillary, and a parotid. None of these are poisonous; but the saliva which they secrete is for moistening the food during mastication, and for the conversion of starch into sugar.

From the pharyngeal region are developed the respiratory organs, — gills and lungs, — as well as certain other structures, the thyroid gland, thymus gland, etc.

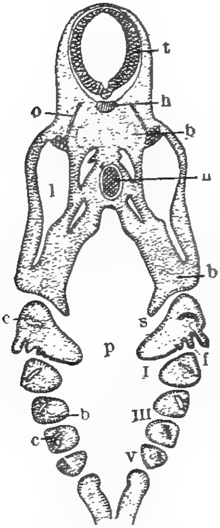

FIG. 23. Horizontal section through head and pharyngeal region of *Acanthias* embryo, showing the gill slits. *b*, blood-vessels; *c*, cœlomic cavities of gill arches; *f*, developing gill filaments; *h*, hypophysis; *n*, notochord; *o*, oculomotor nerve; *p*, pharynx; *s*, spiracular cleft; *I*, first (mandibular) head cavity; *I–V*, gill clefts.

Gills. — Gills arise as a series of paired or bilateral outpushings of the entodermal lining of the pharynx. These push out through the mesodermal and mesenchymatous tissues until they reach the ectoderm on the sides of the neck. The two layers now fuse, and then an opening is formed at the point of fusion, so that there arise a series of openings (**gill-, branchial-,** or **visceral-clefts**) on either side, connecting the pharyngeal cavity with the external world. In the septa between the clefts are developed skeletal structures (gill- or branchial-arches, see skeleton), and also blood-vessels. From the walls of the clefts develop vascular leaves or filaments, the gills proper. These are arranged on the anterior and posterior walls of the clefts, those on a side constituting a **demibranch.**

The number of gill pouches differ in different groups. In *Bdellostoma* a (cyclostome) there may be 14 pairs; in the notidanid sharks 7 or 8; in other sharks 6, and from this down to 5 in reptiles, and 4 in mammals. In the ichthyopsida all, or nearly all, of these pouches break through as described above, but in the amniotes but one or two open to the exterior; the statements regarding the mammals being conflicting. In the amniotes these gill pouches or clefts never develop gill filaments; and in the adult all traces of them, except of the first, are lost. Their presence in this group can only be explained as inheritances from branchiate ancestors. The first gill pouch in the anura and the higher groups form the Eustachian tube (see ear).

In elasmobranchs and some ganoids the anterior visceral cleft is smaller than the others, and opens on the top of the head. This **spiracle** bears well-developed gills in the lowest sharks (notidanidæ), but in others it may have but a vascular network in its walls. In ganoids and embryonic teleosts it has a gill-like structure; but it is here termed a **pseudobranch,** since it receives arterial blood from the opercular gill. The opercular gill is a secondary and ectodermal structure developed on the inner or posterior face of the operculum (see below).

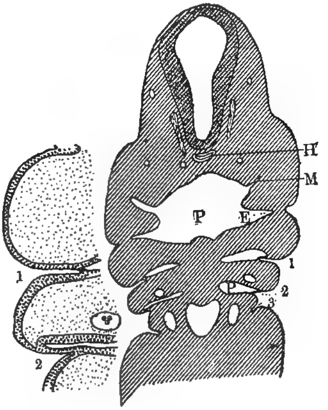

FIG. 24. Section through the head of a pig embryo 6.5 mm. long, showing the gill slits (1, 2, 3,) closed by a thin wall. At the left a small portion enlarged. *E*, Eustachian cleft; *H*, hyphophysis; *M*, mandibular cleft; *P*, pharynx.

In the typical elasmobranchs the interbranchial septa extend to the outside of the body, and the gill clefts open directly to the exterior, either on the sides of the neck (selachii, Fig. 26) or on the ventral surface (raiæ). In the cyclostomes, *Myxine* excepted, there is also a separate opening for each gill cleft. In the holocephali a fold of skin on either side grows back over the gill clefts, thus enclosing a space into which these empty, and which in turn connects with the exterior by a slit-like gill opening behind. In the ganoids and teleosts the same relations occur; but in these the fold, known as the **operculum,** has a cartilaginous or bony internal skeleton. In the amphibia the opercular fold is also found, but

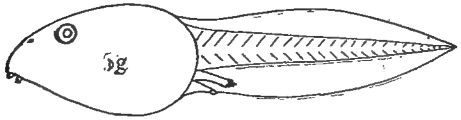

FIG. 25. Tadpole of frog, showing at *g* the external gill opening.

in urodeles and cæcilians it develops but slightly. In the anuran tadpole, on the other hand, the opercular folds of the two sides unite beneath the throat, thus connecting the extra branchial chambers of the two sides, and then the folds unite to the sides of the body, usually leaving but a single opening on the left side through which water is discharged from both right and left gills[1] (Fig. 25).

In the cyclostomes the gill slits are narrow tubes widened in the middle into a saccular shape (whence the name marsipobranchs, pouched gills, often given the group). In these sacs are the demibranchs. In the elasmobranchs the septa extend to the external surface, the gills not extending so far. In ganoids and teleosts, on the other hand, the septa are reduced to small rods while the demibranchs are greatly enlarged.

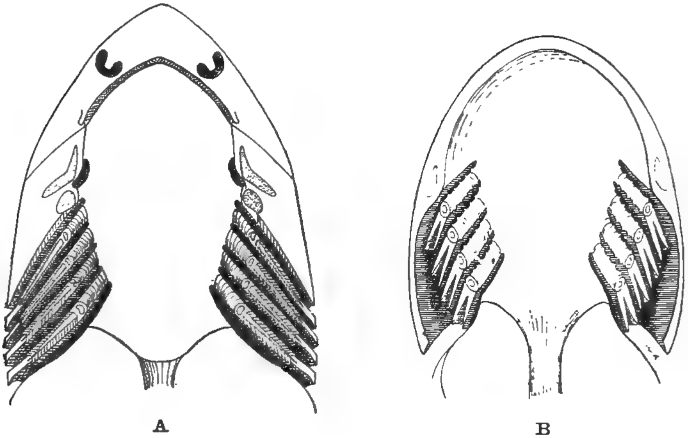

FIG. 26. Relations of gill clefts, etc., in an elasmobranch, *A*, and a teleost *B*.

In the embryonic amphibia external gills occur. These are ectodermal structures developed from the outer surface of the gill septa[2] even before the gill clefts break through. In

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[1] No operculum is developed in the amniotes; but there is some plausibility in the view which regards the external ear of the mammals as a derivation of the ichthyopsidan operculum.

[2] Relations, blood supply, and nerves go to show that the fleshy processes (so called **balancers**) of the urodele larvæ are the modified external gills of the hyoid arch (see Fig. 199).

the perennibranch urodeles these external gills persist through life.[1] In the other urodeles they are lost without replacement.

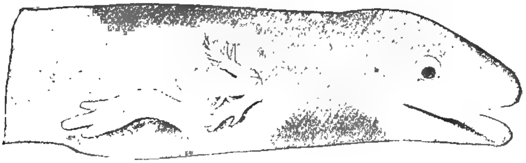

FIG. 27. Head of young *Amphiuma* showing the external gills, partially covered at the base by the backward extension of opercular fold.

In the anura, on the other hand, the external gills are early lost, and are replaced by internal gills upon the sides of the clefts, which, however, are said to be of ectodermal origin.

Air-bladder. — From the pharyngeal or œsophageal region there arises also in most ganoids and teleosts the **air-** or **swim-bladder.** It starts as a diverticulum from the dorsal [2] wall of the pharynx, the distal portion of which enlarges into a thin walled sac, the air-bladder or **pneumatocyst**; the proximal portion forms the **pneumatic duct.** This duct remains open throughout life in the ganoids and the lower teleosts, but in the higher teleosts it closes and is reduced to a fibrous cord.[3] The bladder itself usually lies dorsal to the aorta and urogenital system next the vertebral column. In

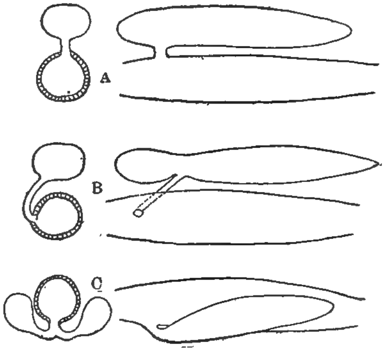

FIG. 28. Relations of the air-bladder to the alimentary canal, after Dean. *A*, in most physostomous teleosts; *B*, in *Erythrinus*; *C*, in *Polypterus*, *Calamoichthys*, and dipnoans.

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[1] Cope, however, claims that in *Siren* the embryonic gills are lost, and that the persistent gills of the adult are new structures.

[2] The pneumatic duct empties laterally in some characinidæ, ventrally in *Polypterus*, into the œsophagus; but until the development is known, we cannot say how far this condition is secondary.

[3] The teleostei were formerly subdivided into physostomi, with permanent pneumatic duct, and physoclisti with it closed.

shape it varies greatly; it may be unpaired, or it may consist of two paired lobes. It may be a simple sac, or it may be subdivided into two or several successive chambers. Its internal walls are usually smooth, but they may be considerably convoluted, thus greatly increasing the surface. Occasionally its walls are calcified. Its chief function is that of a hydrostatic apparatus. It is not respiratory, as it receives arterial blood and returns venous blood. In some fishes (ostariophysiæ) it is connected with the ear by a **Weberian apparatus,** consisting of a chain of small bones. According to the latest conclusions this apparatus seems to be for a recognition of variations in hydrostatic pressure. The swim-bladder is absent in some bottom-living fishes (pleuronectids, etc.).

In the pharyngeal region of the elasmobranchs are cæca, which may be the structures from which the swim-bladder has developed. The swim-bladder, in turn, is usually regarded as having given rise, by substitution of functions, to the lungs. On the other hand, there are some who regard the lungs as new formations in the air-breathing vertebrates, and as having arisen by modification of a pair of gill pouches which have grown backwards instead of outwards, and consequently have failed to form connection with the ectoderm. The method of origin of the lungs and the relations of the cartilages of the larynx, shortly to be described, favor the latter view.

Lungs. — The lungs arise as an outgrowth from the ventral wall of the pharynx, just posterior to the last gill pouch. The outgrowth almost immediately divides into right and left halves, which grow back, laterally to the heart, into the anterior part of the body cavity, and the distal portions enlarge into thin walled sacs, the **lungs** proper. The proximal portions of the paired outgrowths form the **bronchi,** while the unpaired portion gives rise to the windpipe or **trachea,** the opening by which the trachea communicates with the pharynx being the **glottis.**

In this backward growth there is added to the entodermal epithelium of these organs mesenchyme tissue, while the lungs, invading the cœlom, become covered externally with a thin layer of epithelium (peritoneum, see cœlom). Between the two epithelia run numerous blood-vessels, — arteries, veins, and capillaries, — conveying blood to and from the lungs.

In the lower amphibia the lungs develop scarcely beyond the condition of simple sacs with respiratory ducts.[1] In other forms, however, there is increase of surface by a folding of the internal wall, to be described later; and in those still higher there is a division of the primary bronchi into bronchi of secondary and tertiary orders, each of which connects with a separate division of the pulmonary organ.

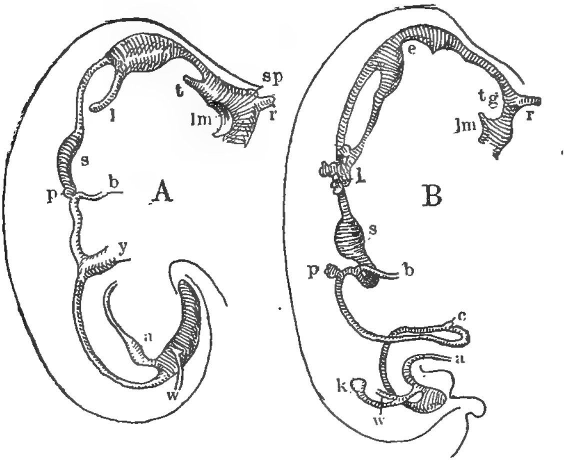

FIG. 29. Alimentary tract of human embryo, *A* at four weeks, *B* at five weeks, after His. *a*, allantois stalk; *b*, bile duct; *c*, cæcum; *e*, epiglottis; *k*, kidney; *l*, lung; *lm*, lower jaw; *p*, pancreas; *r*, Rathke's pocket; *s*, stomach; *sp*, Seessel's pocket; *t*, thymus; *tg*, tongue; *w*, Wolffian duct.

In the dipnoi the trachea and bronchi are without skeletal supports in their walls; but in all other forms cartilaginous parts are present, which tend to keep the tube from collapse. In the lower air-breathers these consist of separate pieces of cartilage on either side of the trachea; but from the reptiles upwards they consist of rings of cartilage, incomplete in mammals, the gap on the dorsal surface of such being crossed by membrane so as to allow the passage of food through the overlying

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[1] A considerable number of salamanders have recently been shown to be lungless; even the trachea has disappeared, and respiration is carried on by the skin.

œsophagus. The jointing of this tracheal skeleton permits of flexibility. In the bronchi there occur only irregular cartilaginous elements, which never form rings or semi-rings like those of the trachea. As a rule, the trachea pursues a straight course; but in certain birds (swans, cranes, birds of paradise, etc.) it becomes extensively convoluted, its windings being either between the sternum and the breast muscles, or within the breastbone itself.

At its upper end the trachea becomes widened and specialized, and is known as the **larynx,** which, like the trachea, has a cartilaginous framework. In the lower amphibia this support consists of a pair of cartilages, the **arytenoid cartilages,** one on either side, to which are added in the higher amphibia a ring cartilage, the **cricoid,**[1] which reappears in a similar shape in the reptiles. In the birds the larynx is somewhat rudimentary, its place being taken by the syrinx to be mentioned below. In the mammals, besides the cricoid and arytenoids, there is added as a development an incomplete ring of cartilage farther in front, the **thyroid cartilage.** This arises for the most part from the third of the visceral arches, the fourth contributing to a considerable extent. Other and smaller cartilages are also added in the same group, but need no description here.

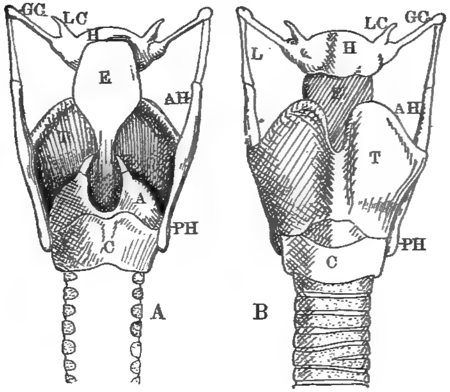

FIG. 30. Dorsal (*A*) and ventral (*B*) views of human laryngeal apparatus. *A*, arytenoid cartilage; *AH*, anterior horn of thyroid; *C*, cricoid cartilage; *E*, epiglottis; *GC*, greater (posterior) horn of hyoid; *H*, hyoid; *LC*, lesser (anterior) horn of hyoid; *L*, ligament connecting hyoid and thyroid; *PH*, posterior horn of thyroid; *T*, thyroid cartilage.

[1] This may be the product of fusion of the cartilages of the fifth gill arch, a view which receives support from the fact that the muscles of the larynx are innervated by the hypoglossal nerve.

Inside the larynx are the **vocal cords.** These are folds of the inner lining which stretch in pairs between the thyroid and the arytenoids, and, by the motion of these cartilages, can be tightened or relaxed. The upper pair of these are the false vocal cords, so called since they play no part in the production of the voice. The second or lower pair are the vocal cords proper. Between the two is a depression, the **ventricle of the larynx,** or **sinus of Morgagni,** which in certain apes becomes greatly developed as a vocal sac or resonator. In many anura the floor of the mouth is capable of distention, and here serves as a resonator.

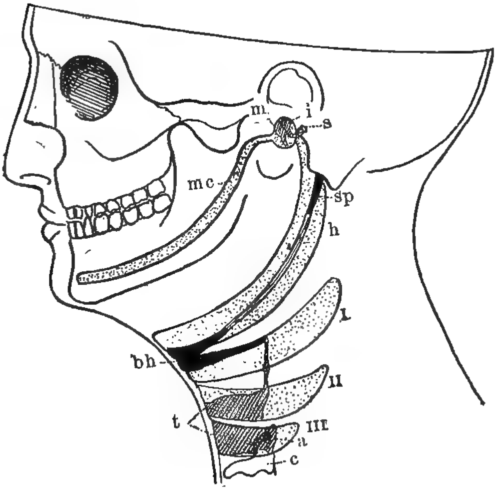

FIG. 31. Diagram of the relationships of the visceral arches in man, after Wiedersheim. *a*, arytenoid; *bh*, basihyal; *c*, cricoid; *h*, hyoid arch; *i*, incus; *m*, malleus; *mc*, Meckel's cartilage; *s*, stapes; *sp*, styloid process; *t*, thyroid cartilage; *I–III* branchial cartilages.

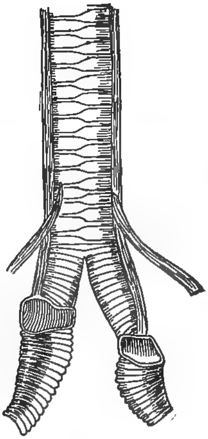

FIG. 32. Syrinx of *Steatornis*, after Stejneger.

In the mammals the anterior part of the larynx becomes closely connected with the hyoid arch (see skeleton).

In the birds, as was said above, the larynx tends to become rudimentary. Its place as a vocal organ is taken by a 'lower larynx,' the **syrinx,**[1] developed at the lower end of the trachea, or at the upper end of the bronchi where these arise from the

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[1] Rudimentary in ostriches and some buzzards.

trachea. Here the cartilage rings are modified and coalesced into a tympanic chamber, inside of which are vibratile membranes which take the place of vocal cords, while muscles running from trachea to bronchi alter the tension of the tympanic walls.

The lungs are all but universally paired. In *Ceratodus* the single sac is without trace of separation into halves; while in some elongate vertebrates (snakes, cæcilians) one lung is very small, the other attaining great development.

The lungs in the lower amphibia are but simple sacs with smooth internal walls; but in the frogs the internal surface becomes folded so that a number of chambers, the **infundibula,** are formed, the walls of which in turn are thrown into a number of hemispherical cups (**alveoli**) lined with pavement epithelium. In the walls of the alveoli run capillary blood-vessels. The infundibula open into a large central space connected with the bronchus, and which may be compared directly with the bronchioles (*infra*) of higher forms.

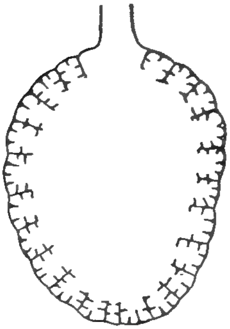

FIG. 33. Diagram of lung of frog. Around the margin are shown the infundibula, the walls of which are folded into alveoli.

In many reptiles the conditions are much as in the amphibia, some (snakes) having the distal portion of the lung without infundibular sacs, others having these complications of the surface extending throughout the organ. In others the bronchus divides into secondary bronchi as it enters the lungs, each of which is continued as a bronchiole; or we may have several bronchioles radiating from a single bronchus (*Alligator*, *Heloderma*). In some forms (*Chamæleon*) the bronchioles may connect with each other distally, a matter of interest in connection with the parabronchi of the birds (*infra*).

The mammalian lung may be regarded as a complex of lungs like those of a frog. The primary bronchus runs through the lung, giving off on either side secondary bronchi, which in turn bear tertiary bronchi. Each of these latter connects with small tubes, the **bronchioles,** which lead to infundibula, as in the amphibia. These bronchioles may be as large as, or even larger than, the smaller bronchi; but they differ from them in the absence of cartilage and glands in the wall, in the absence (usually) of cilia on the internal surface, and in the existence of alveoli arising directly from their walls. Besides the lobulation implied by this branching of the respiratory ducts, the lungs may also be divided into lobes, varying in number, clearly recognizable from the exterior.

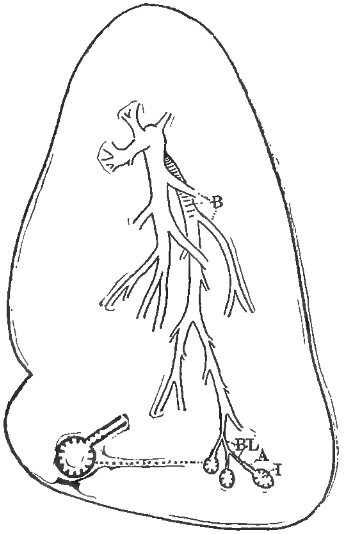

FIG. 34. Diagram of lung structure in man. *B*, bronchi; *BL*, bronchioles; *A*, alveolar duct; *I*, infundibulum, surrounded by alveoli. Only a very few bronchi shown.

The lungs of birds are peculiar in several respects. The primary bronchus, after entering the lung, continues along the ventral surface to near the end of the organ. Near its entrance it gives off several **lateral bronchi,** which also course along the ventral surface, and extend onto its sides. The primary bronchus also gives off from its dorsal surface a larger number of secondary bronchi, which extend through to the dorsal surface. From these dorsal and lateral bronchi arise numbers of slender tubes, the so-called lung-pipes or **parabronchi,** which are to be regarded as modified bronchioles, since they have similar walls, and since they connect with the infundibula. They differ, however, from the bronchioles of the mammals in that they unite or anastomose frequently with each other, thus converting the whole lung into a network of tubes (compare the condition in chameleon, above).

In the embryonic avian lung thin-walled sacs arise from the outer surface of the lung. These **air sacs** increase in size, and extend themselves in every direction,—into the abdominal cavity, where they enter between the viscera, in between the muscles, and beneath the skin; they enter many of the bones (especially the humerus, femur, sternum, and pelvis), so that the whole body is penetrated by these cavities. While this great extension of air sacs is especially characteristic of birds, it has its forerunners in the reptiles, where, as in the chameleons, similar air sacs invade the abdominal region, while in the fossil dinosaurs some of the bones contain cavities which are regarded as having been occupied by similar air sacs.[1] The function of these air sacs in the birds is not certainly known. The chief suggestions made are that they largely increase the respiratory surface, and by introducing air into close connection with the tissues, they lessen the demands upon the circulatory system; they also to a slight extent lessen the specific gravity of the animal; and it may be that compression of them in one region or another causes a shifting of the position of the centre of gravity, a matter of no little importance in flight. Another view is that they allow the air to flow twice over the respiratory surface, thus allowing a more complete exchange of gases.

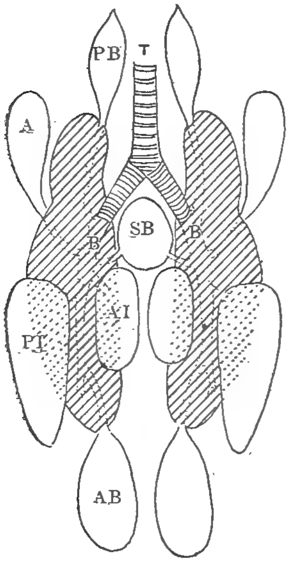

FIG. 35. Diagram of air-sacs of bird, the lungs shaded. *A*, axillary sac; *AB*, abdominal sac; *AI*, anterior intermediate sac; *B*, bronchus; *PI*, posterior intermediate sac; *PB*, prebronchial sac; *SB*, subbronchial sac; *T*, trachea.

Thyroid Gland. — The thyroid gland arises from the floor of the pharynx in the neighborhood of the anterior gill slits. In the typical condition there is a median or unpaired invagination of the oral epithelium, which later becomes cut off as a hollow vesicle or a solid body. Farther back, in most if not in all vertebrates, a pair of secondary invaginations are formed.[2] Like the anterior invagina-

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[1] A somewhat similar *pneumaticity* of certain bones is found in mammals, and especially in monotremes, where air cavities occur in certain bones, especially those of the skull. These cavities, however, are not connected with the lungs.

[2] In reptiles but one of these paired structures comes to full development, the other being rudimentary.

tion, these also separate from the parent epithelium, and become joined to the anterior portion in mammals, but retain their distinctness in the lower forms. The thyroid takes first the shape of numerous cylindrical cords with internal lumen. The cords branch and anastomose, and blood-vessels and connective tissue enter the network thus formed.

By most students the unpaired portion of the thyroid gland is considered as a derivative of the hypobranchial groove of the tunicates and *Amphioxus*, while the paired portion is probably to be regarded as derived from an additional pair of gill slits which never break through to the exterior. The function of the thyroid is apparently to form some compound of iodine necessary to keep the system in good condition.

Thymus Gland. — Closely connected with the gill clefts in development are a pair of structures of problematical functions, — the **thymus glands.** Each arises from the epithelial tissue on the dorsal margin of one or more gill slits. Later this tissue becomes invaded by leucocytes, while ingrowths of connective tissue divide it up into small lobules. In the fishes the glands remain near these points of origin just above the gill slits; in the amphibia they occur above and behind the angle of the jaw. In the reptiles the glands occur in the neck, sometimes far anterior, sometimes, as in the snakes, just in front of the heart. In the birds these glands extend nearly the whole length of the neck, while in the mammals they pass backwards into the thoracic region ~~immediately behind the sternum~~, and ventral to the heart.[1] In mammals the thymus glands undergo more or less complete degeneration with age; in man they reach their highest development in the second year.

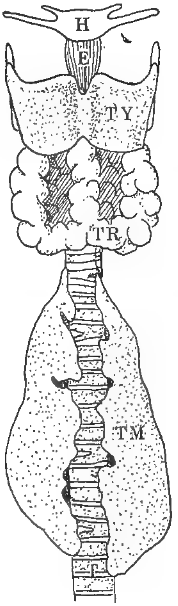

FIG. 36. Relations of thyroid (*TR*) and thymus (*TM*) glands in an infant, after Wiedersheim. *E*, epiglottis; *H*, hyoid bone; *T*, trachea; *TY*, thyroid cartilage.

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[1] The thymus glands of calves are the 'throat sweetbreads' of the market.

Digestive Tract. — The alimentary tract proper begins behind the pharyngeal region and extends to the vent. In *Petromyzon*, of the cyclostomes, a growth from the floor of the hinder portion of the pharyngeal region extends forward above the gill slits, so that separate respiratory and digestive tubes occur in this region. In other vertebrates there is no such separation. In the cyclostomes the alimentary tract shows but slight differentiation into regions, the point of entrance of the liver duct serving to divide it into pre- and post-hepatic portions. In the latter division a slight fold of the internal surface forms a rudimentary spiral valve recalling that to be described below in elasmobranchs and ganoids. In the holocephali, some teleosts, and the lower urodeles there is scarcely more differentiation of the digestive canal.

In all other forms the digestive canal is more or less clearly divided into regions. Thus we find the pre-hepatic portion differentiated into an anterior slender tube, the **gullet** or **œsophagus,** and a posterior widened portion with glandular walls, the **stomach.** The œsophagus calls for few remarks. Its length is correlated with that of the neck, and only in certain birds is any marked differentiation in its walls to be seen. Here it becomes widened near its middle into a glandular sac of variable form, the **ingluvies** or **crop,** which serves as a reservoir of food, and in the pigeons furnishes a food for the young.

The stomach, on the other hand, presents numerous modifications. Behind it is usually sharply marked off from the rest of the alimentary tract by an internal fold, and by a well-developed sphincter muscle in its walls. This forms the **pylorus.** The opposite end of the stomach is the **cardiac** region, so called since in man it lies nearest the heart. The stomach may be parallel with the axis of the body, but usually, as in most fishes, it is loop-like, or comes to lie more or less at right angles to that axis, conditions brought about by a lengthening of the tract more rapidly than the body increases in length. Correlated with the absence of teeth, the stomach of the bird acquires a great development, and becomes divided into two chambers, — an anterior glandular portion, the **proventriculus,** and a posterior muscular portion, commonly known as the **gizzard.** When most developed, as in grain-eating birds, the muscles of this gizzard develop a tendinous disk on either side, while the inner surface is frequently lined with a firm horny coat which aids greatly in grinding the food.

In the mammals the line of division between stomach and œsophagus is more sharply drawn than elsewhere in the vertebrates. In the seals alone is the stomach parallel to the body axis; elsewhere it is twisted into a transverse position. In the mammals it also shows greater variations of form than in any other group, modifications doubtless to be explained by differences in food. It may be either a simple sac, or it may be partially subdivided into chambers. In the simpler forms we may distinguish regions in the stomach, the cardiac and pyloric already mentioned, and between them a **fundus** region characterized by difference in the glands lining the walls. When the subdivision occurs, the chambers correspond more or less closely to these glandular regions. This division reaches its extreme in the ruminants, where usually four divisions are recognized. These are in order (Fig. 38), (1) **rumen** (paunch), (2) **reticulum** (honeycomb), (3) **omasum** or **psalterium** (manyplies), and (4) **abomasum** (rennet). In the cetacea there are a number of diverticula about the pyloric region. It must, however, be kept in mind that the rumen and reticulum are not truly gastric but œsophageal in nature, and that they serve not as digestive organs, but for the storage of food.

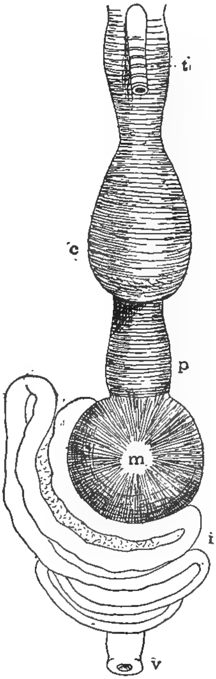

FIG. 37. Digestive tract of a bird of prey. *c*, crop; *i*, intestine; *m*, muscular stomach; *p*, glandular stomach; *t*, trachea; *v*, vent.

In the lower forms the liver duct opens close behind the pylorus, but in the higher vertebrates a tract of some length, the **duodenum**, may intervene between the two. While usually considered as a part of the intestinal region, this duodenum is really pre-hepatic. The post-hepatic portion of the alimentary canal is more or less clearly divided into two regions, an anterior **mid gut,** the small intestine, and a posterior **hind gut,** the large intestine of higher forms. In the lower vertebrates this distinction is not so sharp, being largely indicated by the character of the internal walls, or, as in the elasmobranchs, by the development of a cæcal tube (**rectal gland** or **digitiform appendix**) at the boundary between the two. From the amphibia upwards the line of division is more sharp, an internal constriction, the **ileocolic valve,** forming the line of demarcation.

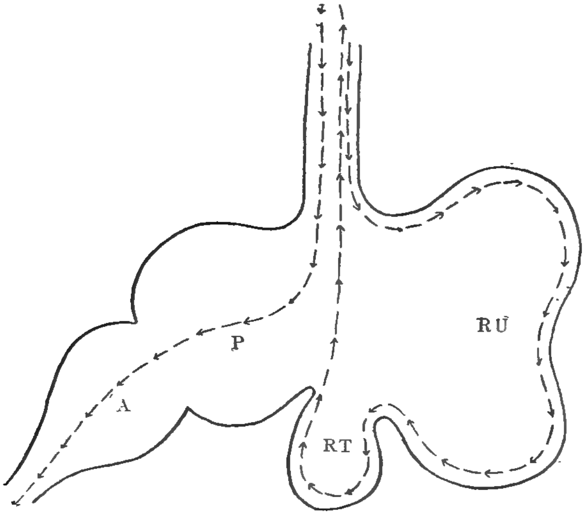

FIG. 38. Diagram of ruminant stomach, after Wiedersheim. *A*, abomasum; *P*, psalterium (manyplies); *RT*, reticulum (honeycomb); *RU*, rumen (paunch).

The mid gut is the chief seat of intestinal absorption, and various means are introduced of increasing the intestinal surface. In the cyclostomes there is an infolding of the inner wall which follows a slightly spiral course. In the elasmobranchs this **spiral valve** acquires great development, either growing out so that the interior of the intestine resembles a spiral staircase, or more like a roll of paper, the free edge projecting into the lumen of the tube. This spiral valve reappears in the ganoids, but is not

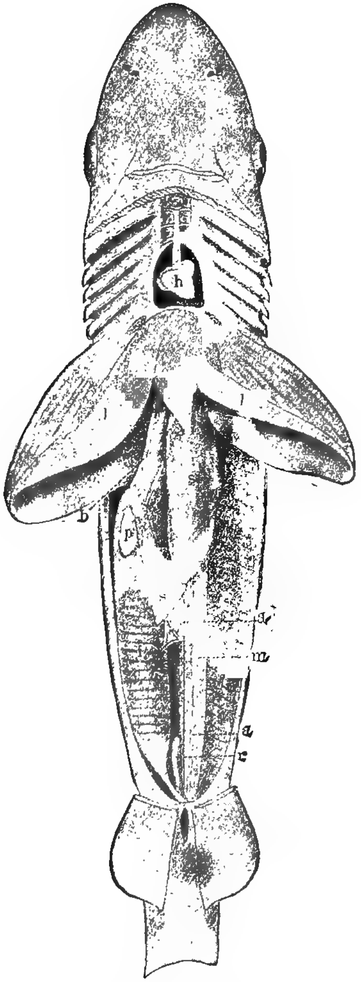

FIG. 39. Alimentary tract of dogfish (*Acanthias*). *a*, dorsal aorta; *b*, bile duct; *h*, heart; *i*, intestine, the spiral valve showing through; *l*, liver; *m*, mesonphros; *p*, pancreas; *r*, rectal gland; *s*, spleen; *st*, stomach.

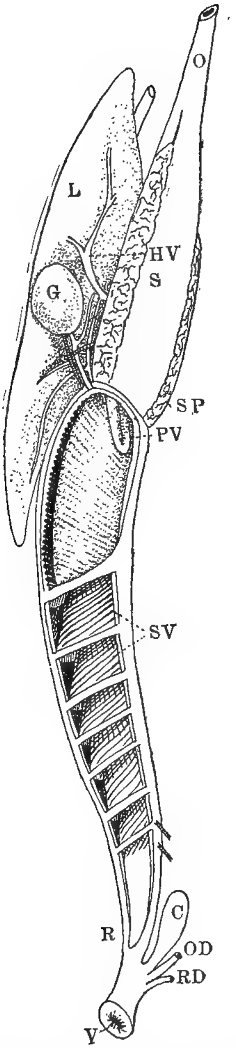

FIG. 40. Alimentary canal of *Protopterus*, after Parker. *C*, cloacal cæcum; *G*, gall bladder; *HV*, hepatic vein; *L*, liver; *O*, œsophagus; *OD*, oviduct; *PV*, pyloric valve; *R*, rectum; *RD*, renal (mesonephric) duct; *S*, stomach; *SP*, spleen; *SV*, spiral valve; *V*, vent.

FIG. 41. Ichthyosauran coprolites, one in section. The spiral character is taken as evidence of the presence of a spiral valve in these reptiles. After Leunis.

found higher in the scale.[1] In the higher fishes it is replaced by cæcal tubes (**pyloric appendages**) developed close to the pylorus. The number of these varies from one in certain ganoids to over one hundred and fifty in the mackerel.

In the amphibia and reptiles the mid gut is nearly straight in the elongate forms, more convoluted in the shorter types, the convolutions increasing in extent in the birds and mammals. In the birds, at about the middle, the mid gut bears a blind tube, the **vitelline cæcum,** the remains of the yolk stalk of development, by which, in the earlier stages, the intestine was connected with the yolk. In these higher forms increase of intestinal surface is brought about in part by the lengthening of the intestine, and in part by the development of numerous small folds (**valvulæ conniventes**) and minute finger-like projections (**villi**) resembling the pile of velvet.

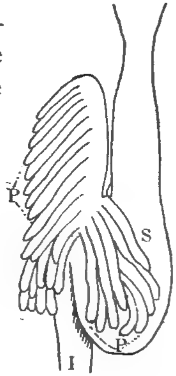

FIG. 42. Stomach and pyloric cæca of Salmo, after Rathke. *I*, intestine; *P*, pyloric cæca; *S*, stomach.

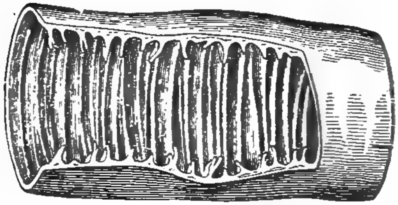

FIG. 43. Part of small intestine of man, showing the valvulæ conniventes, from Martin.

The hind gut is hardly distinct in fishes, as viewed externally, but from the amphibia on it acquires greater individuality. It may consist merely of a straight tube, **rectum,** or it may have a terminal rectum connected with the mid gut by a more or less convoluted tube, — the **colon.** Just behind the ileocolic valve in the forms from the turtles upwards is developed a

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[1] The marks on certain reptilian coprolites indicate that some extinct reptiles may have had a spiral valve (Fig. 41).

blind tube, the **intestinal cæcum,**[1] which is clearly connected with increase of digestive surface. In certain birds there may be two of these cæca, and in the ostrich there is developed on its inside a spiral fold. In the mammals the cæcum shows great variations. It is lacking entirely in certain groups (edentates, cheiroptera, some carnivores). In the herbivorous forms, on the other hand, it may equal the body in length. In man and some apes and rodents all parts of the cæcum are not equally developed, the terminal portion, known as the **appendix vermiformis,** remaining smaller than the rest.

In the elasmobranchs, dipnoans, amphibians, sauropsida, and the monotremes among the mammals, the rectum does not open directly to the exterior, but into a terminal enlargement, the **cloaca,** into which the urinary and reproductive ducts also empty; and from this chamber all contents pass to the exterior through the vent. In the other vertebrates no cloaca is formed. In connection with the cloaca in birds is developed a sac (**bursa Fabricii**), which comes to lie in the pelvic cavity between the vertebræ and the terminal portion of the hind gut. Its function is unknown. The bursa is said to be of ectodermal origin.

The alimentary tract is here placed among the entodermal structures, but only the lining coat is derived from that germ layer. Other constituent parts are derived from the mesenchyme. Beneath the entodermal epithelium and following closely its contour is a layer of loose connective tissue, the **sub-mucosa,**[2] which carries blood and lymph vessels. Outside of this are the muscular layers, two in number, an inner circular and an outer longitudinal, each of smooth or non-voluntary muscle. These by their action produce peristaltic movements of the contents of the tube. Where it passes through the body cavity the alimentary canal receives a third or **peritoneal layer** of pavement epithelium derived directly from the splanchnic layer of the cœlom.

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[1] The rectal gland of the elasmobranchs is possibly homologous with the cæcum of the amniotes.

[2] Occasionally the sub-mucosa may be divided by a muscular layer, in which case that portion nearest the entodermal epithelium is called the tunica propria, the deeper portion retaining the name sub-mucosa.

Liver. — The liver, as was said above, develops as a diverticulum from the ventral side of the primitive alimentary canal. This outgrowth branches again and again, the result being a greatly branched tubular gland, the proximal portion of the tubes being specialized as the ducts leading to the intestine. In the amphibia and reptiles this tubular condition is retained throughout life, the minute lumen of the glandular portions being known as the **gall capillaries.** In birds and mammals the tubular condition soon disappears, the gall capillaries running, without much regularity, between the cells. By the ingrowth of connective tissue the liver glands are divided into lobules, the so-called 'liver islands.' In this connective tissue run the larger gall ducts (which connect with the gall capillaries), and also branches of the hepatic artery and of the portal vein (see circulation). From their position these vessels are often spoken of as interlobular. In the centre of each island (intralobular in position) is a branch of the hepatic vein, while capillaries extend through the lobules from the interlobular to the intralobular blood-vessels. As a rule, there is but a single duct emptying from the liver into the intestine, and this, as a rule, has connected with it by a lateral branch (**cystic duct**) a thin-walled **gall-bladder.** When these conditions occur, the duct leading from the liver as far as the mouth

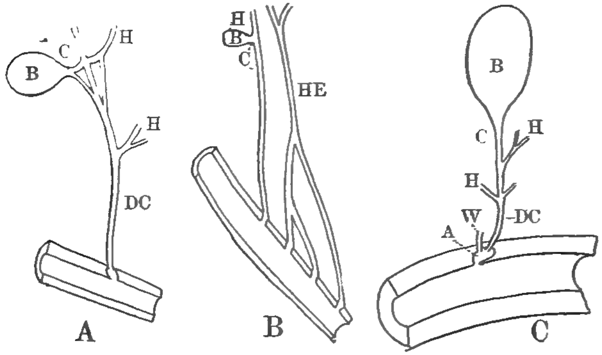

FIG. 44. Hepatic ducts of A, frog; B, emeu; and C, cat. *A*. ampulla of Vater; *B*, gall-bladder; *C*, cystic duct; *DC*, ductus choledochus; *H*, hepatic ducts; *HE*, hepatoenteric duct; *W*, duct of Wirsung (pancreatic).

of the cystic duct is called the **hepatic duct;** from that point to the intestines, the **ductus choledochus.** Again, besides these ducts there may also be a separate **hepatoenteric duct** leading directly from the liver to the intestine, as well as other modifications not necessary to mention, aside from the numerous ducts in lizards and snakes.

The liver thus formed is a large compact organ, largest in the lower vertebrates, and larger in flesh (fat) eating forms than in the herbivorous groups. In many fishes it forms a single, undivided mass, but in the great majority of vertebrates two lobes are present, and these in turn may be lobulated. The blood-vessels leading to the liver (portal vein, hepatic artery) enter in close relations to the gall ducts, while the veins (hepatic) leaving it are widely separate from these, in contrast to the conditions occurring in most organs. The liver is supported by a mesentery (**gastro-hepatic omentum**) which connects it to the ventral wall of the alimentary tract, and which is frequently continued below as the suspensory ligament of the liver.

The pancreas develops in much the same way as the liver, — as an outgrowth from the entodermal walls just behind the liver outgrowth. There is the same increase in size, while branching gives rise to glandular portions and ducts. The pancreas has recently been found to occur in several vertebrates where its existence was formerly denied, and farther research may reveal one in the cyclostomes where none has yet been found. Thus in certain teleosts its condition as a delicate tube lying in the mesentery, and its position in the dipnoi just outside the muscular walls of the alimentary canal, caused it to be overlooked for a long time. In the elasmobranchs and other teleosts it is a well-marked gland. In other forms it is more complex in its origin. Thus in the ganoids (sturgeon) it arises by two dorsal and two ventral outgrowths; in the amphibia and all higher forms, from one dorsal and two ventral outpushings, these later uniting into one glandular mass. The ducts can undergo various modifications, all persisting, or either dorsal or ventral disappearing; or finally the ducts may come into connection with those leading from the liver (Fig. 44 *C*, *W*).

Two other structures, the spleen and the urinary bladder, are closely connected with the entoderm in origin, but they are better described in connection with those structures — circuatory and excretory — with which they become associated in later life.

ECTODERMAL STRUCTURES.

THE derivatives of the ectoderm may be subdivided into epidermal, nervous, and sensory organs, the differentiation of the nervous from the epidermal structures beginning with or even before the completion of the process of gastrulation.

THE CENTRAL NERVOUS SYSTEM.

The central nervous system begins its development as a structure distinct from the rest of the ectoderm by the formation of a **neural** or **medullary plate** on the dorsal surface of the embryo. On either side of the primitive groove (fused blastoporal lips, p. 7) the ectodermal cells become elongated (cylindrical or fusiform), while in those regions destined to give rise to the epidermis they retain their more flattened character, the line between the two regions being sharply drawn. Soon after being outlined the lateral edges of the medullary plate begin to bend upwards and inwards, the whole thus forming a **medullary groove** bounded by the **medullary folds,** the outer portion of each fold being formed by unaltered ectoderm (Fig. 45). This inward bending of the medullary folds continues until the edges meet, the medullary plate being converted by this process into the walls of a tube, which later develops into brain and spinal cord. The edges of the fold now fuse, — neural parts with neural, epidermal with epidermal, — so that the nervous portion becomes internal, and

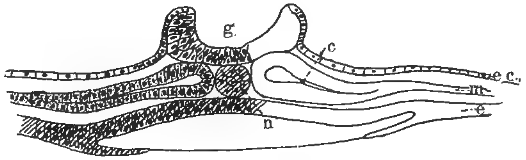

FIG. 45. Section through embryo *Acanthias* before the closure of the medullary groove, *g*. *c*, cœlom; *e*, entoderm; *ec*, ectoderm; *m*, mesothelium; *n*, notochord.

is covered by a continuous sheet of epidermis. This process of infolding and fusion proceeds from in front backwards, but at the very front end a small opening (**anterior neuropore**) may persist for some time. The important points to be kept in mind in this connection are that the central nervous system develops by the infolding[1] of a part of the primitively external surface of the body, and that the inner surface of the neural tube is morphologically external in origin.

Before the infolding of the neural tube is completed, its anterior end enlarges, the first step in the process of differentiation into brain and spinal cord. The latter division must be described first, since it presents much simpler conditions than does the brain.

The spinal cord frequently retains, to a certain extent, its tubular character throughout life, although the central canal does not materially increase its primitive diameter. In the earlier stages the cord is oval in section, its sides being thickened; while in the median line, above and below, it is much thinner (Fig. 48). These halves rapidly increase in size while the central median portion lags behind, the result being that the cord soon becomes marked along its ventral surface by a longitudinal groove. Later a corresponding cleft appears on the dorsal surface. These are the **anterior** and **posterior fissures** of human anatomy.

In sections of the adult cord one clearly distinguishes an outer white matter and an inner gray substance; the latter takes the shape of the letter H, the ends of the uprights being called the **horns** or **cornua**,[2] while the cross-bar is produced by fibres running from one half to the other between the bottoms of the fissures and the central canal. The horns extend towards the surface, above and below, thus dividing the white matter of each half of the cord into three **columns**, — dorsal, lateral, and ventral; the lateral column being between the two horns, the dorsal and ventral between the horns and the

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[1] In some forms (*e.g.*, teleosts, marsipobranchs, some ganoids) the development of the central nervous system varies considerably from that outlined above, but the final result is the same.

[2] A lateral horn (Fig. 46, **cornu lat.**) must also be recognized on the grounds of physiology and nerve origin.

fissures. In the later studies each of these columns has been subdivided (Fig. 46).

During the increase in size of the cord, the cells produce protoplasmic outgrowths (axis cylinders, p. 11), some of which run forwards and backwards in the ventral and lateral columns, while others pass outwards from the cord as the motor roots of the spinal nerves, to be described a moment later. From this it will be seen that the white matter is composed of nerve fibres, the gray matter of nerve cells. Later the dendrites — association fibres — are formed, while with increase in size blood-vessels and supporting-tissue press into the cord.

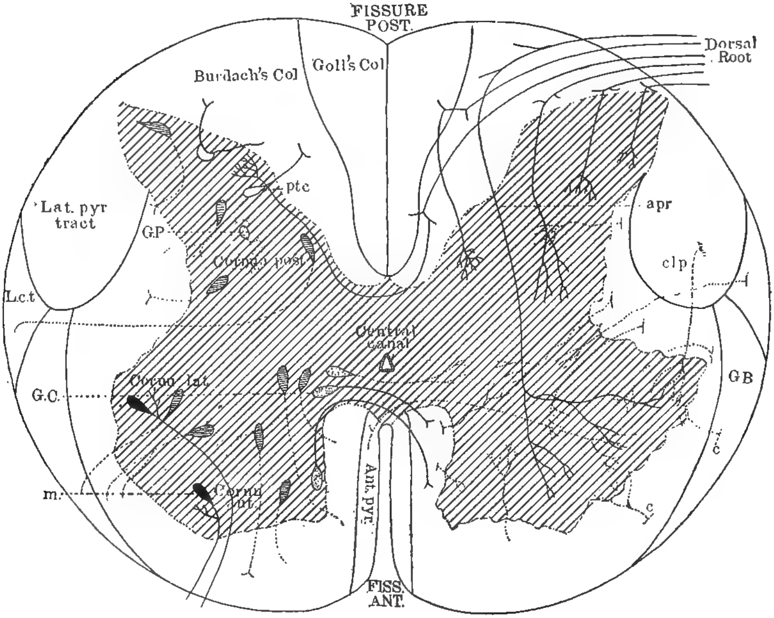

FIG. 46. Diagrammatic section of spinal cord, after von Lenhossék. *Ant. pyr.*, anterior pyramid tract; *apr*, anteroposterior reflex fibre; *c*, collaterals entering the gray substance; *clp*, collateral of the lateral pyramidal tract; *GC*, Golgi's commissural cell; *GP*, Golgi's cell of posterior horn; *Lct*, lateral cerebellar tract; *m*, motor cell of anterior horn; *ptc*, posterior tract cell.

In its early stages the spinal cord shows a marked segmentation or repetition of parts one after the other. This **metamer-**

ism consists in alternate expansions and contractions of the cord and its contained canal.[1] This early segmentation disappears with growth, but the same segments are later indicated by the roots of the spinal nerves.

The spinal nerves are paired structures passing off from either side of the cord (Fig. 47), each nerve arising by two **roots,** one dorsal the other ventral in position. These roots differ markedly in structure and function. The **dorsal roots** are connected with the dorsal horn of the gray matter, and soon after leaving the cord each becomes enlarged into a ganglion composed of those ganglion cells which give rise to the fibres of which this root is composed. The **ventral roots,** on the other hand, are not ganglionated, but their fibres are connected with the ganglion cells of the gray matter of the ventral horns of the cord, from which they pass out into the root. Just beyond the ganglion of the dorsal root the two roots of a spinal nerve unite, and the fibres of each follow a common course.

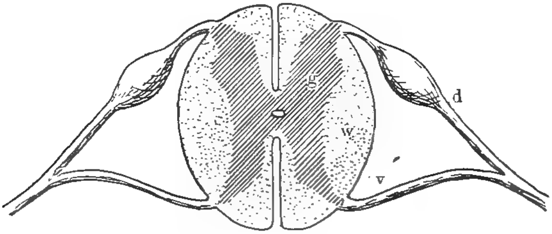

FIG. 47. Section through spinal cord showing the roots of a spinal nerve. *d*, dorsal root with its ganglion; *g*, gray matter of cord; *v*, ventral root; *w*, white matter.

Experiment shows that the dorsal roots are **sensory**; i.e., they carry impulses from the terminal sensory structures to the central nervous system. The ventral roots are **motor** in function; that is, the nervous impulses which they transmit come from the central nervous system, and are carried to peripheral portions (muscles, glands, etc.) which they cause to act. Since the dorsal roots convey stimuli from without to the

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[1] It must be understood that this metamerism is not necessarily primitive in its character.

central nervous system, they are often spoken of as **afferent roots,** while for analogous reasons the ventral roots are termed **efferent.**[1]

These roots differ also in their mode of development. Certain features of the origin of the dorsal root are still in dispute, but the following statements are pretty generally accepted. At the time of closure of the neural tube a thin sheet of cells is visible on either side of the line of closure between the epidermis and the tube. By unequal growth this sheet of cells, or **neural crest,** becomes converted into segments, each segment developing into a ganglion of a dorsal root. Apparently fibres grow out from this ganglion to enter the cord, while others grow peripherally to connect with the sense organs. No such crest is formed for the ventral root; but the fibres forming this are connected with the ganglion cells of the cord, and they lengthen with the growth of the animal, so as to connect with the muscles, glands, etc.

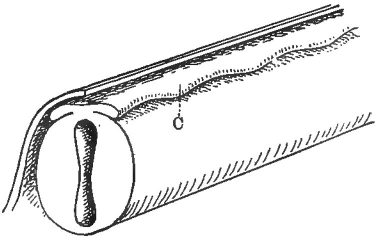

FIG. 48. Diagram of embryonic spinal cord with neural crest, *C*.

Each spinal nerve soon divides into two chief branches, — a **ramus dorsalis** supplying the dorsal region, and a **ramus ventralis** distributed upon the sides and ventral surface. This latter also gives off a **ramus intestinalis** to the viscera. These latter connect with the **sympathetic system,** a pair of longitudinal nerve cords with ganglia (derived from the spinal ganglia) lying near the junction of the mesentery with the dorsal wall of the cœlom. This system supplies the digestive tract, the vascular system and many glands, and in certain ichthyopsida it may extend into the head.

Typically the spinal nerves follow the myocommata or septa between the muscle plates (to be described later), but in all forms above fishes in the region of the limbs several of the ven-

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[1] Later studies show that we must distinguish visceral and somatic motor fibres; visceral and somatic sensory tracts. (See the section on cranial nerves.)

tral rami interlace to form a **plexus** (**cervical** and **brachial** in front, **lumbar** and **sacral** for the hind limb), from which nerves are distributed to the appendage.[1] The spinal cord is enlarged where the spinal nerves forming these plexuses are given off.

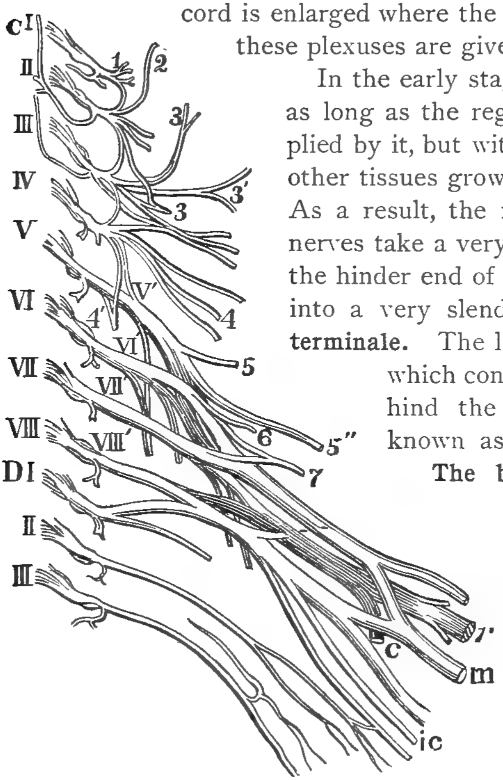

FIG. 49. Right human cervical and brachial plexuses (from Martin) showing the interlacing of nerve trunks. *C*, *I–VII*, roots of cervical nerves; *D*, *I–III*, three anterior dorsal roots; 1–4, nerves of cervical plexus; 4′, phrenic nerve (to diaphragm); *c*, circumflex; *r*, musculo-cutaneus; *ic*, internal cutaneus; *m*, median; *i*, intercostals; *u*, ulnar.

In the early stages the spinal cord is as long as the region of the body supplied by it, but with increase in size the other tissues grow faster than the cord. As a result, the more posterior spinal nerves take a very oblique course, while the hinder end of the cord is drawn out into a very slender thread, the **filum terminale.** The large bundle of nerves which consequently extends behind the cord forms what is known as a **cauda equina.**

The brain is an enlarged and immensely complicated anterior end of the central nervous system, and yet we can trace in it some of the constituents we have come to recognize in the spinal cord. Very soon after the closure of the neural tube the region which is to form the brain becomes differentiated into three hollow enlargements or vesicles, which have received the names, according to position, of **fore, mid,**

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[1] A brachial plexus is formed in snakes and footless lizards. None is found in the cæcilians. *Siren* lacks a sacral plexus.

and **hind brains.** That these three regions are not exactly comparable to the segments of the spinal cord is shown by the fact that the same neuromeres characteristic of the cord (p. 46) appear in the mid and hind brains. Each of these vesicles contains an enlarged portion (called **primary ventricle**) of that cavity, which in the cord is called the central canal.

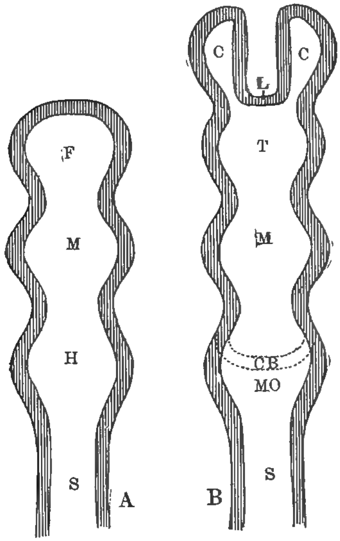

FIG. 50. Diagrams of the development of the brain. In A the three primary vesicles; in B the differentiation of the definitive regions. *C*, cerebrum; *CB*, cerebellum; *F*, fore brain; *H*, hind brain; *L*, lamina terminalis; *M*, mid brain; *MO*, medulla oblongata; *S*, spinal cord.

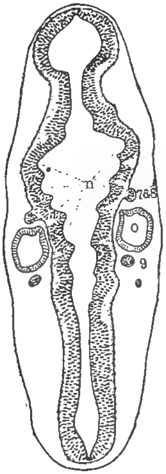

FIG. 51. Section through the brain of embryo pig, 6.5 mm. long, showing the segmentation (neuromeres) of the hind brain (*n*). *o*, otic capsule; 7 & 8, facial and auditory nerve; 9, glossopharyngeal nerve.

Soon these three vesicles become differentiated by unequal growth into five regions, the fore and hind brain each giving rise to two, the mid brain remaining unaltered.

From the fore brain arise the **prosencephalon (telencephalon, cerebrum** or **cerebral hemispheres**) and the **thalamencephalon (optic thalami, diencephalon** or **twixt brain**) in the following manner. The extreme tip of the fore brain in the median plane remains stationary, and forms a thin membrane, later known as the **lamina terminalis.** On either side of this the fore brain grows outwards, and especially forwards, thus producing two lobes, right and left. These are the **cerebral hemispheres,** while the rest of the primitive fore brain is the **thalamencephalon.** The ventricle of the primitive fore brain participates in this outgrowth, giving rise to a cavity in each of the lobes; so that now we have three ventricles in the fore-brain region, the first and second forming a pair, while the third unpaired ventricle remains in the thalamencephalon. The paired ventricles remain in connection with the third by small openings, the **foramina of Monro.**

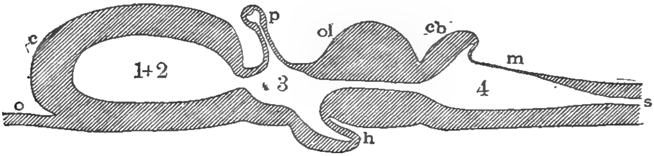

FIG. 52. Sagittal section through vertebrate brain, in front passing through a cerebral lobe. *c*, cerebrum; *cb*, cerebellum; *h*, infundibular (hypophysial) outgrowth; *m*, medulla oblongata; *o*, olfactory nerves; *ol*, optic lobes; *p*, pineal structures; *s*, spinal cord; 1–4, ventricles.

While this differentiation is taking place in the fore brain the mid brain (known under various names, — **mesencephalon, optic lobes, corpora bi-** or **quadrigemina**) remains almost stationary, the chief change being a thickening of its walls so that (except in teleosts where a part remains as the **epicœle**) the primitive ventricle of its earlier condition becomes a narrow tube, the **iter** or **aqueduct,**[1] connecting the third ventricle with the ventricle in the hind brain.

In the hind brain the differentiation is largely confined to the dorsal surface. It consists in the outgrowth from the anterior dorsal wall of a lobe of tissue which extends backward over the rest, and forms the **cerebellum** or **metencephalon,** the rest of the hind brain forming the **medulla oblongata** or **myelencephalon,** which passes into the spinal cord behind.

The different regions of these five divisions of the brain become variously developed, the walls being thickened in parts

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[1] *Iter e tertio ad quartum ventriculum; aqueductus Sylvii.*

while in others they remain but a cell or two in thickness. In the cerebral hemispheres the lower or ventral surface develops a large ganglionic mass, the **corpus striatum,** in either hemisphere. The rest of the cerebral wall is known as the **pallium** or **mantle,** and undergoes great modifications in the different groups. In some fishes (cyclostomes, ganoids, and teleosts) it is epithelial in character. In other vertebrates it is largely nervous in nature,[1] its outer surface (**cortical substance**) being composed of ganglion cells. In all the lower vertebrates the surface of the cerebrum is smooth, but in the higher mammals

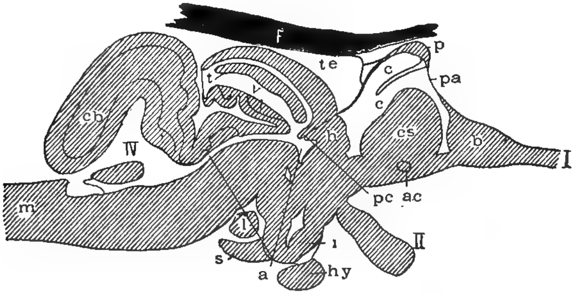

FIG. 53. Nearly median section of brain of trout, after Rabl-Rückhard. *a*, aqueduct; *ac*, anterior commissure; *b*, bulbus olfactorius; *c*, ventriculus communis (composed of first three ventricles of typical brain); *cb*, cerebellum; *cs*, corpus striatum; *F*, frontal bone; *h*, habenular ganglion; *hy*, hypophysis; *i*, infundibulum; *l*, lobus inferior; *m*, medulla; *p*, pinealis; *pa*, pallium of cerebrum; *pc*, posterior commissure; *s*, saccus vasculosus; *t*, torus longitudinalis; *te*, tectum of optic lobes; *v*, valvula cerebelli; *I*, *II*, olfactory and optic nerves; *IV*, fourth ventricle.

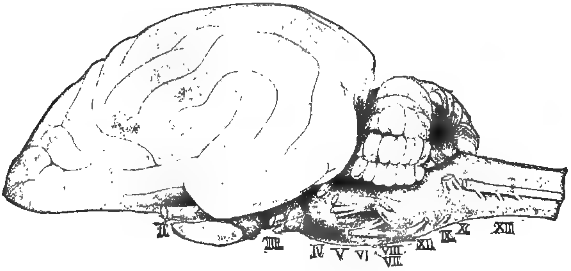

FIG. 54. Brain of dog (after Wiedersheim), showing fissures and gyri of cerebrum. *II–XII*, cranial nerves.

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[1] Even in mammals a portion — the **septum pellucidum** — retains an epithelial character.

(educabilia) **fissures** appear in its surface, separating **convolutions** or **gyri,** and the higher the mammal the more numerous the convolutions. It will readily be seen that this produces an increase in surface, and consequently of cortical (ganglionic) substance ; and it is noteworthy that this increase is correlated with increase of intelligence.

From its anterior ventral region each hemisphere gives off an **olfactory lobe** (**rhinencephalon**) into which a part of the ventricle may extend. Connected with each olfactory lobe is an **olfactory ganglion** which may be placed either in the cerebrum itself, or may be carried out towards the end of the olfactory lobe. From these lobes arise the olfactory nerves (see below).

In the diencephalon the lateral walls become thickened into large tracts, the **thalami,** while the dorsal wall as a whole retains its epithelial character, becoming variously folded to form the anterior **choroid plexus,** which carries blood-vessels into the three anterior ventricles. From this dorsal surface are also developed three structures, — pinealis, epiphysis, and paraphysis, — to be mentioned again in connection with the sense organs. From the pinealis a pair of nerve tracts, the **habenulæ,** run along the inner sides of the thalami. The floor of the thalamencephalon gives rise to a hollow outgrowth, the **infundibulum,** which extends backwards and downwards, developing from its extremity tissue, which unites with other cells, derived directly from the ectoderm, to form the **hypophysis** or **pituitary body.** This ectodermal portion arises from the ectoderm between the nose and the mouth, or from the mouth itself, and grows upwards and inwards to join the infundibular portion. For a time it retains its connection with the parent layer by means of a cord of cells, the **hypophysial duct,** which later disappears. The significance of these ventral structures of the twixt brain is very obscure.

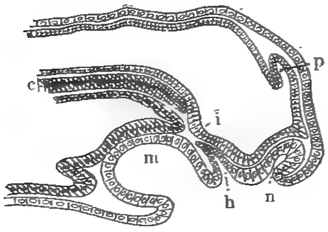

FIG. 55. Sagittal section through head of larval *Petromyzon*, after von Kupffer. *c*, notochord; *h*, invagination for hypophysis; *i*, infundibulum; *m*, mouth cavity; *n*, nasal involution; *p*, pineal outgrowth.

A plausible suggestion is that the infundibulum represents the invertebrate mouth, the ectodermal portion of the hypophysis a modified pair of sense organs. The optic nerves are outlined as hollow outgrowths from the sides of the twixt brain, while on its ventral surface may be developed accessory structures, — the **lobi inferiores, sacculi vasculosi, corpus albicans** (**corp. mammilare**) **tuber cinereum**, etc.

A topographic point is to be kept in view, — the cerebral hemispheres and the diencephalon are in front of the anterior end of the notochord — are **prechordal**.

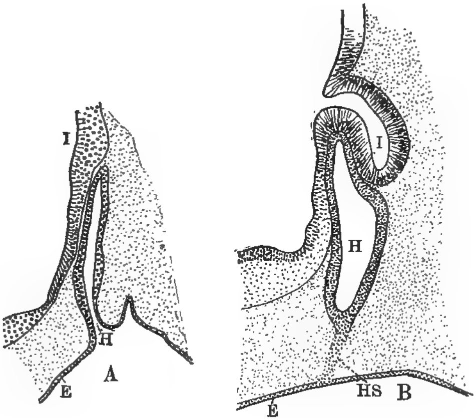

FIG. 56. Two stages in the development of the hypophysis in the pig; A in an embryo 10 mm. long, B in 15.5 mm. long. *E*, epithelium of roof of mouth; *H*, hypophysis connected with the mouth cavity in A by the hypophysial duct, in B by the solid hypophysial stalk *HS*; *I*, infundibulum.

The mesencephalon has its walls thickened so that its contained ventricle, in the higher groups, is reduced to the narrow aqueduct already mentioned. Its dorsal surface is divided by a longitudinal groove into right and left lobes (**corpora bigemina**), and these in turn may each be subdivided transversely into two (**corpora quadrigemina**).[1] Leading ventrally and forwards from these lobes in all except the cyclostomes are the optic tracts connecting with the optic nerves. The floor of the mid brain is formed by a pair of fibre tracts — **crura cerebri** — separated by a longitudinal fissure.

The cerebellum or metencephalon is a thickening of nervous matter on the dorsal anterior end of the hind brain. It may exist as a small transverse fold, or it may be greatly enlarged, extending forwards over part of the mid brain, and backwards over the anterior end of the medulla. It may be

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[1] In older works the anterior of these lobes were called **nates**; the posterior, **testes**.

unpaired in appearance, or it may consist of a pair of lateral lobes or hemispheres separated by a median portion or **vermis,** terminating in a small lobe, the **valve of Vieussens,** which roofs in the fourth ventricle in front.

The myelencephalon or medulla oblongata is the cranial extension of the spinal cord, presenting behind but slight differences from that structure. In front it widens, while its roof thins out and becomes epithelial and folded, to form the posterior choroid plexus for the underlying fourth ventricle. This region of thinning is known, from its shape, as the **fossa rhomboidalis.** It is bounded in front by the valve of Vieussens, and on either side by the diverging dorsal columns of the cord (p. 44), which are frequently subdivided into a median **fasciculus gracilis** (**Column of Goll**) and a more lateral **fasciculus cuneatus** (**Burdach's Column**). (Fig. 46.) Each dorsal column receives in front fibres from the lateral column, the whole forming an enlargement, **corpus restiforme,** on either side, from which the **posterior peduncles of the cerebellum** pass forward and upward into the metencephalon. On the ventral surface are the anterior ends of the ventral columns (p. 44), here known as the pyramids. These can be followed forward until they pass into the crura cerebri already mentioned. In the higher vertebrates the anterior ends of the pyramids are crossed by transverse bundles, forming the **pons Varolii,** which act as commissures connecting the two halves of the cerebellum. The medulla oblongata is further noticeable since it gives rise to the greater part of the cranial nerves.

The various parts of the brain are connected by longitudinal fibre tracts and by transverse fibres or **commissures.** Some of these have already been mentioned, and some others may be noticed here. The chief longitudinal tracts are those of the pyramids, which may be followed through the crura cerebri to the corpus striatum. Some of the fibres of the lateral column and a part of those of the dorsal column enter the cerebellum through the posterior peduncles of the cerebellum, while the majority from these columns end in the medulla. From the cerebellum, fibres extend forward into the mid brain through two bands of tissue known as the **anterior peduncles of**

the cerebellum, which enter the posterior portion of the optic lobes. The habenulæ are also to be regarded as longitudinal tracts; while the **fornix,** a part of which lies ventral to the corpus callosum (*infra*), is to be placed in the same category, although its fibres seem in places to run transversely.

Among the transverse fibres most constant are the **anterior** and **posterior commissures** in the region of the twixt brain.[1] The anterior crosses from side to side in the anterior wall of this region, the other is nearer the junction of twixt brain and optic lobes. In the higher vertebrates the cerebral hemispheres are connected by a large

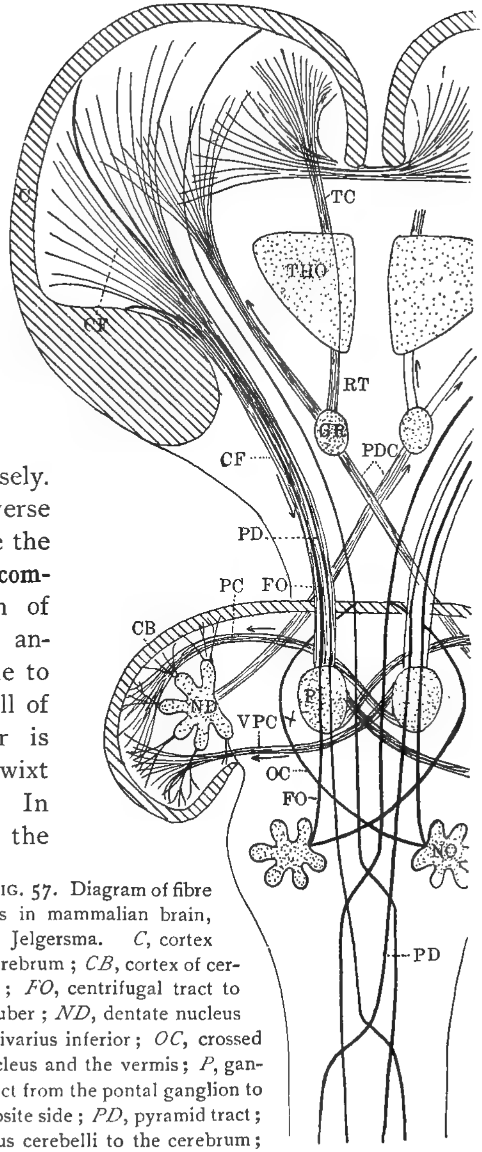

FIG. 57. Diagram of fibre tracts in mammalian brain, after Jelgersma. *C*, cortex of cerebrum; *CB*, cortex of cerebellum; *CF*, centrifugal tract; *FO*, centrifugal tract to olivary nucleus; *GR*, nucleus ruber; *ND*, dentate nucleus of cerebellum; *NO*, nucleus olivarius inferior; *OC*, crossed connective between olivary nucleus and the vermis; *P*, ganglion of the pons; *PC*, dorsal tract from the pontal ganglion to the cerebellar cortex of the opposite side; *PD*, pyramid tract; *PDC*, tract from the pedunculus cerebelli to the cerebrum; *RT*, fibre course from nucleus ruber to optic thalamus; *TC*, connection of thalamus with cerebral cortex; *THO*, optic thalamus; *VPC*, ventral tract from portal ganglion to cerebellar cortex of the opposite side.

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[1] The so-called median commissure is not a fibre tract.

transverse band, the **corpus callosum.** Traces of this occur in amphibia and reptiles, but it acquires its highest development in the higher mammals. The pons Varolii, passing beneath the anterior pyramids of the cord, similarly connects the cerebellar hemispheres in the higher vertebrates. Here, too, must be numbered the **decussation,** or crossing of the fibres of the anterior pyramids from one side to the other.

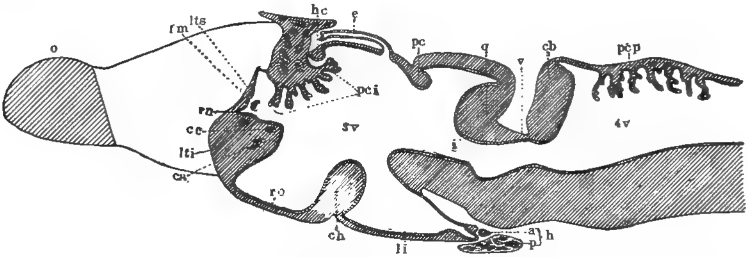

FIG. 58. Longitudinal section of the brain of a frog, after Gaupp. The epithelium blocked. *ah*, anterior part of hypophysis; *ca*, anterior commissure; *cb*, cerebellum; *cc*, corpus callosum; *ch*, optic chiasma; *e*, epiphysis; *fm*, foramen of Monro; *hc*, habenular commissure; *i*, iter; *li*, infundibular lobe; *lti*, lamina terminalis, infraneural portion; *lts*, lamina terminalis, supraneural portion; *o*, olfactory lobe; *pc*, posterior commissure; *pci*, inferior and median choroid plexus; *pcp*, posterior choroid plexus; *q*, posterior portion of mid brain; *rn*, recessus neuropori; *ro*, recessus opticus; *v*, velum medullare ant.; 3*v*, 4*v*, third and fourth ventricles.

In its earlier stages the brain lies in the same horizontal plane with the spinal cord. Soon, by unequal growth of its dorsal and ventral surfaces, bends or flexures appear. Most constant of these is the **cephalic flexure** between fore and mid brains, by which the axis of the fore brain is bent ventrally at nearly right angles to the rest. Two other flexures may also appear; they are most prominent in mammals. The **pontal flexure,** in the region of the pons Varolii, is in the opposite direction; the **nuchal flexure,** in the medulla, is ventral again. In the ichthyopsida these flexures largely disappear with growth; in the amniotes they persist throughout life.

In the lower groups the five divisions of the brain are subequal in size, but the higher vertebrates are characterized by a great increase in size of the cerebellar, and especially of the cerebral, regions, so that these completely cover over the twixt and mid brains. The backward extension of the cerebrum is especially marked in mammals. Connected with this overgrowth is the formation of the **fifth ventricle,** or pseudo-ventricle, a cavity in no way connected with the true ventricles, but lying morphologically outside the brain, between the septa pellucida, the fornix, and the corpus callosum.

The brain and spinal cord are enclosed in envelopes of mesenchymatous origin, which hold them in position, and serve as the bearers of nutrient vessels, etc. These membranes from outside to inside are the **dura mater** and the **pia mater.** Of these the dura is a more dense connective tissue, consisting of two lamellæ in the lower vertebrates; its blood-vessels being distributed to the walls of the spinal canal and the skull. The pia is more delicate, and bears the blood-vessels of the brain and cord. Between the two layers is a large lymph space, and in the amphibia and higher vertebrates this is divided by a third membrane, — the **arachnoid.** The pia enters all the fissures and depressions in the brain and cord, carrying nourishment into the nervous mass.

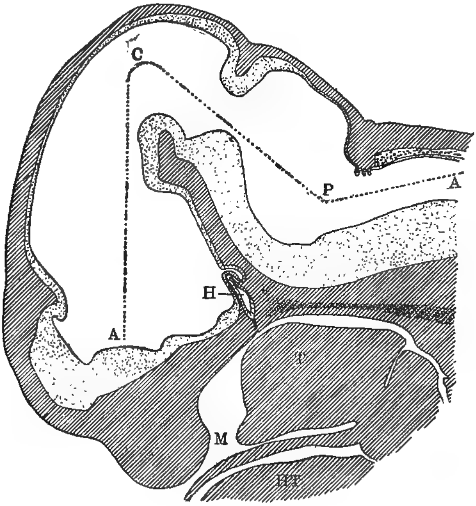

FIG. 59. Sagittal section through the head of pig embryo of 15.5 mm. length, showing the cranial flexures. *AA*, axis of brain; *C*, cephalic flexure; *H*, hypophysis; *HT*, heart; *M*, mouth; *P*, pontal flexure; *T*, tongue. The nervous tissue dotted.

Cranial Nerves. — Like the cord, the brain gives rise to nerves, but these nerves present many differences from those of the spinal region. The last word concerning these has yet to be written, but the following outline summarizes our present knowledge, as well as indicates some of the directions in which modifications of our ideas may be expected.

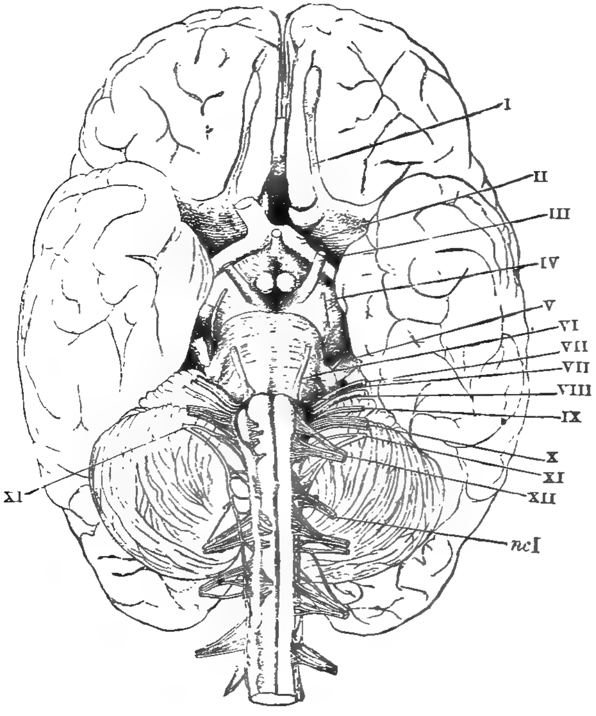

FIG. 60. Base of human brain (from Martin), showing roots of cranial nerves, *I–XII*. *ncI*, first cervical nerve.

The nerves arising from the brain (cranial nerves) are in pairs, which have received names and numbers in man; and these have been transferred to the corresponding structures in the lower vertebrates as follows: —

I. Olfactory.
II. Optic.
III. Oculomotor.

IV. Trochlearis (or Patheticus).
V. Trigeminal (or Trifacial).
VI. Abducens.
VII. Facial.
VIII. Auditory.
IX. Glossopharyngeal.
X. Vagus (or Pneumogastric).
XI. Spinal Accessory (or Accessory of Willis).
XII. Hypoglossal.

As has been described, the spinal nerves contain both sensory and motor roots. The cranial nerves present some differences from this. Thus nerves I., II., and VIII. are purely sensory; III., IV., and VI. are solely motor; while the others are *mixed*, i.e., contain both motor and sensory fibres.

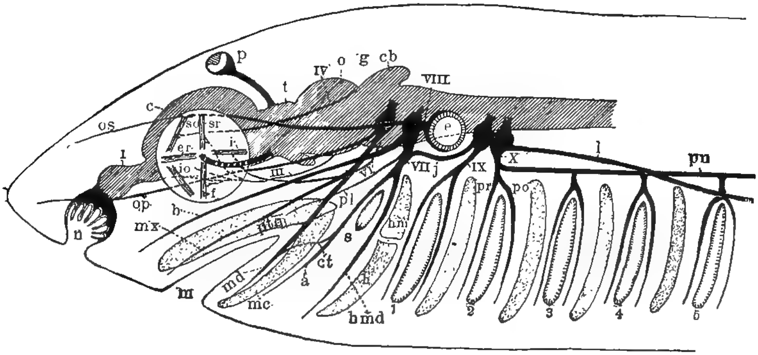

FIG. 61. Diagram of cranial nerves (shark). *a*, alveolaris; *b*, buccalis; *c*, cerebrum; *cb*, cerebellum; *ct*, chorda tympani; *e*, ear; *er*, external rectus muscle; *f*, inferior rectus muscle; *g*, Gasserian ganglion; *h*, hyoid cartilage; *hm*, hyomandibular cartilage; *hmd*, hyomandibular nerve; *i*, internal rectus muscle; *io*, inferior oblique muscle; *j*, Jacobson's commissure; *l*, lateralis branch of vagus; *m*, mouth; *mc*, Meckel's cartilage; *md*, mandibularis; *mx*, maxillaris superior; *n*, nose; *o*, optic lobes (mesencephalon); *op*, ophthalmicus profundus; *os*, ophthalmicus superficialis; *p*, pinealis; *pl*, palatine; *po*, post-trematic branch; *pn*, intestinal (pneumogastric) branch of vagus; *pr*, pre-trematic branch; *ptq*, pterygoquadrate cartilage; *s*, spiracle; *so*, superior oblique muscle; *sr*, superior rectus muscle; *t*, thalamencephalon; *I–X*, cranial nerves; 1–5, gill clefts.

Both the olfactory and the optic nerves are usually regarded as differing from all other cranial nerves in that they arise as hollow outgrowths of the brain itself.[1] The olfactory nerve arises from the olfactory lobe, and is distributed to the sensory epithelium of the nose. Like all other sensory nerves it is provided with its own ganglion, which may either be included in the brain, or it may be carried out into close proximity with the olfactory organ. It is evident that the two cases are really different, and that we can only speak of true **olfactory nerves** distal to the olfactory ganglion. The connection between the olfactory ganglion and the brain is made by the **olfactory tract.**

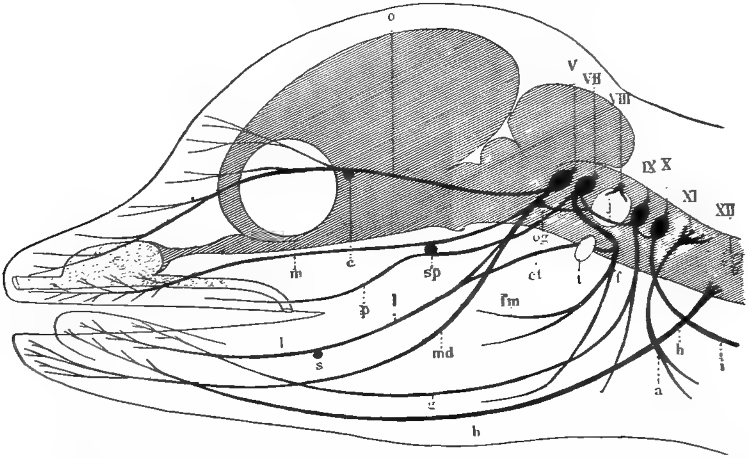

FIG. 62. Diagram of cranial nerves in an amniote; nerves *II* to *IV* and *VI* much as in the ichthyopsida, and hence omitted. *a*, accessorius; *c*, ciliary ganglion; *ct*, chorda tympani; *f*, facialis: *fm*, branches of facialis to facial muscles; *g*, glosso-pharyngeal; *h*, hypoglossal; *i*, ramus intestinalis of vagus; *j*, Jacobson's commissure; *l*, ramus lingualis; *m*, maxillaris; *md*, mandibularis; *o*, ophthalmic; *og*, otic ganglion; *p*, palatine; *s*, submaxillary ganglion; *sp*, sphenopalatine ganglion; *t*. tympanum.

The optic nerves, which arise primitively from the ventral sides of the diencephalon, have their ganglia lying upon the superficial portion of the retina (see eye, below). They retain their connection with the thalamencephalon throughout life in

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[1] In connection with nerves I. and II. it is to be noted that the posterior cranial and the spinal nerves of selachians are at first hollow outgrowths from the brain (or neural crest). Farther, that the definitive nerve of the adult grows back from the ganglion to join the brain in both. These facts tend to invalidate the distinction drawn between nerves I. and II. and the others.

the cyclostomes, but in the higher group they become connected secondarily with the optic lobes by means of the **optic tracts.** These optic tracts are so formed that the nerves cross beneath the thalami, that from the right eye going to the left optic lobe, and *vice versa.* There may be a simple crossing or an interlacing of fibres, or a complete union of the trunks (**optic chiasma**).

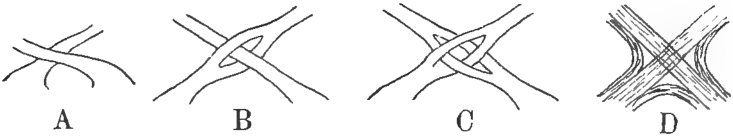

FIG. 63. Diagrams of optic chiasma, after Wiedersheim. *A*, most teleosts; *B*, herring; *C*, Lacerta; *D*, higher mammals.

Nerves III., IV., and VI. are purely motor nerves, supplying the muscles which move the eye. The oculomotor arises from the crura cerebri, and supplies the muscles rectus superior, internus, inferior, and obliquus inferior. The trochlearis arises from the posterior dorsal portion of the mid brain, although its centre inside the brain lies ventrally. It supplies the superior oblique muscle. The abducens arises from the anterior pyramids, and is distributed to the externus rectus muscle and to the retractor bulbi, when this muscle is present. The oculomotor is always distinct, but the others may be fused with the fifth, and in some animals their existence has not yet been demonstrated.

The trigeminal nerve arises from the anterior end of the sides of the medulla. It is always large, and in the higher vertebrates at least has two distinct roots,[1] the dorsal root bearing a ganglion (**Gasserian** or **Casserian ganglion**). As its name implies, it has three branches, — *a*, **ophthalmicus profundus,** distributed chiefly to the nose and lachrymal region; *b*, **maxillaris superior,** supplying the region of the upper jaw; and *c*, the **mandibularis** or **maxillaris inferior**, going to the lower jaw, and in amniotes to the tongue. Frequently the last two are united for a distance as a **maxillaris nerve.**[2] Branches *a* and *b* are

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[1] In at least some of the ichthyopsida these two roots can be distinguished by microscopic study, although not by ordinary dissection.

[2] The terminology of the trigeminal and facial used here is believed best to express the relations of the branches.

largely sensory, most of the motor fibres, together with sensory, going to branch *c*. Each of these branches may have a secondary ganglion connected with it, — the **ciliary ganglion** on *a*, the **sphenopalatine** on *b*, and the **otic** on *c*.

In many ichthyopsida the seventh nerve is closely connected with the fifth, and by mere dissection the roots of the two cannot be distinguished.[1] In the higher vertebrates the two nerves are distinct throughout. The facialis is more complicated than the trigeminal, and may contain four components. In the lower vertebrates it is a mixed nerve, but in the higher it is purely motor, and is connected largely with the muscles of expression. In its greatest development (ichthyopsida) it gives rise to four branches, — *a*, **ophthalmicus superficialis**;[2] *b*, **hyomandibularis**; *c*, **buccalis**; and *d*, **palatinus**. The first of these has its own ganglion and is purely sensory, supplying the lateral line organs (see sense organs, *infra*) on the top of the head. It is found only in aquatic ichthyopsida, the frog, for instance, losing it at

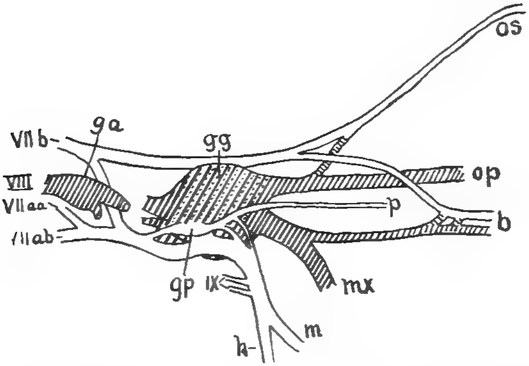

FIG. 64. Diagram of the relations of the fifth (shaded), seventh, and eighth nerves in an aquatic amphibian, after Strong. *b*, buccalis; *ga*, auditory ganglion; *gg*, Gasserian ganglion; *gp*, palatine ganglion; *h*, hyoid nerve; *m*, mandibular nerve; *mx*, superior maxillary nerve; *op*, ophthalmicus profundus; *os*, ophthalmicus superficialis; *p*, palatine nerve; *VII a*, *aa*, *ab*, the three roots of the seventh nerve; *VIII*, root of auditory nerve; *IX*, communication of seventh with ninth nerve (Jacobson's commissure).

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[1] Microscopic study shows that they are usually as distinct here as in the higher forms.

[2] Fibres from the fifth accompany the ophthalmicus superficialis.

the time of metamorphosis. The hyomandibularis soon divides into an anterior or mandibular branch and a posterior division, which supplies the muscles of the gill cover, and some of those of the jaw. When the first visceral cleft or spiracle is present, this division takes place just above it, so that one branch (mandibularis) is **pre-trematic,** *i.e.*, is in front of the opening, the other being **post-trematic** (Fig. 61). The mandibularis goes to the lower jaw; and one of its branches, which unites with the mandibularis branch of the fifth nerve, is known among the higher vertebrates as the **chorda tympani.** The palatine branch supplies the palate and the roof of the mouth. In the lower forms it is a mixed nerve; in the mammals it innervates only the muscles of the soft palate. It may unite with either branch, *a* or *b*, of the fifth. The buccal branch runs in the upper jaw, uniting with the ophthalmicus profundus.

The auditory nerve is closely connected with the seventh, and is often regarded as its dorsal root. It goes directly to the ear, dividing almost immediately into two branches, which may leave the skull through separate foramina.

The vagus complex is composed of the ninth, tenth, and eleventh nerves, which are closely connected, and present many similarities to each other. In many features they resemble more closely the spinal nerves, especially in the presence of distinct dorsal and ventral roots. The ear intervenes between these and the nerves in front. The complex arises from the side of the medulla by from four to eight or more roots, the anterior pair being considered as those of the glossopharyngeal. Usually in the aquatic vertebrates its ganglion is fused with that of the vagus.

The glossopharyngeal nerve splits into two branches,[1] the anterior going to the pharyngeal region, the other (**lingualis**) to the muscles and mucous membrane of the gill in fishes, and to the sense organs of the tongue in the mammals, etc. The pharyngeal branch also gives off a nerve (**Jacobson's anastomosis**) which unites with the hyomandibularis of the facial.

The vagus or pneumogastric has a wide distribution. In

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[1] In the branchiate vertebrates the division occurs above the first true gill slit, so that here, too, we have pre- and post-trematic branches.

aquatic vertebrates it divides into two main trunks, a **ramus lateralis** (possibly equivalent to the r. dorsalis of a spinal nerve), which is lacking in the terrestrial forms, and a **ramus intestinalis.** The lateralis branch runs the length of the body, either close beneath the skin, or deeper in the muscles near the vertebral column. It is purely sensory, and is distributed to the lateral line organs of the trunk; and the absence of these structures in the amniote vertebrates explains the disappearance of the nerve. The ramus intestinalis is the **pneumogastric** nerve of human anatomy. It is largely motor (or better, inhibitory) in its functions. It is distributed to pharynx, stomach (air-bladder of fishes), and the respiratory apparatus, gills and lungs. Of the branches to the gills there are as many as there are gill clefts behind the one supplied by the ninth nerve. Each branch divides above the gill cleft into pre- and post-trematic branches.

The accessory of Willis is apparently a spinal nerve which in the amniotes enters into close association with the vagus. Its distribution is chiefly to the muscles connected with the neck and shoulder girdle, *e.g.*, sternocleidomastoid and trapezius.

The hypoglossal nerve is, in the adult vertebrate, purely motor, its branches being distributed to the muscles of the tongue and to some of those of the hyoid region. It is only in the amniotes that this can be considered as a cranial nerve; in the ichthyopsida it does not enter the skull. It is interesting to find that in the larval stages of some forms this nerve has a dorsal ganglionated root, while in certain species two such roots have been found, a fact which tends to show that the nerve is really compound.

Within recent years it has been recognized that the components of the spinal and cranial nerves were more numerous than is implied by the account given on pages 46 and 59. In the spinal nerve it is clear that a distinction must be made between the nerves of the body (somatic nerves) and those of the viscera (visceral nerves). Each of these is made up of sensory and motor parts, so that four components are to be recognized: (1), somatic sensory (general cutaneous); (2), somatic motor; (3), visceral sensory; and (4), visceral motor. The ganglion cells of the first are situated in the spinal ganglia, and the nerves terminate in the dorsal horn. The ganglion cells of the somatic motor nerves lie in the ventral horn, and the nerves leave by the ventral roots. The internal relations of the visceral system are not so evident ; but both are possibly related to the lateral horn region, the visceral sensory nerves, whose centres in the trunk region are in the sympathetic ganglia, entering by the dorsal roots, while the visceral motor nerves leave by both dorsal and ventral roots (not proved for mammals)

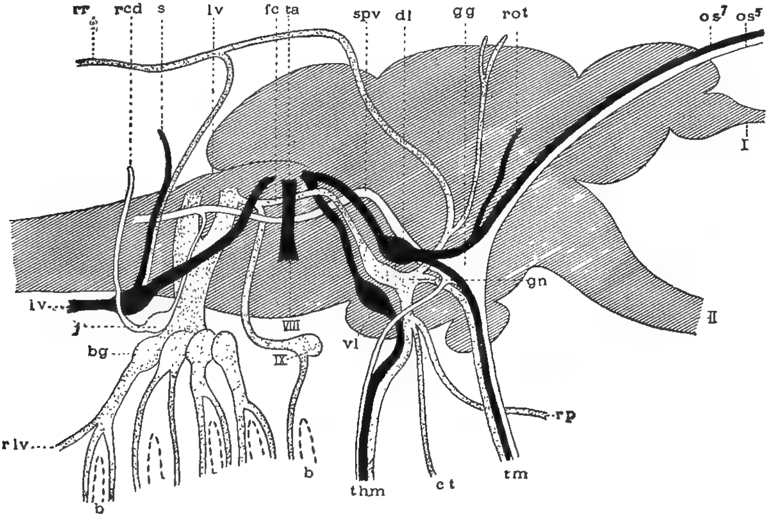

FIG. 65. Diagram of the sensory components in the cranial nerves in *Menidia*, after C. J. Herrick. General cutaneous component white; communis (visceral) dotted; lateralis black; the outline of the brain shaded. *b*, gill clefts; *bg*, branchial ganglia of the vagus, the last containing the ganglion of the ramus intestinalis; *ct*, pre-trematic branch (chorda tympani) of facialis ; *dl*, dorsal lateral line ganglion of the facialis ; *fc*, fasciculus communis ; *gg*, Gasserian ganglion ; *gn*, geniculate ganglion ; *j*, general cutaneous (jugular) ganglion of the vagus ; *lv*, lobus vagi ; os^5, os^7, ophthalmicus superficialis of fifth and seventh nerves ; *rcd*, ramus cutaneus dorsalis of vagus ; *rlv*, ramus lateralis of the vagus ; *rot*, ramus oticus ; *rp*, ramus palatinus of the facialis ; *rr*, ramus recurrens of the facialis ; *s*, ramus supratemporalis of the vagus ; *spv*, spinal V tract (ascending root of the trigeminal) ; *ta*, tuber acusticum ; *thm*, hyomandibular trunk ; *tm*, inferior trunk, containing the rami maxillaris and mandibularis of the trigeminal, the buccalis of the facial and communis fibres ; *vl*, ventral lateral line ganglion of the facialis ; *I*, olfactory ; *II*, optic ; *VIII*, auditory ; *IX*, glossopharyngeal.

In the cranial region the matter is still further complicated by the appearance of a lateralis system, the nerves of which are distributed to the ear and to the lateral line system, and to no other organs. In terrestrial vertebrates, where the lateral line system is lost, the lateralis nerves, with the exception of the eighth (auditory), are lacking. The fibres of the lateralis components terminate in the tuber acusticum. The relations of the sensory components of the cranial nerves are shown in Fig. 65, in which, for clearness, the motor elements have been omitted. The somatic motor nerves of the head include only the eye-muscle nerves (III., IV., VI.). Visceral motor fibres are found in the fifth, seventh, ninth, and tenth nerves.

SENSE ORGANS.

All sensory organs of vertebrates arise from the ectoderm. Some remain throughout life connected with the surface of the body, — epidermis, — while others sink into special structures for their protection, the **sense capsules.** With few exceptions sense organs are formed of specialized cells, — **sense cells,** — each of which is connected by afferent nerve fibres with the central nervous system. Between the sense cells there may be other ectodermal cells which have a supporting function, or which serve to isolate the sensory cells from each other.

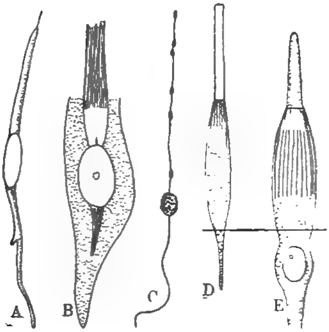

FIG. 66. Sense cells, after various authors. *A*, taste cell of rabbit; *B*, hair cell from lagena of pigeon; *C*, olfactory cell of Proteus; *D* and *E*, rod and cone cells from the human eye.

These sense organs which are situated in the epidermis are the more generalized, and among them are distributed the sensations of touch, pressure, and temperature. In the aquatic ichthyopsida (Fig. 67) these organs are composed of rod-like, club-formed, or pear-shaped cells, the free extremities of which may reach the surface; but in all terrestrial vertebrates where the surface of the skin is dry, the sensory structures sink to a deeper position.

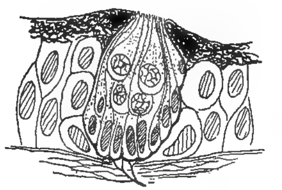

FIG. 67. Lateral line organ of *Amblystoma*, showing, beneath, the nerve fibres; on the free surface the sensory hairs.

Lateral Line Organs. — Some of these organs are irregularly distributed, while others are grouped into regular series, and form what are known as the **lateral line organs.** In their early stages these lateral line organs are upon the surface. Later they sink, in the amphibia, into pits, in pisces into longitudinal grooves which may be closed into tubes, with openings at regular intervals. With increase in size of the animal, the number of openings also increases by division. The openings frequently perforate scales, while the canals between them may become enclosed in bone, especially upon the head. By the presence of grooves and canals in the skulls of many fossil forms, we infer that they possessed lateral line organs. There is considerable variation in the distribution of the lines of these organs, but the following are the most constant series: (1), the lateral line of the trunk (may be double) which extends the length of the body between the dorsal and ventral musculature; this series gives the name to the whole system; (2), occipital series, crossing the back of the head and connecting the systems of the two sides; (3), supraorbital, and (4), infraorbital series, running respectively above and below the eye; (5), mandibular series, upon the lower jaw. In these grooves or canals are the groups of sensory cells, the groups on the head being innervated by the ophthalmicus superficialis, buccalis and

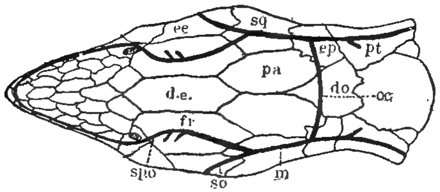

FIG. 68. Dorsal view of head of sturgeon, showing the distribution of the lateral line canals, after Collinge. *de*, dermethmoid; *do*, dermo-occipital; *ee*, dermoectethmoid; *ep*, epiotic; *fr*, frontal; *m*, main canal; *oc*, occipital commissure; *pa*, parietal; *pt*, post-temporal; *so*, suborbital canal; *spo*, supraorbital canal; *sq*, squamosal.

mandibularis externus branches of the seventh nerve, those on the trunk by the lateralis branch of the tenth nerve. These organs occur in the aquatic stages of the amphibia ; but upon the assumption of terrestrial life, as in salamanders, frogs, etc., the organs are lost and their nerves disappear.

In selachians and ganoids are found, especially on the snout, other sense organs, known as ampullæ and Savi's vesicles, the functions of which are more problematical than even those of the lateral line organs. The ampullæ may be organs of pressure sense.

Allied to the sense organs of the lateral line are structures known as **end buds.** These consist of a number of sensory cells, each bearing sensory hairs, compacted into a bud-like mass, and surrounded by supporting cells. In the cyclostomes and fishes they are scattered over the surface, but from dipnoi upwards they are confined to the cavities of the mouth and nose, and in the higher vertebrates to the oral cavity. In the mammals, these function as organs of taste, and the same is probably true of the lower vertebrates, since certain fishes have been shown to be capable of tasting with the external skin.

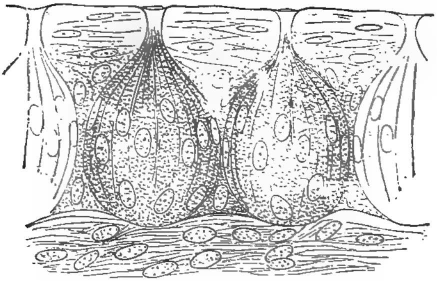

FIG. 69. Taste buds (end buds) from the human mouth (from Martin).

Sense Corpuscles. — In the terrestrial vertebrates the epidermal sense organs take a great variety of shapes due to the modifications of the accessory structures — sometimes unicellular, sometimes multicellular in character ; but in all these we probably have to do with free nerve terminations on or between the accessory cells. In all cases these structures are buried in the deeper layer of the epidermis or in the dermis beneath. The simplest are oval cells, the deeper face of each seated in a cup-like expansion of a nerve termination. In the compound tactile cells (**Grandry's** or **Merkel's corpuscles**), found only in

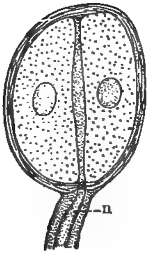

Fig. 70. Grandry's corpuscle, after Böhm and Davidoff. *n*, axis cylinder of nerve.

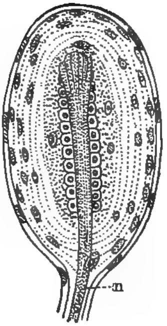

Fig. 71. Pacinian corpuscle. *n*, axis cylinder of nerve.

birds, two or more biscuit-shaped cells are included in a connective tissue, while the connecting nerve becomes flattened out into disks between each two cells. A more complicated type is found in the **corpuscles of Vater** or **Pacini,**— elliptical structures composed of layers of cells like the layers of an onion, into the centre of which projects the axis cylinder of a sensory nerve. Under the heading of **tactile corpuscles (Wagner's** or **Meissner's corpuscles)** are included club-shaped aggregations of cells, around which are coiled the terminal fibrillæ of a nerve. These last are scattered all over the body in the amphibia, but are more restricted in their distribution in the higher groups.

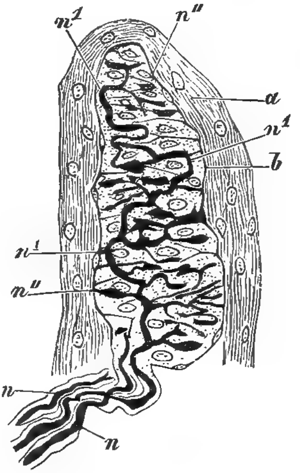

Fig. 72. Meissner's corpuscle from human finger, after Lawdowski from Wiedersheim. *a*, fibrous tissue envelope; *b*, corpuscle with its cells; *n*, entering medullated nerves; *n′*, ramifications of nerves; *n″*, club-shaped nerve terminations.

Among tactile organs must also be enumerated the long facial hairs (**vibrissæ**) of mammals, the base of each being surrounded by a network of nerves. Besides these special tactile organs there are numerous free nerve terminations in the epidermis of all vertebrates from cyclostomes to mammals to which sensory functions must be ascribed.

The ears in all vertebrates are paired structures on either side of the head between the seventh and ninth nerves. In the most highly developed ears three portions are to be distinguished,— inner, middle, and outer,— the first of which only is sensory and essential, and is the only part occurring in the fishes;

the other two are accessory in character. The sensory portion of the inner ear arises from the ectoderm. At first it is a cup-like depression on either side of the head. Then it sinks deeper and its edges unite, converting the cup into a closed sac,[1] the primitive **otic vesicle.** In all forms the closure lags at one point, and in this way, by the insinking of the rest, a slender tube, **ductus endolymphaticus** or **aqueductus vestibuli,** is formed, reaching to the parent ectoderm; and in the elasmobranchs this tube opens throughout life to the exterior by a small opening near the middle line of the top of the head. In other forms it becomes closed, and in some groups the ducts of the two sides may connect above the brain. Distally each duct expands into a **saccus endolymphaticus,** which in the lamprey, according to Ayers, is sensory.

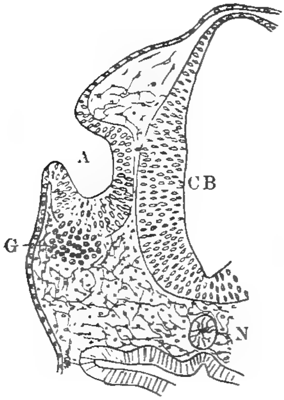

FIG. 73. Involution of auditory epithelium, *A*, to form the auditory vesicle in the embryo tern. *CB*, cerebellum; *G*, auditory ganglion; *N*, notochord.

The otic vesicle is at first spherical, or oval, but it soon divides by constriction into an upper portion, the **utriculus,** and a lower, **sacculus,** connected by a narrower **utriculo-saccular** canal. Flattened outgrowths arise from the walls of the utriculus, the walls of which become pinched together so that each outgrowth becomes converted into a **semicircular canal,** opening at either end into the utriculus. In the myxinoids there is but one of these canals; the lampreys have two, and all other vertebrates three. Two are in vertical planes at nearly right angles to each other, and from their position are known as the anterior and posterior canals; the third is horizontal in position, and is called the external canal. Each canal bears an enlargement, the **ampulla,** at one end,[2] — at the anterior end of the horizontal canal, at the ventral ends of the vertical canals.

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[1] In some forms (*e.g.*, amphibia) only the deeper layer of the ectoderm participates in the formation of the otic vesicle. Otherwise the history is much the same.

[2] The single semicircular canal of the myxinoids has an ampulla at either end.

The sacculus is always connected with the ductus endolymphaticus, and it gives off behind an outpushing known in the lower vertebrates as the **lagena.** In the mammals this lagena becomes greatly developed, and forms the scala media of the cochlea described below.

As long as the otic vesicle remains a simple sac, it bears on its surface a single patch of sensory epithelium ; but with differentiation of parts, the epithelium becomes correspondingly divided into a number of **maculæ** (the sensory cells of which bear short sense hairs) and **cristæ** (provided with long hairs). In the lampreys, where there is no sacculus, there are but three of these patches, — a crista in each ampulla and a macula in the vesicle. In other forms there are three cristæ, and at least one macula in the utriculus, two in the sacculus, and one in the lagena.

These parts, derived from the ectoderm, form the **membranous labyrinth.** It is filled with a fluid, the **endolymph,** in which are **otoliths** or particles of calcic carbonate, sometimes of microscopic size, but in the teleosts forming 'ear stones' of considerable magnitude.

The membranous labyrinths are protected by the otic capsules described in connection with the skull. These are laid down in

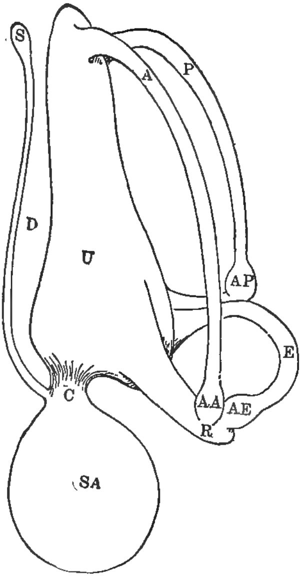

FIG. 74. Diagram of the membranous labyrinth. *A*, anterior canal; *AA*, anterior ampulla; *AE*, external ampulla; *AP*, posterior ampulla; *C*, utriculo-saccular canal; *D*, ductus endolymphaticus; *E*, external (horizontal) canal; *P*, posterior canal; *R*, recessus utriculi; *S*, saccus endolymphaticus; *SA*, sacculus; *U*, utriculus.

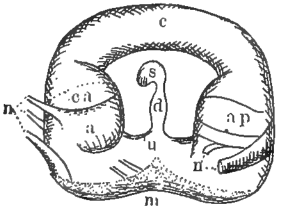

FIG. 75. Ear of *Myxine*, after Retzius. *a*, ampullar crista ; *ap*, posterior ampulla ; *c*, semicircular canal ; *ca*, anterior ampulla ; *d*, ductus endolymphaticus ; *m*, macula ; *n*, nerves ; *s*, sacculus endolymphaticus.

cartilage, but in all except the lower vertebrates the cartilage is finally replaced by bone. The inner walls of these capsules follow more or less closely the contour of the membranous labyrinth, thus constituting the skeletal labyrinth, between which and the membranous portions is a space filled with the **perilymphatic fluid.** The walls of these capsules are perforated internally for the passage of nerves, etc., while on their lateral surfaces, in all groups above amphibia, are two openings, — the **fenestra ovalis** and the **fenestra rotunda** (the latter crossed by membranes),— through which sound waves pass to the parts described.

In the mammals the skeletal labyrinth follows very closely the membranous portion, and in one part these structures need a further description. That part called the lagena in the lower vertebrates is greatly developed here, and is drawn out and coiled in a spiral. which is accompanied,

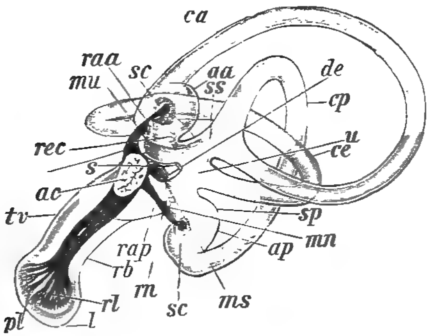

FIG. 76. Membranous labyrinth of thrush (*Turdus*), after Retzius, from Wiedersheim. *aa*, anterior ampulla; *ac*, eighth nerve; *ap*, posterior ampulla; *ca*, anterior canal; *ce*, external canal; *cp*, posterior canal; *de*, ductus endolymphaticus; *l*, lagena; *mn*, macula neglecta; *ms*, macula sacculi; *mu*, macula utriculi; *pl*, papilla lagenæ; *raa*, nerve to anterior ampulla; *rap*, to posterior ampulla; *rb*, basilar nerve; *rec*, recessus utriculi; *rl*, nerve to lagena; *rn*, nerve to macula neglecta; *s*, sacculus; *sc*, septum conciatum; *sp*, posterior utricular sinus; *ss*, superior utricular sinus; *tv*, tegmentum vasculosum; *u*, utriculus

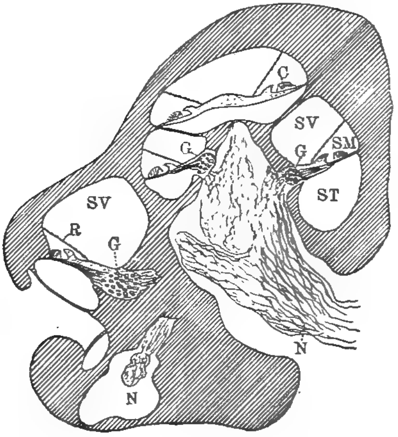

FIG. 77. Section through the cochlea of a cat. Bone, shaded. *C*, organ of Corti; *G*, spiral ganglion; *N*, nerve; *SM*, *ST*, *SV*, scalæ media, tympani, and vestibuli; *R*, Reissner's membrane.

above and below, by similar outgrowths of the perilymphatic space. From the resemblance which these structures present to a spiral stairway these divisions are called **scalæ,** that part connected with the membranous labyrinth being the **scala media,** the upper of the perilymphatic spaces being the **scala vestibuli,** the lower the **scala tympani.** This whole structure, from its resemblance to a snail-shell, is called the **cochlea.** In the scala media the macula lagenæ of the lower vertebrates becomes developed into a highly specialized sensory structure, — the **organ of Corti.** Besides 'hair cells' (sensory cells) and other cells, the organ consists of series of hard rods (**pillar cells**) arranged like a Λ at right angles to the axis of the scala. As the spiral diminishes in size, from apex to base these Λ's also diminish in size, a fact which led to the view formerly held that these were in some way connected with the recognition of pitch.

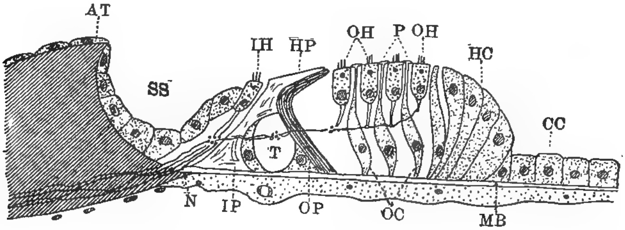

FIG. 78. Organ of Corti in section, after Stöhr. *AT*, auditory tooth; *CC*, cells of Claudius; *DC*, Deiter's cells; *HC*, Hensen's cells; *HP*, head plate; *IH*, inner hair cells; *MB*, basal membrane; *N*, nerve; *OH*, outer hair cells; *IP*, *OP*, inner and outer pillar cells; *P*, phalanges; *SS*, sulcus spiralis; *T*, tunnel. The 'membrana tectoria,' being decidedly problematic in character and relations, omitted.

The middle ear or **tympanum** first appears in the anura.[1] It is formed by the expanded end of the first visceral cleft (spiracle of elasmobranchs), which does not break clear through to the exterior, but is closed externally by a thin **tympanic membrane,** with an external wall of ectoderm, an inner of entoderm, and a middle layer of mesenchyme. Internally the tympanic cavity remains in connection with the pharynx by means of the proximal portion of the cleft, here known as the **Eustachian tube.** Sound waves are conducted across the tympanic

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[1] In the urodeles and cæcilians the tympanic cavity is lacking, and there is but a single auditory ossicle, the stapes, which usually articulates with the quadrate.

cavity by means of **auditory ossicles** which extend from the tympanic membrane to the fenestra ovalis. In the anura and sauropsida there are two of these ear bones, the **stapes,** situated in the **fenestra** ovalis, and the **columella,** extending from the stapes to the tympanic membrane. In the mammals the columella is replaced by two bones, the incus and the malleus, neither of which can be homologized with the columella.

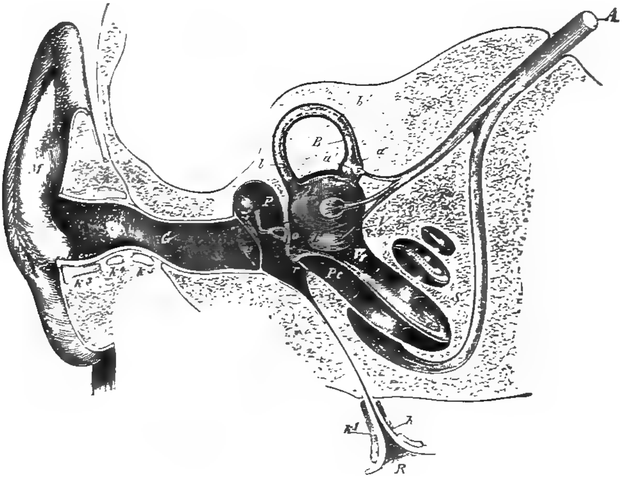

FIG. 79. Diagrammatic section of human ear, from Martin after Czermak. *A*, auditory nerve; *a*, ampulla; *B*, *b*, semicircular canal; *G*, external meatus; *k*, cartilages; *M*, concha; *o*, fenestra ovalis; *P*, tympanic cavity with chain of bones; *Pt*, scala tympani, *r*, fenestra rotunda; *R*, Eustachian tube; *S*, cochlea; *Vt*, scala vestibuli.

The stapes arises as a chondrification, and, later, ossification of the membrane closing the fenestra ovalis; the columella is post-spiracular, and may in part correspond to the hyomandibular; the incus is apparently the quadrate of the lower vertebrates; while the malleus is the proximal end of Meckel's cartilage (? os articulare) which becomes cut off from the rest.[1]

In all anura and in many reptiles the tympanic membrane is on the outer surface of the body, but in higher groups the mem-

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[1] There is great uncertainty upon some of these points, different students having different ideas of the homologies. The view given here is based upon personal studies. Further details are given in the section dealing with the skeleton.

brane is placed at the bottom of a tube, the **external auditory meatus,** the outer end of which is frequently protected by movable dermal flaps. In most mammals an external ear, supported by cartilages, is developed; and there is considerable evidence to show that this external ear is a derivative from the operculum of fishes, or from the external branchial structures of the amphibia.

Recent experiments tend to show that in the fishes the ears are without auditory functions and are solely organs of equilibration. In terrestrial vertebrates they are both organs for hearing and for the maintenance of the equilibrium.

Olfactory Organ. — The organ of smell is a single sac in the cyclostomes, paired in all other vertebrates. Its essential portion is the sensory epithelium, in which sensory cells are interspersed with supporting or isolating cells. Its nerve supply is the olfactory nerve already described. The powers of smell are directly proportional to the extent of sensory surface, and in order that this may be increased the surface is folded, usually in the longitudinal direction. In the more primitive forms the sensory surface is not uniformly distributed, but is gathered in patches separated by large masses of isolation cells. In some ganoids and amphibians the nasal epithelium has a peculiar radiate appearance, as seen in transverse section. From the amphibia upwards outgrowths of cartilage or bone (**turbinals**), either from the ethmoid or lateral walls, tend to divide the cavity still further. In the petromyzontes and pisces only external nostrils occur, and in the cyclostomes there is but one of these. In the forms with paired cavities there is primitively but a single

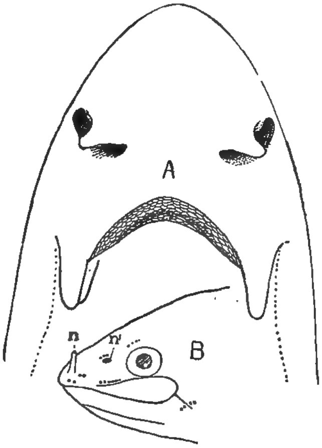

FIG. 80. Divided nostrils of fishes; upper figure *Acanthias*, showing them divided by a movable flap. Lower, young *Amia*; *n*, *n'*, anterior and posterior narial openings.

nostril to each olfactory sac, but in the selachians and ganoids a fold of skin practically divides each nostril (external **naris**) into two. In many teleosts this is carried farther, and two distinct nostrils may occur on either side. These modifications clearly are to permit a current of water over the olfactory epithelium (Fig. 80).

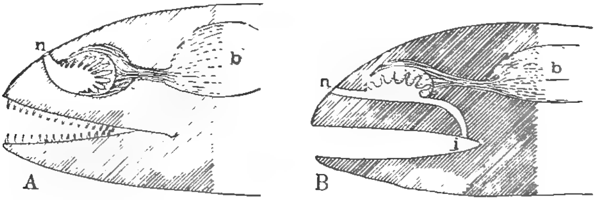

FIG. 81. Relations of nasal organs to the cavity of the mouth; *A*, in fishes; *B*, in terrestrial vertebrates. *b*, brain; *i*, internal nares; *n*, external nares.

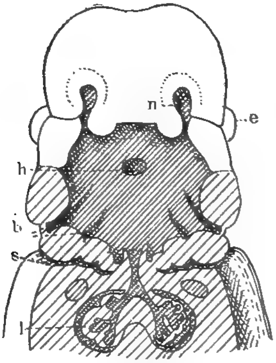

FIG. 82. Head region of a human embryo, after His, showing the method of formation of the respiratory nasal tract leading from the nostril, *n*, into the oral cavity, and the naso-lachrymal duct leading from the eye, *e*, into the nasal cavity. *b*, rudimentary gill clefts; *h*, hypophysial pocket; *l*, lungs; *s*, cervical sinus.

In all vertebrates above fishes both external and internal nares (**choana**) are present, the latter opening into the oral cavity. This condition is foreshadowed in the selachians, where an **oronasal groove** leads back from the external nares of either side to the angles of the mouth. In the higher vertebrates this groove becomes converted, during growth, into a tube by the union of its edges.[1] In this way a **respiratory tract** is formed on one side of the olfactory surface, the posterior end of which opens inside the cavity of the mouth. In a similar way a **naso-lachrymal** duct is formed leading from each eye into the corresponding nasal passage. In terrestrial vertebrates **nasal glands** are frequently present in connection with the nose, the secretion of which moistens the olfactory epithelium.

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[1] The process is modified in certain groups, where a solid cord of cells, instead of a groove, is formed, the respiratory passage appearing later in the cord.

Connected with the nose in all vertebrates above the fishes is a pair of accessory sensory organs, — the **organs of Jacobson.** They are outpushings of the wall of the olfactory surface, supplied by branches of the first and fifth nerves. In the lower amphibia these organs are placed on the medial side of the nasal cavities ; a little higher they are ventral in position ; in the highest amphibia they have rotated to the lateral side of the olfactory organ. In the amniotes they are either medial or ventral in position. In the lower forms these sacs are connected only with the nasal cavities ; but in the mammals a duct (**Stenson's duct**) sometimes leads from them into the mouth through the foramina incisiva, between the premaxillary and the palatine processes of the maxillary bones. In many mammals, however, these foramina are closed by membrane, and are vestigial in character.

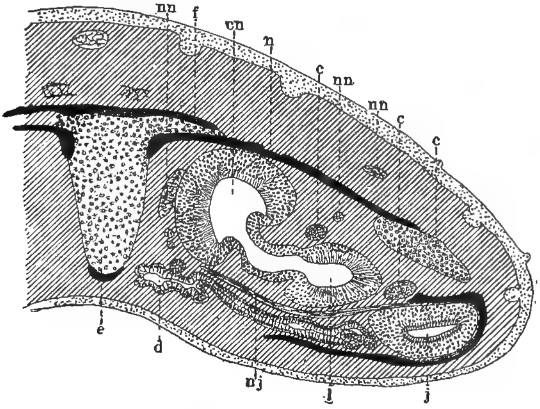

FIG. 83. Section through the nasal region of the Surinam toad, *Pipa*. *c*, cartilage; *cn*, cavum nasale; *d*, Jacobson's gland and duct; *e*, ethmoid cartilage; *f*, frontal bone; *j*, organ of Jacobson; *l*, lateral portion of nasal passage; *n*, nasal bone; *nj*, branch of olfactory nerve to organ of Jacobson; *nn*, branches of nasal nerve of trigeminal.

In the mammals for the first time appears an external nose supported by cartilage. In some, like the tapirs and elephants, this organ becomes enormously developed, and forms in the latter the well-known trunk.

Visual Organs. — The sensory portion of the eyes arises from the brain, and in the embryos of some vertebrates (elasmobranchs, urodeles) optic areas can be recognized in the medullary plate before its involution. The accessory portions are furnished by ectoderm, mesothelium, and mesenchyme.

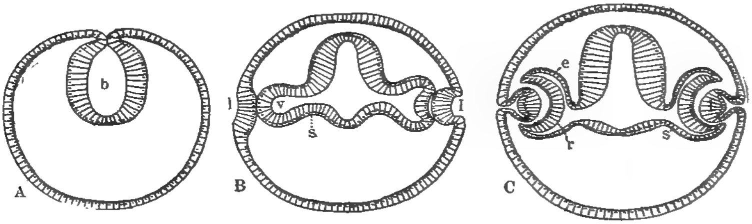

FIG. 84. Diagrams showing the inversion of the layers in the formation of the retina. In all the figures the nuclei are placed in the morphologically deeper ends of the cells. In *A* the brain (*b*) has been closed in, in *B* the optic vesicle (*v*) has reached the thickening for the lens (*l*), and on the right side the vesicle is being converted into the double-walled cup with, as shown in *C*, a medial epithelial (*e*), and an outer retinal layer (*r*), the deeper face of which is turned towards the lens.

A hollow outgrowth arises on either side of the primitive fore brain, and extends towards the skin. The distal portion expands into a globular **optic vesicle,** while the proximal portion retains its smaller size, and is known as the **optic stalk.** Thus the cavity of the vesicle is in connection with the ventricle of the thalamencephalon by means of the hollow stalk. The distal surface of each optic vesicle comes in contact with the ectoderm of the side of the head at the place where the lens is to form (see below), and with the formation of this structure the distal half of the optic vesicle becomes invaginated into the proximal part, thus partially obliterating the cavity of the vesicle, and converting the whole into a two-layered cup. The distal invaginated part of

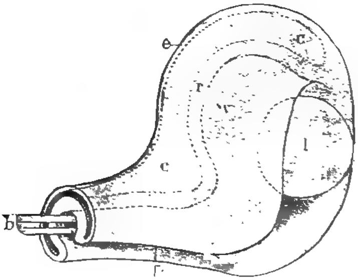

FIG. 85. Diagram of early development of eye, modified from Hertwig. *b*, blood-vessels; *c*, cavity of optic vesicle; *e*, epithelial layer; *f*, choroid fissure; *l*, lens; *r*, retinal layer; *v*, cavity of optic cup, later occupied by vitreous body.

this cup eventually becomes the **retina,** while the outer layer forms the **pigmented epithelium** (pigment layer of the choroid of older works) of the eye.

Connected with the invagination of the retinal layer is another phenomenon, an account of which is necessary for the understanding of other features of the eye. This invagination is not confined to the distal portion of the optic vesicle, but extends along its lower surface and continues upon the optic stalk in a manner readily understood from Fig. 85, the result being a gap, the **choroid fissure,** in the ventral wall of the optic cup, produced as a groove along the lower side of the optic stalk.

Through this choroid fissure mesenchyme cells, and later blood-vessels, enter the optic cup. Later, when the fissure closes, the walls of the stalk unite around the blood-vessels, which hence, apparently, enter the optic cup through the centre of the optic stalk. A loose watery tissue, the **vitreous humor,** is developed from the immigrant mesenchyme cells, and fills the optic cup, or as it is called in the adult, the **posterior chamber,** of the eye. The blood-vessels serve to nourish the retina, etc.

At first the retinal layer is thin ; but it gradually increases in thickness by cell division so that it eventually consists of several layers of cells, and finally these become differentiated so that several strata can be distinguished. Those nearest the lens become the **ganglion cells,** those farthest away the **rod-** and **cone-cells,** and between these a so-called **granular layer,** this last being separated from the other two by an inner and outer **molecular layer.** From some of the rod- and cone-cells, which are the sensory strictures of the eyes, slender **rods** and **cones** (Fig. 66), grow out towards and into the pigmented epithelium, while others of this layer develop into supporting or isolating cells. From the other side of each rod cell and cone cell a nerve fibre grows out towards the front of the eye, and breaks up into dendrites which interlace with other dendrites coming from the cells of the granular layer, their fibrillations producing the inner molecular layer. The outer molecular layer is similarly an interlacing of dendrites from the granular cells and from the ganglion cells, the minute granulations which occasioned the name molecular layer being the sections of the nerve fibrillations. The ganglion cells in their turn produce from these outer or free surfaces axons which rapidly grow from the cells to the choroid fissure (thus forming a layer of nerve fibres over the ganglion cells), and thence, through the groove in the optic stalk, to the brain. These axons form the optic nerve,[1] which, as will readily be understood, appears, after the closure of the choroid fissure, as if it left the eye through the centre of the retina. As all sense cells are lacking at the point of exit of the optic nerve, this region forms the 'blind spot' described in all physiological text-books.

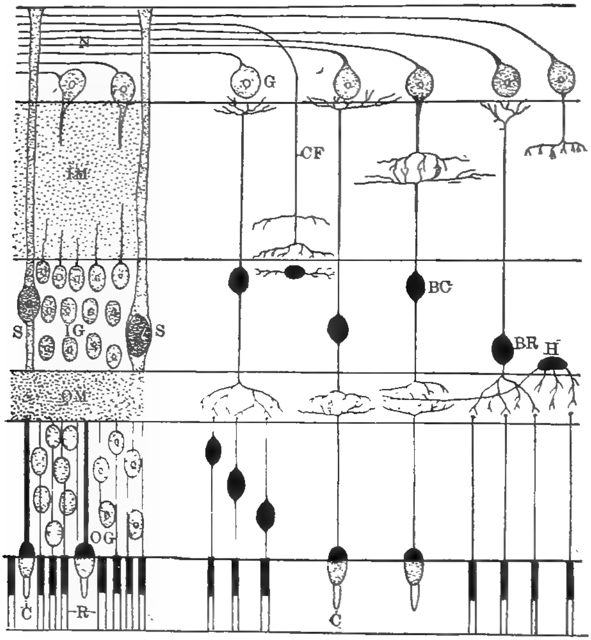

FIG. 86. Retinal elements, after Ramon y Cajal. *BC*, bipolar cone cell; *BR*, bipolar rod cell; *C*, cone; *CF*, centrifugal fibre; *G*, ganglion cell layer; *H*, horizontal cell; *IG*, inner granular layer; *IM*, inner molecular layer; *N*, nerve fibres; *OG*, outer granular layer; *OM*, outer molecular layer; *R*, rods; *S*, supporting cells.

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[1] It was formerly thought that the optic nerve arose by a modification of the cells of the optic stalk. Later, nerve fibres were described as growing from the brain to the eye; but while some fibres may arise in this way, the majority arise as described above. So far as method of nerve formation is concerned, the optic nerve resembles the dorsal root of a spinal nerve (pp. 47 and 60, foot-note.)

One point regarding the eye was formerly emphasized. As will be seen from the method of formation of the eye by involution from the skin (see Fig. 84), the layer of rods and cones is homologous with the superficial layer of the skin, while the ganglionic layer corresponds to the deeper surface of the epidermis. Hence light passing into the eye transverses the transparent deeper layers in order to reach the morphologically superficial sense structures, the rods and cones,[1] a condition which is unlike that occurring in any invertebrate eye, with the exception of the peculiar dorsal eyes described as occurring in the slug *Onchidium.*

At the place where the optic vesicle reaches the ectoderm of the side of the head, the latter thickens, and then a portion of it becomes invaginated, and is at last cut off as an epithelial sac, — the vesicle of the **lens.** This body, which comes to lie in the aperture of the optic cup, has an anterior wall of cubical cells, while those of the posterior surface are so strongly columnar that the cavity is nearly obliterated. With growth the cavity entirely disappears, while the lens of the adult is developed by the addition of elongate fibres produced by budding from the cells of the equator of the structure. These fibres are arranged in layers, like the coats of an onion, and where they meet on the inner and outer surfaces of the lens, they produce peculiar figures like a three-rayed star.

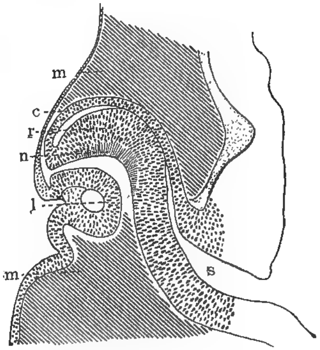

FIG. 87. Development of eye in pig. *c*, pigmented epithelium; *l*, lens; *m*, mesenchyme; *n*, nervous layer of retina; *r*, deeper layer of retina; *s*, optic stalk.

After the lens is cut off from the ectoderm the latter becomes a smooth, transparent sheet over the front of the eye, forming the epithelium known as the **conjunctiva,** continuous with the superficial layer of the skin.

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[1] In man there are from 250,000 to 1,000,000 rods and cones to a square millimetre of retinal surface.

We are now in position to describe the eye of the adult vertebrate. The eye proper is approximately spherical, although, as in fishes, it may be flattened, or, as in birds, somewhat conical in front. In the ichthyopsida it is without any well-developed external accessories for protection;[1] but in the amniotes movable lids, which can close over the organ, occur. There are typically three of these folds of the skin, — an upper and a lower lid, moving in a vertical plane, and inside of these a third transparent lid, the **nictitating membrane,** which is attached at the anterior or inner angle, and which closes horizontally. In

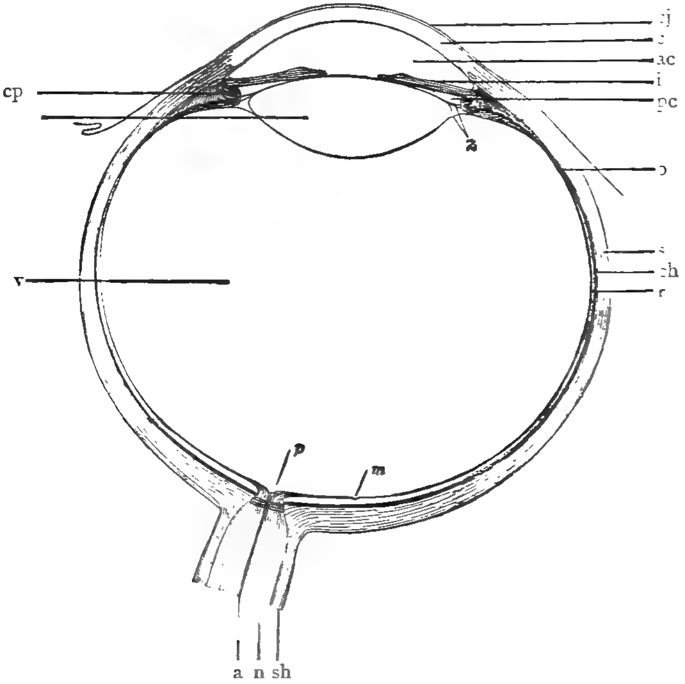

FIG. 88. Horizontal section through human eye, from Hertwig after Arlt. *a*, arteria centralis; *ac*, anterior chamber of eye; *c*, cornea; *ch*, choroid; *cj*, conjunctiva; *cp*, ciliary process; *i*, iris; *l*, lens; *m*, macula lutea, point of distinct vision; *n*, optic nerve; *o*, ora serrata; *p*, papilla of optic nerve; *pc*, posterior chamber of eye; *r*, retina; *s*, sclerotic; *sh*, sheath of optic nerve; *v*, vitreous body; *z*, zonula Zinnii.

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[1] Some salamanders have feebly developed eyelids.

man the nictitating membrane is reduced to a vestigial fold, the **plica semilunaris,** visible at the inner angle of the eye.

The free surface of the eye is covered by the conjunctiva already mentioned; and beneath this is a thicker, dense transparent layer, the **cornea,** composed of connective tissue fibres produced from mesenchyme cells, which penetrate between the conjunctiva and the lens. Laterally the cornea is continuous with a hard white capsule, the **sclerotic coat,** which envelops the whole eyeball, its anterior portion being the well-known 'white of the eye.' This sclerotic is usually cartilaginous, and in the sauropsida and in monotremes, bony structures, **sclerotic bones,** may be developed in it. This sclerotic forms a sense capsule, comparable in a way to those enclosing the ears and olfactory organs, but never, like them, uniting with the skull.

Between the cornea and the lens is the **anterior chamber** of the eye, filled with a watery fluid, the **aqueous humor**, less dense than the vitreous humor already mentioned.

Inside of the sclerotic is a highly vascular layer, the **choroid,** which carries numerous blood-vessels to nourish the eye. The choroid extends forward nearly to the edge of the optic cup; but beyond this point it becomes muscular, a portion of it forming the contractile portion of a circular curtain, which extends from the edge of the optic cup into the anterior chamber. This curtain, known as the **iris,** is opaque, and is usually colored by pigment derived from the edge of the optic cup. The opening in the centre of the iris, the **pupil,** can be enlarged or contracted by means of the muscles already referred to, and thus the amount of light admitted to the retina can be regulated.

Just inside the iris the inner wall of the optic cup becomes developed into a strong ridge, the **ciliary process**, which extends inwards towards the lens to which it is attached by a fenestrated, suspensory ligament (**zonula Zinnii**), thus partially separating the anterior from the posterior chambers. Close to this region the choroid develops a layer of **ciliary muscles,** which by their action can move the lens nearer to or farther from the retina, and at the same time, by stress conveyed by the suspensory ligament, can slightly alter its shape. This forms the apparatus of accommodation necessary for viewing objects at different distances.

In the lower vertebrates accessory glands connected with the eyes are but slightly developed, but with the assumption of a terrestrial life (amphibia) **lachrymal glands** for lubricating the surface appear. These arise as inpushings of the epidermis near the lids. In the lower amphibia the glands are on the lower side of the eye and form a continuous series; but higher this becomes divided into two, — a **Harder's gland** near the inner angle, a true lachrymal gland at the outer. In reptiles[1] and birds these remain on the lower side of the eye, but in mammals the lachrymal gland passes to the upper lid. The Harderian gland, which has for its function the lubrication of the nictitating membrane, becomes reduced in the mammalia. The lachrymal duct has already been mentioned (p. 76).

The eye is provided with muscles which move it as a whole. Some of these are remarkably constant through the whole vertebrate series. There are four **rectus muscles**, known from their position as the superior, inferior, external, and internal. These arise from the bottom of the orbit near the foramen for the optic nerve, and are inserted at about equal distances around the ball. The two **oblique muscles** (superior and inferior) arise in front of the rectus muscles, and are inserted on the ball above and below the internal rectus. Besides, there may be a well-developed **retractor bulbi** attached near the optic nerve, and serving to pull the eye back into its socket. In the sauropsida are also muscles connected with the nictitating membrane, but these are reduced or absorbed in the mammals.

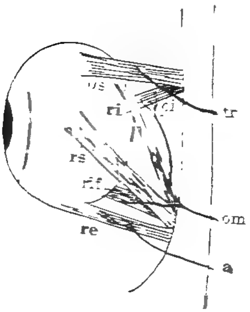

FIG. 89. Eye muscles and related nerves in shark. *a*, abducens nerve; *oi*, inferior oblique; *os*, superior oblique; *om*, oculomotor nerve; *re*, rectus externus; *ri*, r. internus; *rif*, r. inferior; *rs*, r. superior muscles.

Epiphysial Structures. — Several structures which are connected with that part of the primitive fore brain which subse-

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[1] An interesting fact is the absence of lachrymal glands in crocodiles.

quently becomes the twixt brain are best considered in connection with the sense organs. These are best developed in the lizards, and hence these animals serve as the basis of the following account. At an early stage there arises from the epithelial roof of this region a hollow outgrowth (the **epiphysis**) directed upwards and forwards, its distal end at first being in contact with the epidermis of the top of the head. The extremity of this outgrowth expands into a more or less spherical vesicle, the **pineal** or **parietal eye,** which may come to lie at some distance in front of its point of origin, above the cerebral hemisphere, and usually on the right side. The cells of this pineal vesicle increase in number, producing a thickening of the walls; while the distal and proximal surfaces of the vesicle become

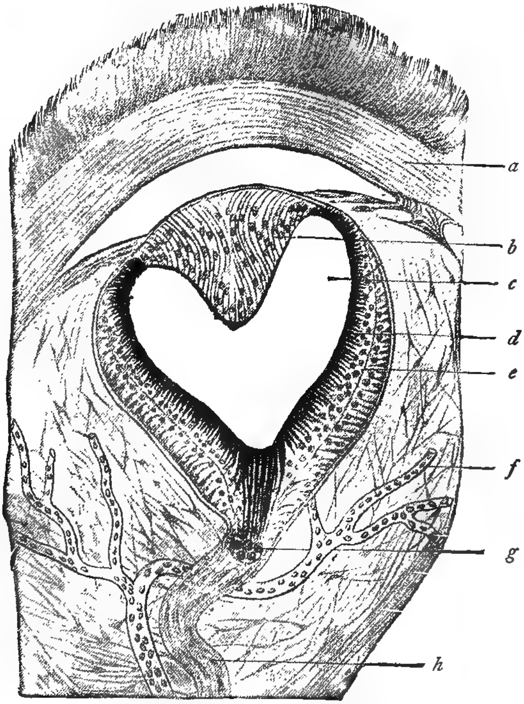

FIG. 90. Section of pineal eye of *Hatteria*, after Spencer from Wiedersheim. *a*, capsule; *b*, lens; *c*, vesicle; *d*, retina; *e*, molecular layer; *f*, blood-vessels; *g*, large cells; *h*, nerve.

differentiated, the former into a transparent lens-like body, the latter into sense cells, supporting cells, and pigment cells, the whole making up a retina. Thus is formed a camera eye; and in the lizards this comes to lie on the top of the head just beneath the skin, one of the plates of the dorsal surface bearing a transparent spot through which light can reach the organ. This parietal eye, however, differs from the paired eyes already described in the relations of the nerves to the retina (p. 81). These proceed from the deeper ends of the sense cells, but it must be kept in mind that there has been no inversion of the retinal layer in the parietal eye.

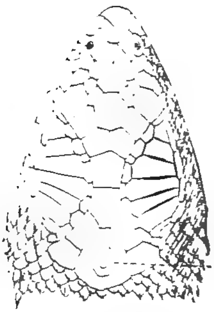

FIG. 91. Dorsal view of head of *Sceloporus undulatus*; *p*, parietal organ.

After the parietal eye has been budded off from the epiphysis, there is frequently formed a less perfect eye-like organ, the **parapinealis**, from the distal end of the stalk. In some cases the epiphysis is double, in which case the pinealis arises

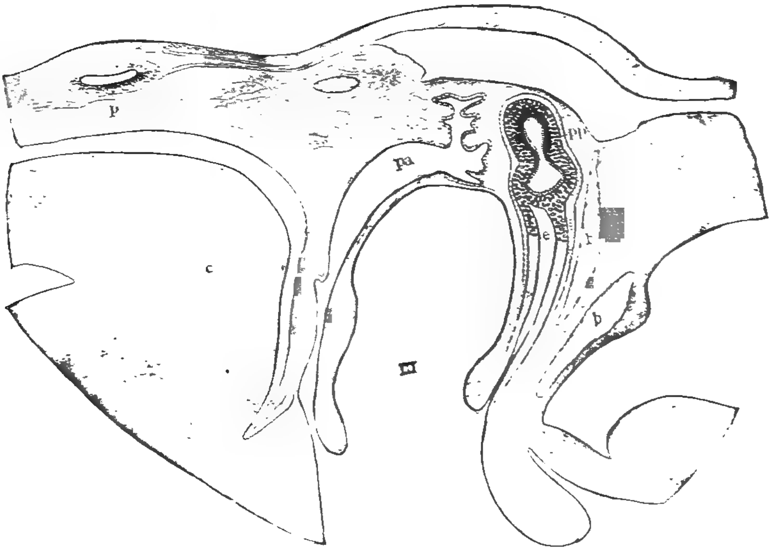

FIG. 92. Pineal apparatus in an embryo lizard (*Sceloporus*). *b*, blood-vessels; *c*, cerebrum; *e*, epiphysis; *p*, parietal eye; *pa*, paraphysis; *pp*, parapinealis.

from the anterior, the parapinealis from the posterior, outgrowth. Besides these, a third outgrowth, the **paraphysis,** may arise in front of the epiphysis; it never develops sensory elements.

The parietal eye has different fates even in the lizards. In some, as *Hatteria* (Fig. 90), it retains its parts well developed throughout life, and its nervous connection with the brain persists, so that here it is apparently to some extent functional. In other lizards it has lost this power, either through the extensive deposit of pigment in all parts, or by the degeneration of its nerve supply. In other groups these structures of the pineal apparatus are much more rudimentary, and are usually entirely enclosed within the skull; although at times, as in the anura, the parietal eye may lie between the bones and the skin, but here all nervous connection is lost. In many extinct vertebrates, if we may judge by the large parietal foramen in the skull, the pinealis was well developed and functional.

EPIDERMAL AND DERMAL STRUCTURES (SKIN).

The Skin. — That portion of the ectoderm which remains on the surface of the embryo after the differentiation and involution of the central nervous system forms the **epidermis,** which, together with the underlying mesenchymatous tissue, the **derma,** makes up the skin. In its earliest stage the epidermis is usually but a single cell in thickness, but later, by division of these cells, other layers are formed on the outside of this first or basal layer. In ganoids, teleosts, and amphibia the epidermis is two cells thick from the first, and in the amphibia (the only instance in vertebrates) the outer layer is ciliated in the young. The basal layer is the active portion, producing by cell division the more superficial layers. In those forms with two-layered epidermis, the basal layer also gives rise to nerves and sense organs, and is therefore often spoken of as the **nervous layer,** the outer one being the **cuticular layer.**

The derma (often called **cutis** or **corium**) is of mesenchymatous origin, and consists largely of layers of fibrous connective tissue intermingled with smooth muscle cells, blood-vessels, nerves, etc., the whole being separated from the deeper tissues by a layer of much looser connective tissue, usually containing considerable fat.

The structure of the adult epidermis varies considerably in the different groups. In all it becomes several layers in thickness, and is thicker in the terrestrial than in the aquatic forms. In the ichthyopsida there is slight differentiation between the layers, the cells showing less stratification than in the higher groups. Among them are numerous unicellular glands, usually spherical in shape, and loaded with a slimy substance (mucus); and as these cells approach the surface they break, and their contents spread over the body, producing the slimy condition so familiar in these forms. In the amniotes, on the other hand, the outer layers of the epidermis undergo a hardening process, and are converted into a horny layer (**stratum corneum**), Fig. 95, the beginnings of which are seen in the frogs. Apparently the first layer to be budded from the basal layer persists through a large part of the embryonic life as a distinct sheet on the outside of the corneum, known as the **epitrichium,** so called because in embryonic mammals it extends in an unbroken sheet over the developing hairs. The non-corni-

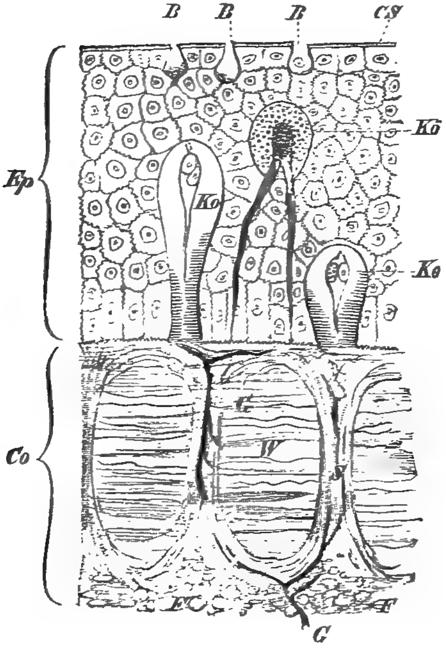

FIG. 93. Section of skin of lamprey eel (*Petromyzon planeri*) from Wiedersheim. *B*, mucous cells; *Co*, derma: *CS*, cuticular layer; *Ep*, epidermis; *F*, fat; *G*, blood-vessels: *Ko*, club cells: *Kö*, granular cells; *S*, *W*, fibres of connective tissue running vertically and horizontally.

fied layers of cells are known as the **Malpighian layer**, the cells of which are polygonal in outline and rich in protoplasm In the mammals, between horny and Malpighian layers, is a thin **stratum lucidum**, consisting of extremely flattened cells closely compacted together.

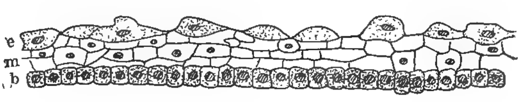

FIG. 94. Skin of mammalian embryo, showing the epitrichium, *e*, after Minot. *b*, basal layer ; *m*, Malpighian layer.

As will readily be understood, the cells of the basal layer are continually dividing, thus producing new cells, which come to lie between the basal layer and those layers previously formed, and in this way tending to increase the thickness of the epidermis. As these cells grow older they gradually pass into the conditions found in the different layers, — lucidum, corneum, — and at last are cast off from the outer surface, either a few cells at a time, or in larger sheets, as in the amphibians and reptiles. The strata corneum and lucidum are clearly protective in nature, and only in the turtles is there an absence of this shedding of the external layers of the skin.

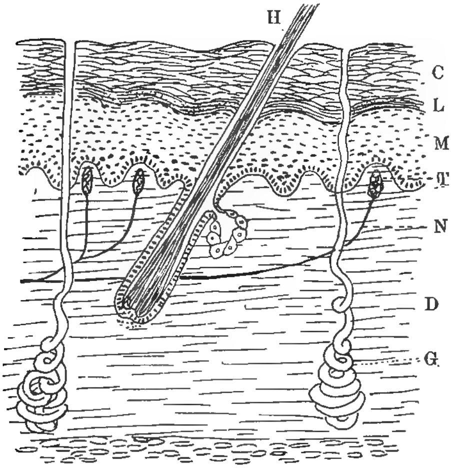

FIG. 95. Diagrammatic section through mammalian skin. *C*, stratum corneum; *D*, derma; *G*, sweat gland; *H*, hair; *L*, stratum lucidum; *M*, Malpighian layer; *N*, nerve; *T*, tactile corpuscles.

Dermal Glands. — The epidermis gives rise to numerous glands. In the fishes the unicellular mucous glands have already been referred to. In some fishes (teleosts) in addition the skin also contains poison glands, sometimes upon the back, sometimes on the operculum, and sometimes in the axilla, but always in connection with a strong spine. Of our native fishes the poison glands in the axilla of certain catfishes (*Noturus*) are best known. In the toadfish (*Batrachus*) a gland in similar position is well known, but apparently its secretion is not poisonous.

In the amphibia, glands in the skin which secrete an acrid juice are abundant, and in the toads their presence causes the warty skin so noticeable in these animals. In the sauropsida, glands are few in number. In certain snakes stink glands occur in the skin, the secretions of which give these animals a disagreeable odor. In the lizards, glands are found only on the inside of the femoral region of the hind limbs, the openings of which (**femoral pores**) are of considerable value in the classification of these forms. In the birds, glands are developed on the reduced tail (**uropygial glands**), the oily secretion of which is used in oiling the feathers. These glands are best developed in the water birds. In the rasores there are in addition glands in the neighborhood of the eye.

In the mammals, glands are well developed, and acquire a great variety of form. These glands may be arranged in two categories, the **tubular** and the **racemose**, the characters of which are indicated by their names. To the tubular type belong the **sweat glands**, which extend deep into the derma, and in their deeper portions become coiled and convoluted (Fig. 95). The racemose (**acinose**) glands, in their simplest condition, form the sebaceous glands, and are normally placed in close connection with the roots of the hair. In some mammals the sebaceous glands of certain regions of the body become converted into scent glands, the secretions of which may serve for

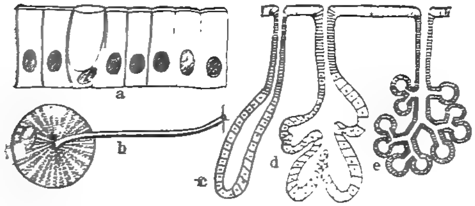

FIG. 96. Different types of glands. *a*, intestinal epithelium with a gland-(goblet) cell; *b*, unicellular gland with duct; *c*, simple tubular gland; *d*, simple racemose gland; *e*, compound racemose gland.

offence or defence; or again may be of value at the rutting season, as attractions for the other sex. Of the defensive glands those of the skunk and polecat come immediately to mind; to the other category belong the peculiar glands of the beaver, civet cat, musk deer, etc. These glands may be placed near the eyes (deer), on the back (musk swine), on the legs (ordinary swine), on the ventral surface (musk deer), or near the vent (skunks, etc.).

A more extreme modification of the sebaceous glands is found in the **milk glands** of all mammals except monotremes,[1] the secretion of which serves to nourish the young. These milk glands are in pairs upon the ventral surface, the number being roughly correlated to the number of young brought forth at a time. The ducts of each group of glands open upon a limited extent of surface, and this becomes converted into a teat or nipple, either by the elevation of the skin in which the ducts open (Fig. 97, *A*), or by the extension of the surrounding skin into a tubular form (*B*).

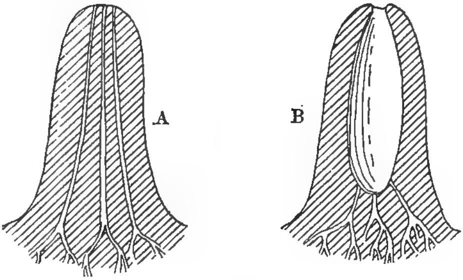

FIG. 97. Two types of nipple.

In the skin, pigment is of common occurrence. It may be found in the epidermis, but is more common in the derma. It may consist of scattered pigment granules, or there may be special pigment cells (**chromatophores**) which enlarge or contract under control of the nervous system, producing those color changes so noticeable in many lizards, and to a less degree in amphibia and fishes.

EXOSKELETON.

Either or both layers of the skin may participate in the formation of firmer parts constituting a tegumentary skeleton, which may take the form of scales or bony plates; and it is to

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[1] The milk glands of the monotremes are apparently derivatives of sweat glands.

be noted that most of the membrane bones of the skull (*infra*) belong in this category. Here, too, may be enumerated feathers, hair, horn, claws, etc., as well as cornifications of the skin of more limited distribution.

Scales. — The most primitive type of this exoskeleton is found in the scales of the elasmobranchs. Here papillæ of the derma (dentinal papillæ), arranged in quincunx, push up into the epidermis, carrying the basal layer of the latter before them. The external surface of each papilla and its base secretes a little plate of bone or dentine with a central spine; while the epidermis covering the papilla becomes converted into an enamel organ, the deeper face of which secretes a hard enamel cap upon the dentine base, the enamel being thickest upon the central spine. These scales are known as placoid scales, and in their development they show the closest similarity with teeth (see p. 19).

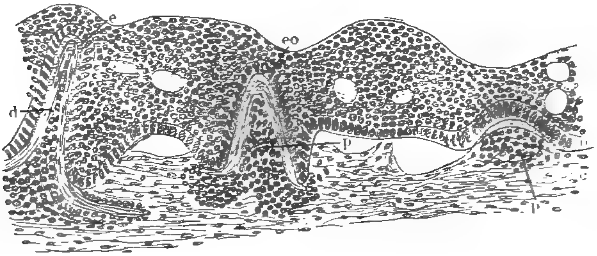

FIG. 98. Developing scales of dogfish (*Acanthias*). *b*, basal layer of ectoderm; *c*. derma (corium); *d*, dentine; *e*, enamel; *eo*, enamel organ: *p*, pulp.

In the ganoids (*Lepidosteus*) the early development is as in elasmobranchs, including the formation of plate, spines, and a rudimentary enamel cap. Later the spines and enamel cap disappear, while the outer side of the dentinal plate becomes covered by a hard, smooth layer known as **ganoin,** which differs from enamel in that it arises from the derma. In the higher ganoids and in the teleosts, dentinal papillæ are formed; but the resulting scales are entirely of dermal origin, and, whether soft and flexible, hard and bony, show no differentiation into layers. At first these scales are arranged in quincunx parallel to the external surface of the body, but usually with growth the anterior end of each extends beneath the posterior margin of the scale in front, so that as a result the scales come to lie in dermal pockets oblique to the surface. In some cases (South American siluroids, many plectognaths, etc.) the scales may fuse into a firm dermal armor enclosing the body, while in many fossil ganoids this external skeleton was highly developed; the parts uniting in some instances into large armor plates.

FIG. 99. Position of scales (black) in skin of teleost. *D*, derma; *E*, epidermis.

All existing amphibia except some cæcilians are without scales.[1] In the latter group and in many fossil amphibia they are (or were) well developed. In cæcilians the scales are dermal, and lie in the rings which encircle the body. In the stegocephalans these plates were in some cases confined to the ventral surface, in some they covered the entire body.

In the reptilia of all groups forms are found with a well-developed dermal skeleton of bony plates, the plates in *Stegosaurus* (one of the extinct dinosaurs) being nearly two feet across. In recent forms similar but smaller dermal bones occur in alligators and many lizards, and reach their extreme in the turtles, where these bony plates unite to form a bony box, composed of an upper carapace and a lower plastron, enclosing the trunk. This shell becomes firmly united with the true skeleton, and to a certain extent replaces it in some species, the vertebræ and parts of the ribs being correspondingly reduced.

Besides this bony skeleton reptiles are also provided with scales, in the formation of which a papilla of the derma is formed, but the scales themselves arise from cornifications of the outer epidermal cells. This horny envelope is periodically moulted by all reptiles except turtles. It may come away piecemeal, or again, as in snakes and lizards, as a continuous whole; the process of separation being aided by the formation of hair-like processes developed from the deeper cells which lift up those

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[1] Some tropical toads have bony plates beneath the skin of the back.

portions which are to be cast. The claws of the reptiles and the horny beaks of the turtles and birds are also cornifications of the epidermis.

Scales (upon the legs and feet) and claws of the same character (*i.e.*, epidermal cornifications) reappear in the birds, but dermal bones are never found. Birds have besides a peculiar epidermal covering, the feathers, which must have more attention. In the following account it must be borne in mind that in the development of the feathers, as in the scale of a snake, a dermal papilla takes the initiative, and that the ultimate structure is entirely formed of cornified epidermis.

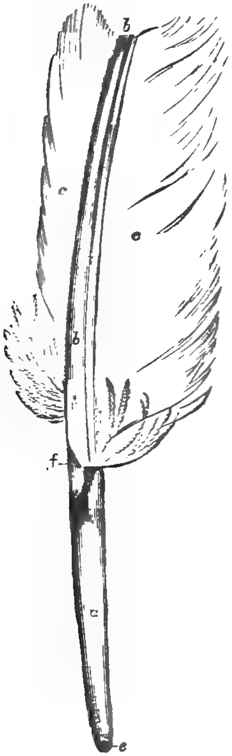

FIG. 100. Contour-feather. *a*, quill; *b*, shaft; *c*, barbs.

Feathers occur only in the group of birds, and here three principal types are found, — down-feathers, pin-feathers, and contour-feathers, differing much in appearance, but of essentially the same structure. Contour-feathers are those which cover the body in the adult bird, giving it its outlines, and forming the broad expanse of wings and tail. In a typical contour-feather are to be distinguished an axial portion, composed of a proximal hollow part, the **quill,** and a distal and more solid **shaft,** the latter bearing on either side lateral outgrowths, the **barbs**; shaft and barbs making up the **vane.** Inside the quill occur thin structureless partitions, the **pith,** while the shaft bears on its so-called inferior surface a longitudinal groove, the **umbilicus.** The barbs bear on their sides smaller projections, the **barbules,** which are usually provided with minute hooks; these, interlocking with similar hooks on the adjacent barbules, convert the whole vane into a continuous sheet. In many cases a second or **aftershaft** joins the axis of the feather on the lower surface near the junction of the main shaft with the quill. The vane supported by this after shaft is usually more downy than the others.

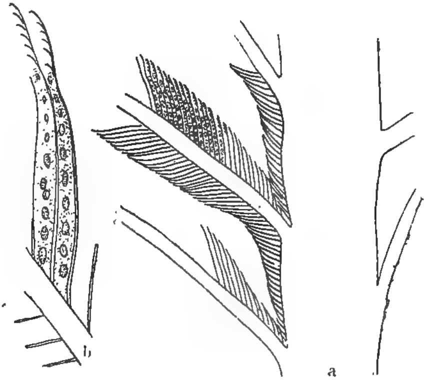

FIG. 101. Part of a feather, enlarged. *a*, portion of shaft showing a part of a barb with its barbules; *b*, two barbules greatly enlarged.

Down-feathers differ from contour-feathers in the absence of a shaft, the barbs arising directly from the end of the quill; these barbs never interlock, but remain soft and free from each other. In pin-feathers (**filoplumes**) there is merely the development of a hair-like shaft without barbs.

Except in the penguins and some ratite birds, feathers are not uniformly distributed over the whole surface of the body, but occur in well-marked **feather-tracts** or **pterylæ,** the rest of the surface (**apteria**) being sparsely covered with down- or pin-feathers. The tertiary penguins also possessed feather-tracts, so that their absence in existing penguins must be a secondary character. The arrangement of the feather-tracts is of importance in the classification of birds.

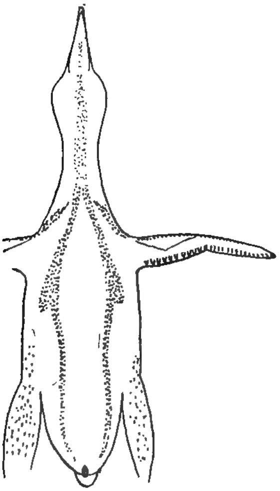

FIG. 102. Feather tracts in young of common crow (*Corvus americanus*).

In development down-feathers precede contour-feathers. There first appears in each spot where a down feather is to develop a rapid multiplication of dermal cells, thus producing a rudimentary papilla, over which the epidermis, elsewhere consisting of basal layer and epitrichium, becomes several cells in thickness. By continuous growth the papilla becomes long and cylindrical, projecting from the body, the axial derma forming the pulp of the future quill, while the epidermis surrounds the outgrowth. A circular depression around the base of the papilla is the beginning of the formation of the future feather follicle. In the distal portions of this outgrowth there next appear longitudinal ridges of the pulp which gradually encroach upon the epidermis, dividing this layer into a series of cylindrical rods (Fig. 104), which at last are held in position by only the layer of epitrichium. Now the derma retracts into the feather follicle, carrying with it the basal layer of the epidermis, so that there remains a hollow epidermal outgrowth, the quill, bearing at its extremity a number of epidermal rods. The cells of these portions rapidly dry and become cornified, and, the epitrichium breaking away, the rods separate as the down of the down-feather.

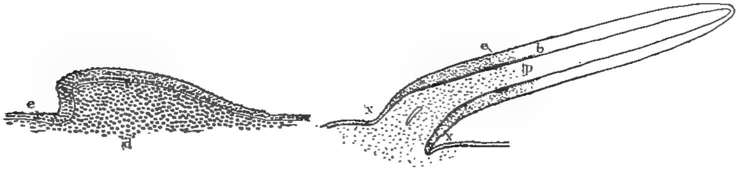

FIG. 103. Two stages in the development of a feather, after Davies. *b*, basal layer of epidermis; *d*, derma; *e*, epitrichium; *p*, pulp; *x*, beginning of depression for feather follicle.

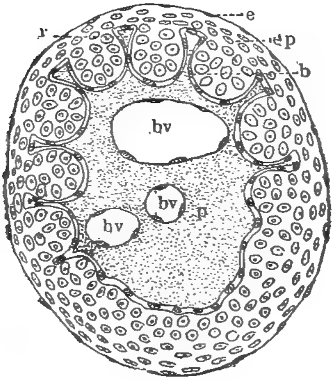

FIG. 104. Transverse section of developing down-feather of tern (*Sterna wilsoni*). *b*, basal layer of epidermis; *bv*, blood-vessels; *e*, epitrichium; *ep*, epidermis; *p*, pulp; *r*, ridges of pulp extending into epidermis.

Later the contour-feathers are developed from the retracted pulp which grows out again as before. In general these develop like their predecessors, excepting in certain details. The rods of pulp are not longitudinal, but oblique to the axis of the outgrowth, the result being that the cornified rods (which form the barbs) proceed from an undivided portion (shaft) on the dorsal side of the outgrowth; and when the epitrichium breaks away, these expand so as to form the vane. One point needs a little more detail. On that side where the shaft is to be formed are two longitudinal thickenings (Fig. 105); with growth these become larger and bend inwards to meet each other. Near the tip the result is a solid rod (Fig. 105, *A*), but farther down the ingrowth includes a space (Fig. 105, *B* and *C*), so that the proximal portion of the shaft is hollow. The umbilicus is formed by these ingrowing ridges. As will readily be understood, the so-called dorsal and ventral sides of the feather correspond to the outer and inner surfaces of the epidermis of the feather papilla.

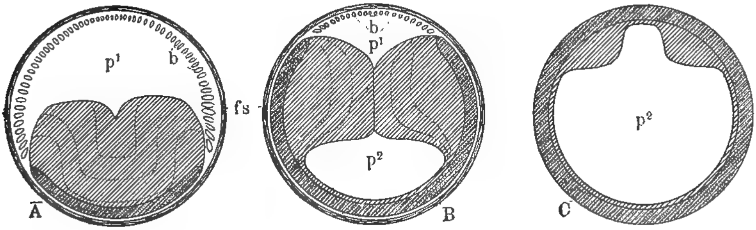

FIG. 105. Diagrammatic sections through a developing contour-feather: *A* at about the middle of the vane, *B* near the base of the vane, and *C* through the quill, after Davies. *b*, barbs; *fs*, feather sheath; p^1, p^2, different portions of the pulp cavity.

At regular intervals the bird sheds or molts its feathers, the old ones dropping out, while new ones arise to take their place by a repetition of the process just described.

Hair is as characteristic of mammals as feathers are of birds. In its formation the epidermis apparently takes the initiative, the result being the formation of a solid ingrowth of epidermis into the underlying derma, the deeper end of which becomes cupped (Fig. 106) to accommodate a small collection of dermal cells, the rudiment of the hair papilla. Next a circular depression appears in their ingrowth, separating a central portion, the future hair, from the surrounding epidermis which forms the

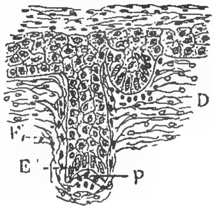

FIG. 106. Two stages in the early development of the hair of the mouse, after Maurer. *D*, derma; *E*, epithelial hair-forming cells; *F*, follicle; *p*, hair papilla.

hair follicle. In both hair and follicle several layers may be distinguished. In the follicle there is the basal layer and the more superficial layers of the epidermis, without, however, any clear differentiation of strata corneum and lucidum. At the bottom of the follicle (root of the hair) these pass directly into the hair itself, on the outside of which is the so-called inner root-sheath (the walls of the follicle forming the outer root-sheath) composed of two layers of cells (the outer called Henle's layer; the inner, Huxley's layer). This inner root-sheath does not reach the external surface. The hair proper consists of a central core or medulla, around which are several layers of cells, the cortex, and on the outside is a cuticular layer. The growing point is at the bottom of the follicle, where the basal layer of the epidermis, by repeated cell division, adds to the base of the hair. As the cells grow older they become cornified, and the whole is gradually pushed out of the follicle by additions below.

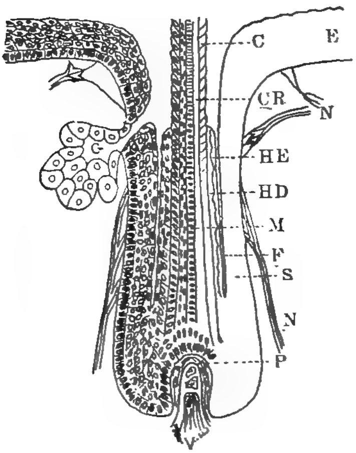

FIG. 107. Diagrammatic section of a hair and its follicle, after Maurer. *C*, cuticle; *CR*, cortex; *E*, epidermis; *F*, follicle; *G*, oil gland; *HE*, Henle's layer; *HD*, Huxley's layer; *M*, medulla; *N*, nerves; *P*, hair papilla; *S*, outer root sheath (the inner root sheath is composed of Henle's and Huxley's layers); *V*, vein.

Like feathers, hairs appear at first in well-defined tracts, but later, by multiplication, this regularity is lost. Hairs are least abundant in the whales, where they may be reduced to from two to eight pairs in the neighborhood of the mouth, and even these sometimes only occur during fœtal life. Hairs may also be enormously developed into organs of defence, as in the case of the 'quills' of the hedgehog and porcupines, while in the case of the vibrissæ ('whiskers') near the mouth, they may serve as sense organs (p. 69).

Oil glands of the racemose type are usually found connected with the hair follicles, while a system of smooth muscle fibres (especially strong in porcupines) serves to erect the hairs.

Closely related to hair are the nails, claws, and hoofs of mammals, and the horn of sheep, goats, and cattle; in fact, these structures may be regarded as composed of agglutinated hairs.

Somewhat different in character are the scales which cover the body in the pangolins (manids), and are found on the tail of the rodent *Anomalurus*, although these are both of epidermal origin. True dermal bones in the skin occur only in the armadillos among recent forms, where they form an armor upon the dorsal surface of the body. In the fossil glyptodons the body was enclosed in a similar bony case, while some extinct cetacea possessed dermal bones.

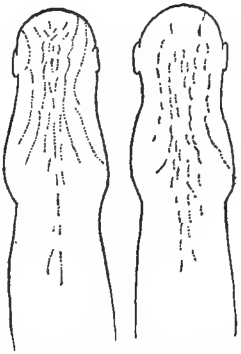

FIG. 108. Hair tracts on early cat embryos, after Maurer.

MESOTHELIAL STRUCTURES.

THE mesothelial structures, as we left them on a preceding page (p. 8), consisted of a pair of compressed sacs or pouches, one on either side of the entodermal tube. Each pouch consists of an inner or visceral, and an outer or somatic, wall, the cavity between them being the primitive cœlom, which is now entirely cut off from all other cavities. The derivatives of this mesothelial tissue are now to be described, but it must be kept in mind that there are many exceptions to the details as given below. The statements regarding the somites apply most nearly to the elasmobranchs, but they are generalized in many respects.

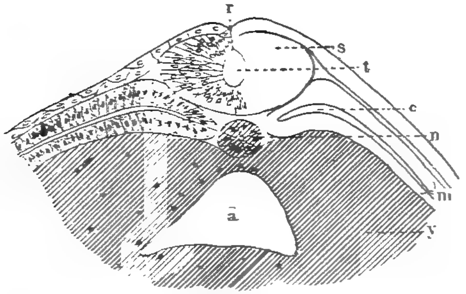

FIG. 109. Transverse section of *Amblystoma* embryo after the separation of the mesothelium. *a*, archenteron; *c*, cœlom; *m*, mesothelial walls of cœlom; *n*, notochord; *r*, groove of closure of neural tube; *s*, spinal cord; *t*, canal of spinal cord; *y*, yolk.

First in order is the development of the primitive segments or **somites** of the body. It is to be noted that while other parts are segmentally or **metamerically** arranged (nerves, blood-vessels, skeleton), this metamerism primarily arises in the mesothelium, and becomes secondarily impressed upon other structures. The process of somite formation is best seen in the trunk region.

As a result, partly of the change in the shape of the embryo caused by the infolding of the medullary plate (see nervous system), in part of the growth of the mesothelium itself, the cœlomic pouches extend upwards from their primitive position along either side of the notochord and the central nervous system, while below the pouches grow until they meet in the mid ventral line, below the entoderm. In each cœlomic pouch three horizontal zones are to be distinguished, — a dorsal muscle-plate or **myotome zone (epimere)**, a ventral **lateral plate zone (hypomere)**, and between these a much narrower **middle zone (mesomere)**.

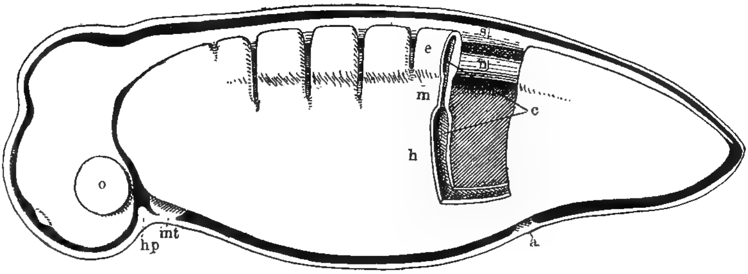

FIG. 110. Diagram of the mesothelial pouch and the beginning of segmentation, based upon *Amblystoma*. *a*, anus; *c*, cœlom; *e*, epimere; *h*, hypomere; *hp*, hypophysis; *m*, mesomere; *mt*, mouth; *n*, notochord; *o*, eye; *s*, spinal cord.

By a series of constrictions not easily described, but readily made out from the figure, epimere and mesomere become divided transversely to the body axis into a series of cubical bodies, the **protovertebræ** of older authors, the **myotomes** of recent embryology. These divisions do not extend into the hypomere, and so do not divide the ventral part of the cœlom. As a result we have below a single cœlomic space extending the length of the trunk, which connects with a number of dorsal cœlomic diverticula, extending, one into each myotome. Later, horizontal constrictions cut the epimeral portions off from the rest, so that from this region there arises, on either side of the body, a series of completely closed cavities with epithelial walls, — the myotomes. To avoid confusion with that portion of the primitive body cavity (**metacœle** or **splanchnocœle**) which remains between the lateral plates, and to which the term cœlom as usually applied is given, the cœlomic pouches in the myotomes have been called the **myocœles.** The myotomes give rise to the voluntary muscles cf the body in a manner shortly to be described; the modifications in other parts of the cœlomic wall must be outlined now.

As will be seen by the diagram above (Fig. 110), the middle zone becomes segmented at the same time and in the same way as the myotomes, and when the latter cut loose from the rest of the mesothelial tissue, the contained cœlom becomes roofed in above. From the inner or visceral wall of these mesomeric segments there is now a rapid proliferation of cells upon the deeper surface, the products of which migrate inward around the notochord, where they eventually give rise to the skeletal structures (vertebræ) surrounding the notochord and central nervous system, from which fact these immigrant cells, divided at first into segments like the cœlomic walls which gave them origin, are called **sclerotomes.** From the method of formation — budding of separate cells instead of an involution of epithelial tissue — these sclerotomes must be regarded as mesenchymatous in nature, and their future fate must be described in connection with that layer. It is only necessary to say here that these

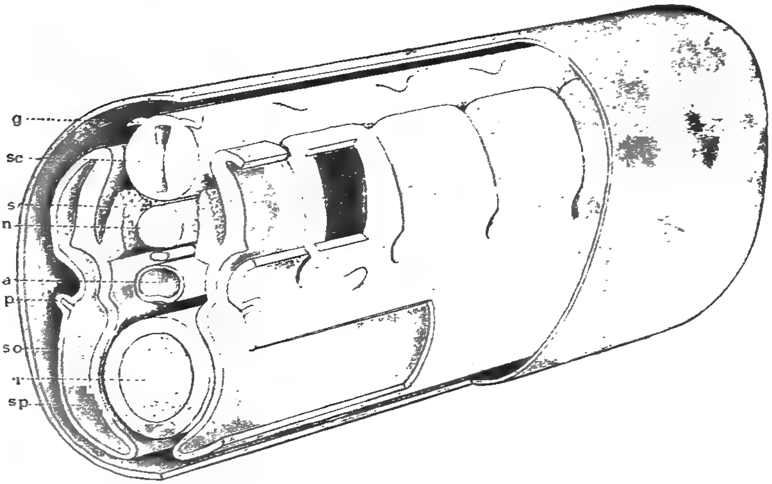

Fig. 111. Diagram of a part of the trunk of an embryonic vertebrate showing the development of the mesothelial tissues. *a*, aorta; *g*, neural crest (anlage of spinal ganglion); *i*, intestine; *n*, notochord; *p*, rudiment of pronephric tubule; *s*, sclerotome; *sc*, spinal cord; *so*, somatic layer of mesothelium; *sp*, splanchnic layer. (For later conditions compare with Fig. 127.)

cells are not wholly used up in building the solid skeleton, but that some wander in between splanchnic mesothelium and entoderm, where they give rise to the smooth muscles and connective tissue of the alimentary canal, some pass between the myotomes, where they form the partitions (**myocommata**[1]) between these structures, while others press farther and give rise, in part, to the deeper layers (cutis) of the skin, etc. This same middle zone also gives rise to a part of the excretory system (nephridia), which is also primarily divided into segments (**nephrotomes**).

The lateral plate region (hypomere) shows but slight traces of segmentation. From the dorsal portion of its splanchnic wall arises the glomus of the pronephros (see below) and the gonads (reproductive structures), but whether or not these latter are truly segmented, and whether we have metamerically repeated **gonotomes**, is as yet a disputed question. The account of these reproductive and excretory organs will be given later.

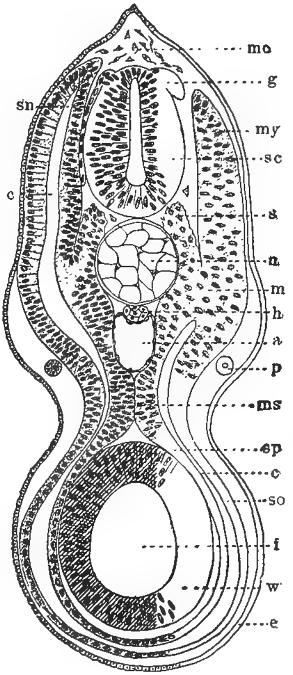

FIG. 112. Transverse section of embryo dogfish (*Acanthias*). *a*, aorta; *c*, cœlom; *e*, ectoderm; *g*, ganglion of spinal nerve; *h*, hypochorda; *i*, intestine; *m*, mesomere; *mc*, mesenchyme; *ms*, mesentery; *my*, myotome; *n*, notochord; *p*, pronephric duct; *s*, sclerotome; *sc*, spinal cord; *so* and *sp*, somatic and splanchnic layers; *sn*, spinal nerve; *w*, wall of intestine. The section passes on the left side through the middle of a myotome, on the right near the edge of one.

Mesenteries. — The greater portion of the lateral plates develops into the flattened epithelium (**peritoneum**) lining the body cavity (**splanchnocœle** or **metacœle**), and plays an important part in the development of the walls of the alimentary tract and the membranous supports

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[1] The term myocomma is sometimes regarded as a synonym of myotome; the usage adopted here is preferable; **myoseptum** is another term for it.

(**mesenteries,** in the broader sense of the word) which connect the various viscera to the walls of the body cavity. The conditions in the abdominal region will be described first.

Here the splanchnic layer of the mesothelium applies itself to either side of the walls of the alimentary tract, it being of course kept in mind that mesenchymatous tissue has migrated in between entoderm and mesothelium in this region (see p. 103), while above and below the digestive tract the dorsal and ventral walls of the hypomere press inwards towards the median line, insinuating themselves dorsally between the alimentary canal and the notochord, ventrally between the entoderm and ectoderm. As a result there is formed a double partition between the metacœles of the two sides both above and below the intestine, with a small amount of mesenchymatous tissue between the two epithelial walls. These partitions, which thus come to support the alimentary canal (Fig. 113), are the dorsal and ventral mesenteries.

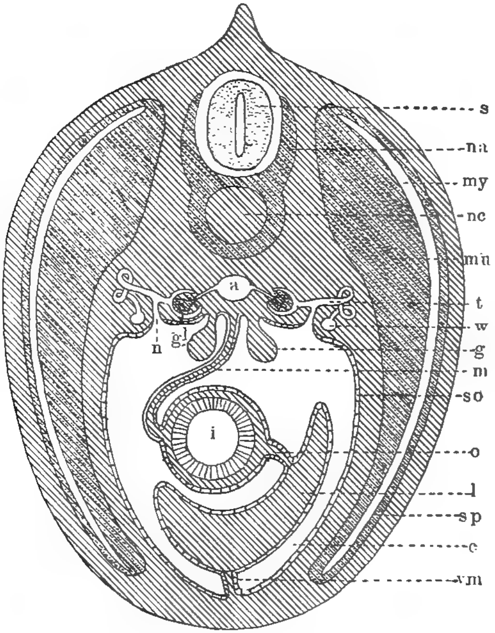

FIG. 113. Diagrammatic section of vertebrate through abdominal region. *a*, dorsal aorta; *c*, cœlom; *g*, gonad; *gl*, glomerulus; *i*, alimentary canal; *l*, liver; *m*, mesentery; *mu*, muscular layer of myotome; *my*, myocœle; *n*, nephrostome; *na*, neural arch; *nc*, notochord; *o*, omentum; *s*, spinal cord; *so*, somatic layer of peritoneum; *sp*, splanchnic layer of peritoneum; *t*, nephridial tubule; *vm*, ventral mesentery; *w*, Wolffian duct.

The ventral mesentery is never perfect throughout the abdominal cavity. In the posterior portion the partition walls break down, placing the cœloms of the two sides in free communication. In front a part of this ventral mesentery persists, binding the liver to the anterior abdominal wall, and in many ichthyopsida carrying the sub-intestinal vein to that organ. Another portion, known as the **small omentum** (or **gastro-hepatic**) and the **duodeno-hepatic omentum** extends from the dorsal surface of the liver to the stomach and duodenum (Fig. 113).

The dorsal mesentery is usually far more complete.[1] In it are recognized various regions, named according to the organs which they support, — **mesogaster, mesentery proper, mesocolon, mesorectum,** etc. It is attached to the dorsal wall in a straight line, and in those vertebrates with a straight alimentary canal the mesentery is a plane membrane, but with increasing convolution of the alimentary canal, the membrane becomes correspondingly plaited. Besides this complication, the mesenteries can form secondary unions with the body wall, or with the

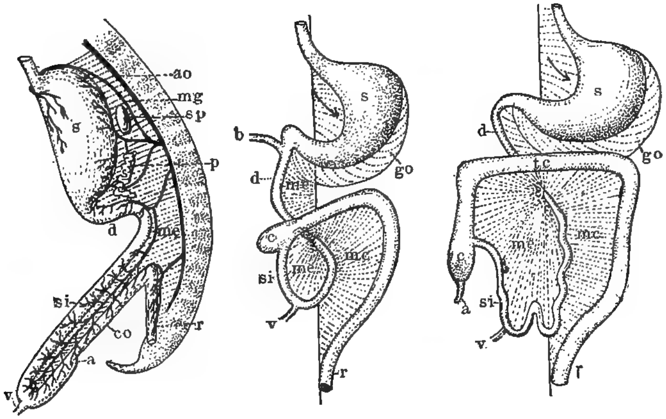

FIG. 114. Three stages in the development of the alimentary canal and the mesenteries of man, after Toldt and Hertwig. *a*, appendix vermiformis; *ao*, aorta; *b*, bile duct; *c*, cæcum; *co*, colon; *d*, duodenum; *go*, great omentum; *mc*, mesocolon; *me*, mesentery; *mg*, mesogaster; *p*, pancreas; *r*, rectum; *s*, stomach; *si*, small intestine; *sp*, spleen; *tc*, transverse colon; *v*, vitelline duct. The arrow points to the opening of the omentum.

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[1] In *Petromyzon* (cyclostome) it has entirely disappeared, except a few shreds in the rectal region.

mesenterial regions, the details of which must be sought in special works.

Those mesenterial folds which bind the various regions of the alimentary canal to each other have received the special name of **omenta.** The small omentum has just been mentioned; the **gastro-splenic omentum** connects the spleen with the stomach; while in the higher vertebrates the **great omentum** is a large double fold formed from the mesogaster and the mesocolon, which connects the stomach to the transverse colon.

In the region of the heart and of the lungs (when these organs are present) the splanchnic layer of the cœlomic wall becomes similarly related to these structures, and in a similar way similar supporting folds (**mediastinum** for the lungs, **mesocardium** for the heart) are formed. In the abdominal region similar mesothelial folds (**mesorchium** in the male, **mesovarium** or **mesoarium** in the female) support the reproductive organs (gonads).

Divisions of Splanchnocœle. — So far, that part of the cœlom enclosed between the lateral plates has been considered as a single space on either side, as it is in the early development. Soon, however, the anterior portion becomes cut off from the rest and forms a sac, the **pericardium,** enclosing the heart, the relations of which are described in connection with the circulatory organs. In the lower vertebrates the posterior wall of this pericardium is known as the **false diaphragm** or **septum transversum,** and in many is perforated by one or more small **pericardio-peritoneal canals,** connecting the pericardium with the abdominal cavity, a result of incomplete closure.

In the mammals the true diaphragm appears, although rudiments, sometimes even muscular, appear in some sauropsida. This **diaphragm** is a transverse muscle, usually described as crossing the abdominal cavity from side to side, completely dividing it into two cavities, an anterior or **pleural,** in which the lungs are placed, and a posterior or peritoneal cavity containing the remaining viscera. This statement is not exactly correct. In the lower forms the liver abuts directly against the septum transversum. In the mammals these relations are the same. The diaphragm is therefore to be regarded as a paired structure, extending from the lateral walls behind the lungs to middle part of the septum transversum. This explains why it is that the pericardium appears as if enclosed in the pleural cavity, although it is morphologically outside of it.

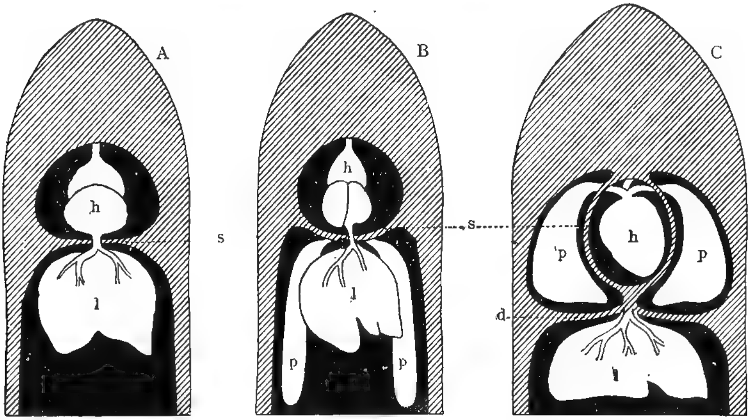

FIG. 115. Diagrams illustrating the relations of the pericardium to the rest of the cœlom: *A* in fishes, *B* in amphibia and sauropsida, *C* in mammalia. *d*, diaphragm; *h*, heart; *l*, liver; *p*, lungs; *s*, septum (false diaphragm) between pericardium and the rest of the cœlom. In *B* the lungs project into the general cœlom (pleuro-peritoneal cavity), in *C*, by the formation of the diaphragm, pleural and peritoneal cavities are distinct, while the pericardial cavity, containing the heart, has been shoved backwards between the two pleural cavities.

The abdominal cœlom is not completely closed off from the outer world; for the urogenital ducts, to be described later, form a means of communication. Besides these there occur in cyclostomes, many fishes, dipnoi, turtles, and crocodiles, from one to two small openings (known as **abdominal pores**), beside or behind the vent, by means of which the cœlom is connected with the outside world. Little is known as to their function.

MUSCULAR SYSTEM.

The history of the muscle plates or myotomes is next to be taken up. After their separation from the other portions of the primitive mesothelial tissue, these form a series of approximately cubical hollow bodies on either side of the notochord and central nervous system. From the early idea that these bodies gave rise to the vertebræ, they were formerly called protovertebræ. We now know that they contribute little or nothing to the skeletal structures, but give rise to the voluntary musculature of the body. The processes involved in the conversion of these epithelial walls into muscle — the histogenesis of muscle — must be traced first.

In the majority of the vertebrates the cells of the mesal wall (*i.e.*, that towards the notochord and nervous system) rapidly increase in number, thus obliterating the myocœle. In this process the cells lose their original shape and arrangement as a cylindrical epithelium, and form elongated cylinders, the axes of which are parallel to the longitudinal axis of the body. Each of these primitive muscle cells at first contains but a single nucleus; but by division several arise, which may either eventually lie in the centre (amphibia) or on the periphery (mammals) of the cell. At the same time the peripheral protoplasm of the cell becomes differentiated into numbers of fine longitudinal fibrillæ, which increase in number so that at last all except a small amount of protoplasm in the immediate vicinity of the nucleus has been converted into these contractile structures, — the epithelial cell becomes a muscle fibre. The lateral or outer wall of the myotome does not participate in this muscle formation, but is said to give rise to the deeper layer (corium or derma) of the skin. The process of the histogenesis of muscle in the cyclostomes differs in some particulars from that given above.

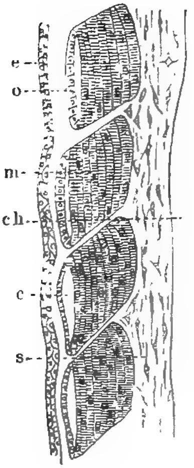

FIG. 116. Myotomes of *Amblystoma* in process of conversion into muscle-plates. *c*, remains of myocœle; *ch*, chorda; *e*, epidermis; *m*, muscle developing from inner plate of myotome; *o*, outer plate of myotome; *s*, skeletogenous tissue.

The myotomes, after their separation from the mesothelial tissues, increase rapidly in their dorso-ventral dimensions, and gradually push in between the lateral plate and the ectoderm in the ventral half of the body, thus giving rise to the musculature of this region, while dorsally their extension is less marked (Fig. 113). In this process the myocommata also participate, so that the whole body is enveloped on either side by a series of muscle-plates, the fibres of which have a generally longitudinal direction, and are interrupted at regular intervals by the intermuscular ligaments, the derivatives of the earlier myocommata. This primitive condition can readily be recognized in the trunk region of a fish, but it becomes greatly modified in the birds and mammals; yet even here traces of the primitively segmented condition can be made out in the ventral abdominal region and in the intercostal muscles.

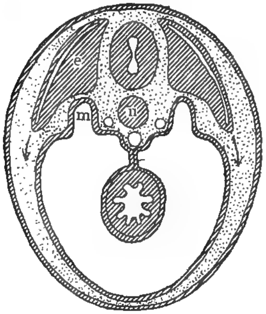

FIG. 117. Illustrating the downward growth of the myotomes. *e*, epimere (myotome); *m*, mesomere.

In the fishes the resulting muscles of the trunk and tail become subsequently divided into dorsal and ventral or **epiaxial** and **hypaxial** systems, the line of division between the two following more or less closely the lateral line, and being marked by a partition of connective tissue. In the amphibia these epi- and hypaxial portions are clearly visible in the tail, but farther forward the hypaxial system is reduced. This reduction is carried to a greater extent in the aminotes, where almost the sole traces

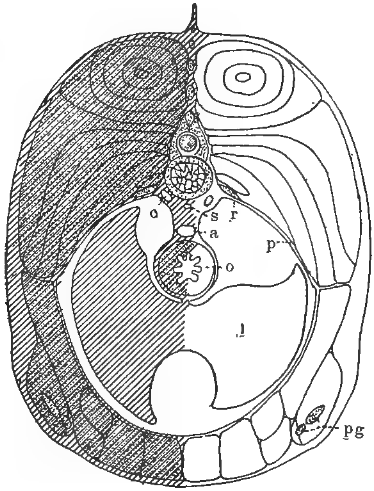

FIG. 118. Transverse section through young *Amblystoma*, showing the final result of the downward growth of the myotomes (deeply shaded); *a*, aorta; *c*, cardinal vein; *l*, liver; *o*, œsophagus; *p*, peritoneum; *pg*, pectoral girdle; *r*, rib; *s*, subvertebral vein.

of the hypaxial system are to be found, greatly modified, in the pelvic and neck regions.

The subsequent modifications of the primitive musculature in the higher groups cannot be traced here in detail, even were it better known. Only the origin of the limb muscles can be referred to. This is best known in the fishes, there being only scattering observations relating to the air-breathing vertebrates; but these few accounts justify us in the assumption that in the amniotes the phenomena are essentially the same. In the fish-like forms several of the somites almost immediately behind the head bud from their lower surfaces cords of cells which extend out laterally, lose their distinctness, and form a common matrix out of which the definitive muscles are later developed (Fig. 120). In the amniotes more somites intervene between the

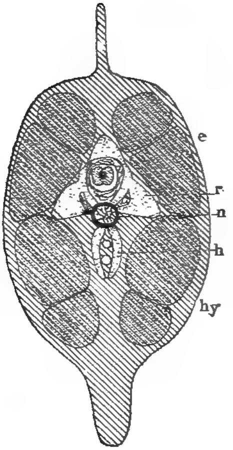

FIG. 119. Section through the tail of *Amblystoma*, showing (*e*) epiaxial and (*hy*) hypaxial muscles; *h*, hæmal arch; *n*, notochord; *r*, ribs.

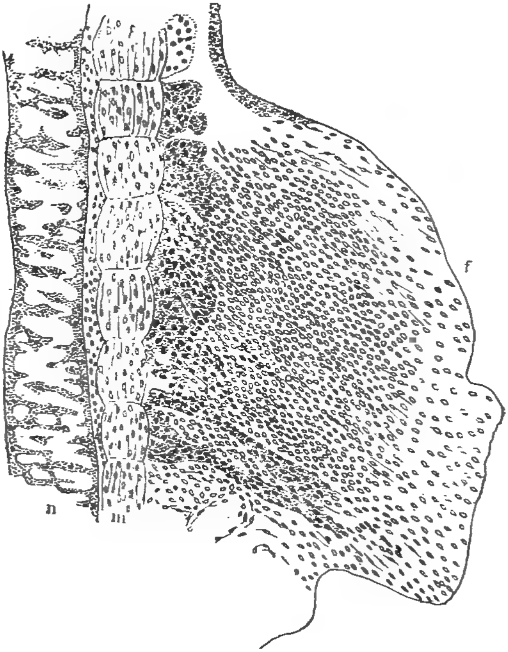

FIG. 120. Developing fin of trout, after Corning. *f*, fin; *m*, myotomes; *n*, notochord. Strands of cells can be traced from several myotomes into the fin.

head and those myotomes which form the muscles of the limb. The process for the formation of the posterior fin is essentially the same.

In the head region, although no little study has been devoted to the subject of the mesoderm segments, naturalists are not in unison as to their results. Not only is there a difference of opinion as to the number of myotomes developed in this region, from the nine recognized by van Wijhe to the seventeen or more claimed by Dohrn and Killian, but it is even disputed whether these be true somites. The questions involved will be taken up in another place. Setting these points aside, it may briefly be said that in those forms which have been most carefully studied (the elasmobranchs) there are ten[1] myotomes developed in the head region. Each of these which occur in front of the ear is completely separated from its fellows, a fact which leads some to believe that we have to do here, not with the whole mesothelial structures as in the trunk region, but with merely the myotome zone. This matter, however, would seem to have less importance than is sometimes given to it; for we must remember that the vertebrate head is an extremely complicated structure, all the parts of which have been greatly modified, while the appearance of the gill slits is of itself sufficient to explain the absence of a continuous metacœle.

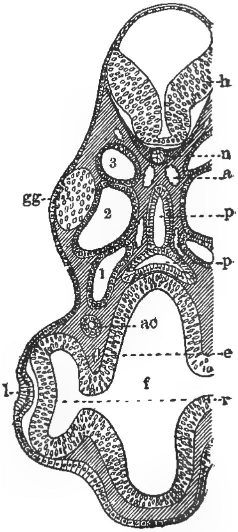

FIG. 121. Section through the head of embryo *Acanthias* at about the stage of Fig. 122. *a*, aorta; *ac*, anterior (premandibular) head cavity; *e*, pigmented epithelial layer of eye; *f*, fore brain; *gg*, Gasserian ganglion; *h*, hind brain; *l*, lens of eye; *n*, notochord; *p*, pharynx; *r*, retinal layer; 1, 2, 3, head cavities.

To the muscle fibres, the development of which was outlined above, other parts of mesenchymatous origin are added in the development of the definitive muscle. This connective

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[1] There is clearly *one* pair of cœlomic cavities in front of the first recognized by van Wijhe (Fig. 121, *ac*).

tissue wanders in among the separate muscle cells, forms an envelope (**perimysium**), and binds these together into bundles, and bundles into muscles. This perimysium, which extends beyond the contractile or true muscular portions, also forms the means of attachment[1] of the muscles to the parts which are to be moved; it gives rise to what are known as tendons, sometimes, as in the extremities, of considerable length. Tendons may occur not only at the ends, but in the middle of muscular tracts. When forming broad, flat sheets, tendons are called **fascia** or **aponeuroses.** Frequently ossification may occur in tendons, familiar examples being found in the patella or knee-pan of man, the bony tendons in the 'drumstick' of many birds (turkeys), etc.

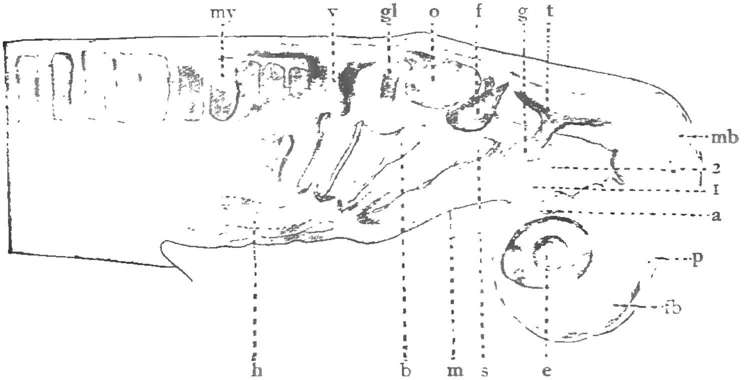

FIG. 122. Anterior end of embryo dogfish, *Acanthias*, viewed as a transparent object. *a*, anterior head cavity; *b*, first true gill cleft; *e*, eye; *f*, facial nerve; *fb*, fore brain; *g*, Gasserian ganglion; *gl*, glossopharyngeal nerve; *h*, heart; *m*, position of mouth; *mb*, mid brain; *my*, myotome; *o*, auditory capsule; *p*, pinealis; *s*, spiracular cleft; *t*, trigeminal nerve; *v*, vagus nerve; 1, 2, first and second head cavities of van Wijhe.

In shape the muscles vary extremely. In the trunk region, as a rule, they are short and more or less flattened; in the extremities they are usually prismatic or cylindrical, and greatly elongate. They may have one or several 'heads' or points of

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[1] That attachment of a muscle which usually remains without motion in the contraction of a muscle is spoken of as its **origin**; the attachment to a movable portion as its **insertion**.

origin (biceps, triceps, etc.); one or several points of insertion (pinnate, bipinnate, serrate, etc.).

In the fish-like vertebrates the trunk muscles clearly show their myotomic origin, for myotomes and the intervening myocommata are strikingly in evidence. Even here there is a tendency toward specialization, for a horizontal connective tissue partition divides the muscles of each half of the body into dorsal and ventral portions (p. 109); while in the ventral region occurs a subdivision into a median **rectus** muscle, and a more lateral **oblique** muscle (the names being indicative of the direction of the muscle fibres). These same features can be traced more or less clearly in the higher vertebrates, complications being introduced by the greater development of those muscles which, while having their origin on the trunk, serve to move the limbs, and by the subdivision of the others, into distinct regions. Thus the **rectus** may be divided into a **rectus abdominis,** extending from the

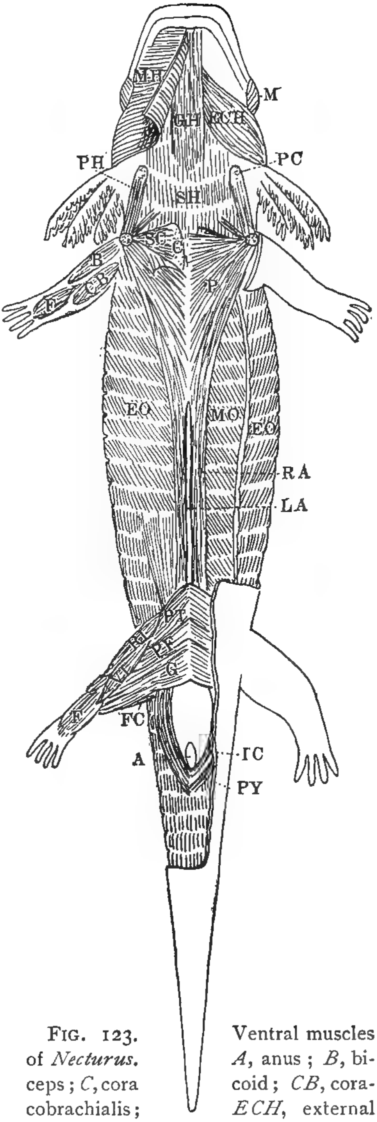

FIG. 123. Ventral muscles of *Necturus*. *A*, anus; *B*, biceps; *C*, coracoid; *CB*, coracobrachialis; *ECH*, external ceratohyoid; *EO*, external oblique; *F*, flexor communis; *FC*, femorocaudalis; *G* gracilis; *GH*, geniohyoid; *IC*, ileocaudalis; *LA*, linea alba; *M*, masseter; *MH*, mylohyoid; *MO*, middle oblique; *P*, pectoralis; *PC*, procoracoid; *PF*, pubofemoralis; *PH*, procoracohumeralis; *PT*, pectineus; *PY*, pyriformis; *RA*, rectus abdominis; *RI*, rectus internus; *SC*, supracoracoid; *SH*, sternohyoid; *VI*, vastus internus.

pelvis to the breast-bone, a **sterno-hyoid** from the sternum to the hyoid region, and a **genio-hyoid** from the hyoid to the extremity of the lower jaw. Similarly the oblique muscles may be subdivided into three or more layers (**internal** and **external oblique, transverse,** etc.); **intercostals,** between the ribs; **scalenes,** from the anterior ribs to the side of the neck, and **sterno-** and **cleido-mastoid** from the breast-bone and clavicle to the skull. In the dorsal half of the trunk also a large number of separate muscles may be distinguished, — **spinales,** between the spinal processes of the vertebræ; **inter-transversales,** between the transverse processes; **longissimus dorsi,** arising from the ribs and transverse processes, and extending along the back (continued in the cranial region as the **trachelo-mastoid**); **recti capitis,** etc. The muscles of the diaphragm are indirectly derived from the ventral portion of the myotome.

In the gill region of the branchiate vertebrates special muscles are developed from the corresponding myotomes to open (**levator** and **depressor arcuum**) and to close (**constrictors**) the gill slits. With the loss of the gills these muscles change in their functions, and become connected with the hyoid or disappear. The jaws are opened by a **digastric** muscle arising from the base of the skull, and inserted on the angle of the jaw, while closure of the mouth is effected by adductors, called **masseter, temporalis,** or **pterygoid,** according to their origin from different regions of the skull.

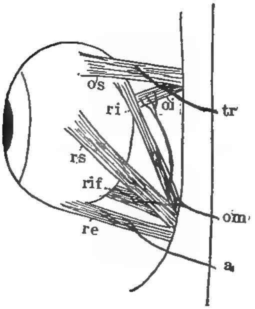

FIG. 124. Eye muscles and nerves in shark. *a*, abducens; *om*, oculomotor; *t*, trochlearis nerves; *oi*, *os*, inferior and superior oblique muscles; *re*, *ri*, *rif*, *rs*, external, internal, inferior, and superior rectus muscles.

The muscles which move the ball of the eye are, in all vertebrates, six in number, and are derived from the three anterior head somites of van Wijhe (p. 111). The most anterior of these develops into three **rectus** muscles, — **superior, internal,** and **inferior,** and into the **inferior oblique**; the second furnishes the **superior oblique,** and the third the **external rectus.** It is interesting to note that the nerve supply of these muscles corresponds to this origin (see cranial nerves). These muscles move the eye, and in many forms are re-enforced by a **retractor bulbi,** apparently derived from the third head segment.

Beneath the skin of mammals there occurs a general muscular layer, the **panniculus carnosus,** concerning which our information is none too extensive. From this layer are developed in the facial region 'muscles of expression,' which serve to move the skin, especially that around the mouth and eyes. The fact that these muscles of expression are innervated by the facial nerve would apparently indicate their point of origin as behind the jaws.

The muscles which move the limbs are divided into **intrinsic** (those which have their origin and insertion on the bones of the limb or of the supporting girdle) and **extrinsic** (which arise from the trunk and are inserted on the girdle or on the limb). In the fishes neither series acquires extensive development; but with the more varied movements necessary in a terrestrial life both sets, and especially the intrinsic, attain a high grade of differentiation. Both series may be grouped as dorsal and ventral, and these divisions again may be considered accordingly as they are preaxial or postaxial in position; i.e., accordingly as they are in front of or behind the axis of the limb. The proximal extrinsic and intrinsic preaxial muscles act as **protractors,** serving to move the limb forwards, the postaxial as **retractors,** which move it in the opposite direction. The other intrinsic muscles are divided between **flexors,** which bend the limb upon itself, and **extensors,** which straighten it after flexion. For the details of these muscles reference must be made to special works.

Eletrical Organs. — In certain fishes, *Torpedo,* electrical eel (*Gymnotus*), *Malapterus,* and to a less degree in some skates (*Raia*), certain of the muscles become metamorphosed into an electrical organ. This organ lies in the *Torpedo* on either side of the head; in the others in the trunk or tail near the backbone. In all the organ consists of a series of capsules of connective tissue filled with a gelatinous substance in which are the 'electrical plates,' in which the nerves terminate, and which are apparently the modified motor end-plates of the muscle.

The discharge of the organ is under control of the will, and varies in strength according to the size of the organ and its condition of fatigue: in the torpedo and electrical eel it is sufficient to knock a man down, but in the others it is much less in amount.

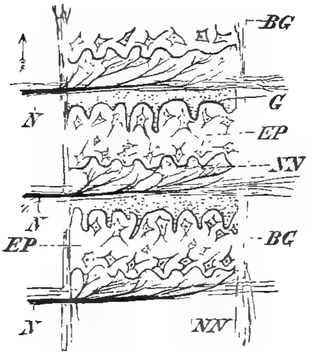

FIG. 125. Diagrammatic section of electrical apparatus, from Wiedersheim. The arrow points dorsally or anteriorly. *BG*, connective tissue framework; *EP*, electrical plates; *G*, gelatinous tissue; *N*, nerves entering through the septa; *NN*, terminations of the nerves.

UROGENITAL ORGANS.

The excretory and the reproductive organs of the vertebrates are so closely related to each other that it is impossible to treat them separately. The excretory glands (**nephridia**), reproductive organs proper (**gonads**), and the ducts to carry away the nitrogenous waste and the reproductive elements, stand in close relation to each other in position, development, and function. Hence we speak of urogenital organs.

Nephridia. — Under the head of nephridia are to be included three different structures which appear in the vertebrates, — a **pronephros** ('head kidney' of older writers); a **mesonephros** or **Wolffian body**; and a **metanephros,** which is the functional kidney in the amniotes. Pronephros and mesonephros appear only as embryonic structures in the amniotes; but in the lower groups the pronephros is usually functional for a time, the mesonephros assuming its work in the adult.[1] These organs have a regular succession in time, and hence in our account we follow the order of development and begin with the pronephros.

It will be remembered (p. 101) that the walls of the mesothelial cavities on either side are divisible into three zones, and that segmentation only affects the dorsal and middle of these, the hypomere being unsegmented. The nephridial structures

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[1] In the elasmobranchs the pronephros is never functional, while apparently in *Bdellostoma* (a cyclostome) the whole excretory organ is pronephric.

arise almost entirely from the mesomeric segments (nephrotomes). The pronephros arises from a few[1] nephrotomes immediately behind the head. From the outer wall of each of these an outgrowth occurs, — sometimes solid at first, but usually hollow from the beginning, — its apex directed towards the skin. These outgrowths form the **pronephric tubules,** each of which opens at the inner end, by means of the remains of the cavity of the mesomere, into the body cavity, the opening being funnel-shaped and, in its full development, ciliated. These openings are the **nephrostomes.** Distally the tubules of the successive segments fuse together, thus giving rise to a longitudinal tube, the **pronephric duct,** which gradually extends backwards behind the pronephric segments, until at last it fuses with the cloaca or with the skin immediately adjoining. An opening now forms between the duct and the cloaca, and thus, through the system of tubes leading from the nephrostomes to the vent, the body cavity is placed in connection with the external world.

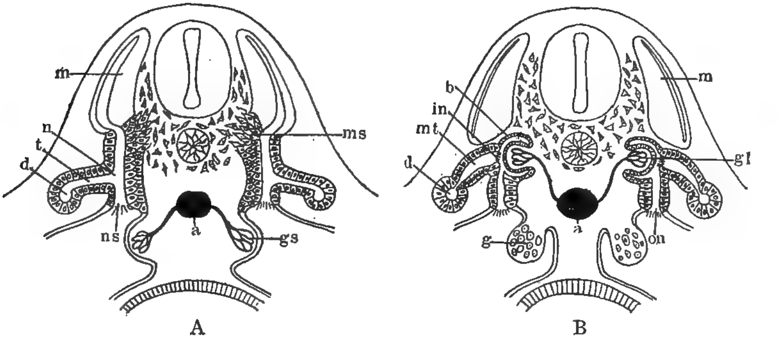


FIG. 126. Diagrams of the relations of pro- and mesonephros, based on Semon. Mesomeric structures shown with conventionalized cells. *A*, pronephros; *B*, mesonephros. *a*, aorta; *b*, Bowman's capsule; *d*, pronephric duct; *g*, gonad; *gl*, glomerulus; *gs*, glomus; *in*, inner nephrostome; *m*, myotome; *ms*, formation of mesenchyme; *mt*, mesonephric tubule; *n*, cavity of nephrotome; *ns*, nephrostome; *on*, outer nephrostome; *t*, pronephric tubule.

[1] Two in most urodeles and amniotes; three in lampreys, some sharks, anura, and some amniotes; four in some sharks, seven or eight in skates, and a dozen in cæcilians. It has been pointed out that in general terms the number of pronephric nephrotomes is roughly correlated to the number of segments in the whole body.

This backward growth of the pronephric duct is apparently (at least in most forms) the result of growth of the duct itself, without any cellular additions from other sources; although a few years ago the duct was described in most vertebrates as being wholly of ectodermal origin, a view arising from the fact that the duct in its progress fuses with that layer.

A second pronephric element is the **glomus.** The dorsal arterial blood-vessel (aorta) gives off an arterial twig on either side opposite each nephrostome. Each artery breaks up into a vascular network just beneath the dorsal splanchnic epithelium of the hypomere (Fig. 126, *A*), and pushes out so that the structure projects into the dorsal portion of the body cavity. This vascular outgrowth is the glomus. In most vertebrates it is unsegmented, but forms a continuous rete mirabile, and projects freely into the cœlom. In certain forms, however (*e.g.*, *Ichthyophis*), the glomus becomes distinctly segmented, while the dorsal portion of the body cavity becomes cut off from the rest, forming a separate envelope (Bowman's capsule) around each glomar segment, so that here we have a series of vascular capsules almost exactly comparable to the Malpighian bodies to be described in connection with the mesonephros.

There is considerable evidence to show that the pronephros originally had a much greater extent than in most existing forms; and indeed the structure may have extended nearly to the vent, as is apparently the case in *Bdellostoma,* if we may judge by recent studies. Its fate in all vertebrates except this cyclostome will be better understood after a history of the mesonephros.

The mesonephros or Wolffian body is usually confined to segments behind the pronephros, and is often spoken of as a later generation of excretory structures. The fact, however, that pro- and mesonephric tubules can occur together in the same segment tends to show that the two structures are distinct.

The mesonephric tubules are formed in a manner similar to the pronephric tubules, except that they arise from the more dorsal portion of the nephrotome. They grow outwards, and finally connect with the pronephric duct, although they do not participate in its formation. From this time on the pronephric duct is usually called the **mesonephric** or **Wolffian duct.** The aorta likewise forms segmental twigs, which grow out towards the splanchnic layer of the nephrotome, and give rise to a series of vascular networks, the **glomeruli,** which differ from the glomus of the pronephros in that they project not into the larger body cavity (splanchnocœle), but into the cavity of the nephrotome, and in their segmental arrangement. The walls of the nephrotome close over each glomerulus, and are henceforth known as **Bowman's capsule,** while the whole complex of capsule and glomerulus form a **Malpighian body** or **corpuscle.** The mesonephric tubule opens into Bowman's capsule by means of an **inner nephrostome,** while the lower portion of the nephro-

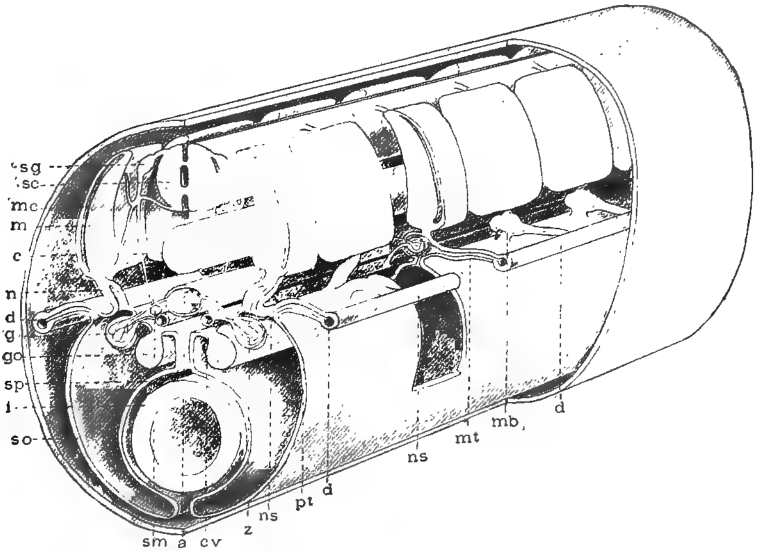


FIG. 127. Diagram of the development of the nephridial system in the vertebrate. The pronephric system is according to the views of Semon; it is more probable that they arise from the nephrotomes instead of from the somatic layer. *a*, aorta; *c*, notochord; *cv*, cardinal vein; *d*, pronephric duct; *g*, glomus; *go*, gonad; *i*, intestinal epithelium; *m*, myotome (muscular layer); *mb*, Malpighian body; *mc*, myocœle; *mt*, mesonephric tubule; *n*, nephrotome; *ns*, nephrostome; *pt*, pronephric tubule; *sc*, spinal cord; *sg*, spinal ganglion; *sm*, sympathetic ganglion; *so*, somatic layer; *sp*, splanchnic layer; *z*, cavity of nephrotome. Compare with Fig. 111.

tome cavity retains its connection with the metacœle, the opening forming the outer nephrostome (Fig. 126, *B*).

As was stated above, pro- and mesonephros are the only excretory organs in the ichthyopsida. They appear as larval structures in the amniotes, and only in certain reptiles does either of them function after hatching. In the adult ichthyopsidan the pro- and mesonephros are usually readily distinguished, the pronephros being in front, rudimentary in character, and separated by a greater or less distance from the Wolffian body, which usually extends along the greater part of the dorsal wall of the body cavity.

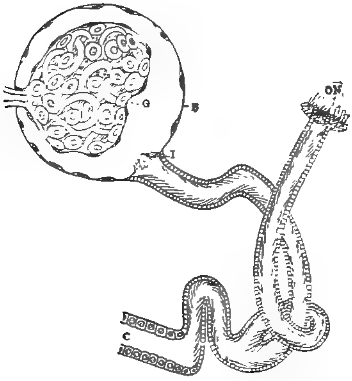


FIG. 128. A single tubule of the mesonephros of *Proteus anguineus* modified from Spengel. *C*, beginning of collecting tubule; *B*, Bowman's capsule; *G*, glomerulus; *I*, *ON*, inner and outer nephrostomes.

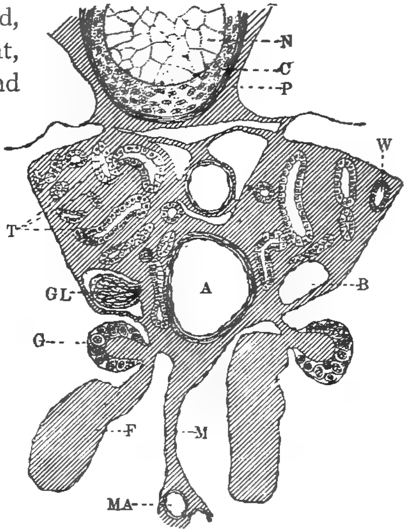


FIG. 129. Section through the mesonephric region of *Amblystoma*, 45 mm. long. *A*, aorta; *B*, Bowman's capsule, from which the glomerulus has dropped out; *C*, cartilage, and *P*, bone of vertebral centrum; *C*, gonad; *GL*, glomerulus; *M*, mesentery; *MA*, mesenteric artery; *N*, notochord; *T*, mesonephric tubules; *W*, Wolffian duct.

The pronephros acquires a varying development in different vertebrates. In the elasmobranchs its tubules never become convoluted, and in very early embryonic life the nephrostomes fuse so that a single large opening connects the cœlom with the pronephric duct, and forms the anterior end of the Mullerian duct to be described below. In the amniotes, also, the pronephros never advances beyond a very rudimentary condition, and soon degenerates, and, to a greater or less extent, disappears. In ganoids, teleosts, and amphibia the pronephros is functional for a time. The tubules become greatly convoluted, and between them is developed a rich plexus of sinus-like blood-vessels. Later it degenerates in all except a few teleosts (*Fierasfer*, *Dactylopterus*), where it remains functional throughout life, while in others it retains its excretory character until the approach of sexual maturity. In these teleosts with functional pronephros the funnels connect with the pericardial cavity (the same condition has been described in cyclostomes), a relation readily understood from the method of formation of the pericardial walls. In its degeneration the pronephros contributes to the formation of the supra-renal bodies to be described below.

In its development the mesonephros progresses beyond the stage at which it was left above. The tubules, instead of being short and transverse, become greatly convoluted, and they also increase greatly in number, new tubules, with funnels and Malpighian bodies, being developed by budding dorsal to the primary tubules; and after a convoluted course these secondary and tertiary tubules join the distal ends of the first, which thus become converted into collecting tubules, emptying into the pronephric duct. With this formation of new tubules the mesonephros largely loses the segmental character that it earlier possessed.

With the convolution and increase in number of the tubules blood-vessels enter between these structures, and form a rich capillary plexus surrounding them. The cells of the tubules become cubical and excretory in character. This increase in number and size of the tubules increases the size of the organs, so that they protrude into the cœlom as a ridge on either side of the mesentery.

The physiological action of pro- and mesonephros is apparently as follows: Blood from the aorta enters the glomus or glomeruli, through the walls of which it loses water, which passes (pronephros) into the cœlom or (mesonephros) into Bowman's capsule, and from thence into the tubules. From the glomeruli the blood next passes into the plexus surrounding the tubules, and here, by means of the cubical cells, loses its nitrogenous waste (uric acid, urates, etc.). By means of the cilia surrounding the nephrostomata, watery matter is also taken from the cœlom, and all of these waste products are passed via the pronephric duct to the exterior.

In teleosts and ganoids all of the mesonephros is excretory; but in elasmobranchs and amphibians the anterior end loses this function and becomes largely degenerate (females), or enters into the service of the reproductive structures (males), as will be described below. In the amniotes the whole mesonephros degenerates and disappears, except in so far as it enters into connection with the gonads, and is represented by the paradidymis and parovarium (*infra*).

To compensate for this disappearance a third excretory organ, the **metanephros**, or **kidney** proper, is developed in the amniotes. Its developmental history is not so well known as that of the pro- and mesonephros, and the following statement is only tentative. A hollow diverticulum arises from the dorsal surface of each pronephric duct, near its entrance into the cloaca. This grows rapidly forward near the aorta, and develops into the excretory duct (**ureter**) of the metanephros. As it grows forward the mesoderm behind the Wolffian body rapidly proliferates, and becomes richly vascular. When the ureter reaches the hinder end of the Wolffian body it expands, giving rise to the pelvis of the kidney, and produces, by budding from its tip, cords of cells which soon become tubular, and form the collecting tubules of the kidney. In the proliferated mesoderm other tubules also appear (the method of their formation is not clear) connected with Malpighian bodies, essentially like those of the mesonephros. These metanephric tubules become greatly convoluted, and at

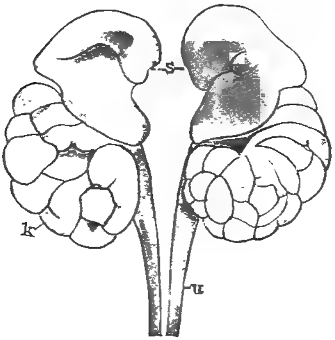


FIG. 130. Kidneys (*k*) and suprarenals (*s*) of a human embryo, after Wiedersheim. The figure shows the lobulated appearance of the early kidney.

last open into the collecting tubules; but it is important to note that at no time are nephrostomata developed in connection with them, and the body cavity is without communication with this nephridial system. While this process is going on the whole metanephros pushes farther forward, dorsal to the pronephric duct, the ureter increasing correspondingly in length. In the subsequent history the kidney becomes strongly lobulated, the lobes corresponding to the groups of collecting tubules of which it is composed. This lobular appearance is retained throughout life in the sauropsida, but is subsequently lost in all mammals except the whales and some carnivores.

The kidney never extends through as many segments as does the mesonephros, but forms a relatively smaller and more compact body lying within or a little in front of the pelvic region. In the mammals the anterior end of the ureter becomes widened out, inside of the mass of the kidney, into a considerable chamber, the **pelvis** of the kidney, into which the collecting tubules empty, the openings of these being placed on one or more papillæ, which extend into the pelvis renalis, partially dividing it into smaller chambers or **calyces.**

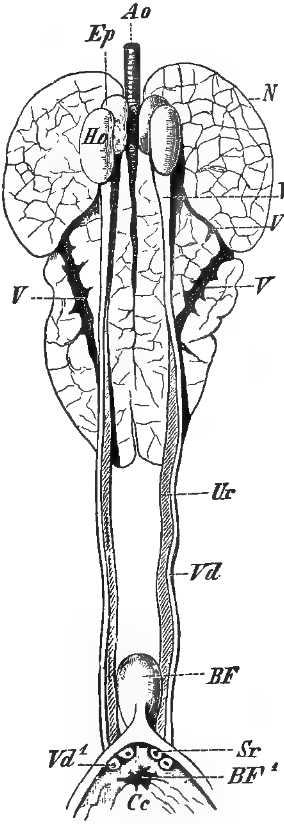
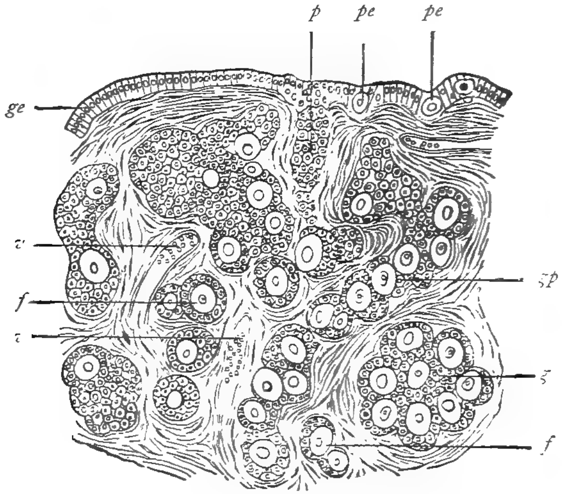


FIG. 131. Urogenital system of male heron (*Ardea*), from Wiedersheim. *Ao*, aorta; *BF*, bursa Fabricii, opening at *BF′* into the cloaca, *Cc*; *Ep*, epididymis; *Ho*, testes; *N*, kidney; *Sr*, opening of ureter; *V*, furrows for veins on ventral surface of kidney; *Vd*, vasa deferentia; *Vd′*, their opening into cloaca.

The ureter does not long retain its primary connection with the distal end of the pronephric duct, but acquires its own opening into the dorsal portion of the cloaca; and then this cloacal region becomes constricted off from the rest to form a urinary bladder, which is connected directly or indirectly with the exterior by a single duct, — the urethra. The bladder persists throughout life in lizards, turtles, and mammals, but disappears in the other amniotes.

Reproductive Organs. — To those structures which are to produce the reproductive cells, — eggs and spermatozoa, — the term **gonads** has been given. These are paired (unless fusion or abortion of one occur), and arise from the epithelium lining the body cavity, nearer the median line than the nephrostomata (see Fig. 127, *go*). In this region, which may extend nearly the length of the body cavity or which may be more restricted, the epithelium retains its original columnar character, and even increases it, while in all other regions it becomes converted into a pavement epithelium. The underlying mesenchyme increases in amount, pushing the germinal epithelium out into the body cavity as a longitudinal ridge. It is usually stated that in the earlier stages the gonads are segmental in



IG. 132. Section of ovary of new-born child, from Hertwig after Waldeyer. *f*, single egg surrounded by follicle cells; *g*, group of egg cells and follicle cells; *ge*, germinal epithelium; *p*, egg strings; *pe*, primordial ova; *v*, blood-vessels.

character; *i.e.*, are divided into segments, which, in harmony with the names given other regions, have been called **gonotomes,** but the accuracy of these statements has been disputed recently. In the earlier stages certain of the epithelial cells become larger than their fellows; and these are called the **primordial ova** and the **primordial seminal cells,** accordingly as they are to give rise to eggs or spermatozoa. For a considerable length of time one cannot say, from an examination of these primordial cells, whether they are to develop into one or the other of these reproductive cells; but other structures enable us to decide at an early date, in most vertebrates, whether we have to deal with a male or a female, and so between testes and ovaries.

The **ovaries** are those gonads which are to give rise to the eggs or **ova.** Briefly stated, portions of the epithelium covering the gonad sink into the deeper portion of the ovary, carrying with them the primordial ova, while the other cells arrange themselves as **follicles** around these ova. In this position the ova increase rapidly in size, in part by what must be called a devouring of their neighbors, in part by nourishment furnished through the follicular cells from the richly vascular mesenchyme adjacent. In the mammals these follicles undergo a peculiar modification, and have secured the special name of **Graafian follicles.** The follicular epithelium becomes several cells in thickness and then splits, thus forming an internal cavity, filled with fluid, to one side of which the ovum, surrounded by a few follicular cells, remains attached (Fig. 133). This region is the **discus proligerus.** When fully formed the follicle rises to the surface of the ovary, and at the proper time,

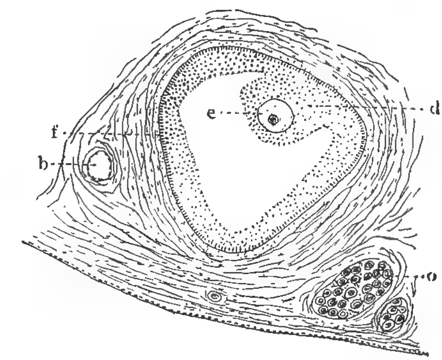


FIG. 133. Portion of ovary of cat. *b*, blood-vessel; *d*, discus proligerus; *e*, nearly mature ovum; *f*, follicle epithelium; *o*, clusters of immature ova.

by rupture of the surrounding walls, the egg escapes. In the higher vertebrates usually but a single egg escapes at a time, but in the ichthyopsida hundreds or even thousands may pass out from the ovary in a few hours. As will be understood from the relations of the ovary, the eggs upon their escape pass into the cœlomic cavity, from which they pass to the exterior, in the case of some fishes, by means of the abdominal pores, but in most vertebrates through the Müllerian duct.

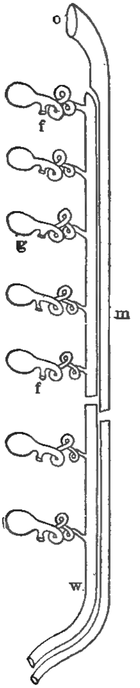


FIG. 134. Division of pronephric duct into Müllerian (*m*) and Wolffian (*w*) ducts in elasmobranchs; *f*, funnels; *g*, glomeruli of mesonephros; *o*, ostium tubæ formed by fusion of pronephric funnels.

At first the ovaries are simple ridges projecting slightly into the cœlom, but as they increase in size they become more distinct from the body wall, until at last they are only supported by a double fold of the peritoneum, like a mesentery, the **mesovarium.**

The male gonads which produce the spermatozoa are called **testes,** and, like the ovaries, their essential portions are derived from the germinal epithelium. This in places sinks into the underlying mesenchyme as cords of cells. Later these cords become hollow (**canaliculi seminiferi**), and from certain large round cells in their walls, the spermatozoa are formed by cell division. In the case of the testes there is the same formation of a mesenterial support (**mesorchium**) as was noted for the ovary.

The Urogenital Ducts. — In teleosts, ganoids, and cyclostomes the pronephric duct remains without essential alteration, functioning solely as an excretory duct. In the elasmobranchs it divides into two tubes. In the mesonephric region its lumen becomes oval in section, the collecting tubules emptying into the dorsal portion. It now divides lengthwise back as far as the cloaca, while in front the division stops just in front of the mesonephros (Fig. 134). The dorsal of the two resulting tubes is the **Wolffian (Leydig's) duct,** the ventral the **Müllerian** duct.

The former retains its connection with the menesophros; but the Müllerian duct loses all connection with the Wolffian body, and opens into the cœlom by means of the fused nephrostomes of the pronephros, — the **ostium tubæ abdominale.**

In all other vertebrates a Müllerian duct is formed, according to the older accounts in the same way as in the elasmobranchs, but according to most recent writers as a new formation. An ingrowth of cœlomic epithelium begins at the anterior end of the mesonephros, and continues backward until the cloaca is reached. During its growth it becomes tubular, and at its anterior end it opens widely into the cœlom, behind into the cloaca. It thus forms a Müllerian duct essentially like that of elasmobranchs in structure, but greatly different in origin. In all cases the duct receives, in addition to the epithelium, mesenchymatous tissue, which makes up the bulk of its walls.

The Müllerian duct in the female of both elasmobranchs and of higher vertebrates henceforth functions as an oviduct. The eggs, which escape from the ovary, pass into its funnel (ostium), and are thence conducted to the exterior. It may remain a simple tube, or more usually distinct regions may be specialized in it, each with distinct functions. Most constant of these, except in mammals,[1] are regions which secrete the protective envelopes — shell, egg membrane, etc. — around the egg. In those forms which bring forth living young (mammals, many elasmobranchs, etc.) one portion of the duct becomes specialized to retain the egg during its development, and receives the name **uterus** in those forms where the growing young acquires attachment to the lining walls. With the development of the uterus that portion of the Müllerian duct in front is called the **Fallopian tube,** while the post-uterine portion forms a **vagina.** In the lower mammals as in the lower vertebrates the Müllerian ducts usually remain distinct from each other throughout their length, the result being two uteri and two vaginæ; in the higher mammals a fusion of the posterior end of the ducts of the two sides occurs, resulting in a single vagina, and usually of an unpaired uterus, the latter showing more or

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[1] The monotremes differ from the other mammals in this respect.

less clearly traces of its double origin, as in cases of bicornuate uteri.

In the male the Müllerian duct almost entirely disappears, a portion of its anterior end persisting as the **stalked hydatid** (or **hydatid** of **Morgnani**), somewhat closely connected with the epididymis (see below), while the posterior end occasionally retains its lumen, and is known as the **uterus masculinus.**

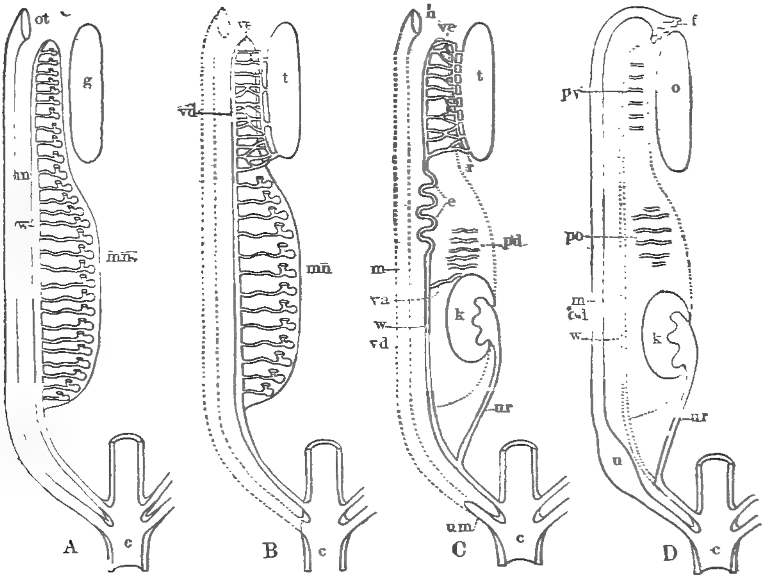

FIG. 135. Diagram of the modifications in the urogenital apparatus. *A*, indifferent and also the female ichthyopsidan: *B*, male amphibian; *C*, male amniote; *D*, female amniote. *c*, cloaca; *e*, epididymis: *f*, fimbriated extremity of Fallopian tube; *g*, gonad; *h*, stalked hydatid; *k*, kidney (metanephros); *m*, Müllerian duct; *mn*, mesonephros (Wolffian body); *o*, ovary; *od*, oviduct; *ot*, ostium tubæ; *pd*, paradidymis; *po*, paroöphoron; *pv*, parovarium: *r*, rete; *t*, testes; *u*, uterus; *um*, uterus masculinus; *ur*, ureter; *va*, vas aberrans; *vd*, vas deferens; *ve*, vasa efferentia; *w*, Wolffian duct.

The history of the Wolffian duct is somewhat different. In the female its anterior end degenerates; and in the amniotes, where the metanephros usurps the functions of the mesonephros, this degeneration extends to the whole tube. The only portions which persist are, a rudimentary structure behind known as **Gärtner's duct,** and in front where it comes in connection with a small body known as the **parovarium** or **epoöphoron**[1] formed from the degenerate tubules of the mesonephros.

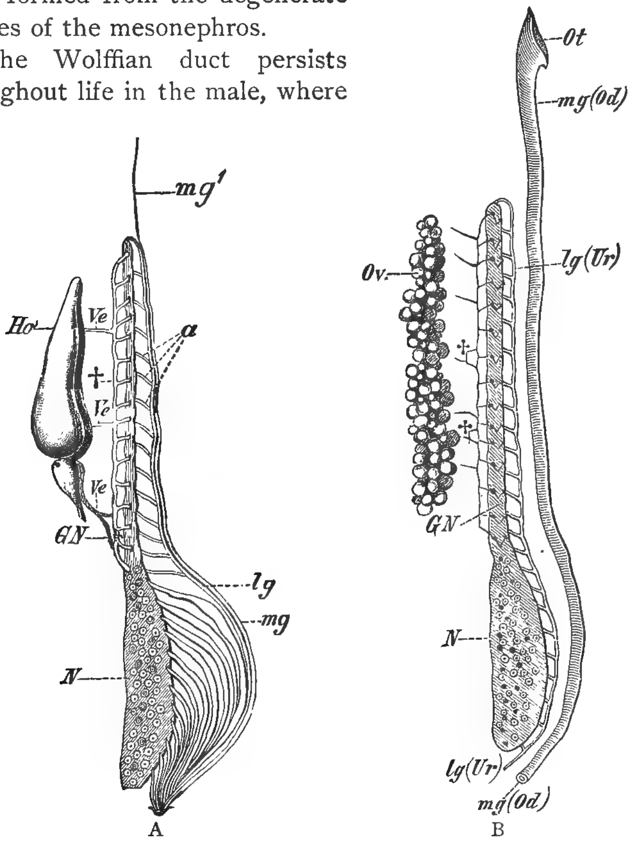

FIG. 136. Scheme of urodele urogenital system based on *Triton,* from Wiedersheim after Spengel. *A,* male; *B,* female. *a,* excretory ducts; *GN,* sexual part of mesonephros; *Ho,* testis; *lg,* Leydig's duct (ureter); *mg,* Müllerian duct (oviduct in *B*); *mg',* its vestigial end in the male; *N,* functional portion of mesonephros; *Ov,* ovary; *Ot,* ostium tubæ; *Ve,* vasa efferentia; + collecting duct of the vasa efferentia (rudimentary in *B*).

The Wolffian duct persists throughout life in the male, where it acquires new functions. Here the anterior end of the mesonephros loses its excretory powers, and enters into con-

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[1] In amniotes, where the whole mesonephros degenerates, the posterior portion of the Wolffian body in the female forms a **paroöphoron** behind the ovary, a structure of only vestigial importance.

nection with the testis. Its tubules branch and anastomose, and also connect with the seminiferous canaliculi, forming a system of ducts conducting the spermatozoa into the anterior end of the Wolffian duct. This plexus of tubules nearest the testis is the **rete,** nearer the duct it forms the **vasa efferentia.** The Wolffian duct, by this assumption of reproductive functions, is converted into a **vas deferens,** the anterior part of which becomes greatly coiled, this portion being known as the **epididymis.** More distally the duct may develop marked muscular walls and form an ejaculatory structure.

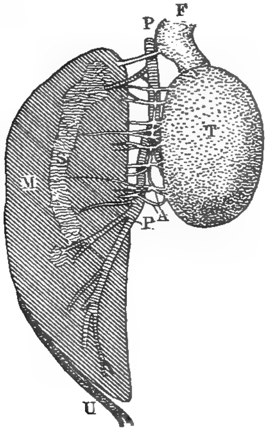

Fig. 137. Urogenital organs of male frog; the testis, *T*, turned to one side to expose *A*, the vasa efferentia passing from the testis to *M*, the mesonephros. *F*, posterior end of fat body; *P*, postcava; *S*, suprarenal; *U*, ureter.

As was said above, the posterior portion of the mesonephros retains its excretory powers in the ichthyopsida, and as it pours its secretions into the Wolffian duct, this tube in the male is at once excretory and reproductive in character. In the male amniotes, when the metanephros is developed, the posterior part of the mesonephros degenerates into a small body close to the epididymis known as the **paradidymis** (**organ** of **Giraldi**), and occasionally forms one or more blind tubes (**vasa aberrantia**), opening into the vas deferens.

In some vertebrates the Wolffian and Müllerian ducts open directly into the cloaca, but in most they unite into a **urogenital sinus,** which, in turn, empties by a single opening into the cloaca. In the mammals (monotremes excepted) the separation of the urogenital sinus from the hinder end of the alimentary canal is complete, a muscular partition (**perineum**) separating the vent from the urogenital opening.

Connected with the urogenital structures outlined above are many accessory parts, — glands, external genitalia, copulatory organs, etc., — some of which will be described in connection with the groups in which they occur. Others will be found in the larger manuals to which reference must be made. Only one of these structures seems to demand attention here. This is the **suprarenal body,** which derives its name from the fact that in the mammals it forms a capsule-like structure on the anterior end of the kidney. In the sauropsida it is in closer connection with the gonads. In the amphibia (Fig. 137) it is either on the ventral surface of the mesonephros (anura), or upon its medial margin (urodeles). In the teleosts it is either closely connected with the mesonephros, or is farther forward in the region of the degenerate pronephros. In the elasmobranchs the suprarenal is replaced by two structures: (1), an **interrenal,** a long, slender body just medial to the ureter, those of the two sides being connected behind; (2), a series of **adrenals,** on either side closely connected with the sympathetic ganglia.

Development teaches that the suprarenals consist of two portions different in origin and corresponding to the inter- and adrenals of the elasmobranchs. One portion (the cortical substance, interrenals) arises from the mesothelium, and according to recent observations, largely by a metamorphosis of the glomus of the pronephros, the mesonephros possibly contributing to some extent. The medullary substance (equivalent to the adrenals) is derived in part from the sympathetic nervous system, and contains ganglion cells, and in part is mesenchymatous in nature, this tissue arising from cells proliferated by the septum transversum.

MESENCHYMATOUS STRUCTURES.

As was stated on a preceding page (p. 8), the mesenchyme may arise from ectoderm, entoderm, or mesothelium, either by the separation of isolated cells, as is usually the case, or by the immigration of large masses of cells into the space (i.e., the remains of the segmentation cavity) between the other body layers. This immigration in large masses from the mesothelium is shown in the formation of the sclerotomes in Fig. 112, and from the ectoderm into the region of the head to form the gill cartilages in Fig. 138. The mesenchyme is characterized by the fact that it never gives rise to epithelial structures,[1] and as a rule, by the great development in it of intercellular substance, as seen in fibrous or areolar connective tissue, cartilage, bone, blood, etc. Smooth muscle tissue, however, is an exception in this respect.

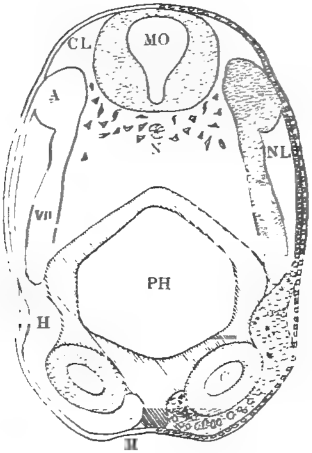

FIG. 138. Section through the head of an embryo *Amblystoma*, showing the points, *H* and *M*, where the ectoderm is producing the mesenchyme to form the hyoid and mandibular arches. *A*, auditory ganglion; *C*, cœlom of mandibular arch; *CL*, cuticular layer of ectoderm; *MO*, medulla oblongata; *NL*, nervous layer of ectoderm; *VII*, facial nerve.

Besides the connective tissues proper, which extend through all parts of the body, forming a support and connection for tissues and organs, the mesenchyme also gives rise to most of the skeletal and circulatory structures.

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[1] It is possible that the epithelium (endothelium) lining the cavities of the vascular system is of mesenchymatous origin, but the weight of evidence goes to show that some of it at least is of entodermic origin.

THE SKELETON.

The skeletal structures of the vertebrates may be either membranous, cartilaginous, or bony (osseous) in character; and in development certain portions may pass successively through all of these phases in attaining the adult condition; or the cartilage stage may be skipped, the membrane developing directly into bone; or again, the cartilaginous condition may be the final stage of the skeleton.

The membranous skeleton consists of connective tissue cells, and in its highest development forms sheets or masses of fibrous tissue. From it cartilage is developed by a great increase in the number of cells, the tissue in what has been called the **procartilage** stage consisting of closely compacted polygonal cells with large nuclei. These cells rapidly secrete an intercellular substance (chondrin), and thus the tissue becomes converted into cartilage, the extent and solidity of which are dependent upon the amount of this matrix. In the conversion of cartilage into bone this matrix is dissolved; and around the margins of the cavities thus produced bone-forming cells (**osteoblasts**) arrange themselves, and these, secreting lime salts (carbonate and phosphate) around themselves, gradually build up the bone. In the lower vertebrates this process begins upon the outside of the cartilages and proceeds toward the interior; but in the higher forms, besides this perichondrial ossification, **centres of ossification** appear within the cartilage, and from these the ossification extends peripherally. In the conversion of membrane into bone there is the same appearance of osteoblasts in and upon the tissue as described above, and these produce the bony substance in the same way. The result in either case is the same, and it is not possible by histological means to distinguish between cartilage bones and membrane bones; this depends entirely upon development. As will appear later, the distinction between the two is very important.

Increase in the size of membranes and cartilage is accomplished by additions to the exterior as well as by increase in the interstitial substance. In the case of bone this interstitial increase is impossible. Increase in size is effected here by additions to the exterior, and in the case of the long bones, bodies of the vertebræ, etc., by the appearance of more than one centre of ossification in the cartilage. From these centres ossification extends in all directions, but for a time there remains a cartilaginous region between the ends (**epiphyses**) and the main portion in which increase in length is possible. Later these epiphyses usually become so united or anchylosed to the main portion that the line of division cannot be traced.

The skeleton may be divided into internal and dermal portions, and the internal in turn is composed of an axial portion, including the vertebral column, skull, ribs, and breast-bone; and an appendicular portion, consisting of the skeleton of the appendages and the girdles supporting them.

The vertebral column is developed around the notochord (p. 17). This, as will be remembered, is a rod-like structure of entodermal origin which lies between the alimentary tract and the central nervous system, extending from just behind the infundibulum to the posterior end of the body. Its cells gradually become gelatinous, and migrate toward the periphery, where they finally become arranged in a manner recalling epithelium; while the mass of the notochord is composed of a reticulum, in the meshes of which is the rather solid jelly. The cellular envelope thus formed and its derivatives are frequently called the **elastica interna**. It is clearly of entodermal origin. The notochord has different fates in the various divisions of the vertebrates, as will be detailed later. In the cyclostomes it continues to increase in size throughout life, and constitutes the major portion of the skeletal axis; but in other vertebrates the development of vertebræ relegates it to a very subordinate position in the adult, where it may persist as a very inconspicuous remnant.

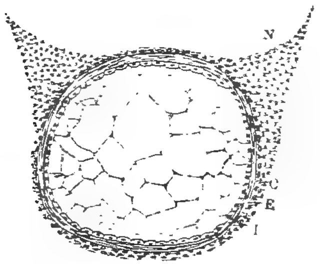

Fig. 139. Section through notochord of embryonic shark (*Acanthias*). *C*, centrum of vertebra; *E*, *I*, elastica externa and interna; *N*, neural process.

The vertebræ proper arise from mesenchymatous cells, which bud off as sclerotomes (p. 102 and Fig. 111) from the developing mesothelial tissues. Some of these cells arrange themselves as a continuous envelope around the notochord (the **notochordal sheath** or **elastica externa**), while others wander inwards, between the spinal cord, notochord, and muscle plates. It is to be noted that this skeletogenous tissue loses all segmental character, and that the segmentation later to be seen in the vertebræ is secondary, and is the result of the relations of myotomes and nerves. In the cyclostomes the notochordal sheath increases in thickness with age, and in these forms reaches its highest development.

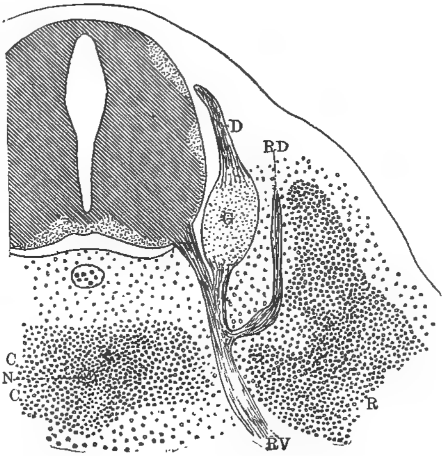

FIG. 140. Section through a developing vertebral centre of the pig, showing the multiplication of the mesenchyme cells where cartilages are to arise. *C*, vertebral centrum; *D*, dorsal; *V*, ventral roots of a spinal nerve; *G*, ganglion of dorsal root; *N*, notochord; *R*, rib; *RD*, *RV*, rami dorsalis and ventralis of nerve.

The earliest appearance of the segmental skeletal structures is seen as an increasing density of the mesenchyme between the inner surface of each myotome and the spinal cord. These more dense portions are soon converted into cartilage, the result being a series of pairs of backwardly directed rods (the **neural processes** or **neurapophyses**), which tend to arch in the spinal cord. A little later similar condensations of mesenchyme take place around the notochord, a ring of this tissue occurring opposite to each pair of myotomes. This forms the rudiment of the **body** or **centrum** of the vertebra. Its subsequent history varies greatly in different groups; and the final account cannot be written until we know more of the development, especially in the ichthyopsida. As usually described these membranous rings become directly converted into cartilage and, in the higher forms, into bone; but the little we know of development, together with the conditions occurring in the ganoids, and especially in certain fossil amphibia (stegocephali), make it probable that a vertebral body or centrum is more complicated than it was once thought to be.

The most complicated condition known is found in the fossil *Archegosaurus.* Here there occurs on the dorsal surface of the notochord on either side between two successive neural processes (Fig. 141) a skeletal plate, — the **pleurocentrum.** On the ventral surface, opposite the base of the neural process, is an arched band, the **hypocentrum**[1] (or **hypocentrum arcale**), which extends across the notochord from one side to the other. Behind this and opposite the pleurocentra are a pair of skeletal plates, — the **hypocentra pleuralia.** More usually (Fig. 142) the hypocentra pleuralia are absent. These forms belong to the **rhachitomous** type of vertebræ.

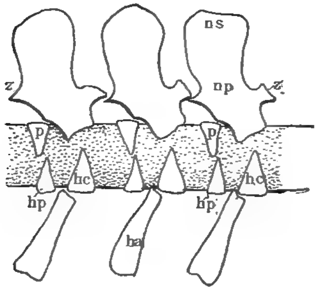

FIG. 141. Diagram of rhachitomous vertebræ, based on *Archegosaurus. ha*, hæmal process; *hc*, hypocentrum arcale; *hp*, hypocentrum pleurale; *np*, neural process; *ns*, neural spine; *p*, pleurocentrum; *z*, zygapophysis.

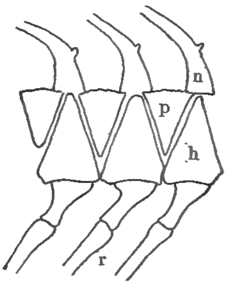

FIG. 142. Trunk vertebra of extinct stegocephalous *Eurycormus speciosus*, showing rhachitomous condition, after Zittell. *h*, hypocentrum; *n*, neural arch; *p*, pleurocentrum; *r*, radialia.

In the **embolomerous** type (Fig. 143) a vertebral body is composed of two rings, one of which is directly opposite the base of

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[1] The terms centrum and **intercentrum** often used for these parts lead to unnecessary confusion; the intercentrum is in most cases the hypocentrum arcale.

the neural process, the other between two of these rings. In development (*Amia*) this embolomerous condition is derived from the rhachitomous type by the fusion of hypocentra pleuralia with the pleurocentra to form one ring (centrum, *auct.*), while the other (intercentrum) is developed by a dorsal extension of the hypocentrum arcale. In others it may be that no hypocentra pleuralia occur, the centrum arising by a ventral extension of the pleurocentra.

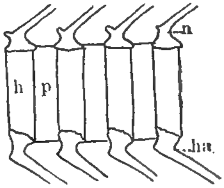

FIG. 143. Tail vertebræ of extinct stegocephalous *Eurycormus speciosus* showing embolomerous condition, after Zittell. *h*, hypocentrum; *ha*, hæmal arch; *n*, neural arch; *p*, pleurocentrum (intercentrum).

In the birds and mammals the vertebra arises at first by what has been called a vertebral bow, passing beneath the notochordal sheath and obliquely upwards and backwards to the posterior limits of the somite, while a little later the centrum proper forms behind the bow. This of course suggests a comparison with the rhachitomous vertebra.

Concerning the fates of these parts in the higher vertebrates there is a difference of opinion. American students, as a rule, regard the pleurocentra as giving rise to the body of the vertebræ in the amniotes, the intercentrum appearing as the chevron bones well known in mammals. In amphibia and teleosts, on the other hand, the vertebral body is said to arise from the intercentrum; *i.e.*, from the hypocentrum arcale. Thus the vertebræ cannot be regarded as exactly homologous throughout the vertebrate phylum. Many European authorities, on the other hand, claim that the centrum of the vertebrates arises from the hypocentrum arcale, and that the pleurocentra either contribute or give rise to the anterior zygapophyses to be mentioned later.

A third type of vertebra is the **phyllospondylous,** the relations of which to the foregoing has yet to be made out. In this the vertebral body is composed of right and left halves. This type is found in the fossil Branchiosauridæ (stegocephalous batrachia).

To the parts of the vertebræ so far described others may be added. In the embryo a ligament (interspinous ligament) runs the length of the body just dorsal to the spinal cord. Where this passes between the dorsal ends of the neural processes it becomes converted into cartilage, thus giving rise to an additional element (**spinous process** or **neural spine**), which, together

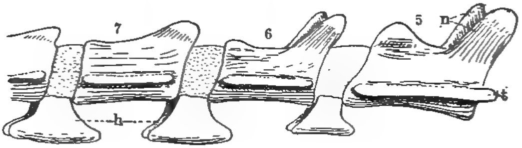

FIG. 144. Fifth to seventh caudal vertebræ of *Perameles gunni*. *h*, hæmal arch; *n*, neural processes; *t*, transverse processes.

with the two neural processes, form a **neural arch** enclosing and protecting the spinal cord. In the caudal region of the ichthyopsida and some higher forms, the vertebra is completed below by a similar **hæmal arch,** which encloses the caudal artery and vein. This arch is composed of a pair of **hæmal processes** (**hæmapophyses**) and a **hæmal spine.** These various parts of the vertebræ arise separately; but they exhibit in recent forms a tendency to fuse together in the adult, the fusion being most complete in the higher groups.

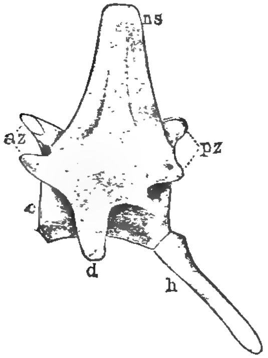

FIG. 145. Caudal vertebra of alligator. *az*, prezygapophysis; *c*, centrum; *d*, diapophysis; *h*, hæmal arch; *ns*, neural spine; *pz*, postzygapophysis.

The vertebræ are laid down at an early stage in development, and their number is not subsequently increased. Increase in length of body is therefore accomplished by longitudinal growth of the centra of the vertebræ. In the fishes additions are made, as it were, in layers, on the circumference of the centrum first formed, each new layer being slightly longer than its predecessor. As a result the centrum becomes concave on either end, — is **amphicœlous**. The parts of the centrum first formed prevent any farther increase of the notochord in the intravertebral regions; but intervertebrally it expands, filling up the cavities between the successive vertebræ, and thus assuming the appearance of a string of beads (Fig. 146). In the amphibia we have at first the conditions just described, and in the perennibranchiate forms this amphicœlous condition persists throughout life. Higher still, there appears an intervertebral growth of cartilage (Fig. 147, *A*) which produces a secondary series of constrictions in the notochord. A later stage in the process is shown in Fig. 147, *B*, where an absorption of a part of the intervertebral cartilage is taking place in such a way as to result in the formation of a cup at one end of the vertebra, and at the other of a rounded extremity which fits the cup at the end of the next vertebra. The extreme of the process is shown in Fig. 147, *C*, where the intervertebral cartilage has been cut completely in two, the result being the formation of a ball and socket joint between the successive vertebræ; while ossification has extended so far that almost the entire centrum as well as a part of the intervertebral cartilage has been converted into bone. When this process results in a centrum rounded in front and hollow behind, we have an **opisthocœlous** vertebra; when rounded behind and hollow in front, it is **procœlous.** A statement of the occurrence of these three types of vertebræ centra may be given here.

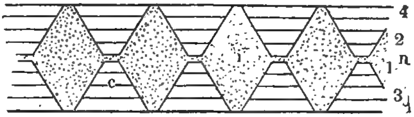

FIG. 146. Diagram of method of growth of amphicœlous vertebræ. *c*, centrum; *i*, intercentral enlargements of, *n*, notochord; 1–4, successive layers of centra.

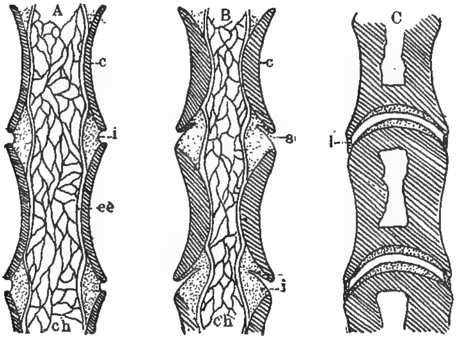

FIG. 147. Diagrams of developing vertebræ of urodeles, modified from Wiedersheim. *c*, centrum; *ch*, chorda; *e*, elastica externa; *i*, intercentral cartilage; *l*, ligament; *s*, incisure in cartilage. Bone lined, cartilage dotted.

Amphicœlous: most fishes, most perennibranch urodeles, some salamanders, some stegocephali, gymnophiona, many dinosaurs,[1] plesiosaurs, ichthyosaurs, precretaceous crocodiles, geckos, rhynchocephalia, and the fossil birds *Archæopteryx* and *Ichthyornis*.

Opisthocœlous: *Lepidosteus*, most salamanders, *Pipa*, *Discoglossus* (anura), most dinosaurs, some vertebræ in penguins and auks, and the neck vertebræ of most ungulates.

Procœlous: the majority of anura, reptiles, and birds.

In the majority of mammals the vertebræ are flat upon each end of the centrum, — **amphiplatyan.**

In forms with amphicœlous vertebræ there was no true articulation of the separate elements of the vertebral column; but with the assumption of pro- or opisthocœlous conditions the vertebral centra articulate with one another, and frequently accessory portions are developed to lock the vertebræ more firmly together. Most common of these are what are known as **articular processes (zygapophyses)**. Of these there are two pairs, arising from the anterior and posterior surfaces of the neurapophyses. The anterior or **prezygapophyses** have their flattened surface turned dorsally so that they can articulate with the ventral surfaces of the posterior process (**postzygapophyses**) of the vertebra in front. In the snakes and some lizards (iguanidæ) these are re-enforced by articular surfaces developed from the neural spine. On the anterior surface of the base of the spine a wedge-shaped process (**zygosphene**) projects forward, its

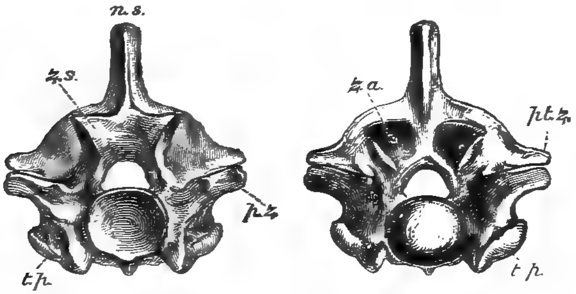

FIG. 148. Anterior and posterior faces of a vertebra of *Python*, from Huxley. *ns*, neural spine; *ptz*, postzygapophysis; *pz*. prezygapophysis; *tp*, transverse process; *za*, zygantrum; *zs*, zygosphene.

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[1] In *Camarasaurus* the first caudal is convex on either end.

articular surfaces directed obliquely outwards and downwards. This fits into a corresponding cavity (**zygantrum**) on the posterior surface of the neural spine of the vertebra in front.

In all forms above fishes, what are known as **transverse processes** (**pleurapophyses**) occur. The homologies of these are not settled. In general terms there may be said to be two of these on either side, a **diapophysis** connected with the neural process, and a **parapophysis** connected with the vertebral centrum. One or the other of these may excel in development, and occasionally either may be rudimentary. In addition the names **anapophysis** and **metapophysis** have been given to certain projections upon the neural processes which seem to be without great morphological significance.

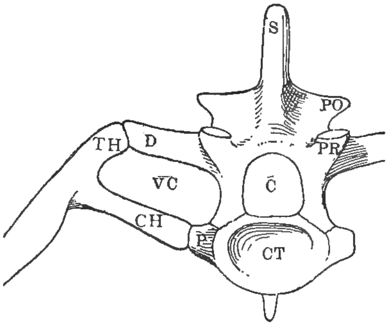

FIG. 149. Anterior thoracic vertebræ of alligator. *C*, canal; *CH*, capitular head of rib; *CT*, centrum; *D*, diapophysis; *P*, parapophysis; *PO*, postzygapophysis; *PR*, prezygapophysis; *S*, spinous process; *TH*, tubercular head of rib; *VC*, vertebrarterial canal.

The vertebral column or backbone is built up of these vertebræ, and in this structure two or more regions can always be clearly distinguished. In the fishes there are two of these regions, **trunk** and **caudal**, the caudal being distinguished by the presence of a complete hæmal arch in connection with each vertebra, while in the trunk the hæmal processes diverge and become converted into so-called ribs (see below). In the amphibia two other vertebral regions — cervical and sacral — occur. The **sacrum** intervenes between trunk and caudal vertebræ, and gives support to the pelvic arch by which the hind limbs are supported. The trunk vertebræ bear true ribs, while the **cervical** vertebra lacks ribs and transverse processes, or these are present in a rudimentary condition. The line between cervical and trunk vertebræ is also loosely drawn by the girdle of the fore limb. In the sauropsida (except in the limbless forms) the same regions can be traced as in the amphibia; but it is to be

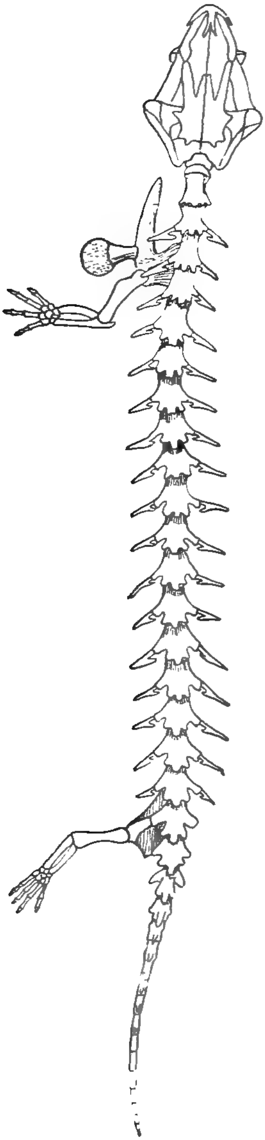

FIG. 150. Skeleton of *Necturus*.

noticed that both sacral and cervical regions are increased in extent, there being two or three sacral and a much larger number of cervical vertebræ. In the mammals these regions are still further increased by a division of the trunk into a **thoracic** ('dorsal') region, the vertebræ of which bear ribs, and a **lumbar** region in which ribs are wanting.

In certain regions there is a strong tendency towards the fusion of vertebræ. Most frequently those of the sacrum unite into a single piece, while fusions in the caudal region are numerous, and are correlated with the partial or entire disappearance of the tail. In modern birds there results from this a short bony complex, the **pygostyle,** while in the anura the caudal vertebræ of the tadpole are coalesced into the rod-like **urostyle.** In other regions this union is less frequent; but the fusion of the anterior vertebræ to form the anterior vertebral plate of the skates and the anchylosis of the cervical vertebræ in the whales, and the occasional fusion of some dorsals in birds, will be recalled.

The anterior two vertebræ in the amniotes call for special notice. The first of these, which joins the skull, is known as the **atlas,** the second as the **axis** or **epistropheus.** The atlas bears on its anterior face articular surfaces for articulation with the skull; its neural arch is well developed, but the centrum is absent, there being below but a thin bony arch, regarded by some as the first intercentrum (*i.e.,* hypocentrum arcale). It arises in development from the ventral part of the vertebral bow (p. 137). The axis is in most respects a normal vertebra, but it bears, projecting from the anterior face of its centrum, a more or less cylindrical outgrowth, the **odontoid process**; this is morphologically the centrum of the atlas, which has lost its connection with its proper neural arch, and has become secondarily united with the centrum of the second vertebra, forming a pivot about which the atlas turns.

In crocodiles, *Hatteria*, and possibly some mammals, a pair of plates (reptiles) or a single plate occurs on the dorsal anterior portion of the neural arch of the atlas. This is the so-called **pro-atlas**; but whether this is the last remnant of a vertebra which has otherwise disappeared from between the existing atlas and the base of the cranium cannot yet be definitely decided. Nor is it possible as yet to say whether the only cervical vertebra of the amphibia is homologous with either atlas or axis of the amniotes.

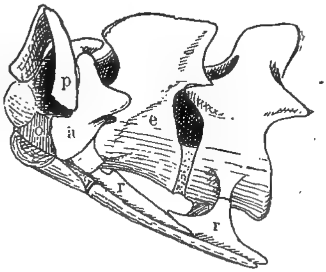

FIG. 151. Three anterior vertebræ of alligator. *a*, atlas; *e*, axis; *o*, odontoid process; *p*, pro-atlas; *r*, ribs.

Ribs. — The name **rib** has been applied to two different structures,[1] one appearing in the ganoids, teleosts, and dipnoi, the other in amphibia and amniotes, and apparently in selachii as far as these latter have ribs.

The ribs of the fish are the hæmal processes of the trunk vertebræ, which, in the region of the body cavity, extend from the vertebral centres towards the ventral surface between the muscles and the cœlomic walls. The transitions from these ribs into the hæmal arches can be traced in any fish skeleton. In the caudal region of the urodeles hæmal arches comparable to those of fishes are present, and besides these the caudal vertebræ also bear transverse processes which extend directly outwards between the epi- and hypaxial muscles. Following

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[1] The view of the ribs adopted here is that which appears to have the better basis. Baur and others hold that ribs are homologous throughout the vertebrates, but their reasons are not conclusive.

the vertebræ forward, it is seen that the transverse process of the sacral vertebra, considerably enlarged, supports the pelvic arch, while in the presacral vertebræ these same transverse processes bear short articulated elements, — the ribs. It follows from this (1) that the amphibian ribs are not equivalent to the hæmal processes in these animals, and (2) that they are structures different from the ribs of fishes. This view is farther substantiated by the conditions which obtain in the ganoid *Polypterus*, where both types of ribs, those of fishes and those of the higher vertebrates, occur in the same segment, the latter lying in the connective tissue between the epi- and hypaxial muscular systems.

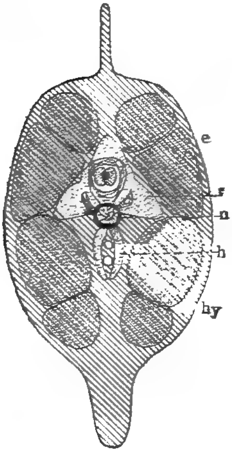

FIG. 152. Section through tail of *Amblystoma*, showing the two types of rib. *e*, epaxial muscles; *h*, hæmal arches; *hy*, hypaxial muscles; *n*, notochord; *r*, true ribs.

The ribs of the amniotes are clearly homologous with those of the amphibia. They are intersegmental in position, and arise by a condrification and more or less complete ossification of part of the myocommatous tissue, a mode of development which readily explains their frequent extension to the ventral surface.

In the fishes the ribs (sometimes lacking, as in some plectognaths and lophobranchs) are usually slender, and are frequently firmly united to the vertebral centra ; or, again, they may be movably articulated to short 'basal stumps.' In many physostomous fishes some of the anterior ribs are modified to give rise to a chain of bones connecting the air-bladder with the ear. Besides these ribs, there frequently occur in fishes slender bones in the fleshy portions, the homologies of which remain to be ascertained. Possibly some of them may represent the ribs of the higher forms. These epimerals, epicentrals, and epipleurals, as they are called, are stated to be without a cartilage stage.

The ribs of the elasmobranchs are small and cartilaginous, and are more or less intimately united with the vertebral centra.

In their relationships to the muscles they resemble the ribs of the amphibia, and are in no way differentiations of hæmal arches.

From the amphibia upwards the ribs are typically articulated with the vertebræ by two heads, a dorsal or tubercular head articulating with the diapophysis, a ventral or capitular head resting upon the parapophysis. There is thus formed a skeletal arch (**vertebrarterial canal**) between rib and vertebra, through which passes a vertebral artery (Fig. 149 VC). In the amphibia the two heads are said to arise separately and to unite later. From these typical conditions various modifications may occur. Thus either head may disappear, while the parapophysis (as in many mammals) may be reduced to an articular surface. Again, as in the anura, the ribs may fuse to the diapophysis, or, as in the neck of mammals, to both di- and parapophysis. In crocodiles both tubercular and capitular heads articulate with the transverse process in most of the thoracic ribs.

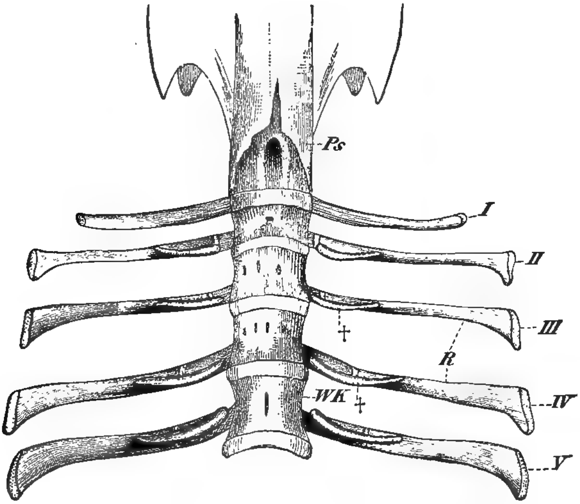

FIG. 153. Anterior end of the vertebral column of *Polypterus*, showing both kinds of ribs from below, from Wiedersheim. *Ps*, parasphenoid; *R*, true ribs (*I–V*); *WK*, vertebral centra; + fish ribs.

In the amphibia the ribs are usually short, and are confined to the region near the backbone.[1] In some forms (*Megalobatrachus* and some stegocephalans) the ribs are not confined to the trunk region, but from three to eight pairs may occur in the tail. It is to be noted that the pelvis does not articulate directly with the transverse process of the sacral vertebra, but that connection is effected by the intervention of a sacral rib, distinct in many forms. In the cæcilians ribs occur on every vertebra except the first and last.

In the amniotes the ribs in the trunk region acquire a much greater development, and, like the hoops of a barrel, extend

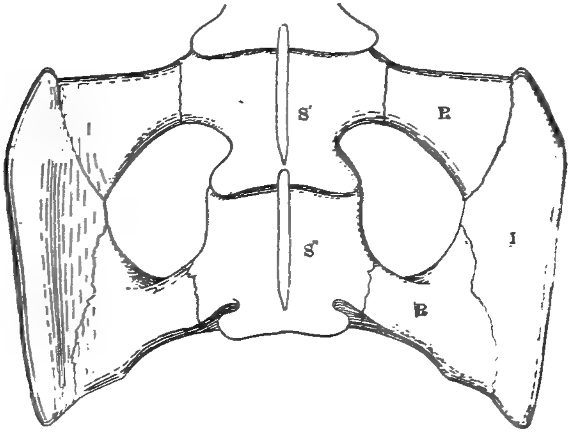

FIG. 154. Pelvis and sacrum of alligator. *I*, ilium; *R*, sacral ribs; *S'*, *S''*, sacral vertebræ.

around the body cavity. They may be ossified throughout their extent, in which case each rib is usually divided into several segments (crocodile),[2] but usually a considerable portion remains cartilaginous. Ventrally they may terminate freely, or they may connect with a sternum to be described later. In the great majority of the birds, as well as in some reptiles (crocodilia, rhynchocephalia), each rib bears a backwardly directed **uncinate process,** which overlaps the rib behind, thus giving additional strength to the thoracic framework.

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[1] Ribs occur in the ventral region of some stegocephali (see p. 147). and cartilaginous ventral ribs have been described in *Necturus* and *Menopoma* (urodeles).

[2] The median segment in crocodiles is not truly ossified, but is cartilage partially calcified.

In the cervical region the ribs are much shorter. They may be freely articulated to the vertebræ (crocodiles, etc.), but usually they are coalesced to transverse processes and centra, the foramen for the passage of the vertebral artery remaining to show the morphological relations. Usually caudal ribs are poorly developed, but in some reptiles they may appear on almost every caudal vertebra.

In some stegocephals, as well as in many reptiles (*Hatteria*, crocodiles, ichthyosaurs, pterosaurs, etc.), so-called abdominal ribs occur. These are chondrifications or ossifications in the ventral wall of the abdomen, usually behind the true ribs, and external to the rectus muscles. From the fact that these are not homologous with the true ribs, the name **gastralia** has been given them. They may, as in crocodiles, equal the segments in number; they are twice as many in *Hatteria*, while in some stegocephals there are several series of ossicles to the somite.

Sternum. — A sternum or breast bone is absent in all fishes, but occurs in the majority of the higher forms; but it is as yet an open ques-

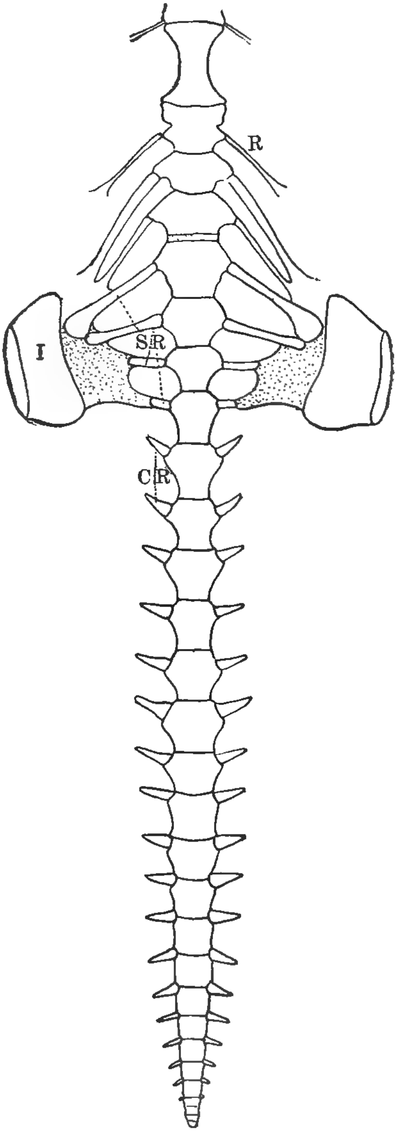

Fig. 155. Posterior vertebral region of *Testudo græca*. *CR*, caudal ribs; *I*, ilium; *R*, trunk ribs; *SR*, sacral ribs.

tion as to how far the sternum of the amphibia is homologous with the similarly named structure in the amniotes.

In the amphibia the sternum arises as a pair of longitudinal cartilaginous rods in the connective tissue on the ventral surface of the body. These rods soon unite, and form an unpaired plate in the median line between the origin of the fore limbs. In the urodeles the sternum remains as a small plate just behind the ventral portion of the shoulder girdle, but in the anura it extends farther forward. Its median portion is caught between the epicoracoids, and is reduced to a very slender thread; but in front of the girdle it expands again in a plate, the so-called **omosternum.** In the urodeles the sternum is cartilaginous; but in the anura portions of the omosternum, as well as of the posterior portion (termed **xiphisternum,** a term adopted from human anatomy), become ossified. The sternum is lacking in the footless amphibia.

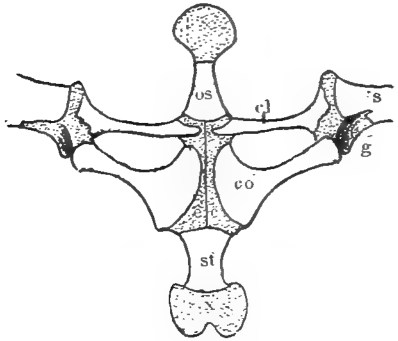

FIG. 156. Sternum and ventral portion of the shoulder girdle of *Rana*, after Wiedersheim. *cl*, clavicle; *co*, coracoid; *ec*, epicoracoid; *g*, glenoid fossa; *os*, omosternum; *s*, ventral part of scapula; *st*, sternum; *x*, xiphisternum.

In the amniotes the sternum arises from the ventral ends of the ribs. The distal ends of these become separated from the rest, and unite to form a pair of ventral rods, which then unite to form the unpaired structure, which in many forms shows evidences of its origin from a series of elements, — **sternebræ.** The sternum is lacking in snakes and turtles. In the dinosaur *Amphicœlias,* it is said to have been paired in the adult, the two halves possibly having been united by cartilage. In the lizards it is usually a broad rhomboidal plate. In the birds but few (at most eight) ribs contribute to the sternum, which is a broad plate, and in the ordinary birds bears a strong keel or **carina** upon its ventral surface. In the flightless birds the keel is absent, and the presence or absence of keel was formerly employed as a means of dividing birds into Ratitæ and Carinatæ. It is interesting to find a keel existing in the bats and in the fossil pterodactyls. In the mammals the sternum is more elongate, and more ribs contribute to its formation than in the sauropsida. It may consist of as many separate sternebræ as there are ribs connected with it, or these may so unite that but three separate bones can be recognized, a **manubrium** in front, a body in the middle, and an **ensiform process (xiphisternum)** behind, the latter extending behind the ribs.

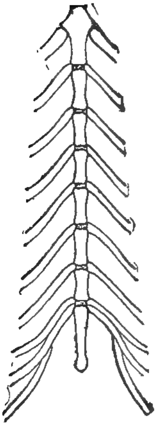

FIG. 157. Sternum of dog, showing sternebræ.

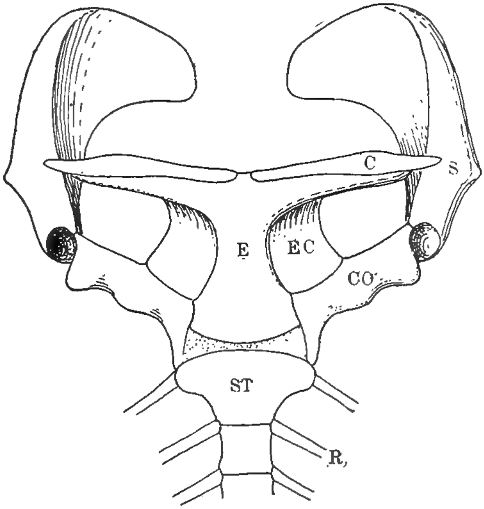

Fig. 158. Shoulder girdle of *Ornithorhynchus.* *C*, clavicle; *CO*, coracoid; *E*, episternum; *EC*, epicoracoid; *S*, scapula; *ST*, sternum; *R*, ribs.

Connected with the sternum in many groups is a structure to which the name **episternum** has been given. This first appears in the stegocephali, but reaches its highest development in the reptiles. It forms usually an unpaired plate connected with the median ends of the clavicles, and in those reptiles where it occurs it is placed ventrally to the sternum proper. It is expanded in front, and frequently takes the shape of a T, the arms supporting the clavicles, while the shaft connects with or may even be fused with the sternum proper. No episternum has been described in the birds; but in mammals one frequently exists, but here it is placed anterior to instead of ventral to the sternum proper. Where best developed it is T-shaped; and it may be movably articulated to the sternum as in the monotremes (Fig. 158), or firmly united to it (marsupials). In certain rodents it becomes divided into three parts, while in the primates it is reduced to the intermediate cartilages by which the clavicles articulate with the sternum. The omosternum of the anura was formerly regarded as an episternum, but it is apparently truly sternal in nature.

The Skull. — The skeleton of the head, the **skull,** is a very complicated structure; and in it two regions may be recognized, — a **cranium** for the protection of the brain and sense organs (eyes, nose, ears), and a **visceral skeleton** which forms the jaws, and gives support to the visceral walls. In the beginning all of these parts are outlined in cartilage; and in marsipobranchs and elasmobranchs they never pass beyond the cartilage stage, although, as in some sharks, the outer portions of the cartilage may be calcified[1] in the adult. In the higher groups this cartilage may be partially or almost completely converted into bone; and in all vertebrates above the elasmobranchs there are added to those portions of the skull which are of cartilage origin numerous other skeletal elements which are not preformed in cartilage, but which arise as ossifications of membranes. It therefore becomes necessary to distinguish in the higher vertebrates between cartilage-bones and membrane-bones, but these distinctions can be made only by tracing the development; there is nothing in the fully developed bone which will decide the question.

In the development of the cartilaginous cranium (**chondrocranium**) there occurs first the formation of a membranous capsule, the **primordial cranium,** which encloses the brain and sense organs. In no vertebrate have the details of this membranous cranium been worked out. Later there is a chondrification of this primordial cranium which proceeds from several distinct centres, which may be spoken of as the parachordals, otic capsules, trabeculæ, and nasal capsules.

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[1] The distinction between calcified cartilage and bone is important.

As will be recalled, the notochord extends forward as far as the infundibulum, and its anterior end is concerned in the formation of the chondrocranium. On either side of this structure there develops a horizontal cartilaginous plate, the **parachordal** cartilage, which grows out laterally until it unites with a cartilaginous box, the **otic capsule,** which forms around the sac-like inner ear (p. 71). From this union of parachordals and otic capsules, there is formed a trough which encloses the medulla oblongata below and on either side. Later, in the typical conditions, the cartilage gradually extends upwards and inwards from the dorsal surface of the otic capsules forming a plate — the **synotic tectum** — which roofs in this region of the brain above. To this region there is added (amphibia) a vertebra or vertebral complex, developed like those of the vertebral column, which becomes finally united to the parachordals and otic capsules, and closes in the cranium behind. Comparative morphology would also lead us to regard the parachordals as formed of coalesced vertebral centra; but in their history, so far as made out, they of themselves afford not the slightest clew as to the number of elements fused together in this region.

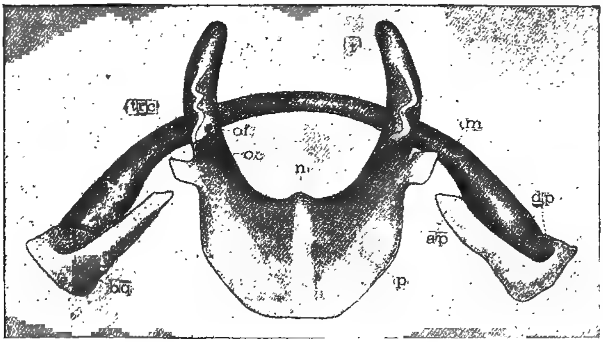

FIG. 159. Early chondrocranium of *Amblystoma*, before the formation of the otic capsules. *ap*, ascending process of quadrate; *bq*, body of quadrate; *dp*, descending process of quadrate; *m*, Meckel's cartilage; *n*, notochord; *oc*, *of*, foramina for oculomotor and optic nerves; *p*, parachordals; *t*, trabecula; *trc*, trabecular crest. From Winslow.

The **trabeculæ cranii** are a pair of cartilaginous rods which extend forward from the anterior end of the parachordals (or of the notochord) on either side of the pituitary body. In front, at about the anterior end of the brain, these trabeculæ turn inwards towards each other and fuse into a median mass which, from its future history, is known as the **ethmoid plate.** Farther forward the trabeculæ separate, and turn outward in front of the developing olfactory organs, the diverging horns thus formed being known as the **cornua trabeculæ.** The farther development of the trabecular region differs considerably in different vertebrates. In general the trabeculæ rapidly increase in height by the development of a crest upon the dorsal surface, and in the elasmobranchs and some ganoids (sturgeon, etc.) this process is continued until the brain is completely roofed in above. In the teleosts, amphibia, and amniotes no cartilaginous roof (**tegmen cranii**) is found in this region;[1] and in lizards, birds, and certain teleosts the trabeculæ retain their condition of simple rods closely applied to each other. In most other vertebrates the trabeculæ gradually grow together beneath the twixt and fore brains, thus forming a complete floor. In the

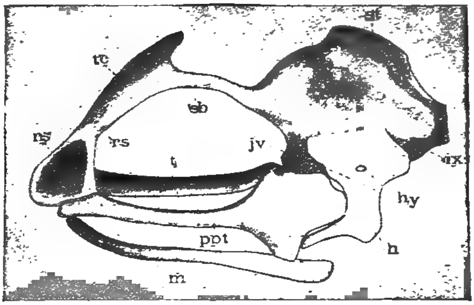

FIG. 160. Chondrocranium of embryo trout (*Salmo fontinalis*). *h*, hyoid; *hy*, foramen for hyomandibular nerve; *ix*, foramen for glossopharyngeal nerve; *jv*, foramen for branch of jugular vein: *m*, Meckel's cartilage; *ns*, nasal septum; *rs*, foramen for ophthalmicus superficialis: *sb*, supraorbital bar; *st*, synotic tectum; *t*, trabecula; *tc*, tegmen cranii. From Winslow.

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[1] The history in the Dipnoi is not known. In nearly adult animals (*Protopterus*) there exists a longitudinal rod of cartilage in the roof of the skull which may be the remains of an earlier complete cartilage roof. The same may also be true of an isolated cartilage plate in the skull of *Polypterus*.

urodeles, crocodiles, lizards, and many teleosts no such cartilaginous cranial floor is formed, the ventral wall of the skull being formed by membrane bones to be described later.

Cartilage walls are also found in the optic and olfactory organs. Since motion is necessary in the eye, the optic capsule (sclerotic, p. 83) never participates in the formation of the cranium. The nasal capsules, on the other hand, unite with the anterior ends of the trabeculæ and with the cornua. They are frequently extensively fenestrated. In the vertebrate series a general law may be observed. The more completely the adult skull is ossified, the less developed is the chondrocranium.

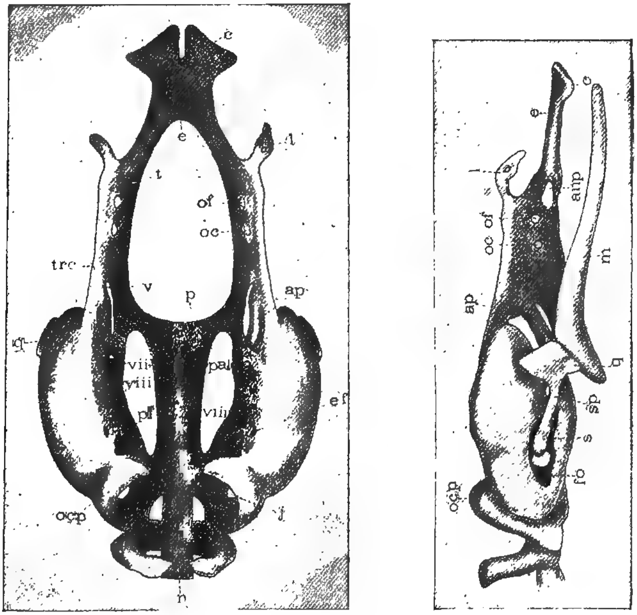

FIG. 161. Dorsal and lateral views of the chondrocranium of *Amphiuma*. *anp*, antorbital process; *ap*, ascending process of quadrate; *c*, cornu trabeculæ; *e*, ethmoid plate; *ef*, foramen for ductus endolymphaticus; *j*, jugular foramen; *l*, lamina cribrosa; *m*, Meckel's cartilage; *n*, notochord; *oc*, foramen for oculomotor nerve; *ocp*, occipital process (vertebra); *of*, foramen for optic nerve; *p*, parachordal; *pal*, foramen for palatine nerve; *pf*, foramen for ductus perilymphaticus; *q*, quadrate; *s*, stapes; *sp*, stapedial process of quadrate; *t*, trabecula; *trc*, trabecular crest; *V*, *VII*, *VIII*, foramina for *V*, *VII*, and *VIII* nerves.

The visceral skeleton consists of a series of paired bars, always preformed in cartilage, in the walls of the pharynx and the oral cavity. Formerly these arches, which partially or completely surround the alimentary canal, were compared more or less closely with the ribs, but that this homology cannot be held is shown by the fact that the ribs develop from the somatic mesenchyme (*i.e.*, that outside the cœlom), while the visceral skeleton arises from the splanchnic mesenchyme. This visceral skeleton is seen in its simplest condition in the region of the gill clefts (p. 22), where there is developed a **branchial cartilage,** a rod-like structure, between each two successive gill slits. In their simplest condition these are simple rods, but usually they become broken up into a series of elements, typically four in number, movably articulated with each other, and named, proceeding from above downwards, **pharyngobranchial, epibranchial, keratobranchial,** and **hypobranchial.** Between the two hypobranchials of each arch is developed an unpaired piece, the **copula** or **basibranchial,** and these

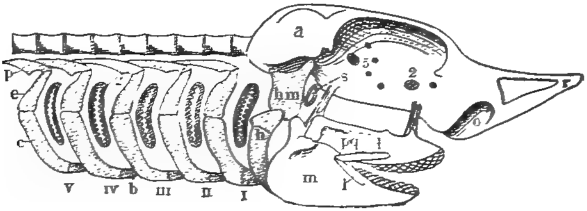

FIG. 162. Diagram of skull and visceral arches of an Elasmobranch. *a*, auditory capsule; *b*, basibranchial; *c*, keratobranchial; *e*, epibranchial; *g*, gill cleft; *h*, hyoid; *hm*, hyomandibular; *l*, labial cartilages; *m*, mandible (Meckel's cartilage); *o*, olfactory capsule; *p*, pharyngobranchial; *pq*, pterygoquadrate; *r*, rostrum; *s*, spiracle; 2, 5, exits of second and fifth nerves; *I–V*, branchial arches.

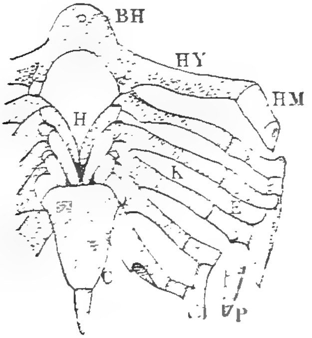

FIG. 163. Visceral arches of *Scyllium*, after Gegenbaur. *BH*, basihyal; *C*, copula (united basibranchials); *E*, epihyal; *H*, hypohyal; *HM*, hyomandibular; *HY*, hyoid; *K*, keratobranchial; *P*, pharyngobranchial.

copulæ become more or less intimately connected with each other, thus forming a support for the whole visceral skeleton.

The two anterior arches have somewhat different fates. The second (counting from in front) is called the **hyoid arch,** and it lies between the first true branchial cleft and the spiracular cleft (Eustachian tube, p. 73). In the fishes this arch is divided into two primary pieces, — a dorsal **hyomandibular** and a ventral **hyoid** proper. The former loses more or less completely its connection with the hyoid, and intervenes between the jaws and the cranium, where it forms the whole (elasmobranchs) or a part (ganoids and teleosts) of a suspensor apparatus which supports the jaws. In all forms higher than the teleosts this hyomandibular element has apparently disappeared.[1] The hyoid proper may divide into three parts, — the **epihyal, keratohyal,** and **hypohyal,** — while a copula (**basihyal**), larger than the basibranchials, is usually developed, and not infrequently grows forward to form an internal skeleton for the tongue.

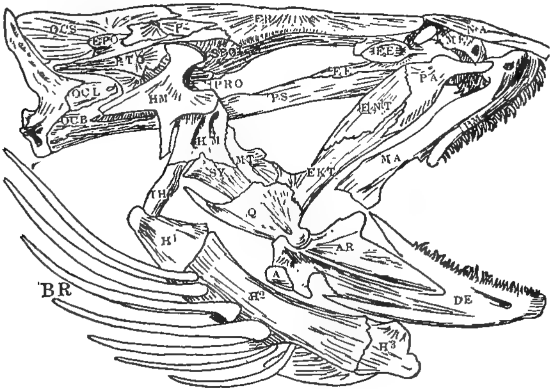

FIG. 164. Skull of cod, the outer membrane bones removed, after Hertwig. *A*, angulare; *AR*, articulare; *BR*, branchiostegals; *DE*, dentary; *EE*, ectethmoid; *EKT*, ectopterygoid; *ENT*, entopterygoid; *EPO*, epiotic; *FR*, frontal; H^{1-3}, hyoid; *HM*, hyomandibular; *IH*, interhyal; *MA*, maxillary; *ME*, mesethmoid; *MT*, metapterygoid; *NA*, nasal; *OCB*, basioccipital; *OCL*, exoccipital; *OCS*, supraoccipital; *P*, parietal; *PA*, palatine; *PRO*, prootic; *PS*, parasphenoid; *PTO*, prootic; *Q*, quadrate; *SPO*, sphenotic; *SY*, symplectic.

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[1] The stapes of the ear may possibly be derived from the hyomandibular.

Each branchial arch may develop cartilaginous outgrowths — the branchial rays — which serve as supports for the gills. These may also occur upon the hyomandibular arch in those forms where a spiracular gill is developed; but in the teleosts the rays of the hyoid portion of the arch are modified into slender bony rods — the **branchiostegal rays** — which support a membrane closing in the gills beneath; while the rays of the hyomandibular are represented by the opercular bones to be described below.

The most anterior of the visceral arches, the **mandibular arch,** has lost all connection with the respiratory region, and has divided into two portions, which are bent on each other so that they meet at a sharp angle behind. The upper of these is the **pterygoquadrate,**[1] the lower is **Meckel's cartilage.** These two cartilages of the two sides form the jaws in the elasmobranchs. Both pterygoquadrate and Meckel's cartilage frequently have accessory **labial cartilages** developed in connection with them. These have been interpreted as degenerate arches in front of the mandibular arch.

The foregoing outline of the cartilaginous skull applies to the gnathostome forms; but before going more into detail, a word must be said concerning the cyclostomes. The chondrocranium is formed of parachordals, otic capsules, and trabeculæ, the cranial cavity being partially roofed in by a narrow tegmen, the so-called occipital arch. In front the cranium is closed by a cartilaginous nasal capsule. The branchial skeleton consists

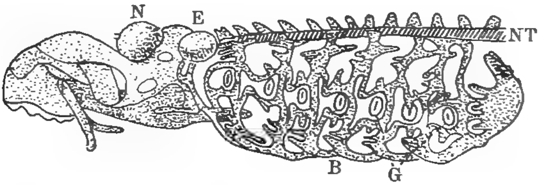

FIG. 165. Cranium and branchial basket of *Petromyzon*, after W. K. Parker. *B*, branchial basket; *E*, otic capsule; *G*, gill slits; *N*, nasal capsule; *NT*, notochord.

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[1] The term palatoquadrate sometimes applied to this is a misnomer, since the palatine bone is a membrane bone.

of a complicated cartilaginous framework, the vertical bars being united by horizontal rods. There occur in connection with the cranium several cartilaginous bars, while in front a series of plates extend to the end of the head. There is no structure comparable beyond a doubt to a hyoid; while instead of movably articulated jaws, the mouth is supported by a cartilaginous ring, and a well-developed cartilaginous framework exists in the tongue, while the filaments around the mouth (*Myxine*) have cartilaginous supports.

In the elasmobranchs the skull is never converted into bone, although calcareous deposits may be formed in its wall. The cranium is a closed capsule, sometimes cartilaginous throughout, sometimes with places in its roof (**fontanelles**), which are not chondrified, but are closed with membrane. Through the walls are openings for the passage of nerves and blood-vessels, but there is no trace of division into separate elements. The pterygoquadrate in the normal sharks is united to the chondrocranium by ligaments and muscles, and by the hyomandibular suspensor. In the holocephali, on the other hand, pterygoquadrate and cranium are firmly anchylosed in the adult (Fig. 166), although free in the young.

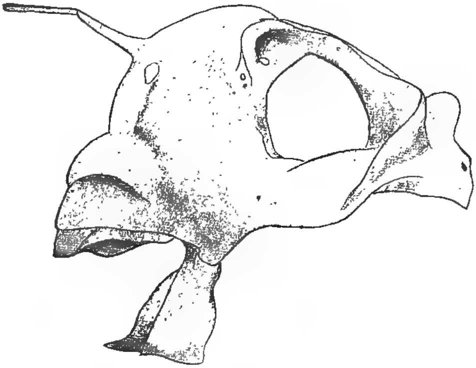

FIG. 166. Skull of *Chimæra monstrosa* (drawn from a dry specimen).

Above the elasmobranchs bones appear in the skull, both as ossifications of cartilage and as membrane bones. The more constant and more important of these are as follows: —

The chondrocranium gives rise to four bones around the large opening (**foramen magnum**) through which the brain is connected with the spinal cord. These are, below, the **basi-occipital**; on either side an **exoccipital**; and above, part of a

supraoccipital. In the floor of the cranium in front of the basioccipital is a **basisphenoid,** and in front of this a **presphenoid.** Still farther in front, in the region of the ethmoid plate and the nasal capsules, a **mesethmoid.** In the trabeculæ are developed two bones on either side, an **alisphenoid** in front of the otic capsules, and an **orbitosphenoid** in the neighborhood of the eye. The otic capsules each ossify into three bones, — a **prootic** in front, an **epiotic** above, and an **opisthotic** behind. These bones form the floor and a part of the lateral walls of the skull. Not all of them are always developed, and again two or more may fuse together or with membrane bones.

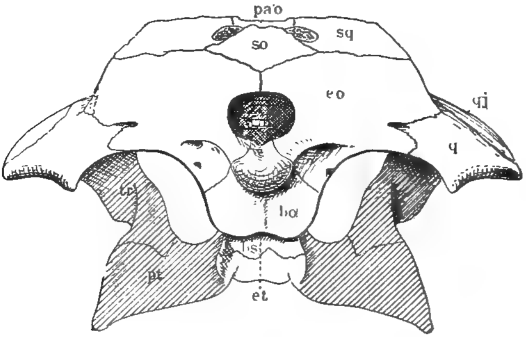

FIG. 167. Base of skull of alligator (*Alligator lucius*). *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *et*, opening of Eustachian tube; *fm*, foramen magnum; *pao*, paroccipital; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal; *tr*, transversum.

The pterygoquadrates of either side develop into a pair of **pterygoid** and a pair of **quadrate** bones, while Meckel's cartilage never ossifies, or at most gives rise to an **articulare** on either side, where the lower jaw articulates with the quadrate. The other visceral arches may ossify to a greater or less extent, but the names of the resulting bones are the same as those given the cartilages.

In all terrestrial vertebrates certain cartilages or bones are developed in connection with the ear, and the most diverse views have been advanced regarding the homologies of these **ossicula auditus.** The following account is based upon personal studies of the development of these ossicles in amphibia, sauropsida, and mammalia.

In the urodeles, where these elements first appear, the lateral wall of the otic capsule is interrupted by an opening, the **fenestra ovalis,** in which a plate, the **stapes,** is supported by membrane. In several urodeles and in all cæcilians this stapes is connected with the quadrate by means of a stapedial process (see Fig. 161, *s*, *sp*). This may be called the urodele type; and it is to be noted that here no tympanum (p. 73) occurs, the first postoral visceral cleft undergoing reduction in development.

In the anura and sauropsida the tympanum is well developed; and this is crossed by a rod, the **columella,** often differentiated into three parts, which reaches from tympanic membrane to stapes, which is situated as in the urodeles. This columella serves to conduct sound waves across the tympanic cavity to the internal ear. In development it arises *behind* the tympanum, and when fully developed it is bound to the posterior wall by membrane. It is therefore clearly postspiracular in character, and its connection with the ventral portion of the hyoid (Fig. 168) indicates that possibly it is to be homologized with the hyomandibular of the pisces. In these groups the quadrate acts as a suspensor of the lower jaw, and has only a ligamental connection — no articulation — with the stapes or columella.

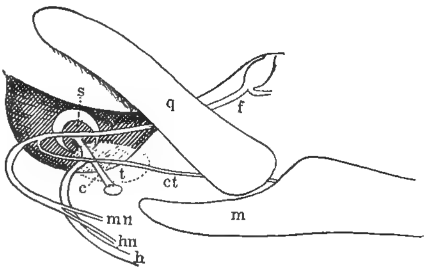

FIG. 168. Diagram of auditory ossicles and related parts in the sauropsida, based on embryos of *Sceleporus undulatus*. *c*, columella; *ct*, chorda tympani; *f*, facialis; *h*, hyoid: *hn*, hyoid branch of facialis; *m*, Meckel's cartilage; *mn*, mandibular branch of facialis; *q*, quadrate; *s*, stapes; *t*, tympanum.

In the mammals two[1] ossicula intervene between the tympanic membrane and the stapes. The more internal of these is the **incus,** the outer the **malleus.** As will be remembered, the lower

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[1] Frequently a third element is mentioned, the os **orbiculare** or os **lenticulare,** which arises in the ligament between incus and stapes.

jaw of the adult is without a quadrate suspensorium. In the embryo mammal, however (Fig. 169), Meckel's cartilage is seen to be connected to the otic capsule by means of a quadrate, from which a stapedial process extends backwards to articulate with the outer end of the stapes, in a manner which strikingly recalls the relations in the urodeles. The proximal end of Meckel's cartilage is expanded, and, besides articulating with the quadrate, sends a long process, the future manubrium, backwards and inwards, between the tympanum and the external auditory meatus, *i. e.*, into the tympanic membrane. Later, with the formation of membrane bone (dentary) around the more distal portion of Meckel's cartilage, the lower jaw acquires a new articulation with the skull, on the under surface of the zygomatic process, while at the same time the proximal end of Meckel's cartilage becomes segmented off from the rest, and gives rise to the malleus. The quadrate, having no longer to serve as a suspensorium, loses its connection with the otic capsule, and becomes the incus. Incus and malleus extend into the tympanic cavity from in front, *i.e.*, are prespiracular, and cannot be homologous with the anuran and sauropsidan columella. Further, it will be noticed that the ossicula of the mammal are on the opposite side of the chorda tympani from what is found in the reptilia (Fig. 168). It is an interesting fact, the bearings of which will be alluded to later, that the quadrate, in both urodeles and mammals, retains its articulation with the stapes throughout life. In the reptiles nothing of the sort occurs.

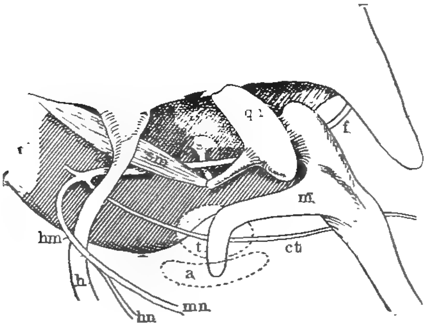

FIG. 169. Diagram of auditory ossicles and related parts in the mammalia, based on the embryo rat. *a*, external auditory meatus; *ct*, chorda tympani; *f*, facial nerve; *h*, hyoid; *hm*, hyomandibular nerve; *hn*, hyoid branch of facialis; *m*, mallear portion of Meckel's cartilage, its process extending down between tympanum and meatus; *mn*, mandibular branch of facialis; *q* (*i*), quadrate, later incus; *s*, stapes; *sm*, stapedial muscle; *t*, tympanum.

In the teleostomous fishes an operculum or fold covering the gill slits occurs; and this is supported by opercular bones, which in their full development may number four on either side, — **operculum, preoperculum, interoperculum,** and **suboperculum.** These are cartilaginous in origin, and are usually regarded as extremely modified branchiostegals of the hyomandibular.

The membrane bones which complete the lateral walls and roof in the cranium are: the dorsal part of the supraoccipital (when distinct called paroccipital), and, proceeding forwards, a pair each of **parietals, frontals,** and **nasals,** meeting in the middle line above, the skull being terminated by a pair of **premaxillaries,** which also appear on the ventral surface. Lodged in the angle between nasal and frontal is a **prefrontal** on either side, while a pair of **postfrontals** are placed in a similar position between the frontals and parietals. Pre- and postfrontals may make up the superior or inner margin of the orbit, or a **supraorbital** may intervene between them. Below the postfrontal and behind the orbit there may be a **postorbital** which may extend beneath the orbit, or the posterior margin of the orbit may be formed by a **squamosal (temporal),** which extends upwards in front of the otic region to reach the supraoccipital and parietal. A **lachrymal** bone is more constant than some that

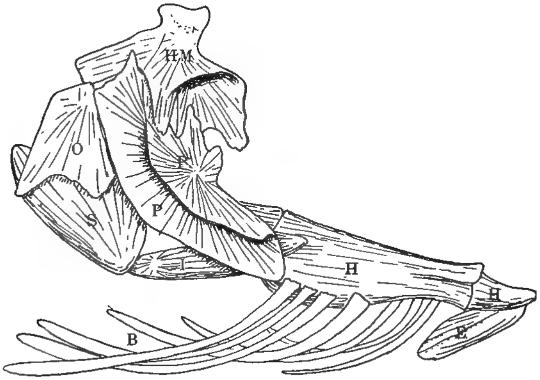

Fig. 170. Hyoid and opercular apparatus of cod. *B*, branchiostegals; *E*, os entoglossum; *H*, hyoid; *HM*, hyomandibular; *I*, interoperculum; *O*, operculum; *P*, preoperculum; *S*, suboperculum.

have been named; it usually enters into the composition of the anterior wall of the orbit, but it may be forced forward by the prefrontal.

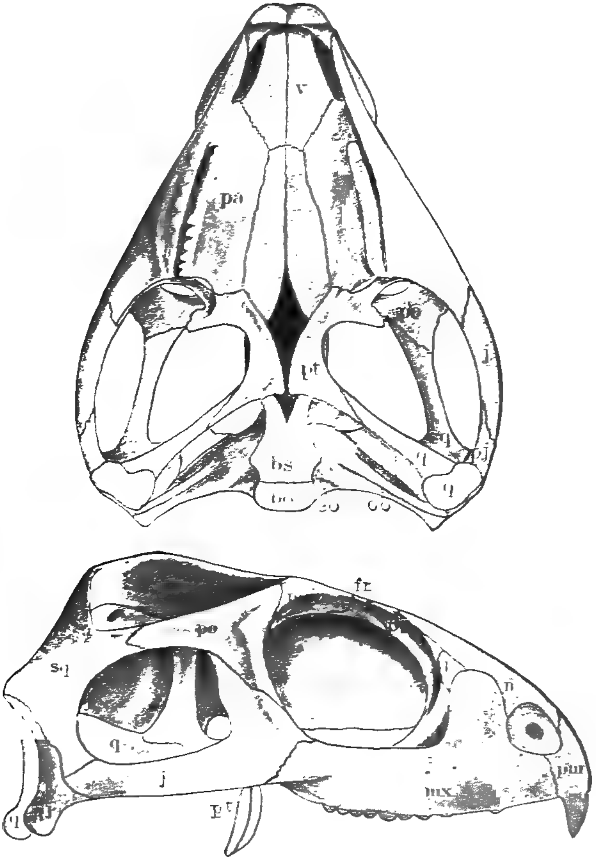

FIG. 171. Ventral and side views of the skull of *Hatteria* (*Sphenodon*), after Günther. *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *fr*, frontal; *j*, jugal; *l*, lachrymal; *mx*, maxillare; *n*, nasal; *oo*, opisthotic; *pa*, palatine; *pf*, prefrontal; *pm*, premaxillary; *po*, postorbital; *ptf*, postfrontal; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *v*, vomer.

In the elasmobranchs the upper jaw is formed by the pterygoquadrate cartilage, but in all higher forms other elements usurp these functions. In front there are a pair of premaxillaries already mentioned, and behind these a pair of **maxillaries** usually occur. These may extend back to the angle of the jaw, or a **jugal (malar)** and a **quadratojugal** may intervene, the latter connecting with the quadrate, and in some cases arising in part from an ossification of a process of the quadrate cartilage. In the roof of the mouth in front are usually a pair of **vomers,** and behind these, and extending back usually to meet the pterygoids, are a pair of **palatines;** while in some groups an **os transversum** occurs, connecting the hinder portion of the mandible with the pterygoid. In the ichthyopsida the floor of the chondrocranium does not ossify; and here the remainder of the roof of the mouth is formed by an unpaired membrane bone, — the **parasphenoid.**

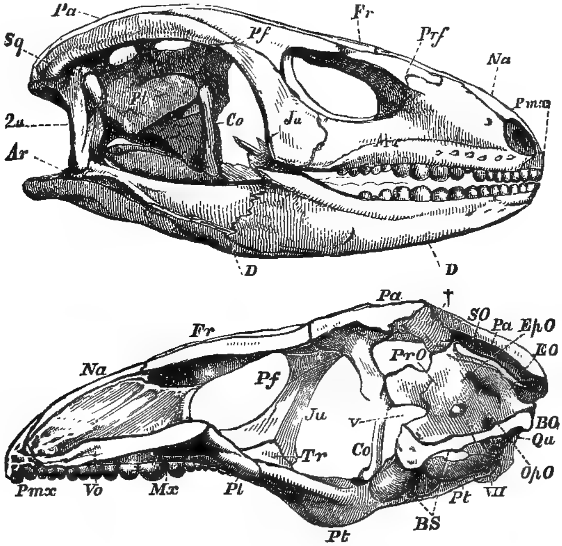

FIG. 172. Skull of *Cyclodus* from the side and split through the middle, from Huxley. *Ar*, articulare; *BO*, basioccipital; *BS*, basisphenoid; *Co*, columella; *D*, dentary; *EO*, exoccipital; *EpO*, epiotic; *Fr*, frontal; *Ju*, jugal; *Mx*, maxillary; *Na*, nasal; *OpO*, opisthotic; *Pa*, parietal; *Pf*, postfrontal; *Pl*, palatine; *Pmx*, premaxillary; *Prf*, prefrontal; *PrO*, prootic; *Pt*, pterygoid; *Qu*, quadrate; *SO*, supraoccipital; *Sq*, squamosal; *Vo*, vomer; *V*, *VII*, exits of fifth and seventh nerves.

In the ganoids and all higher forms membrane bones form around Meckel's cartilage, and these form the functional lower jaw. In their greatest development there may be several of these bones on either side, — a **dentary** in front, a **splenial** farther back on the inner side, and an **angulare** extending forward from the angle of the jaw to meet the other two. In addition, a **supraangulare** is sometimes present behind the articulation of the lower jaw with the quadrate.

Several of these membrane bones may bear teeth. When teeth are present they almost universally occur on the premaxillaries, maxillaries, and dentary; but they may also occur on the vomers, palatines, parasphenoid, and splenials, and occasionally on the pterygoids.

This leads to the question of the phylogenetic origin of these membrane bones of the skull. All the evidence goes to show that not only these teeth-bearing bones, but most of the covering bones of the skull, have arisen from the fusion of dermal plates, much like the placoid scales of the elasmobranchs. In the jaws the enamel-capped spines have given rise to the teeth, while the basal plates, fusing together, form the bones themselves. In many forms this origin of the bones by the fusion of the bases of the teeth can readily be seen (Fig. 173). In the covering bones of the cranium the dental portion has disappeared. The remaining membrane bones have arisen around the canals of the lateral line system, the suborbital chain of bones being the most constant of these.

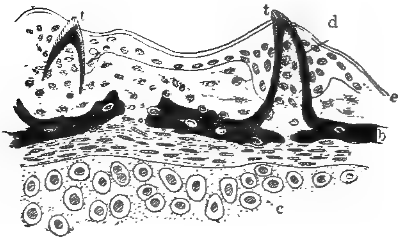

FIG. 173. Development of dermal (maxillary) bone in *Amblystoma* by fusion of the bases of teeth. *b*, bone; *c*, cartilage; *d*, dentine of tooth; *e*, epidermis; *t*, tooth.

Through the walls of the skull formed by these cartilage and membrane bones are foramina for the passage of nerves; and these openings afford important landmarks for the identification of certain bones, especially in those numerous cases where different elements fuse together. The optic nerve passes through the orbitosphenoid. Between the orbitosphenoid and alisphenoid is an opening (**sphenoidal fissure** or **foramen lacerus anterior**) through which pass the third, fourth, and sixth, and the ophthalmic branch of the fifth nerves. The maxillaris superior and mandibularis branches of the fifth nerve leave the skull through the alisphenoid bone, either through a common opening or through two separate foramina (**f. ovale** for the mandibular, **f. rotundum** for the other). The seventh nerve

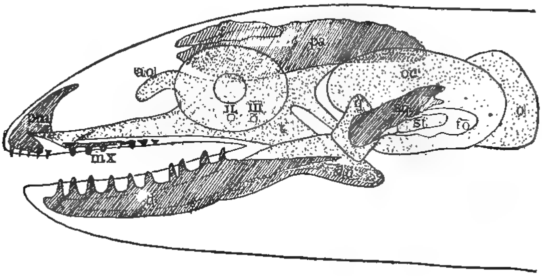

FIG. 174. Developing bones in the head of *Amphiuma*. Cartilage dotted, bone lined. *ao*, antorbital process; *an*, angulare; *d*, dentary; *f*, frontal; *fo*, foramen ovale; *mx*, maxillary; *o*, occipital vertebra; *oc*, otic capsule; *pa*, parietal; *pm*, premaxilla; *q*, quadrate; *sq*, squamosal; *st*, stapes; *t*, trabecula; *II*, etc., exits of nerves.

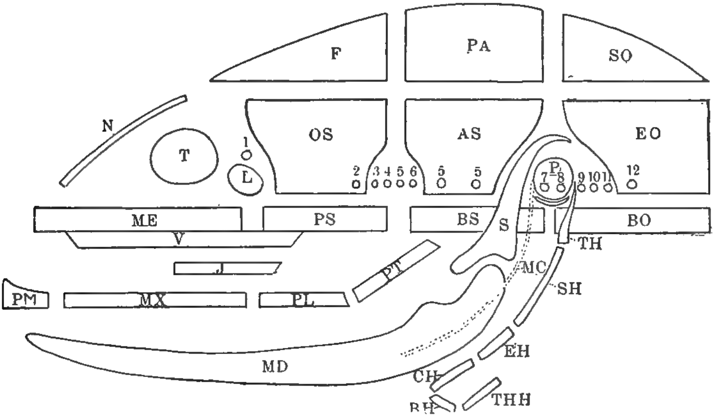

FIG. 175. Diagram of the relations of the bones in the mammalian skull, after Flower. *AS*, alisphenoid; *BH*, basihyal; *BO*, basioccipital; *BS*, basisphenoid; *CH*, ceratohyal; *EH*, epihyal; *EO*, exoccipital; *F*, frontal; *J*, jugal; *L*, lachrymal; *MD*, mandible; *MC*, Meckel's cartilage; *ME*, mesethmoid; *MX*, maxilla; *N*, nasal; *OS*, orbitosphenoid; *PA*, parietal; *PL*, palatine; *PM*, premaxilla; *PS*, presphenoid; *PT*, pterygoid; *S*, squamosal; *SH*, stylohyoid; *SO*, supraoccipital; *T*, turbinal; *TH*, tympanohyal; *THH*, thyrohyal; *V*, vomer; 1–12, exits of the cranial nerves.

passes through the otic bones (petrosal), the ninth and tenth through the **jugular foramen** formed by the junction of basi- and exoccipital and otic bones. Occasional variations from these conditions occur; for instance, the optic nerve may pass through a notch in the orbitosphenoid, or, again, the ophthalmic branch of the fifth may be enclosed in the alisphenoid.

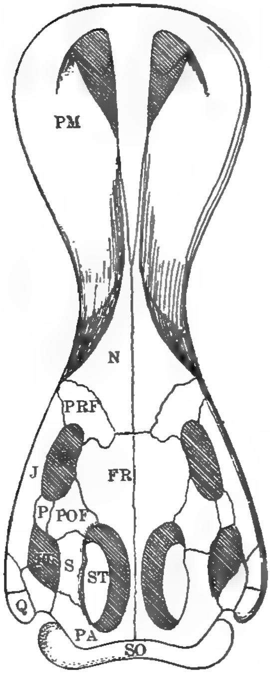

FIG. 176. Skull of the Dinosaur *Hadrosaurus*, showing supra- (*ST*) and infratemporal fossæ (*IT*), after Cope. *FR*, frontal; *J*, jugal, *N*, nasal; *O*, orbit; *P*, postorbital; *PA*, parietal; *PM*, premaxilla; *POF*, postfrontal; *PRF*, prefrontal; *Q*, quadrate; *S*, squamosal; *SO*, supraoccipital.

While the question of the segments of the head will be taken up in a later section of this volume, it may be well to point out here that the bones of the skull form a series of rings surrounding the brain; but it is to be noticed that these rings are formed in part of membrane bones, in part of cartilage bones. The posterior of these rings is formed of basi-, ex-, and supraoccipitals; next in front comes a ring formed of the basisphenoid, alisphenoids, and parietals; third, one of presphenoid, orbitosphenoids, and frontals; and lastly, one of ethmoid and nasals.

In the fishes, stegocephalans, and gymnophiona the membrane bones form a continuous layer on the outside of the skull; but in the higher vertebrates gaps may occur here and there behind the orbit, the fossæ thus formed being bounded by arches of bone. There may be two of these **fossæ,** — a more dorsal **supratemporal,** and a more ventral and lateral **infratemporal.** These fossæ are separated from the orbit by a bridge of bone, usually consisting of postorbital and a process of the jugal. The infratemporal is bounded externally by a zygomatic arch into which the quadratojugal, jugal, and maxillary may enter; while between the two fossæ is an arch usually composed of squamosal and postorbital. By alteration in the position or extent of the bones these two fossæ may unite into a single temporal fossa, and again, the boundaries between this and the orbit may become broken through, the postorbital arch being imperfect or totally disappearing. (For details see Reptilia.)

Appendicular Skeleton. — The appendages of the vertebrates (fins or limbs) arise as paired outgrowths from the sides of the body, one pair, the anterior or **pectoral,** arising a short distance behind the pharyngeal region, the other, or **pelvic** (ventral) pair, a little in front of the vent. In the higher vertebrates each limb grows out as a simple bud, but in some elasmobranchs the appendages arise as differentiations of a continuous lateral fold on either side of the body. Into these outgrowths migrate cells derived from the muscle plates (Fig. 177), which are to

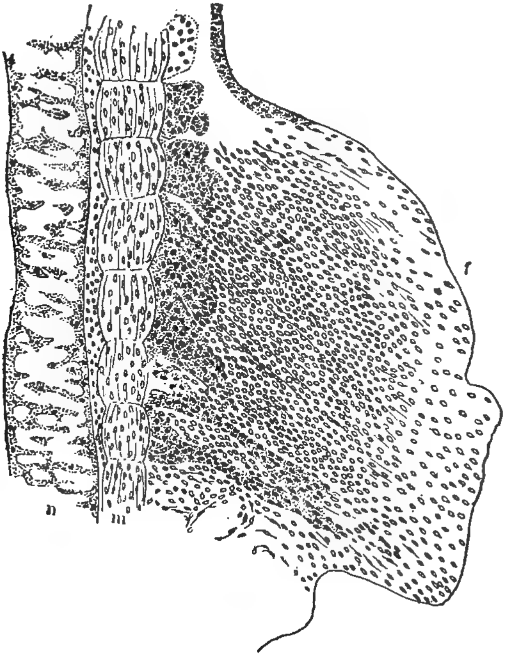

FIG. 177. Developing fin of trout, after Corning. *f*, fin; *m*, myotomes; *n*, notochord; the myotomes are seen to be proliferating strands of cells into the fin.

give rise to the muscles of the appendage, and also mesenchymatous tissue, which becomes transformed in part into the skeleton. This skeleton is, with the exception of the clavicles, preformed in cartilage, the cartilage formation beginning at about the middle of the limb and proceeding thence in both directions.

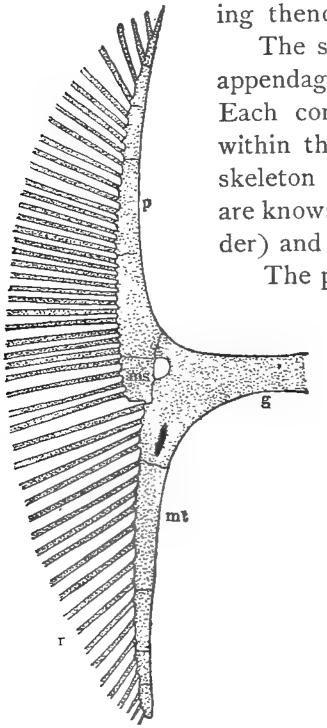

FIG. 178. Shoulder girdle and proximal part of pectoral fin of skate (*Raia*). *g*, right half of girdle; *ms*, mesopterygium; *mt*, metapterygium; *p*, protopterygium; *r*, radii of fin.

The skeletons of both pectoral and pelvic appendages are closely similar in structure. Each consists of a skeletal arch or **girdle** within the trunk, each girdle supporting the skeleton of the appendage. These girdles are known respectively as the **pectoral** (shoulder) and **pelvic** girdles.

The pectoral girdle occurs in its simplest form in the lower fishes, where it is a U-shaped arch of cartilage, the bottom of the U crossing the ventral surface of the body beneath the skin, the arms projecting upwards on either side, and the ends being connected by muscles with the vertebral column.[1] The skeleton of the fin is articulated to either half of the girdle, the point of articulation being usually excavate, and known as the **glenoid fossa.** This fossa serves to divide each half of the girdle into a dorsal or scapular and a ventral or coracoid portion.

With the appearance of bone (ganoids, teleosts) each half of the girdle develops two cartilage bones, — a **scapula**, and a second, usually regarded as a **coracoid**; while the two halves of the girdle proper become separated from each other. In the dipnoi, ganoids, and teleosts, these are re-

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[1] In the skates the pectoral girdle becomes attached to the backbone by means of a so-called **suprascapula**. In many other fishes it is connected with the skull by a chain of bones. Elsewhere, except in some fossil reptiles, it is free from the axial skeleton.

enforced by membrane bones. The chief and largest of these is the **cleithrum** (usually called the clavicle), developed on the outer anterior surface of the girdle, the cleithra of the two sides frequently uniting below. To this is added above a **supraclavicle,** which may connect directly, or by the intervention of a **posttemporal** bone, with the base of the skull. Other membrane bones — **postclavicle, infraclavicle,** etc. — sometimes occur.

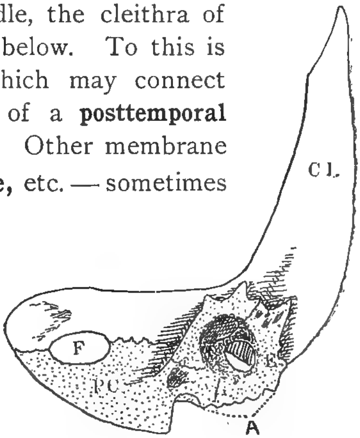

FIG. 179. Shoulder girdle of carp (*Cyprinus carpio*), after Gegenbaur. *CL*, cleithrum; *E*, scapulare; *PC*, coracoid (procoracoid); *F*, foramen between coracoid and cleithrum; *A*, attachment of fin.

In the amphibia and higher groups other portions may be differentiated in the pectoral girdle, and as yet these cannot all be homologized with the conditions found in fishes. In fact, it is probable that no detailed homology exists. The scapular portion of the arch may ossify throughout, or the ossification may be restricted to that portion — the **scapula** — nearest the glenoid fossa, while the dorsal portion may be a distinct element, partly or entirely cartilaginous, — the **suprascapula.** The ventral portion of the girdle gives rise typically to two elements, a posterior **coracoid**

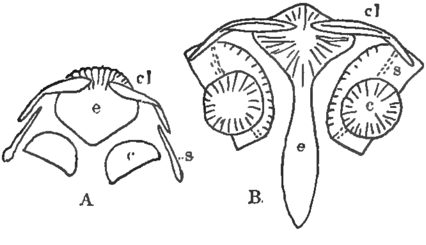

FIG. 180. Pectoral girdles of, *A*, *Archegosaurus* and, *B*, *Palæohatteria*. *c*, coracoid; *cl*, clavicle; *e*, episternum; *s*, scapula, after Credner.

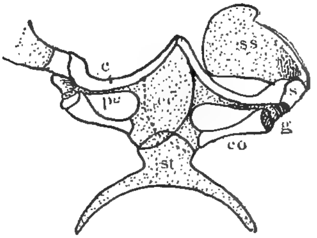

FIG. 181. Shoulder girdle, etc., of *Bombinator igneus*, after Wiedersheim. *c*, clavicle; *co*, coracoid; *ec*, epicoracoid; *g*, glenoid fossa; *pc*, procoracoid; *s*, scapula; *ss*, suprascapula; *st*, sternum.

and an anterior **procoracoid,** both extending inwards; and frequently the inner ends of these are united by a longitudinal cartilaginous band, — the **epicoracoid.** To these may be added a **clavicle,** developed from membrane, in front of the procoracoid, extending inwards from the scapula, and usually connecting with the sternum by means of the episternum. These parts undergo various modifications, and some or all of them, with the exception of the scapula, may, here and there, more or less completely disappear. Possibly the most common is the replacement of the procoracoid by the clavicle. The details of these modifications will be given in connection with the groups in which they occur; but in the majority the two halves of the pectoral girdle are more or less firmly united by means of the sternum.

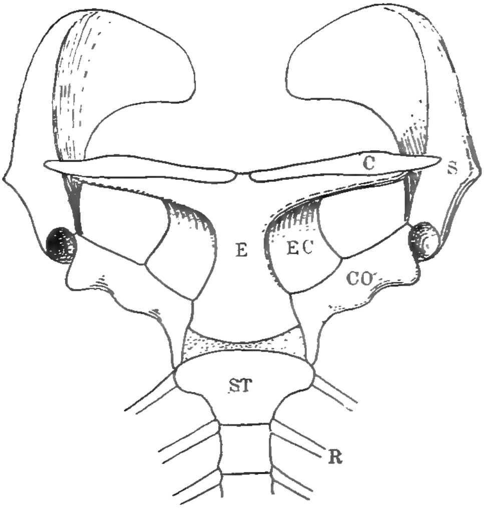

FIG. 182. Shoulder girdle of *Ornithorhynchus*. *C*, clavicle; *CO*, coracoid; *E*, episternum; *EC*, epicoracoid; *S*, scapula; *ST*, sternum; *R*, ribs.

The pelvic girdle presents many similarities to the anterior arch. In the elasmobranchs there is the same transverse arch as in the shoulder girdle; and this supports the ventral fins, there being in some cases a dorsal portion extending beyond the fossa (**acetabulum**) in which the fin articulates. There thus arise a dorsal iliac portion and a ventral ischio-pubic portion in each half of the arch, the ventral part being perforated by an opening (**obturator foramen**) for the obturator nerve. In the other fishes the pelvic girdle is much less developed, and in the teleosts the fins are supported by these enlarged basal elements (*vide infra*). In the amphibia and higher groups the iliac portion is well developed; and when bones are developed in the cartilage, three elements can be recognized in each half, — a dorsal **ilium,** and, below, an anterior **pubis** and a posterior **ischium,** the obturator foramen either forming a part of the opening between these two bones, or passing through the pubis itself. Ventrally these bones can unite with their fellows of the opposite side in a symphysis, while all three of a side meet in the acetabulum.[1] These parts can be well compared with those of the pectoral girdle; pubis with procoracoid, ischium with coracoid, and ilium with scapula; but one difference is to be noted, — the ilium becomes connected with the sacral vertebra or vertebræ by the intervention of short ribs (p. 146). To these parts in the amphibia there is frequently added in front of the pubis a cartilaginous **epipubis.** This reappears again in certain reptiles; and in mammals it may be homologous with the so-called **marsupial bones,** which project forward from the anterior margin of the pubis, there being two views upon this point. These parts may undergo many modifications, but the pelvis is not re-enforced by membrane bones such as play such a part in the shoulder girdle.

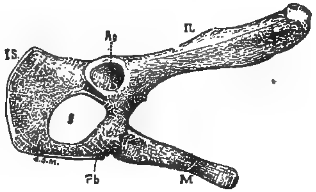

FIG. 183. Side view of pelvis of opossum, after Minot. *Ac*, acetabulum; *f*, obturator foramen; *IL*, ilium; *IS*, ischium; *M*, marsupial bone.

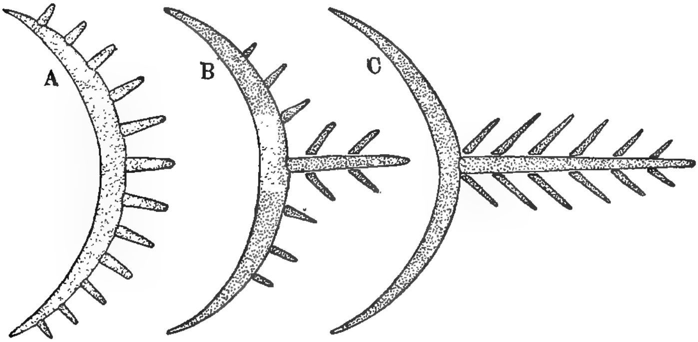

FIG. 184. Modifications of branchial arch and rays according to Gegenbaur's archipterygium theory.

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[1] In many mammals a distinct **acetabular bone** occurs at the junction of the three.

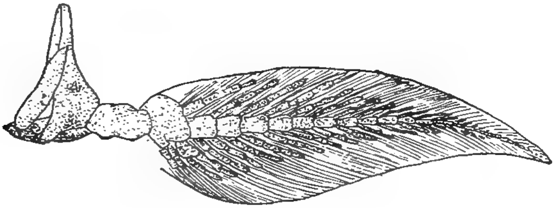

FIG. 185. Skeleton of pectoral fin of *Ceratodus*, after Günther.

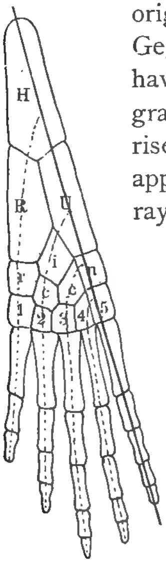

FIG. 186. Diagram of amphibian fore limb, after Gegenbaur. *c*, centrale; *H*, humerus; *R*, radius; *i*, intermedium; *r*, radiale; *U*, ulna; *u*, ulnare; 1–5, carpales. The heavy line is the axis of Gegenbaur's archipterygium, the dotted lines, of the radials of his scheme.

Before beginning the account of the skeleton of the limbs it may be well to summarize the two prominent theories of the origin of these parts. According to the view of Gegenbaur (which he has lately repeated), limbs have arisen from gill structures which have migrated backwards. The gill arches have given rise to the girdles, while the skeletal parts of the appendages have had their origin from the gill rays. With the outgrowth of the limb one of the gill rays near the middle of the arch has correspondingly elongated, and in its outgrowth has carried the neighboring gill rays along with it, the result being a skeletal axis to the limb, on either side of which was a series of smaller skeletal pieces (Fig. 184). A fin closely corresponding to the requisites of this view is found in the dipnoan *Ceratodus*. By suppression of almost all of these accessory skeletal parts on one side of the axis, and a modification or suppression of some on the other side of this **archipterygium,** Gegenbaur derives all types of vertebrate limbs. Fig. 186 shows the relations of the typical pentadactyle leg.

The other view, first advanced by Thacher, assumes that the ancestral vertebrate was provided with two longitudinal folds on either side of the body. The more dorsal of these migrated upwards, those of the two sides uniting to form the dorsal part of the median fin to be described later. From the more ventral folds arose the ventral portion of the median fin, behind the vent; while the pectoral and ventral fins arose as differentiations from the preanal region of the folds. In fact, several existing elasmobranchs exhibit exactly this condition in their development.

In those parts of the fold where the fins are to form, rod-like cartilage supports arose, possibly agreeing in number with the myotomes concerned in the formation of the appendage. At first these were separate and nearly equal in size, but later the basal portions became larger and separated from a more distal (**radial**) part. Such a condition is seen in the extinct elasmobranch *Cladoselache* (Fig. 188); but usually the **basalia** fuse into a few larger elements, connecting the radialia together, and giving stiffness to the whole fin. One of these enlarged basalia acquired prominence over its fellows, and growing in toward the median line fused with a similar ingrowth from the opposite side, thus giving rise to the ventral portion of the girdle. But such a bar would prove too rigid, and would prevent the fin from moving freely, so there appeared a joint on either side, the distal portion now articulating with the median or girdle region at a place known as the glenoid fossa or acetabulum. The skeleton

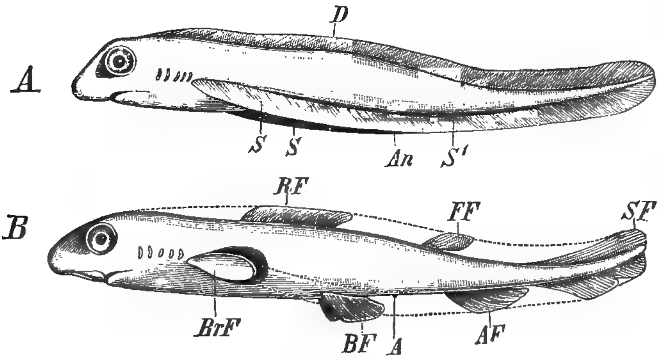

FIG. 187. Diagram of the origin of median and paired fins, from Wiedersheim. *A*, with continuous fin folds; *B*, with differentiated fins. *AF*, anal fin; *An*, anus; *BF*, ventral fin; *BrF*, pectoral fin; *D*, dorsal folds; *FF*, adipose dorsal; *RF*, dorsal fin; *S*, lateral folds; *SF*, caudal fin.

of the fin proper would now consist of the basals and radials plus a number of delicate rods of dermal origin, — the so-called **actinotrichia.** From such an archetypal structure the paired fins of all fish-like forms can readily be deduced; but the transition between this and the limb of the higher vertebrates offers many difficulties, and the intermediate forms have not yet been found. The most plausible view of the homologies is that which derives the limb of the higher vertebrates from one like that of the ganoid or selachian by the loss of most of the basals and radials, a single basal giving rise to the humerus or femur, the proximal portions of a couple of radials forming the ulna and radius (tibia and fibula), while the distal portions of the same radials, with possibly parts of others, producing the distal parts of the limb. The accompanying diagram illustrates the general outlines of the process,

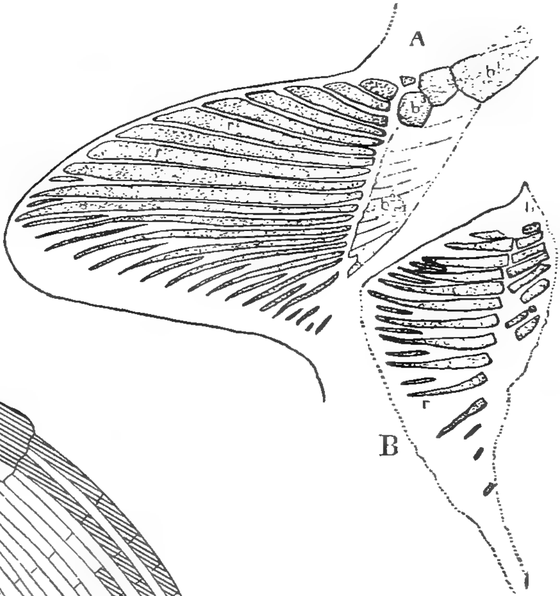

FIG. 188. *A*, pectoral, and *B*, ventral fins of *Cladoselache*, after Dean. *b*, basalia; *r*, radialia.

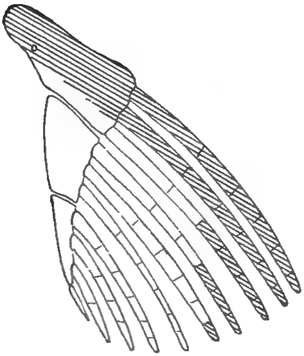

FIG. 189. Diagram illustrating possible evolution of pentadactyle limb from the ventral fin of fishes; the shaded portion represents the persistent parts.

those parts which are shaded being those which persist in the higher vertebrates.

In the fin skeleton of the elasmobranchs two basals, an anterior **protopterygium** and a posterior **metapterygium,** occur in the ventral fin, while in the pectoral fin a third basal, the **mesopterygium,** is intercalated between the other two. These basals support a richly developed radial system, the radialia being with few exceptions developed on one side of the axis formed by the basals. In the lower ganoids, on the other hand, the basals are more numerous, and show the primitive conditions more clearly than do the elasmobranchs. In both of these groups the rays of dermal origin are well developed, and reach their extreme in teleosts in which the cartilage bones of the fin are greatly reduced. In the pectoral fin they are represented by (usually) four bones (**actinosts**) which support the dermal rays, either directly or by the intervention of cartilaginous radials. In the dipnoi there is a well-developed and segmented axial skeleton to the fin which may be without other skeletal parts (*Protopterus,* Fig. 269), or which may bear biserial lateral branches which connect with the dermal rays (*Ceratodus,* Fig. 185).

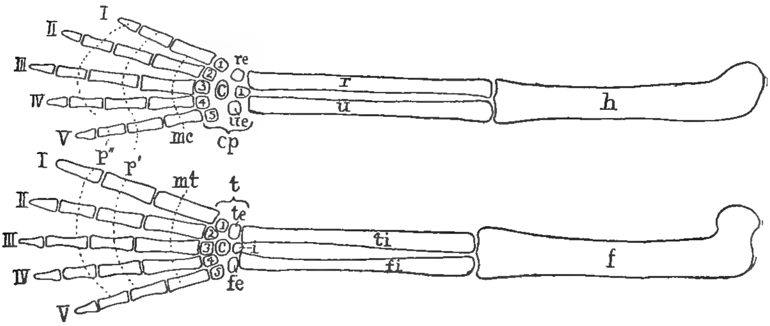

FIG. 190. Typical pentadactyle limbs; above fore limb, below hind limb. *c*, centrale; *cp*, carpus; *f*, femur; *fe*, fibulare; *fi*, fibula; *h*, humerus; *i*, intermedium; *mc*, metacarpals; *mt*, metatarsals; *p'*, *p''*, phalanges; *r*, radius; *re*, radiale; *t*, tarsus; *te*, tibiale; *ti*, tibia; *u*, ulna; *ue*, ulnare; *I–V*, digits; 1–5, carpales or tarsales.

Throughout the higher vertebrates, from the amphibia to man, the same type of limb structure is everywhere found, that of the anterior and posterior limbs being essentially identical. In the fore limb there is in the region corresponding to the upper arm (**brachium**) of man a single bone, the **humerus**; in the fore arm (**antibrachium**) two bones, the **radius** on the anterior, the **ulna** on the posterior side. In the wrist (carpus) there are typically nine small bones, arranged in three series. The first consists of a **radiale** on the radial side, an **ulnare** on the ulnar side, and between these an **intermedium.** The second series consists of a single **centrale**; while the distal series is a row of five **carpales,** numbered from one to five, beginning on the radial (thumb) side. In the hand (**manus**) are recognized **metacarpus** (palm) and **digits** (fingers). There are five metacarpal bones in the palm, while the digits are composed of a number of bones arranged in series (**phalanges**). The fingers are numbered from one to five, beginning at the radial or thumb (**pollex**) side.

In the hind limb the **femur** corresponds to humerus; **tibia** and **fibula** to radius and ulna respectively. The ankle (**tarsus**) consists of **tibiale, fibulare, intermedium, centrale,** and five **tarsales,** and these are succeeded by **metatarsals** and phalanges, which are numbered from one to five, beginning at the **hallux** (large toe).[1]

These parts can be greatly modified, the chief changes consisting of fusion or disappearance of some of these elements. These alterations are usually more marked in the distal portions, while those bones nearer the body are less subject to modification. Occasionally bones may be added to these typical ones; thus, there may be two centrales, and again, there may be membrane (**sesamoid**) bones added to the wrist or ankle. In cases where the details of reduction can be clearly traced, it is found that the outer digits are the first to disappear, the order of disappearance usually being 1, 5, 2, 4.

In human anatomy different names have been given to the carpal and tarsal bones from those employed here; and as in the older works this nomenclature has been transferred to other groups, the following table, which shows the usually accepted homologies, may prove of value.

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[1] The student is referred to special works for a discussion of those cases, like the frog and the mammal *Pedetes*, which seem to indicate the existence of more than five digits.

CARPUS.		TARSUS.	
radiale	= scaphoid.	tibiale	= astragulus.
intermedium	= lunare.	intermedium	
ulnare	= cuneiforme.	fibulare	= calcaneum.
centrale	= centrale.	centrale	= naviculare.
carpale^1	= trapezium.	tarsale^1	= internal cuneiform.
carpale^2	= trapezoid.	tarsale^2	= middle cuneiform.
carpale^3	= magnum.	tarsale^3	= external cuneiform.
carpale^4	= unciform.	tarsale^4	= cuboid.
carpale^5		tarsale^5	

The **pisiform** of the carpus is a sesamoid bone (*i.e.*, a membrane bone developed in a tendon as a result of strain or pressure), while the centrale often fuses with the carpale^3 to form the **os magnum.**

The median or unpaired fins which develop from the dorsal pair of lateral folds and the postanal part of the ventral folds occur only in the ichthyopsida. The result of such a union of folds (p. 172) would be to produce a fin in the median line which, beginning on the back, should continue around the tail and forward upon the ventral surface as far as the vent. Such a continuous fin occurs in the cyclostomes, larval amphibia, and many other forms; but usually it is interrupted, and thus divided into **dorsal, caudal,** and **anal** (on the ventral surface) fins. In the amphibia these fins are without skeletal support; but in the fishes a regular skeleton is formed, consisting of segmentally arranged basalia and radialia like those of the primitive paired fins, and besides, a system of dermal fibrous supports. Occasionally, however, there is to be found an intercalation of radialia, these sometimes being at least twice as numerous as the somites.

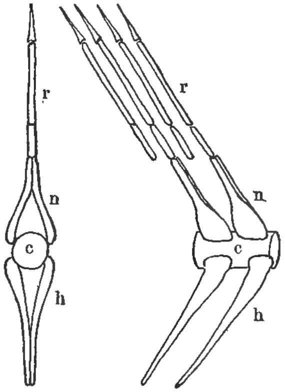

FIG. 191. Dorsal vertebræ of *Pleuracanthus*, after Fritsch. *c*, notochord; *h*, hæmal arch; *n*, neural arch; *r*, radialia of dorsal fin, showing intercalation of elements.

ORGANS OF CIRCULATION.

The circulatory structures of the vertebrates consist of fluids (blood and lymph) and the vessels in which they flow, certain parts of which are specialized for the propulsion of the contained fluid. The general characters of the blood and lymph have already been described; details will be given below when necessary. On *a priori* grounds the lymph system is apparently the older, but it will be more convenient to begin our account with the blood-vascular system. In this we recognize in all vertebrates a central muscular organ, the **heart,** which propels the blood, vessels (**arteries**) which convey the blood to the peripheral portions, and other canals (**veins**) which bring it back to the heart; the extremities of the arteries and veins being connected by minute tubes, — the **capillaries.**

There is considerable evidence to support the view of Bütschli, that the main trunks of the circulatory system are remnants of the segmentation cavity (p. 5) of the embryo, which has otherwise become entirely obliterated by the ingrowing mesoderm. The extension of the cœlomic pouches towards the middle line of the body above and below the alimentary tract narrows the segmentation cavity in these regions into two longitudinal tubes, the main circulatory trunks; while from those portions of the cavity between the myotomes arise semicircular tubes uniting the dorsal and ventral tubes, the result being represented diagrammatically in Fig. 192. A part of the ventral tube near the anterior end becomes specialized as the heart; it forces the blood forward through the anterior end of the ventral tube which is known as the **ventral aorta,** then dorsally through

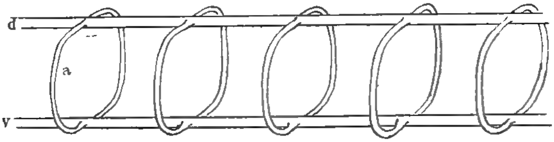

FIG. 192. Diagram of primitive condition of blood-vessels. *a*, transverse vessels; *d* and *v*, dorsal and ventral vessels.

the connecting semicircular vessels (aortic arches), and thence back through the dorsal tube (dorsal aorta) to again enter the posterior (venous) portion of the ventral tube, and thence back to the heart.

In development much of this probable ancestral history has been masked. Many of the vessels which theoretically should appear as spaces between the myotomes are formed as solid cords of cells (often as a single row of cells), which later become canalized and converted into tubes. We may first describe this system of circulatory vessels as they become developed in the lower vertebrates, taking them up in the order — heart, arteries, and veins, and then trace the modifications which occur in the higher groups. This method has the advantage, as it traces the ontogenetic steps by which the amniote circulation arises.

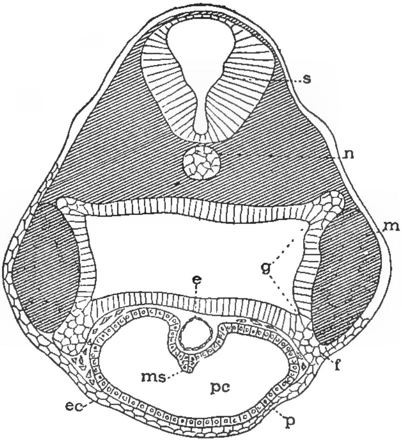

FIG. 193. Section through the throat region of an embryonic *Amblystoma*, illustrating the early formation of the heart. *e*, endothelium of heart; *ec*, ectoderm; *f*, fusion of ectoderm and entoderm through which the gill cleft will develop later from the gill pouch, *g*; *m*, myotome; *ms*, remains of ventral mesocardium, the dorsal mesocardium has not yet formed; *n*, notochord; *p*, pericardial wall; *pc*, pericardial cavity; *s*, spinal cord.

In the development of the heart three parts are to be considered, — the epithelium lining it, its muscular walls, and the cavity (**pericardium**) in which it is suspended.

Just behind the place where the first (hyomandibular) gill slit is to appear, the descending edges of the lateral plates, corresponding in length to several somites, meet just above the ventral epidermis, while more dorsally they enclose a groove-like space open to the yolk above. In this groove appear cells which ultimately develop into the epithelium (endothelium) of the heart ; but the origin of these cells is not certainly known. The evidence tends to show that they are derived from the yolk (entoderm); but the investigation is difficult, and they may arise from the mesothelium, or, less probably, they may be mesenchymatous in origin. These cells arrange themselves into a tube which is to form the lining (epithelium) of the heart and ventral aorta, while behind the heart region they extend backwards as a pair of tubes, the **omphalomesaraic veins** to be described later, on either side of the yolk.

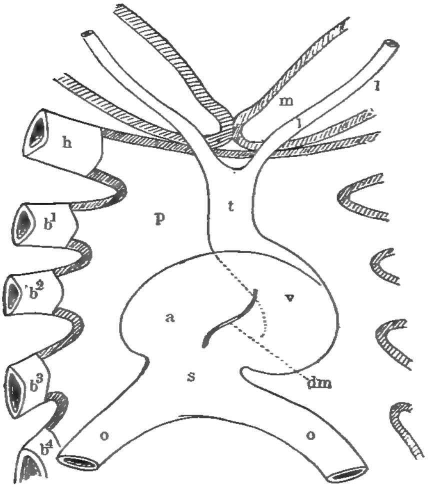

FIG. 194. Early heart of *Amblystoma*, after a reconstruction by Dr. F. D. Lambert. *a*, auricle; *b* ¹, *b* ⁴, branchial arches, 1–4; *dm*, dorsal mesocardium; *h*, hyoid arch; *m*, mandibular head cavity; *o*, omphalomesaraic veins; *p*, pericardial chamber; *s*, sinus venosus; *t*, truncus arteriosus; *v*, ventricle; 1, first aortic arch.

In the heart region the edges of the lateral plates now fuse in the mėdian line above and below the endothelial tube, thus giving rise to two longitudinal folds, a dorsal and a ventral **mesocardium**; while that part of the lateral plates surrounding the endothelium later develops the muscular wall (**myocardium**) of the heart and the ventral aorta. The downward growth of the lateral plates brings the cœlom just outside the myocardium, and this part of the cœlom becomes cut off from the rest, and gives rise to a space, the **pericardial cavity**, surrounding the heart.

At first the dorsal and ventral mesocardia are entire, and while dividing the pericardial space into right and left halves, suspend the tube in this chamber in the same way that the intestine is supported by the mesenteries farther back. Soon the ventral mesocardium breaks down, while a little later the dorsal membrane becomes reduced to a small support for the posterior portion of the heart. At first the tube is straight, and equal in length to the pericardium; but it rapidly increases in length, and as a result becomes twisted into an S-shaped tube, and with this twisting the heart becomes differentiated. In the S are developed two chambers, an anterior **ventricle** and a posterior **atrium** or **auricle**, the tube between these remaining smaller, — the **atrio-** or **auriculo-ventricular** canal. In this twisting only the posterior portion of the tube takes part, and the atrium comes to have the more dorsal position (Fig. 194).

The anterior straight portion of the tube gives rise to the **truncus arteriosus** and the **ventral aorta.** In the truncus region, which immediately adjoins the heart, two parts may be differentiated, — a posterior **conus arteriosus,** containing on its inside membranous valves preventing any backward flow of the blood, and an anterior and muscular **bulbus arteriosus.** Behind the heart the two omphalomesaraic veins unite to form a cavity, the **sinus venosus,** into which, later, other veins entering the heart come to empty. Valves soon arise in the auriculo-ventricular canal, and a little later other valves are formed at the opening of the sinus into the atrium. These valves are fleshy folds which prevent any backward flow of the blood.

In its earlier stages the heart lies in the region of the gill slits (Fig. 122); but as the animal increases in age there is a relative shifting of parts, so that the heart comes to lie behind the gills, and in many forms is removed some distance from them.

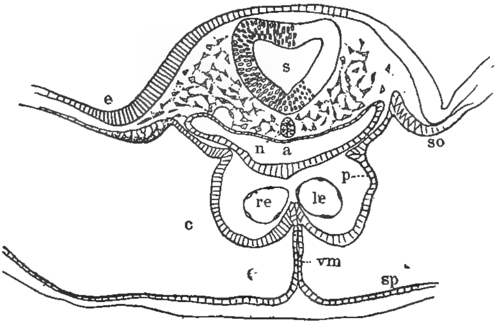

FIG. 195. Early stage in the development of the heart in the tern (*Sterna*). *a*, anterior end of the alimentary canal; *c*, cœlom, later cut off as pericardium; *e*, epidermis; *le*, left endothelial cavity; *n*, notochord; *p*, wall of somatoplure, which later gives rise to muscles of the heart; *re*, right half of heart; *so*, somatoplure; *sp*, splanchnoplure; *vm*, ventral mesocardium.

The conditions so far described are permanent in fishes, and also occur in the younger stages of all higher forms, with the

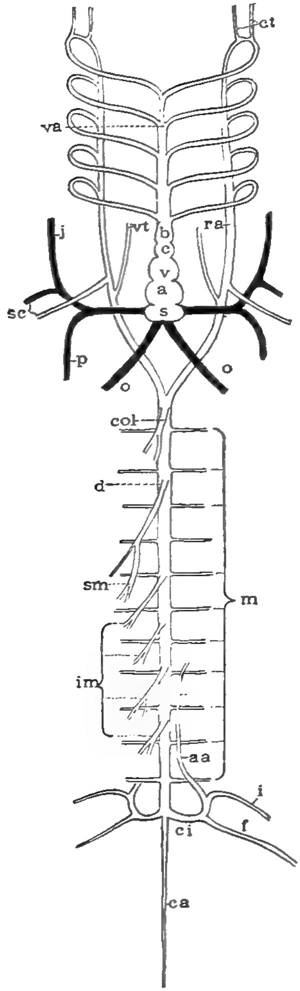

Fig. 196. Diagram of early arterial circulation. *a*, auricle; *aa*, anterior abdominal artery; *b*, bulbus arteriosus; *c*, conus arteriosus; *ca*, caudal artery; *ci*, common iliac artery; *col*, cœliac axis; *ct*, carotids; *d*, dorsal aorta; *f*, femoral artery; *i*, iliac artery; *im*, inferior mesenteric arteries; *j*, jugular vein; *m*, metameric (intercostal) arteries; *o*, omphalomesaraic (hepatic) veins; *p*, postcardinal veins; *ra*, radix aortæ; *s*, sinus venosus; *sc*, subclavian artery; *sm*, superior mesenteric artery; *v*, ventricle; *va*, ventral aorta; *vt*, vertebral artery.

exception of one feature in the amniotes. In these, as a result of the great size of the yolk, the heart at first appears as a pair of widely separated tubes (Fig. 195), which later approach and then unite to form the single tube, which then undergoes the twisting and differentiation already described.

The ventral aorta extends forward from the heart beneath the pharynx. It is a part of the same primitive tube from which the heart arises. From this tube there are given off vessels — right and left — (**aortic arches**) which pass outward in the tissue between the gill slits, then up on either side of the pharynx, and at last those of each side unite dorsally to form a vessel (**radix aortæ**) above the pharynx. Behind the region of the gill slits the radices of the two sides unite to form a tube (**dorsal aorta**), running backward between the notochord (vertebral column) and the alimentary canal to the end of the body.

From these arterial vessels smaller arteries are given off to supply the various regions of the body. From the first or anterior aortic arch of either side arise two arteries, the **external** (ventral) and **internal** (dorsal) **carotids,** which run forward to supply the head; the external being distributed to the muscles of the head and tongue, the internal going up through the floor of the skull to the brain.

Farther back the dorsal aorta gives off vessels, right and left, to the adjacent segments (see p. 188), and then gives off two larger trunks, the omphalomesaraic arteries, which at first connect directly with the omphalomesaraic veins already mentioned. Behind the origin of these arteries the dorsal aorta is a paired structure, but soon the two halves unite into the single vessel found in the adult of all forms. Near the posterior end of the peritoneal cavity the dorsal aorta gives off a pair of **hypogastric arteries** which run downward on the side of the alimentary canal, and behind these the aorta continues into the tail as the **caudal artery.**

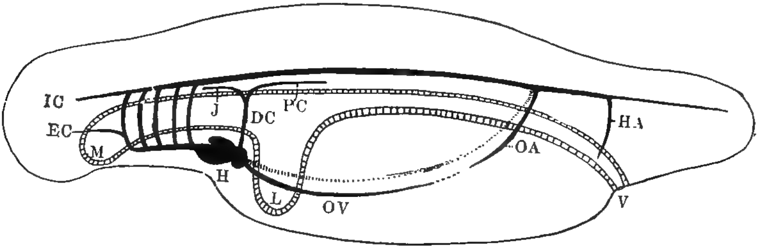

FIG. 197. Diagram of early circulation in a vertebrate with small yolk. *DC*, ductus Cuvierii; *EC*, external carotid; *H*, heart; *HA*, hypogastric artery; *IC*, internal carotid; *J*, jugular vein; *L*, liver; *M*, point of formation of mouth; *OA*, omphalomesaraic artery; *OV*, omphalomesaraic vein; *PC*, posterior cardinal vein; *V*, vent.

A little later another system of veins arises. These are the **jugulars,** or **anterior cardinals,** and the **posterior cardinals.** These run on either side of and a little below the backbone, the jugulars coming from the head, the posterior cardinals from the dorsal wall of the body cavity. These vessels of either side unite just above the heart into a transverse vessel, the **ductus Cuvierii,** which empties into the sinus venosus.

The foregoing gives in outline the great vascular trunks of the body; but these undergo many modifications in the different groups of vertebrates, while other vessels, both veins and arteries, are developed to supply the various organs. The alterations from these outlines are now to be traced.

Heart. — The heart always retains its primitive twist, and the atrium and its derivatives lie dorsal to or even in front of the ventricular portion. In the lower fish-like forms the heart of the adult can be reduced to the condition outlined above, but from the dipnoi and amphibia upwards (that is, with the appearance of lungs) this organ is more or less completely divided into right and left halves by a vertical septum which grows from behind forwards. In the groups just mentioned this septum divides the atrium into right and left halves, — the **auricles** of the heart. The sinus venosus retains its connection with the right auricle, while the pulmonary vein, bringing blood from the lungs, empties into the other. Thus the two auricles receive different kinds of blood. That which enters by way of the sinus comes from all parts of the body, and is consequently poor in oxygen and contains much carbon dioxide; while that coming from the lungs is rich in oxygen and lacking in carbon dioxide. These two kinds of blood are known respectively as **venous** and **arterial.**

In the contraction of the auricles the blood from the left auricle is first forced into the ventricle, while the venous blood follows later, and thus comes to occupy the posterior portion of the ventricle. These two kinds of blood are now forced through different portions of the aortic arches. In the truncus arteriosus a spiral fold or valve occurs, extending as far forward as the posterior aortic arch. When the ventricle contracts, this blood at first flows forward in the ventral aorta into the anterior aortic arches, which consequently receive arterial blood. As the aorta fills, the spiral valve moves in such a way that the venous blood flows into the posterior arches. In the reptiles the cardiac septum extends into the ventricle, dividing it partially or completely (crocodiles) into right and left halves. Even in those cases where the septum between the two halves is incomplete, there is a physiological division, for at the time of contraction the walls and the septum come together so as to separate the two sides. In the birds and mammals the separation is complete. Hence in all amniotes we can recognize an arterial (left) and a venous (right) side to the heart, each side consisting of practically an auricle and a ventricle. In the mammals and birds the division also extends to the truncus as far forward as the first aortic arch, so that these vessels are connected with the right auricle, the other arches being connected with the arterial half of the heart. In the reptiles the division is carried farther; for the fourth arch of the left side has its own trunk, and this is connected with the right side of the heart. The effect of this will be apparent after we consider the aortic arches.

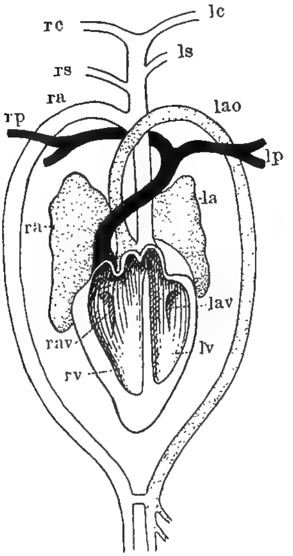

FIG. 198. Diagram of the heart and aortic arches of the alligator, after Hertwig. *la*, left auricle; *lao*, left aortic arch; *lav*, left auriculo-ventricular aperture; *lc*, left carotid; *lp*, left pulmonary artery; *ls*, left subclavian; *lv*, left ventricle. The right side with corresponding letters.

Aortic Arches. — In all vertebrates except the cyclostomes and lower sharks the aortic arches are typically five in number;[1] but in all except the elasmobranchs the number is reduced by the disappearance of the second normal arch. In the following the arches are numbered one to five, although that number may not be actually present. In the ichthyopsida these arches really consist of two parts, one arising from the ventral aorta, the others connecting with the dorsal aorta. In the gill arches these two vessels run parallel to each other, the connection between them being effected by capillary loops which run through the external or internal gill filaments. In passing through these gills the blood loses its carbon dioxide and takes up oxygen, and thus enters the dorsal aorta as arterial blood. In dipnoi, amphibia, and higher groups, in which lungs appear, the posterior (fifth) arch of either side sends a branch, the **pulmo-**

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[1] There is some evidence to show that the number is really six, an arch dropping out between the fourth and fifth of those recognized here.

nary artery, back into the corresponding lung. With the loss of gills in the amphibia and their absence in the higher groups, the lungs become the chief respiratory organs, and the proximal

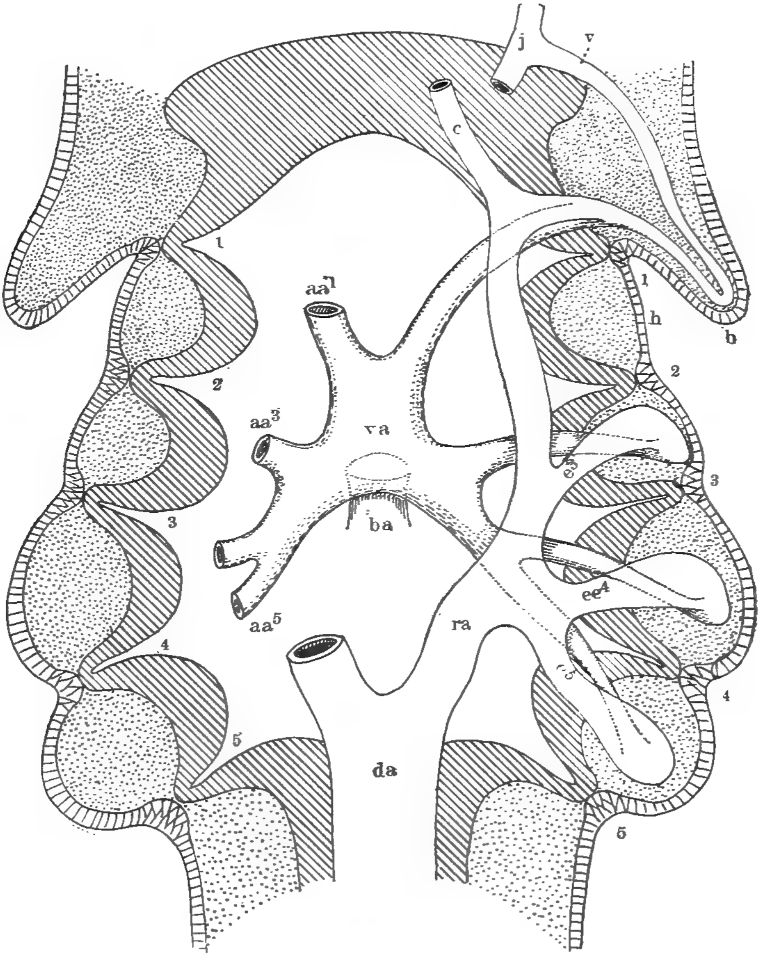

FIG. 199. Aortic arches of *Amblystoma* embryo, after a reconstruction by Dr. F. D. Lambert. *aa* $^{1-5}$, afferent arteries; *b*, balancer; *ba*, extremity of bulbus arteriosus; *c*, common carotid; *da*, dorsal aorta; *e* $^{3-5}$, efferent arteries; *h*, hyoid arch; *j*, jugular vein; *ra*, radix aortæ; *v*, vein from balancer to jugular; *va*, ventral aorta; 1–5, places where gill clefts are to form. Notice that the second aortic arch is lacking.

portion of the arch and the pulmonary artery increase in size, while that portion of the arch between the pulmonary artery and the radix remains undeveloped (**ductus Botalii**) or becomes entirely aborted. In the amphibia also the radix disappears between the first and third arches, so that blood forced through the anterior arches can only go to the head through the carotids.

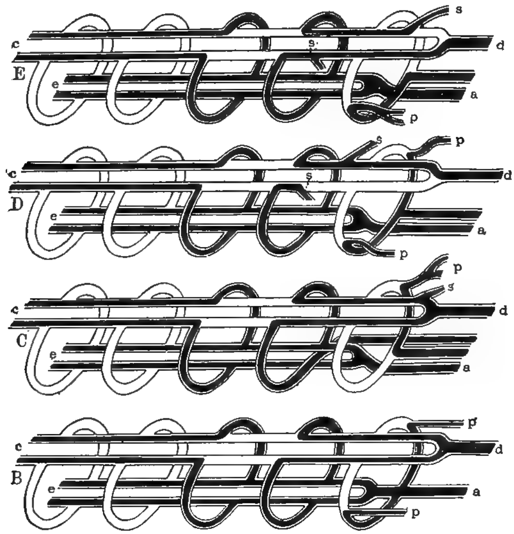

FIG. 200. Diagrams of the aortic arches in different groups of vertebrates. *A*, fishes; *B*, amphibia; *C*, reptiles; *D*, birds; *E*, mammals; *a*, ventral aorta; *c*, internal carotids; *e*, external carotids; *p*, pulmonary arteries; *s*, subclavian arteries. After Lambert.

In the urodeles two arches on either side (three and four) connect with the dorsal aorta by means of the radices; but in the anura, on the assumption of the adult condition, the fourth arch degenerates.

In the reptiles the conditions are somewhat complex. In certain lizards the third arch as well as the fourth may be connected with the radix, so that both arches are aortic in character, while the blood going through the third arch in part goes to the carotids. In the other reptiles the connection between the third and fourth arches disappears (Fig. 200 *C*), and here the third arch is purely carotid in character. The right arch of the fourth pair forms the main trunk of the dorsal aorta, while the left, which as we have seen is connected with the right side of the heart, is largely distributed to the digestive organs, only connecting with the dorsal aorta by a small trunk (Fig. 198). As a result of this distribution of vessels the carotids and the dorsal aorta receive arterial blood, while the stomach receives only venous or mixed blood. The remainder of the venous blood goes through the fifth arch to the lungs.

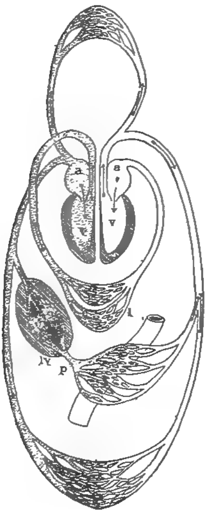

Fig. 201. Diagram of the circulation in a mammal, the arterial parts white, the venous shaded; the arrows show the direction of the flow of blood. *a*, auricles; *l*, lung; *lv*, liver; *p*, portal vein; *v*, veins.

In the birds and mammals where there are but two arterial trunks, all of the venous blood goes to the lungs, all parts of the systemic arteries receiving arterial blood. The chief distinction between these groups lies in the fact that in the birds the right half, in mammals the left, of the fourth arch persists (Fig. 200 *D* and *E*).

Arteries. — As development proceeds other arteries than those mentioned on p. 183 arise from the dorsal aorta and its radices. The chief of these are the following. In the cervical and posterior cranial regions are as many segmental arteries as there are segments. These are united by anastomoses on either side, after which the roots of the segmental arteries themselves disappear, with the exception of the last, which remains as the stem, while the anastomosing vessel on either side persists as the **vertebral artery,** growing forward into the head, where it anastomoses with the carotids. From the stem of the vertebral artery the **subclavian artery** arises as a bud, and with the outgrowth of the limb it extends into that member.[1] In the higher vertebrates the subclavian, on entering the fore limb, is known as the **axillary artery,** and farther down as the **brachial artery,** the brachial dividing in the fore arm into radial and ulnar branches which run near the corresponding bones.

With the absorption of the yolk, the omphalomesaraic arteries undergo changes. They early lose their direct connection with the omphalomesaric veins (Fig. 197), while that of the left side disappears without trace, that of the right carrying blood to the yolk, which finds its way to the omphalomesaraic vein by a system of yolk capillaries. From this persistent vessel a branch grows out

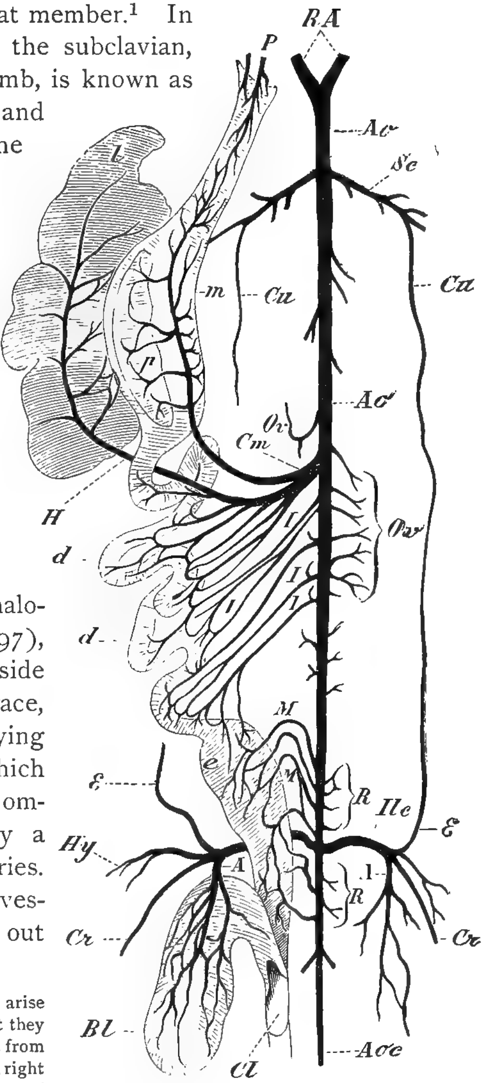

FIG. 202. Arterial system of *Salamandra*, from Wiedersheim. *A*, allantoic; *Ao*, aorta; *Bl*, bladder; *Cl*, cloaca; *Cm*, mesenteric; *Cr*, crural; *Cu*, cutaneous; *d*, intestine; *E*, epigastric; *e*, rectum; *H*, hepatic; *Hy*, hypogastric; *I*, intestinal; *Ilc*, common iliac; *l*, liver; *M*, rectal arteries; *m*, stomach; *Ov*, genital arteries; *P*, arteries to pharynx and œsophagus; *R*, renal arteries; *RA*, radices aortæ; *Sc*, subclavian.

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[1] Typically the subclavians arise from the radix of either side; but they may have their origin in the adult from the dorsal aorta, or, exceptionally, right and left subclavians may be given off from the radix of one side.

through the mesentery to the anterior end of the intestine, and becomes the **superior mesenteric artery** of the adult.

Anterior to the superior mesenteric arise arteries supplying the stomach, spleen, liver, pancreas, and duodenum (**gastric, splenic, hepatic,** and **duodenal**). In the lower vertebrates these are more or less distinct in their origin from the aorta, while in the adults of the higher groups they unite at their base into a common trunk, the **cœliac axis**; and occasionally the superior mesenteric may fuse for a short distance with this, forming a cœliac-mesenteric trunk.

Between the superior mesenteric (omphalomesaraic) and the hypogastric, other arteries (**inferior mesenterics**) supply the hinder end of the intestine; and these again may arise separately from the aorta, or their roots many fuse into one or more trunks.

The **hypogastric arteries** (**allantoics** of amniotes) are rather more complicated in their relations. In the fishes they are distributed on the ventral wall of the body in front of the vent and to the rectal region of the alimentary tract, while branches, the **iliac arteries,** are given off from each to the pelvic appendages. In the amphibia, with the development of an allantoic diverticulum from this region which later forms the urinary bladder, the vessels going to the rectal region enlarge, and are known as the **allantoic** arteries. In the embryonic sauropsida and mammals the allantois becomes greatly developed, and grows out (sauropsida) into close connection with the egg shell, or (mammals) forms the placenta (see Mammalia) which enters into intimate relations with the uterine walls of the mother. Thus in the amniotes the allantois becomes an important organ of respiration, and in mammals of nutrition, and the arteries which reach this distal portion through the umbilicus become very important. After birth (hatching) respiration and nutrition are accomplished in other ways, and these allantoic vessels consequently degenerate.

With the appearance of legs, the iliac arteries increase in importance. Of these there are two, — an anterior **external** and a more posterior **internal**, the latter arising from the hypogastric trunk. External and internal iliacs many arise separately from the dorsal aorta, or they may leave it as a single trunk, — the **common iliac.** From the internal iliac, arteries arise to supply the various viscera of the pelvis, and also an **ischiatic** or **sciatic artery,** which passes out to the dorsal portion of the hind limb, and early forms the chief supply of this appendage. This condition persists in all vertebrates except the mammals. In these the external iliac (after its entrance into the limb known as the **femoral artery**) extends farther into the limb, and usurps the function of the ischiatic, which here supplies only the posterior proximal portion of the appendage. The femoral artery extends down into the bend of the knee, where it is known as the **popliteal artery,** and in the proximal end of the shank divides into an **anterior tibial artery** which runs along the anterior face of the limb, and a **posterior tibial** and a **peroneal** in the calf of the leg.

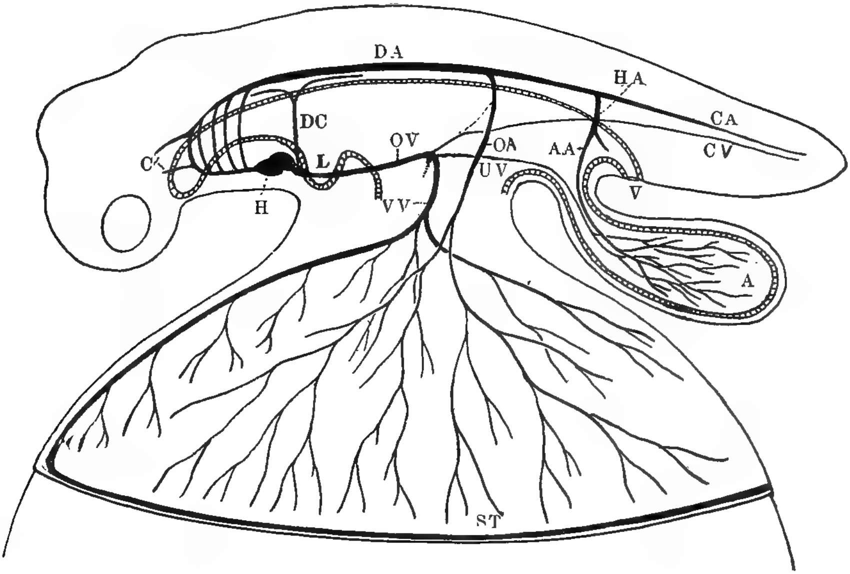

FIG. 203. Diagram of the chief circulatory vessels in an embryonic sauropsidan. The amnion omitted for clearness. *A*, allantois; *AA*, allantoic artery; *C*, carotid arteries; *CA*, caudal artery; *CV*, caudal vein; *DA*, dorsal aorta; *DC*, ductus Cuvierii; *H*, heart; *HA*, hypogastric artery; *L*, liver; *OA*, omphalomesaraic artery; *OV*, omphalomesaraic vein; *ST*, sinus terminalis; *UV*, umbilical (allantoic) vein; *V*, vent; *VV*, vitelline vein. Compare with Fig. 197.

The arteries already described extend ventrally from the aorta; but there arise earlier numerous pairs of vessels, segmentally arranged (see p. 188), which run out in a transverse direction to the muscles and to the urogenital structures. Those which run out in the body wall to supply the muscles, etc., are known, according to their position, as the **intercostal** and **lumbar arteries**; those going to the excretory organs are the **renal arteries**; while the **genital arteries** (**ovarian** or **spermatic**) go to the reproductive organs (gonads). In the lower vertebrates, where the pro- or mesonephros is functional throughout life, the renal arteries retain their metameric character; but with the formation of a metanephros (amniotes) the segmental arrangement is lost, and the kidneys receive their blood through a single pair of renal arteries. The blood-vessels supplying the gonads undergo a similar reduction in the higher vertebrates.

Veins. — The primary venous trunks have been enumerated on a previous page; they are a pair each of omphalomesaraics, jugulars, and posterior cardinals.

The omphalomesaraic veins are the paired posterior continuations of the grooves from which the heart is formed. They continue themselves backwards, and at first are connected with the omphalomesaraic arteries (see Fig. 197). Soon this connection is lost, and the vein of the right side partially disappears, while the other sends out branches, right and left, over the yolk. In those vertebrates which, like the sauropsida, have a large yolk, these **vitelline veins** play an important part in the early development, but with the absorption of the yolk they disappear. From the point where the vitelline veins arise from the persistent omphalomesaraic, two veins grow back along the tail beneath the caudal artery, passing on either side of the rectum. Fusion of these vessels occurs, and there results a single **caudal vein** with a loop around the vent (Fig. 205).

In the beginning the two omphalomesaraics pass on either side of the liver; but as this organ develops, the left omphalomesaraic sends a branch into it from behind, while from the anterior side both omphalomesaraics extend into this gland. There is thus inaugurated a system of circulation (the **portal system**) through the liver, while that part of the left omphalomesaraic which passed around the liver degenerates, and the anterior portions of these veins become converted into the **hepatic veins,** conveying blood from the liver to the sinus venosus. In this process that portion of the omphalomesaraic vein between the liver and the origin of the vitelline vein becomes twisted, so as to surround the intestine in a spiral manner; and this portion persists throughout life as the **portal vein** which brings blood from the intestine to the liver, while that part of the caudal vein which lies in the intestinal region develops into the **subintestinal** vein of the adult. The fate of the posterior part of the caudal vein will be given below.

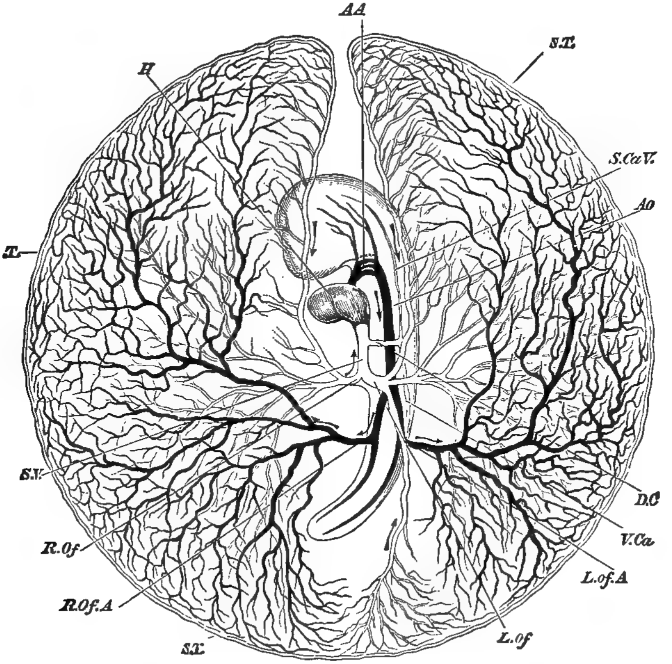

FIG. 204. Scheme of the circulation in a chick of the third day from below, after Balfour from Wiedersheim. *AA*, aortic arches; *Ao*, dorsal aorta; *DC*, ductus Cuvierii; *H*, heart; *Lof*, left omphalomesaraic vein; *LofA*, left omphalomesaraic artery; *ROf*, *ROfA*, right omphalomesaraic vein and artery; *SCaV*, anterior cardinal vein; *SV*, sinus venosus; *ST*, sinus terminalis; *VCa*, posterior cardinal vein.

The posterior cardinals at first extend back to the anterior ends of the pronephros, from which they return the blood to the heart. With the development of the mesonephros they extend farther back until they reach the posterior limits of the abdominal cavity. Each gives off intersegmental veins to bring back a portion of the blood sent into the abdominal walls by the intercostal and lumbar arteries, while in the early stages the veins from both extremities (**subclavians** and **hypogastrics**) empty into the same vessels.

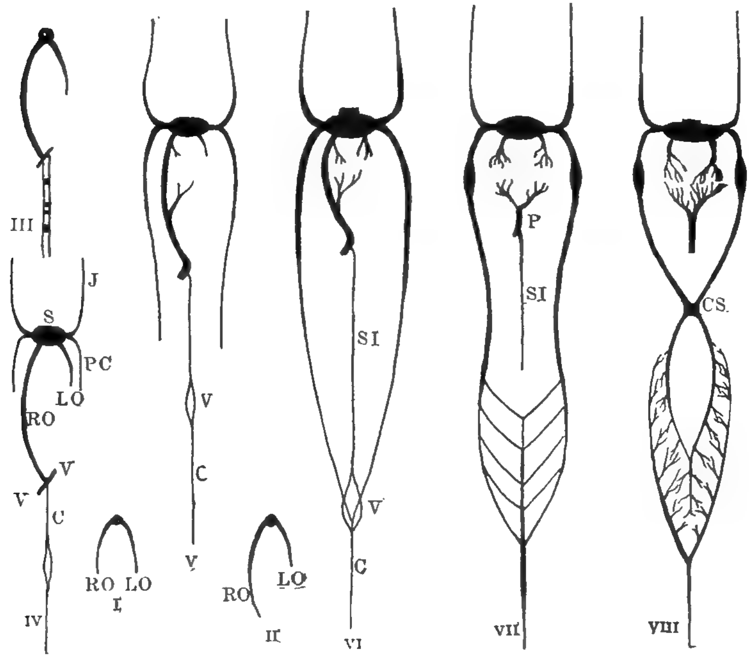

FIG. 205. Development of the venous system of selachians, after Rabl and Hochstetter. *C*, caudal; *CS*, cardinal sinus; *J*, jugular; *LO*, left omphalomesaraic; *P*, portal; *PC*, postcardinal; *RO*, right omphalomesaraic; *S*, sinus venosus; *SI*, subintestinal; *V*, vitelline (in *V* and *VII*, cloacal loop). Compare *VII* and *VIII* with Fig. 206.

These post cardinals gradually develop a rich vascular plexus in the mesonephros, receiving the blood brought from the tail by the caudal vein, which runs forward between the two Wolffian bodies. When this system is established the connection between the caudal and subintestinal veins is lost. Modifications now set up in the capillary system of the mesonephros not easily described in a few words, but readily made out from Fig. 205, the result being that the interrenal part of the caudal vein becomes continuous with both posterior cardinals, while the posterior portion of the caudal vein divides and extends forwards upon the lateral sides of the Wolffian bodies, absorbing the posterior part of the posterior cardinals, and with them receiving the blood from the posterior appendages.[1]

In front of the kidneys in elasmobranchs, the posterior cardinals meet and fuse in the median line, thus forming a **cardinal sinus** between the gonads. In the teleosts the cardinals unite behind with the caudal vein, and then that of the left side closes near the middle, so that the blood from the left kidney usually passes backwards to enter the right cardinal on its way to the heart.

In the dipnoi and amphibia a new vein, the **postcava (vena cava inferior)**, comes into relations with the system just described. It begins as an outgrowth of the right hepatic vein, and extends back and joins the right posterior cardinal just in front of the Wolffian body, so that now a large part of the renal

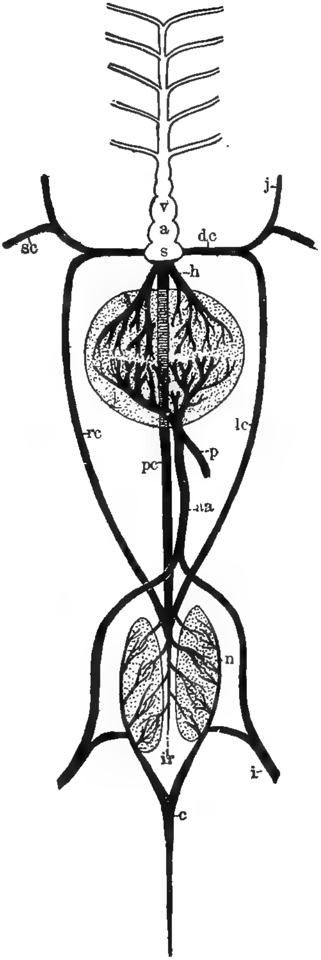

FIG. 206. Diagram of the venous system of an Amphibian. *a*, auricle; *aa*, anterior abdominal vein; *c*, caudal vein; *dc*, ductus Cuvierii; *h*, hepatic vein; *i*, iliac vein; *ir*, interrenal vein; *j*, jugular; *lc*, left cardinal; *n*, mesonephros; *p*, portal vein; *pc*, postcava; *rc*, right cardinal; *s*, sinus venosus; *v*, ventricle.

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[1] This has been greatly abbreviated in mammals.

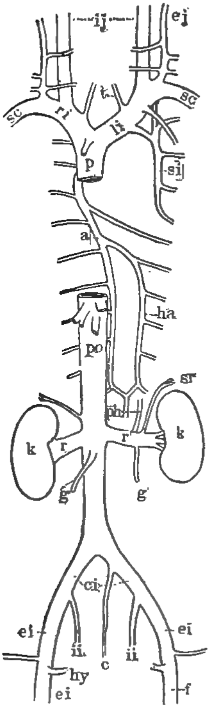

FIG. 207. Venous trunks of man. *a*, azygos; *ι*, caudal (sacralis media); *ci*, common iliac; *ei*, external iliac; *ej*, external jugular; *f*, femoral; *g*, genital; *ha*, hemiazygos (azygos minor); *hy*, hypogastric; *ii*, internal iliac; *ij*, internal jugular; *k*, kidney; *li*, left innominate; *p*, precava; *ph*, phrenic; *pc*, postcava; *r*, renal; *ri*, right innominate; *sc*, subclavian; *sr*, suprarenal; *si*, superior intercostal; *t*, thyroid.

portal blood returns to the heart by way of the postcava, while the posterior cardinals merely receive that which comes back from the body walls by way of the intersegmental veins.

In the amniotes, a renal portal system never reaches that development seen in the ichthyopsida, and is only found in connection with the Wolffian body, *i.e.*, in embryonic life. When first formed, blood is returned from the kidney by the posterior cardinal veins; and these extend back and receive the iliac veins as well, no interrenal vein being formed by the co-operation of caudal and postcardinal veins. When the postcava extends back as far as the permanent kidneys, it sends a renal vein to each; and from this point backwards it absorbs the right postcardinal, while on the other side lateral veins extend out and take the blood formerly brought to the postcardinal of the left side by the intersegmental veins, Fig. 208 C.

Farther in front a transverse vein arises from the right postcardinal, and crosses over and unites with the left, which now loses its connection with the ductus Cuvierii and becomes the **hemiazygos vein,** the blood from which now passes across into the right post cardinal, called in man the **azygos** or **azygos major.** In this way all of the blood from the hinder half of the body (*i.e.*, from the kidneys and behind) flows back to the heart through the postcava. The anterior portion of the left posterior cardinal may retain its connection with the anterior veins (left innominate) of the same side, and become converted into a **superior intercostal vein.**

The blood distributed by the hypogastric arteries is returned to the heart by the derivatives of a pair of hypogastric veins which run on the ventral body wall forward to the omphalomesaraic vein. When the hind limbs appear, external and internal **iliac veins** grow out from the hypogastrics into those appendages, their ultimate distribution coinciding more or less closely with the similarly named arteries. When the posterior cardinals grow back into this region they tap these vessels, and so the blood from the hinder appendages is returned to the heart through them, at first directly, later through the renal portal system (Fig. 206), and in the higher vertebrates by way of the postcava. The ventral portions of the hypogastric veins retain their connection with the iliacs throughout life in the ichthyopsida (Fig. 206), and either as two vessels or as a single **anterior abdominal vein,** run forward in the ventral body wall, and enter the portal system (Fig. 203).

In the amniotes, with the formation of the allantois, the hypogastric veins grow out into this, and are here known as the **umbilical veins.** In the reptiles they retain their distinctness; but in birds and mammals one aborts, leaving the other as a single trunk which empties into the omphalomesaraic. During embryonic life this system is very large and important, but after hatching or birth it becomes reduced to an inconspicuous condition, Fig. 203.

In the fishes the relations of jugulars and the ducts of Cuvier are much as outlined above, with the exception that the jugular veins develop two branches, internal and external. With the formation of lungs (dipnoi and amphibia) this system becomes unsymmetrical, in that the left Cuverian duct is now compelled to reach the right side of the sinus venosus; and here, as in the higher groups, the trunks, formed of united jugulars, subclavians, and posterior cardinals (*i.e.*, the Cuverian ducts), are known as the **precavæ,** right and left. Here, too, is to be noticed a shifting of the veins (**subclavians**) coming from the fore limbs. At first they empty into the posterior cardinals, but later they empty into the jugulars, the common trunks formed by the subclavians and jugulars being known as the **innominate veins.** In the birds a transverse anastomosis forms between the jugulars of the two sides. In the mammals (Fig. 208) a transverse connection forms between the precavæ of the two sides; and then the direct connection of the left precava with the heart is lost, so that all the blood from the right side of the head and the right fore limb passes through the left precava in its way to the heart.

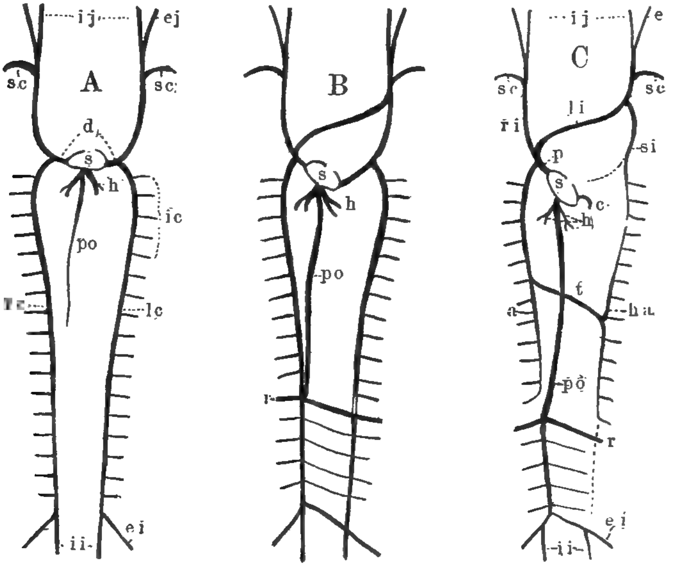

FIG. 208. Diagram (altered from Gegenbaur) showing the modifications of the venous trunks in mammals. *a*, azygos vein; *c*, coronary; *d*, ductus Cuvierii; *ei*, external iliac; *ej*, external jugular; *h*, hepatic; *ha*, hemiazygos; *ic*, intercostals; *ii*, internal iliacs; *ij*, internal jugulars; *li*, left innominate; *lc*, left posterior cardinal; *p*, precava; *po*, postcava; *r*, renal; *rc*, right posterior cardinal; *ri*, right innominate; *s*, sinus; *sc*, subclavian; *si*, superior intercostal. In *B* the postcava has extended backwards and tapped the right posterior cardinal; and a transverse trunk has formed between the jugulars of the two sides. In *C* a transverse vessel, *t*, has united the two postcardinals; and these have lost their other connections, and form the azygos system.

The lymph system forms another series of circulatory vessels which are distinct from the blood-vessels, excepting at one or more points where they connect, the lymph flowing from the lymph vessels into the venous system. The walls of the lymph vessels are always thin; in most places they consist merely of epithelium without muscular or adventitial envelopes, and at times, as in the frogs, they expand into large subcutaneous lacunar lymph spaces, or similar spaces around the gonads and in the mesenteries, as in many ichthyopsida. The system is frequently in connection with the cœlom by means of openings (stomata) in the peritoneal membrane.

The distribution of these vessels varies greatly in the different groups; and a detailed comparative study of the system is still a desideratum, while its development is largely unknown. In the fishes there is a rich plexus of lymph capillaries beneath the skin which extends into the connective tissue between the muscles, while around the heart and the ventral aorta the system is richly developed. In the lower vertebrates (amphibia, reptiles, and embryo birds) pulsating sacs occur in the course of these vessels, — the so-called lymph hearts. These are usually placed near some connection between the lymph and venous systems, as near the pelvis and the caudal vertebræ, or in the thoracic cavity dorsal to the heart; but occasionally lymph hearts occur at more distant points. For instance, in the urodeles a series of these occur beneath the lateral line; none are known in mammals.

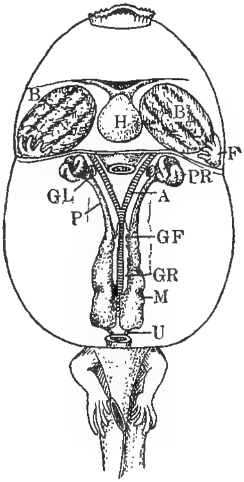

FIG. 209. Urogenital system of tadpole of frog, after Marshall and Bles. *A*, radix aortæ; *B*, gills; *F*, fore foot; *GF*, fat body; *GL*, glomus of head kidney; *GR*, genital ridge; *H*, heart; *M*, mesonephros; *P*, pronephric duct; *PR*, pronephros; *U*, ureter.

In sauropsida and mammals a special trunk, the **thoracic duct,** is developed in connection with the digestive tract which takes the lymph from the hinder extremities, the reproductive and excretory organs as well as the alimentary canal, and carries it forward, pouring it, in the sauropsida, into the right brachiocephalic vein, in the mammals into the left.[1] In birds and mammals valves

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[1] According to the unpublished studies of Dr. F. D. Lambert, a paired thoracic duct is developed in the young of *Amblystoma*, but a little later the right of these vessels becomes obliterated.

are developed in the larger lymph trunks, preventing any back flow.

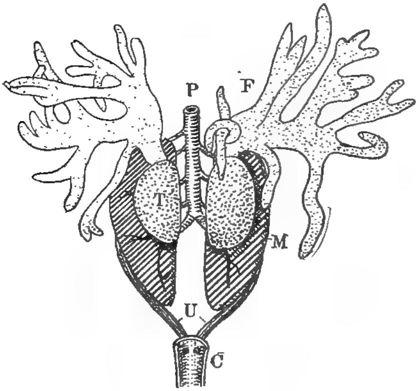

FIG. 210. Urogenital organs and fat bodies of adult frog. *C*, cloaca; *F*, fat body; *M*, mesonephros; *P*, postcava; *T*, testis; *U*, ureters.

In connection with the lymph system lymphoid tissue is developed, especially around the genital organs of the ichthyopsida, where, as in the amphibia and reptiles, this forms the prominent 'fat bodies.' Aggregations of such lymphoid tissue give rise to **lymph glands,** which are variously distributed through the vertebrate body. Of these the most prominent is the **spleen,** the cells of which are said to arise, in the tadpole, from the entoderm. It usually is somewhat close to the stomach, and in *Protopterus* (Fig. 40, *sp*) it is still enclosed in the gastric walls. Among other lymph glands may be mentioned the **tonsils,** which occur at the beginning of the pharynx in reptiles, birds, and mammals.

THE SEGMENTATION OF THE HEAD.

SINCE in the vertebrates the region of the body behind the head is made up of segments repeated one after the other (metamerism), there has naturally arisen the question, Is the head itself similarly composed of somites? If so, how many of these somites are to be recognized? Various attempts have been made to solve these problems, but with varying results. Only the merest outline of the attempted solutions can be given here.

In the trunk and tail regions the parts which are metamerically arranged are as follows: myotomes, spinal nerves, vertebræ, nephridial tubes, and the intersegmental blood-vessels. Each and all of these structures have been employed in the attempt to carry the segmentation forward into the head. The existence of the problem was first recognized by Oken (1807), who attempted its solution upon a vertebral basis. In the mammalian skull he recognized three vertebræ, the centres of which were represented respectively by the basioccipital, sphenoid and ethmoid bones, while the neural arches were formed by ex- and supraoccipitals, parietals, and frontals. Later students recognized four vertebræ in the skull, the increase being effected by recognizing basi- and presphenoid centres.[1] In 1869 Huxley showed that this theory was untenable, and that the 'vertebræ' of the skull could not be homologous with those of the trunk, since they were, in part, composed of membrane bone. He also pointed out that in those vertebrates (elasmobranchs) where one would naturally expect to find the vertebræ best developed, there was a continuous unsegmented brain case. His attempt at the solution of the problem was based upon the nerves and gill clefts, thus transferring the question from the

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[1] The interested student will find the extreme development of this 'vertebral theory of the skull' in the first volume of Owen's 'Anatomy of the Vertebrates.'

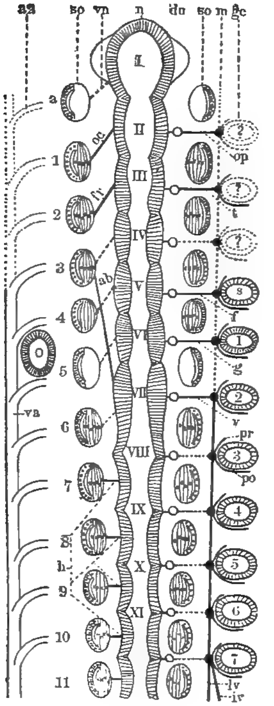

FIG. 211. Diagram of the head segments in a selachian, after Neal. *a*, anterior somite; *aa*, aortic arch; *ab*, abducens nerve; *dn*, dorsal nerves; *f*, facialis nerve; *g*, glossopharyngeal nerve; *gc*, gill clefts; *h*, hypoglossal nerve; *iv*, intestinal branch of vagus; *lv*, lateralis branch of vagus; *m*, mediolateral line; *n*, neuromeres; *o*, otic vesicle; *oc*, oculomotor nerve; *op*, ophthalmicus profundus nerve; *po*, post-trematic nerve; *pr*, pre-trematic nerve; *s*, spiracular cleft; *so*, mesodermic somites; *t*, trigeminal nerve; *v*, vagus nerve; *I–XI*, neuromeres; 1–11, somites of van Wijhe; 1–7, functional gill clefts.

vertebræ to the neural and branchial segments. With these as a basis he recognized nine cranial segments. Two years later Gegenbaur, using the same criteria, also concluded that there were nine segments in the head, although his somites and those of Huxley do not agree in detail.

Both of these authors recognized that the nerves behind the ear (IX–XII.) were like the spinal nerves in the possession of dorsal and ventral roots, and that the ninth divides above the first gill slit into pre- and post-trematic branches (p. 63). The tenth nerve, however, bears similar relations in the ordinary sharks to four gill clefts, and hence is a compound nerve. In front of the ear the facial nerve divides above the spiracular cleft, while the trigeminal nerve splits in a similar way on either side of the angle of the mouth. This last circumstance led Huxley to the view that the mouth has arisen from the coalescence of a pair of gill slits, a view which has received a certain amount of corroboration from embryology. This left a third division (ophthalmic) of the fifth nerve out of consideration; this was supposed to represent another segment further indicated according to Huxley's view by the orbito-nasal groove, while Gegenbaur saw traces of it in a pair of labial cartilages. Both recognized an additional segment in front of the ophthalmic, the details of which are not necessary here.

Balfour introduced another element, the mesodermal somites, into the discussion; and his method, developed by Marshall,[1] and still farther by van Wijhe, is that which has given results most often quoted in connection with this subject. Van Wijhe considered mesodermal somites, gill clefts, and nerves, and tried to utilize the purely motor nerves (III, IV, VI,) as ventral roots of the preauditory nerves. He recognized nine mesodermal segments, and the relations of these to the segmental nerves is given here in tabular form.

SOMITE.	DORSAL NERVE ROOT.	VENTRAL NERVE ROOT.
1.	Ophthalmicus profundus,	Oculomotor.
2.	Trigeminal less op. prof.,	Trochlearis.
3.	Acustico-facialis,	Abducens.
4.		None.
5.	Glossopharyngeal,	None.
6.	Vagus	Not recognizable.
7.		Hypoglossal.
8.		
9.		

Since van Wijhe wrote, others have tried to add to his structure, and some have claimed to recognize eighteen or nineteen of these head somites. It is pretty certain that there is at least one somite in front of the first recognized by him (Figs. 121 and 122 *a*). Others have taken the sense organs as their basis, including in this not only ear and nose, but sensory structures developed in connection with the gills, and considering the facialis as compound, have figured out eleven head segments (Beard). Again, the early condition of the neural tube has shown the existence of nervous segments (neuromeres, p. 49), eleven in number in the head region (Orr, Maclure, Hoffmann) back to and including the vagus. Locy has claimed that the same number of segments can be recognized in the medullary plate of elasmobranchs, amphibia, and birds before it is infolded to form the neural tube, but his conclusions are in dispute.

The questions asked at the beginning of this section cannot as yet be fully and finally answered. That the head is truly

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[1] Balfour recognized eight or nine somites; Marshall nine (eleven in notidanid sharks).

segmented can hardly be doubted; but this region of the vertebrates has been so wonderfully altered and specialized that the original segments have been greatly changed, and in some instances may have disappeared. The postauditory region presents the simplest condition; the tract in front of the ear is much more complex. We can say with great confidence that there are many more than the three somites recognized by Oken; while with some probability we can say that the number is not far from ten or eleven. In the discussion of the problem the greatest weight should be given to the positive evidence of the myotomes, since it is probable that segmentation originated in the mesoderm; next in importance are the cranial nerves, while less weight can be given to gill clefts and their modifications, and even less to the so-called branchial sense organs.

THE EARLY HISTORY OF THE OVUM.

THE formation of the essential parts of the sexual or reproductive cells from the germinal epithelium was mentioned upon a preceding page (p. 125). A brief account of their subsequent history follows. Space does not admit of any extended account of the details of the phenomena of reduction division, maturation, impregnation, etc., and the theories based upon them ; for these, reference must be made to the special text-books upon cytology and embryology.

Both eggs and spermatozoa, as they leave the gonads, are cells specialized for the perpetuation of the species ; and ultimate analysis shows that as they leave the parent tissue these cells contain all the absolute essentials for the reproduction of the kind. In the vertebrates, however, as in most other animals, these essentials are variously modified in shape and in composition by the addition of certain secondary features which demand attention.

As has already been said, the ovum is a specialized cell, which passes into an ovarian follicle, and receives nourishment from the follicular cells, and grows larger than the other cells of the body. At last it escapes from the ovary, passes into the cœlom, and thence to the exterior either through the Müllerian ducts (most vertebrates), through the pori abdominales (some teleosts), or by means of special structures (many teleosts). In its simplest condition an ovum is directly comparable to any other cell of the body, consisting merely of a mass of protoplasm with a specialized portion, the nucleus, near the centre. In most cases, however, it receives other parts of a secondary character, either from the ovarian tissues, or from the walls of the ducts through which it passes.

From the ovarian tissue the egg receives a varying amount of **food yolk** or **deutoplasm.** This is a peculiar substance to be used later as food by the growing embryo. It appears in the shape of small disks, plates, or globules embedded in the protoplasm. In color it is usually white, but in birds (Fig. 212) two kinds of yolk, white and yellow, are arranged in a complicated manner. The amount and distribution of this deutoplasm exercise an important influence upon the early phases of development, while the size of the egg is directly dependent upon the amount of this substance.

In the higher mammals the deutoplasm is scanty in amount, and is regularly distributed throughout the protoplasm (**alecithal**). In the amphibia and in *Petromyzon* the yolk is much more abundant, and the eggs are consequently larger in size. It is still distributed throughout the whole of the egg; but a marked polarity is visible, one pole of the egg containing the bulk of the protoplasm, while the other is as strongly deutoplasmic (**telolecithal**). In selachians, reptiles, birds, and monotremes this polarity is still more marked; while in many teleosts the extreme is reached, for here protoplasmic and deutoplasmic

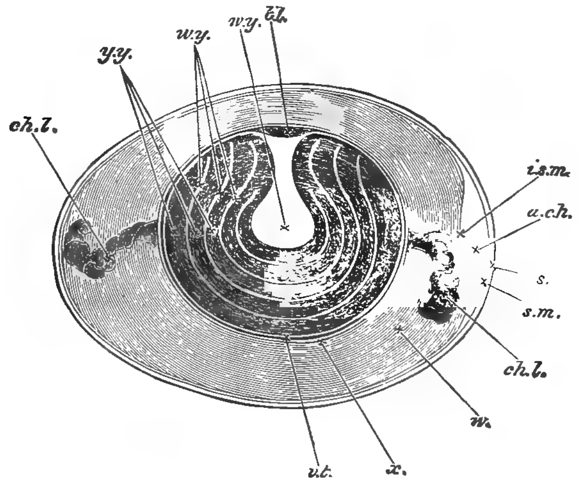

FIG. 212. Diagram of hen's egg, from Hertwig after Balfour. *ach*, air chamber; *bl*, blastoderm; *chl*, chalaza; *ism*, inner shell membrane; *s*, shell; *sm*, outer shell membrane; *vt*, vitelline membrane; *w*, white; *wy*, white yolk; *x*, inner layer of white; *yy*, yellow yolk.

portions are sharply distinct, the protoplasm resting as a small cap upon the large sphere of pure food yolk.

The egg is surrounded by primary and secondary envelopes, the former arising before the ovum has escaped from the ovary, the latter from the ovarian ducts. In the vertebrates the primary envelopes are at most three in number. These are, from without inwards, (1), a **vitelline membrane,** structureless in character; (2), a **zona radiata** (or **zona pellucida**) traversed by minute pores; and (3), a thin and delicate inner membrane. These are not constant, and any one or two may be lacking in a given egg. In some cases (teleosts and *Petromyzon*) an opening (**micropyle**) exists, through which the spermatozoon obtains entrance to the egg.

Of the secondary envelopes one of the simplest conditions is found in *Petromyzon,* where the outer surface of the egg is covered with a thin layer of adhesive mucus, which serves to fasten the egg to stones, etc. In the myxinoids the egg envelope is more horny, and is provided at either end with anchoring hooks. The descriptions would also imply that at the time of laying there was an outer sheathing capsule.[1] In the amphibia the eggs receive a coating in their passage down the oviduct which swells into a jelly when in contact with water. In the elasmobranchs the eggs are enclosed in a horny capsule, usually quadrangular in outline, while in the reptiles and monotremes the oviducts secrete around each egg a calcareous shell.

The birds present the most complicated condition. Here the eggs, after they have entered the oviduct, receive first a layer of albumen (the 'white'), a portion of which, firmer than the rest, is twisted into a spiral **chalaza** at either end. Outside of this there is next deposited a double **shell membrane,** and then, by the next division of the duct, the calcareous shell (Fig. 212).

The spermatozoa arise in the canaliculi seminiferi of the testes (p. 126), but they present many differences from the eggs. These in merest outline are as follows: In every cell of the

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[1] No one has yet described the origin of these envelopes of the cyclostome egg; it may be that they are ovarian in origin, a view which seems the more probable from the absence of oviducts.

body in any given species the nucleus contains a fixed and definite number of bodies, the **chromosomes,** so called because they are readily colored by the various microscopical stains. At each division of a cell these chromosomes are divided so that each daughter-cell contains exactly as many as did the mother-cell. Each egg before it leaves the ovary contains these chromosomes, and the number in each egg corresponds exactly with the number in any other part of the body of the mother. In the formation of the spermatozoa, however, there is a peculiar cell division, — a so-called **reduction division,** — the results of which are that each resulting spermatozoon contains just half the number of chromosomes normal to the species.

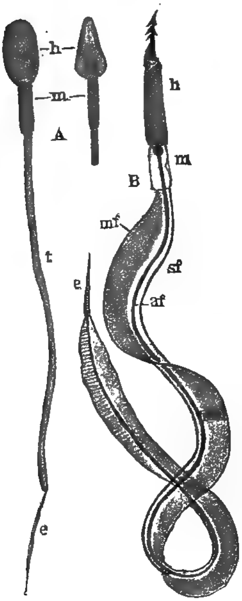

FIG. 213. *A*, human spermatozoon front and side view, after Retzius; *B*, diagram of vertebrate spermatozoon, modified from Böhm and Davidoff. *af*, axial filament; *e*, end piece of Retzius; *h*, head; *m*, middle piece; *mb*, undulating membrane; *mf*, marginal filament; *sf*, secondary filament; *t*, tail.

The spermatozoa also differ from the eggs in their appearance. The egg is passive, and it contains the nourishment and material from which the young is to be developed. The spermatozoon, on the other hand, must be active; for it must seek out and unite with the egg in order that the latter may develop. To this end it is made as small as possible. Deutoplasm is entirely absent, and the extranuclear protoplasm is reduced to the smallest amount. The chromosomes are compacted into a small body, the so-called **head,** while the protoplasm is largely developed into a 'tail,' consisting of an axial filament and a lateral membrane, by means of which the spermatozoon is able to swim.

Impregnation consists of the union of the egg and the spermatozoon, and there is abundant evidence to show that a single spermatozoon is sufficient to impregnate a single egg. This impregnation may take place either outside or inside of the body of the mother, the latter being the prevailing method, external impregnation occurring only in the cyclostomes and in most teleosts and amphibia. Occasionally, as in some urodeles, the spermatozoa are deposited in bunches (**spermatophores**), which are taken into the cloacal opening, effecting internal impregnation; or, as in most elasmobranchs, the ventral fins of the males are modified into copulatory and intromittent organs (**claspers**). In the birds the transmission of the sperm to the female is effected by an apposition of cloacal openings, although in a few birds a copulatory organ, the penis, is developed. In the reptiles this structure acquires a greater development, and reaches its extreme in the mammals.

After the spermatozoon has penetrated into the egg, there occurs, in all eggs accurately studied, certain phenomena which constitute the process known as **maturation.** These chiefly concern the nucleus, and are as follows: The nucleus approaches the surface of the egg and undergoes a normal division, one of the resulting halves, together with a small amount of protoplasm, being cast out of the egg as the first **polar globule.** The nucleus now divides again; but this division is a reduction division, half of the chromosomes being cast out in a second polar globule, while half sink back into the egg, which now contains just as many chromosomes as does the spermatozoon. These chromosomes now unite with those from the head of the spermatozoon, forming the new nucleus of the egg (the **segmentation nucleus**), which thus again contains the number of chromosomes characteristic of the species. Not until this process is complete is the egg really impregnated and ready for segmentation.

The character of the segmentation varies according, among other things, to the amount and distribution of the food yolk in the egg. This substance is inert, and its presence interferes with the living and active protoplasm. Were no deutoplasm present, the egg would divide in a regular and equal manner, and the resulting cells would be equal in size; and the same would be true, other things being equal, were the deutoplasm small in amount and evenly distributed through the protoplasm. Such eggs do occur in the non-vertebrate groups, but none are known among the vertebrates. The simplest conditions presented by these forms may be illustrated by the amphibia, the outlines which follow being to a measure true of *Petromyzon* and some ganoids.

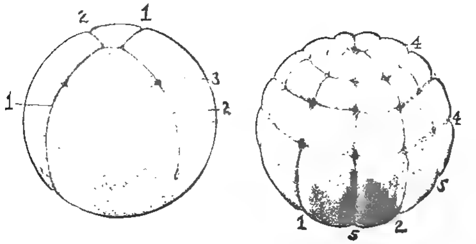

FIG. 214. Two stages in the segmentation of the egg of *Amblystoma;* 1 to 5 the successive planes of segmentation.

In the amphibia the first two planes of division may be compared to two meridians of a globe at right angles to each other. These begin to cut through at the protoplasmic (darker) pole of the egg, and gradually extend to the other. The third plane is at right angles to these, but nearer the protoplasmic than to the deutoplasmic pole. The result is that the eight resulting cells are unequal in size, four being small and four much larger. This disparity in size is continued in the following divisions, and it also affects the position of the internal segmentation cavity (p. 5), which, instead of being central, is pushed toward the protoplasmic pole (Fig. 215). In the amphibia, then, the whole egg divides into cells. Such eggs are called **holoblastic.**

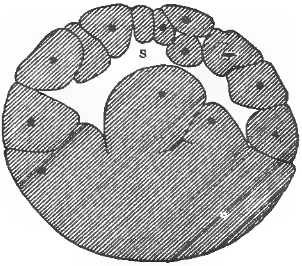

FIG. 215. Early stage of the segmentation of the egg of *Amblystoma*, in section, showing the excentric position of the segmentation cavity, *s*.

In elasmobranchs, reptiles, and birds, where the deutoplasm is much more abundant, and the polar differentiation of the egg is more marked, the planes of segmentation do not cut through the entire egg, but are confined to what is called the germinal area at the protoplasmic pole. Here occur meridional and circular planes of division, so that the germinal area is converted into cells, while the bulk of the egg remains unsegmented. In these **meroblastic** eggs the segmentation cavity is still farther displaced from the centre, so that it comes to lie immediately beneath the protoplasmic pole. The layer of cells formed by this segmentation is known as the **blastoderm.** In the teleosts where protoplasm and deutoplasm are sharply distinct, the protoplasmic portions alone are segmented, the food yolk remaining undivided, and the segmentation cavity here lies between the blastoderm and the deutoplasmic mass.

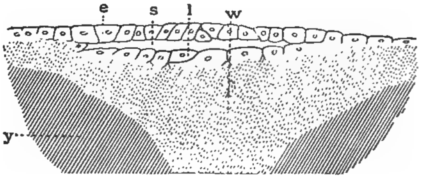

FIG. 216. Early segmentation of hen's egg, after Duval. *e*, ectoderm; *l*, lower layer cells; *s*, segmentation cavity; *w*, white yolk; *y*, yellow yolk. Only a small part of the egg shown; compare Fig. 212.

The little that is known of the development of the eggs of the monotremes shows that in their features of segmentation they are closely like the reptiles and birds, — they are meroblastic; but the other mammals present several peculiarities in their segmentation, which can best be considered after a description of the process of gastrulation in other vertebrates.

In the amphibia and similar forms the segmentation cavity is so small that it would be impossible for the larger yolk-loaded cells to become invaginated in the typical manner (p. 5), and so a modification of the process, not easily described, takes place, the result however being the production of the two-layered gastrula. In a few words the process may be outlined as follows: Since the large cells cannot be pushed inside the smaller ones,

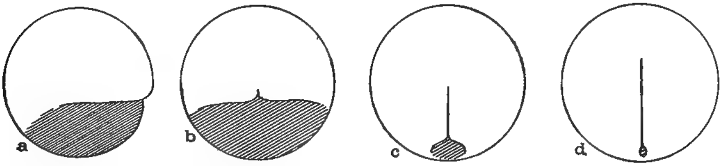

FIG. 217. Diagram of the process of gastrulation in *Amblystoma;* the cells to be invaginated as entoderm shaded. *a* and *b*, front and side views of the beginning of the invagination, the primitive groove beginning in *b*; *c*, a later stage with longer primitive groove; in *d*, the process is nearly complete, a small patch of entoderm being seen behind (yolk plug in the 'anus of Rusconi').

the latter grow down over the others at that side of the egg which is later to form the hinder end of the embryo. This downward growth results in the infolding of a portion of the cells as a sort of pocket, the cells on the upper surface of the pocket being small, those on the lower side the larger yolk-laden cells. This pocket is the archenteron; its walls are entoderm, and its opening is the blastopore. As the process continues, the blastoporal lips of either side come to meet in the median line, producing the primitive streak and groove already described.

In the elasmobranchs the process of gastrulation is still farther modified by the large amount of unsegmented yolk. Here the blastoderm forms a small circular patch of cells resting upon the yolk. At the morphologically hinder portion of this blastoderm the cells begin to turn in between the rest and the yolk, thus differentiating ectoderm and entoderm. As the blastoderm increases in size by continual cell division plus additions from the yolk, this infolded rim grows together, its halves swinging in toward the middle line so that the grooves of either side unite to form a tube, — the archenteron, — the floor of which is formed by the yolk. The rim of the inflected tissue must be regarded as the lips of the blastopore, and as these lips unite in the median line they give rise to the primitive streak.

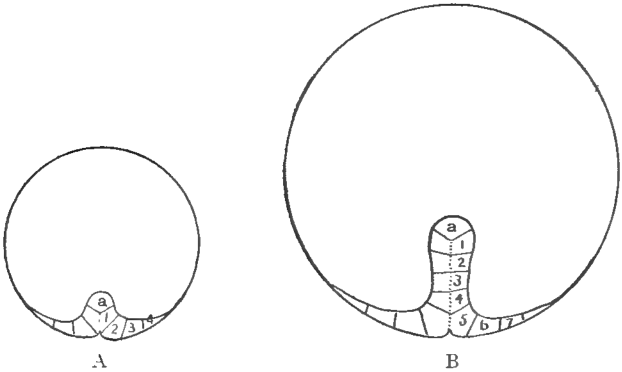

FIG. 218. Diagram of two stages in the formation of the embryo in an elasmobranch egg; the inflected rim of the blastoderm divided up into segments so as to illustrate the formation of the embryo by concrescence.

In birds the first phenomenon of gastrulation is the formation of a crescentic or sickle-shaped groove at the margin of the blastoderm, the anterior margin of which is directly comparable to the rim of inflection in the elasmobranch. The edges of the right and left halves of this groove coalesce as in the sharks, and then the blastoderm grows backward beyond the primitive streak thus formed, so that the streak comes to lie like an island in the centre of the blastoderm. In the reptiles much the same conditions occur as in the birds, except that the blastopore is placed within rather than at the edge of the blastoderm.

A feature to be noticed in all the foregoing types is that in each case the embryo arises from right and left portions, which at first may be widely separate, and which meet and fuse in the middle line. This phenomenon of **concrescence** consists in the formation of the dorsal portions of the embryo, and all of the structures there developed — nervous system, myotomes, sclerotomes, vascular system, and cœlomic structures — from the union of the blastoporal lips.[1] This process is illustrated in our figures (Fig. 218) where the successive portions of the germinal ring (*i.e.*, edges of the blastopore) are shown uniting to form the axial portion of the embryo.

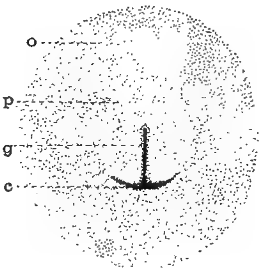

FIG. 219. Early blastoderm of hen's egg, after Kölliker. *c*, crescent; *g*, primitive groove; *o*, area opaca; *p*, area pellucida.

In the placental mammals the eggs are very small and the amount of deutoplasm is small, consequently the eggs are holoblastic. In their segmentation and in the method of formation of the germ layers these eggs present many peculiarities, which are usually explained upon the hypothesis that the mammals have descended from animals with large-yolked eggs, and that the features in which they differ from the other vertebrates as well as from other animals with holoblastic eggs are to be attributed

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[1] Several authors (Sedgwick, Kastschenko, Morgan, and others) have criticised this theory in one way or another, but the actual facts of development seem to negative their arguments.

to loss of yolk and consequent modification of processes. From almost the first the segmentation is irregular; and there results, exactly how is not known, a solid sphere consisting of an outer layer of hyaline cells surrounding a mass of more granular cells, one of which reaches to the exterior through a gap, closed later, between the cells of the outer layer. Now the solid mass expands into a hollow sphere, the blastodermic vesicle, the outer layer of cells becoming greatly flattened, the inner adhering to one side of them in a small lenticular mass, the cavity of the vesicle being filled with fluid. The lenticular mass becomes three layered, increases in extent, and gradually extends around under the outer layer so that the whole vesicle is eventually two layered throughout. The central portion of the lenticular mass remains thicker than the rest, and in this place the embryo arises, a primitive streak being formed, but nothing that can with certainty be called a blastopore appears.

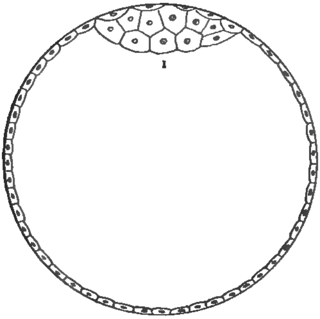

FIG. 220. Diagram of mammalian blastodermic vesicle. *i*, inner cell mass.

So far there is little dispute as to the facts, but as to their interpretation the views are various, some regarding the outer layer as ectoderm, others as entoderm; while the inner cell mass is regarded by some as purely entodermal, by others as giving rise to both ectoderm and entoderm. For details reference must be made to special works on vertebrate embryology.

THE ORIGIN OF THE VERTEBRATES.

THE question as to the ancestors of the vertebrates is one of the most vexed problems of zoology. It has seemed at times as if the solution were near at hand. The recognition of chordate affinities in the tunicates, and, later, in *Balanoglossus*, at the time when these were regarded as invertebrates, raised hopes that were disappointed when it was found that these forms were chordates, and that only superficial resemblances had caused their association with the non-vertebrate groups. It would seem that to-day we are not much nearer the answer to the question than we were when the theory of evolution was new.

Apparently the problem must be solved, if solved it ever be, upon the basis of comparative anatomy and embryology. Paleontology has never thrown the slightest light upon the matter, and it seems as if it never could, because it is more than probable that the ancestral chordate was a soft-bodied animal of small size, incapable of leaving any definite impress in the rocks.

The three most important characteristics of the vertebrates, and of all chordates, are the presence of gill slits, the existence of a notochord, and the occurrence of a central nervous system placed entirely upon one side of the alimentary canal. These features are found in no invertebrate, and we can only speculate upon the way in which they have arisen; for it is one of the canons of evolution that no organ arises *de novo*, but only by modification of some pre-existing structure.

At present the greater weight of evidence, such as it is, points toward an annelid ancestry. Annelids and vertebrates agree in the possession of metamerism, and the homologies of the metameric structures can be traced with some detail. Muscular system, cœlomic pouches, and nephridia agree in their general features, while the fact that the nephridial ducts in both serve to carry away the sexual cells is also suggestive. These ducts, however, afford some difficulties, as it is not easy to see how the continuous pronephric duct of the vertebrates could have arisen from the separate ducts of the annelid. Again, the ventral nervous chain of the annelid can be closely compared with the spinal cord of the vertebrates, the comparison including the dorsal roots of the nerves with the spinal ganglia. The same is true of the similarities existing between the transverse blood-vessels of the annelids and the aortic arches and intercostal vessels of the vertebrates.

The most plausible hypothesis by which to homologize the anterior portions of the nervous system is that which regards the infundibulum and the nervous portion of the hypophysis as representing the invertebrate mouth, while the vertebrate mouth may have arisen by the coalescence of a pair of gill slits. In this case the 'brain' of the annelid would be represented by the vertebrate fore brain. In certain annelids there exists a subintestinal tube of entodermal origin which has been doubtfully compared with the notochord, but as yet no structures are known in the annelids which can be homologized with the gill slits.

Other but less widely accepted views of the ancestry of the vertebrates are those which would derive the group from some arthropod not far from the limuloids, or from the nemertean worms. It must however be kept in mind that the greatest resemblances between vertebrates and annelids are directly or indirectly the result of metamerism; and that it is possible that this vegetative repètition of parts may have arisen independently in the chordate phylum, and that the similarities noted above may be expressions of convergent evolution, and that the chordates may have descended from non-segmented ancestors. This view receives some support from the fact that metamerism also occurs in the echinoderms, where it could not have been inherited from either annelids or vertebrates.

In the following pages are numerous references to the lines of descent of the various groups of vertebrates. The adjacent diagram illustrates some of these. Concerning some points there are differences of opinion. Thus the dipnoans are frequently regarded as the ancestors of the amphibia, a view which receives its chief support from the existence of lungs in both forms. In their skeleton and in other features the two groups seem widely remote. Again, in recent years the tendency has been to regard the mammals as descendants from theromorphous reptiles, a view which receives its chief evidence from paleontology. More lately still the tendency is to revert to the older view of an amphibian ancestry.

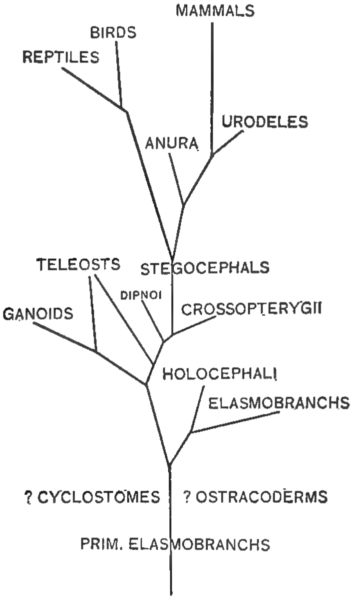

FIG. 221. Lines of descent of the different groups of vertebrates.

PART II.

SYSTEMATIC ZOOLOGY.

SUB-PHYLUM VERTEBRATA.

METAMERIC metazoan animals with a complete alimentary canal, the anterior portion of which, at least in embryonic stages, is provided with gill slits. The central nervous system, consisting of brain and spinal cord, is hollow, and is situated entirely on one side of the alimentary tract. Between alimentary canal and central nervous system is a skeletal axis — the notochord — of entodermal origin, which may persist throughout life. Around this notochord is developed a segmented skeleton, consisting of skull and vertebral column. The heart is on the abneural side of the alimentary canal, and consists of at least two chambers. It connects with a dorsal aorta by arterial arches, which, however, may become greatly reduced and modified in the adult. The blood contains red corpuscles in addition to leucocytes. The reproduction is entirely sexual. The vertebrates are free throughout their entire existence.

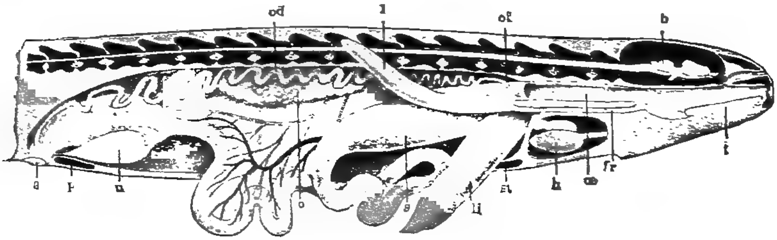

FIG. 222. Anatomy of a vertebrate, based on *Amblystoma*. *a*, anus; *b*, brain; *h*, heart; *l*, lung; *li*, liver; *o*, ovary; *od*, oviduct; *ot*, ostium tubæ; *p*, pelvis; *s*, stomach; *st*, sternum; *t*, tongue; *tr*, trachea; *u*, urinary bladder.

In dealing with the classification of the vertebrates many different ideas exist, not only with regard to the interrelationships of the various groups, but with their co-ordination as well. This is due to several causes. Among them may be mentioned the fact that only in exceptional cases among the fossil vertebrates are other structures than the skeleton preserved, and for this reason our classifications have of necessity been too largely based upon osteological characters. Again, there is a great difference in the numbers of species in the different groups; thus the cyclostomes, one of the two great divisions of vertebrates, contain less than a score of species, while of birds about twelve thousand 'species' are known. As a result, the group of aves has been subdivided to an extent unknown in other classes. Divisions which elsewhere would be regarded as families are here raised to ordinal rank, and other subdivisions correspondingly magnified. In the following pages it has been the attempt to preserve a proper co-ordination of groups, — to maintain a classificatory perspective.

The vertebrate phylum may be divided into cyclostomes and gnathostomes.

Series I. Cyclostomata (Agnatha).

Eel-like vertebrates without paired appendages; mouth suctorial, jaws lacking; olfactory organ single and median; optic nerves going to the eyes of the same side; gills 6–14 pairs in saccular pouches. The cyclostomes include but a single class, — the Marsipobranchii.

CLASS I. MARSIPOBRANCHII (MYZONTES).

The marsipobranchs are undoubtedly the lowest vertebrates; but there is yet a question as to how far their simple structure is the result of a primitive condition, and how far it has been caused by degeneration. The body is eel-like; and all traces of paired fins are absent, unless, as Dohrn suggests, two slight folds near the vent are the remnants of ventral fins. A median fin occurs, which may be continuous, or may be differentiated into dorsals and caudal. The skin is without scales, but is rich in mucus-secreting cells, and in the myxinoids contains also numerous pockets of so-called thread cells, these pockets extending into the underlying muscles. These thread cells have their protoplasm converted into a long thread, and when these are discharged, the threads become unwound ; and these and the mucus are so abundant that one of these animals will convert a bucket of water into a thick jelly.

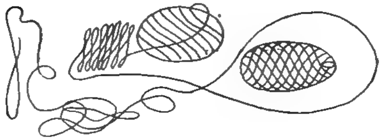
FIG. 223. Thread cells of *Bdellostoma*, one intact, the other 'exploded,' after Ayers.

The mouth is at the bottom of a more or less circular suctorial funnel, the inside of which, like the tip of the mobile tongue, is armed with horny, cuticular teeth, which aid the suckers in anchoring these animals to the fish on which they feed, and also serve to rasp the flesh. The alimentary canal is straight ; a circular fold, the velum, occurs inside the mouth ; no cloaca is present. The brain has well-developed cerebral lobes which may be solid or hollow, but the cerebellum is very small. The nasal organ is median, and is placed at the posterior side of the hypophysial duct, the opening to which thus serves as the nostril, opening either at the tip of the snout (myxinoids) or upon the top of the head (petromyzontes). The deeper end of the hypophysis expands into a large sac, which

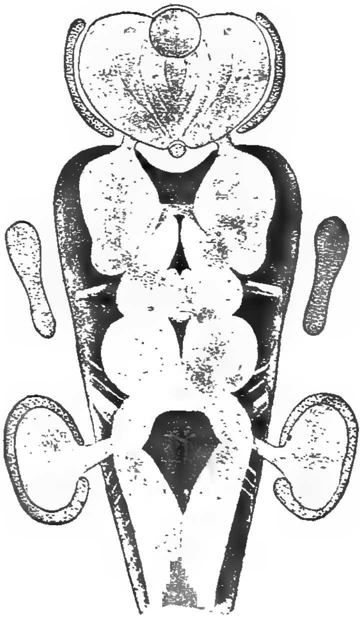
FIG. 224. Brain and nasal organ of *Petromyzon*. In front is (darker) the nasal canal, behind which are the plaits of the nasal membrane. On either side of the twixt brain are bits of the cartilage of the chondrocranium, and farther back the otic capsules.

in the myxinoids, opens into the mouth. The ears are remarkable in the absence of the horizontal (external) semicircular canal, while in the myxinoids but a single canal is present, which, as it bears an ampulla at either end, may be regarded as representing the anterior and posterior canals of the normal ear (p. 71).

The vertebral column consists of a large persistent notochord surrounded by a fibrous sheath and a membranous neural tube, in which (*Petromyzon*) cartilaginous neural arches occur. The cranium is cartilaginous, but is more or less incomplete above, and roofed by membrane. Labial cartilages and cartilages for the tongue occur; but all traces of jaws — pterygoquadrates, Meckel's cartilage — are lacking. The branchial region in the petromyzontes is supported by a complicated cartilaginous framework, the branchial basket; but it is as yet impossible to homologize this with the visceral arches of the higher vertebrates. In the myxinoids the basket is rudimentary.

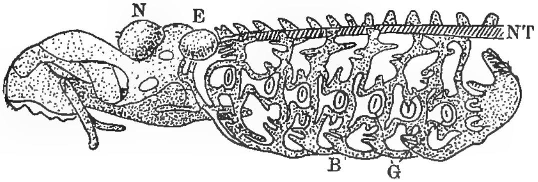

FIG. 225. Cranium and branchial basket of *Petromyzon*, after W. K. Parker. *E*, otic capsule; *B*, branchial basket; *G*, gill clefts; *N*, nasal capsule; *NT*, notochord.

The gill slits are tubular, and the folded gills are borne on the walls of pouch-like enlargements of these tubes. The heart lacks a conus arteriosus, and no renal portal circulation occurs. The excretory organs are elongate bands. In the lampreys and *Myxine* the pronephros is lost in the adult; but in *Bdellostoma* it retains its function throughout life, its nephrostomes opening into the pericardium.[1] The gonads are unpaired, and in the myxinoids are protandric hermaphrodite in character (*i.e.*, the animal is at one time male at another female), the anterior por-

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[1] According to Price, the whole excretory organs of *Bdellostoma* are pronephric in character.

tion being ovary, the posterior testis. The sexual products are discharged into the body cavity, from which they escape to the exterior through genital pores which open into the hinder end of the urinary (pronephic) ducts.

The eggs of the myxinoids are large, and each bears at either end a crown of long-stalked anchoring-hooks. Almost nothing is known of the development. The lampreys have much smaller eggs, the early development of which shows striking similarities to the conditions found in the amphibia. The eggs undergo a total but unequal segmentation, with small cells (**micromeres**) at one pole, and larger yolk-laden cells (**macromeres**) at the other. Gastrulation is effected in a modified manner by a growth of the micromeres over the macromeres, and the blastopore (or rather its posterior end) persists as the anus of the adult. In the development of the nervous system, instead of the typical inrolling of a medullary plate there is formed a solid cord or keel of cells along the middle line of the back, in which later, by splitting, a cavity appears. At the extremity of the head appears an inpushing, from the walls of which both olfactory organ and hypophysis are developed; and it is stated that the olfactory structures are paired at first, the azygos condition of the adult being a secondary feature. The young hatches from the egg in a larval condition known as the *ammocœtes* stage, with rudimentary eyes and a large hood-shaped upper lip. This is later metamorphosed into the adult.

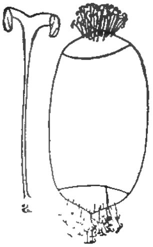

FIG. 226. Egg of *Bdellostoma;* at *a*, a single hook enlarged.

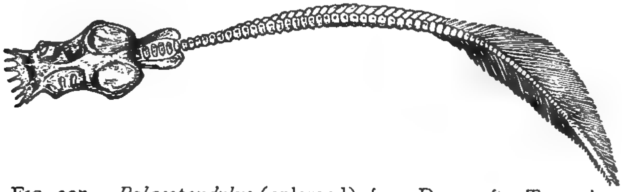

FIG. 227. *Palæospondylus* (enlarged), from Dean, after Traquair.

Fossil marsipobranchs are imperfectly known. Formerly peculiar structures known as conodonts were regarded as myxinoid teeth, but later these have been supposed to be annelid jaws. Traquair has recently described, under the name *Palæospondylus gunni*, a fossil from the Devonian of Scotland, which may prove to be a palæozoic marsipobranch, or possibly the larva of some higher form.

SUB-CLASS I. PETROMYZONTES (HYPEROARTIA).

Marsipobranchs with well-developed dorsal fins; hypophysial duct closed, its external opening on the top of the head; seven branchial openings on either side; branchial basket well developed; pharyngeal region divided by a longitudinal partition into a dorsal food tube and a ventral respiratory duct from which the gill slits arise; a slightly developed spiral valve in the intestine.

The lamprey eels live both in salt and in fresh water, some of the marine species ascending rivers in the spring to lay their eggs. When ovipositing they attach themselves to stones, or take up smaller pebbles with their suckers to make their nests, a fact which is reflected in the generic names *Petromyzon* and *Lampetra*. The lampreys feed upon the mucus and blood which they rasp from fishes to which they attach themselves. The lampreys are included in a single family, PETROMYZONIDÆ, and are grouped in several genera.

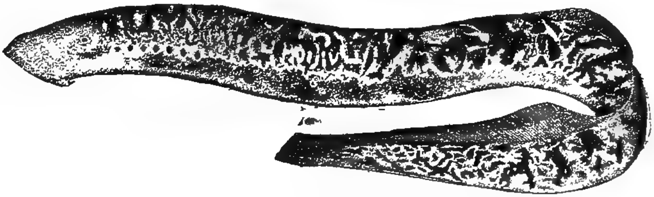

FIG. 228. See lamprey, *Petromyzon marinus*, after Goode.

Petromyzon, second dorsal joined to caudal, supraoral tooth with 2–3 cusps. *P. marinus* (sea lamprey), Europe and North America — Atlantic. *Lampetra*, smaller species (brook lampreys), with broad supraoral tooth with median cusp small or lacking. *L. planeri*, Europe. Scarcely different is *L. wilderi* from New York. Other genera are *Mordacia* and *Geotria* from the southern hemisphere.

SUB-CLASS II. MYXINOIDEI (HYPEROTRETIA).

Dorsal fin small or absent, hypophysial duct opening at tip of snout, posteriorly communicating with mouth cavity. Branchiæ 6–14 pairs, the pharyngeal region not divided. Behind the gill clefts on the left side occurs an œsophageo-cutaneous duct, connecting the pharynx with the exterior. Branchial basket rudimentary, snout bearing eight barbels ; spiral valve absent.

The hag-fishes and borers are the nearest approach to parasites in the vertebrate phylum. They fasten themselves to the gill region of fishes, and work their way into the inside, where they rapidly devour the flesh, leaving merely a hulk of skin and bones.

Family MYXINIDÆ. Branchiæ 6, the clefts uniting external to the branchial pouches to open to the exterior by a single opening. *Myxine*, the only genus. *M. glutinosa*, in the northern Atlantic south to Cape Cod. Family BDELLOSTOMIDÆ. Gills 6–14, each with its own duct. *Bdellostoma* (*Heptatrema*, *Polistotrema*), the only genus, occurs in the Pacific, where *B. dombey* ranges from California to Chile.

OSTRACODERMI.

The ostracoderms are a group of fish-like forms from palæozoic rocks of exceedingly doubtful relations. They have been regarded as ganoids, as cyclostomes, as tunicates, and even as having relations to the xiphosures (*Limulus*). This uncertainty of position is due to the fact that no traces of jaws or of internal skeleton have yet been found. The anterior half of the body was enveloped in an exoskeleton of large bony plates which no one has yet satisfactorily homologized with the bones in any modern form. The hinder part of the body was fish-like, the tail heterocercal. Frequently the anterior plates bear traces of canals supposed to have contained lateral line organs, while the head region contained pits which may have been occupied by eyes.

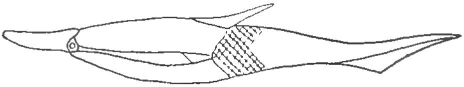

FIG. 229. Restoration of *Pteraspis*, after Lankester.

ORDER I. HETEROSTRACI.

Head region covered above by a few firmly united plates, below by a single ventral plate ; tail sometimes scaled ; orbits lateral ; no paired appendages. *Pteraspis*, the best-known genus, comes from the Devonian.

ORDER II. ASPIDOCEPHALI (OSTEOSTRACI).

Head covered by a large, simple, arcuate shield much like the cephalothorax of *Limulus* in outline, with 'orbits' near its centre. Tail covered with rhomboid scales of varying size. No paired appendages known. *Cephalaspis*, Devonian. *Auchenaspis*, upper Silurian.

ORDER III. ANTIARCHA.

Head and trunk covered with large polygonal plates coated with enamel; tail with small scales, 'orbits' dorsal, close together, a single pair of appendages ('pectoral fins'), covered with strong plates, and each jointed near the middle. *Pterichthys* (lower Devonian), 1–4 inches long. *Asterolepis*, 6 inches long (Devonian). *Bothriolepis*.

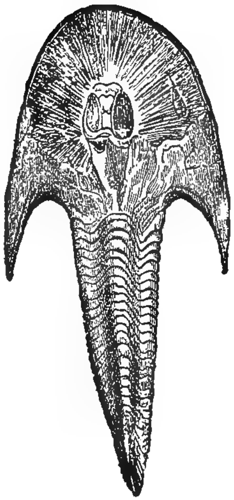

FIG. 230. *Cephalaspis*, from Dean, after Agassiz.

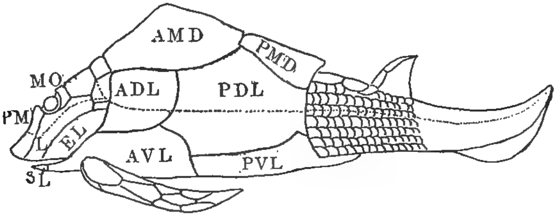

FIG. 231. Restoration of *Pterichthys testudinarius*, after Traquair. *ADL*, anterior dorso-lateral; *AMD*, anterior median dorsal; *AVL*, anterior ventro-lateral; *EL*, extra lateral (opercular); *L*, labial; *MO*, median occipital; *PDL*, posterior dorso-lateral; *PM*, premedian; *PMD*, posterior median dorsal; *PVL*, posterior ventro-lateral; *SL*, semilunar. Lateral line system dotted.

Series II. Gnathostomata.

Vertebrates with jaws; paired appendages normally present; olfactory organs paired, and not connected with hypophysis; optic chiasma present; three semicircular canals in the ear; gills, when present, never more than seven pairs.

The gnathostomes embrace the great majority of vertebrates, and the account of that group given in the first part of this volume applies largely to these forms. The mouth is transverse; paired limbs occur in all, except where, as in certain eels, snakes, etc., they have been lost. The skeleton is well developed, the vertebræ being cartilaginous or osseous, while the skull is more or less completely roofed in with cartilage or bone. The gill slits are narrow clefts, and are never more than seven in number, and the branchial arches are well developed. The gnathostomes are subdivided into two great divisions or grades, —the Ichthyopsida and the Amniota.

GRADE I. ICHTHYOPSIDA (ANAMNIA, ANALLANTOIDEA).

As the name implies, the ichthyopsida include the fish-like forms characterized by the presence of functional gills, either in the larval stages or throughout life, the absence of an amnion and true allantois (see amniota), and the presence in young or adult of median fins.

The surface of the body is rich in glands, and in most forms the skin contains scales largely of dermal origin (p. 92). In the young the skin also bears sense organs belonging to the lateral line system (p. 67) innervated by the seventh and tenth nerves; but in those forms in which the adults assume a terrestrial life (amphibia) this system becomes lost upon leaving the water. In the young, median fins, formed by a fold of the integument, occur; and in the fishes these are supported by rays of dermal origin, or by true skeletal rays, or by both. In the amphibia the rays are lacking, and the fins themselves disappear on the assumption of a terrestrial life.

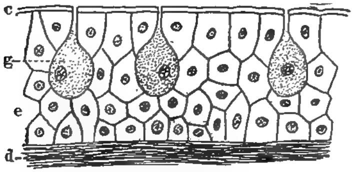

FIG. 232. Diagram of skin of a fish. *c*, cuticle; *d*, dermis; *e*, epidermis, containing, *g*, epidermal glands.

In the skeleton the noticeable features are the small size, or absence, of the basisphenoid, and the large size of the parasphenoid when present. Usually (fishes) no sternum is present; in the amphibia, where it occurs, it is never connected with the ribs. The branchial arches are four or more in number, and these are largely persistent in the adult.

In the brain the separate divisions are subequal in size. The vagus nerve innervates all but the anterior pair of gill slits, and in the aquatic forms bears a large ramus lateralis distributed to the sense organs of the skin. The eleventh nerve is apparently a branch of the vagus, while the twelfth is represented by the first, or first and second, spinal nerves.

The heart, usually far forward in position, has the sinus venosus external to the atrium, the atrium single or divided by a longitudinal septum into right and left auricles, the ventricle always simple and undivided. In the lower forms the conus is large and well developed; in the teleosts it is reduced to a row of valves between the ventricle and the bulbus. At least one pair of aortic arches persists in a complete state in the adult, while some or all are permanently or temporarily (amphibia) connected with the gills. A renal portal system (p. 194) occurs; and the red blood corpuscles are large, oval, and nucleated. The functional kidney is the mesonephros, although rarely the pronephros persists.

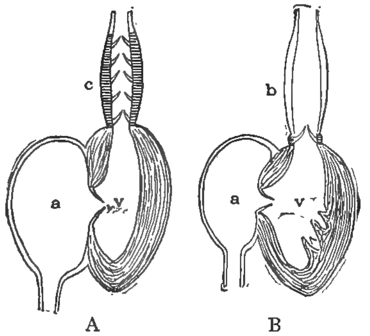

FIG. 233. Relations of the conus, *A*, in elasmobranchs and ganoids; *B*, in teleosts. *a*, auricle; *b*, bulbus arteriosus; *c*, conus, reduced in *B* to a circle of valves; *v*, ventricle.

The alimentary canal is comparatively short, and either terminates in a cloaca (p. 39), or the vent is anterior to the urogenital openings. No metanephros is developed, and the ova are frequently large.

The Ichthyopsida are divisible into Pisces and Amphibia.

CLASS I. PISCES.

Ichthyopsida with persistent gills; paired appendages almost always present in the shape of fins; median fins supported by dermal rays; body usually covered with dermal scales; postcava, Eustachian tube, and stapes lacking. Nostrils (except in dipnoi) never opening into the mouth.

Under the heading Pisces are included all those forms, except the lampreys and hags, commonly known as fishes. The group is well marked off from all other groups of vertebrates to-day, and the only questions of classification are those pertaining to the relationships and arrangement of the various groups composing the class.

The skin usually contains abundant gland cells secreting mucus, but multicellular glands are rare. The body is usually covered with scales of dermal origin ; but these are occasionally absent, as, for instance, in most electrical fishes. Some years ago the scales were of importance in classification, and four types were recognized : (1), placoid scales, occurring in the elasmobranchs, in which there is a basal plate of dentine bearing a central spine (p. 92) of dermal origin, the spine being tipped with ectodermal enamel. This type of scale is regarded as the most primitive, and as having given rise to teeth and dermal bones (p. 164). (2), Ganoid scales ; large, bony (dermal) rhomboidal plates embedded in the skin, and frequently bearing on their outer surface a layer of enamel (ganoin), likewise of dermal origin. This type of scale is found in most ganoids, and was especially characteristic of the early members of this group. (3), Cycloid scales, more horny in character, lacking in enamel, and embedded in dermal pockets ; these have the outline approximately circular. (4), Ctenoid scales differ from these last in having small spines upon the posterior or free margin. Occasionally scales may fuse to form large bony plates or scutes.

Median fins are always present, and, except in degenerate forms, two pairs of paired fins as well. These are supported by rays of dermal origin, and the paired fins also have cartilaginous or bony basal supports (p. 177). In the young the median fins are continuous around the tail, and this condition persists in the adult of a few forms (*e.g.*, eels) ; but usually it is interrupted so that we may recognize fins on the back (**dorsals**), on the tail (**caudal**), and on the ventral surface behind the vent (**anal**). The shapes of these and the number of supporting rays are of importance in the discrimination of species, etc., but more important are some of the peculiarities of the caudal fin.

In the primitive condition the vertebral axis continues straight to the tip of the tail, the caudal fin being developed symmetrically on either side (**diphycercal** fin, Fig. 234, *A*). This is found in but few forms. In elasmobranchs and many ganoids the **heterocercal** type occurs (Fig. 234, *B*). Here the axis of the body is bent abruptly upwards; and besides the caudal of the diphycercal condition a secondary lobe develops on the lower side, giving the tail an unsymmetrical appearance. The **homocercal** condition (Fig. 234, *C* and *D*) is derived from this last by the greater development of the ventral lobe, so that the fin appears symmetrical externally, although, as will be seen from the figures, the skeletal parts are of the heterocercal type.

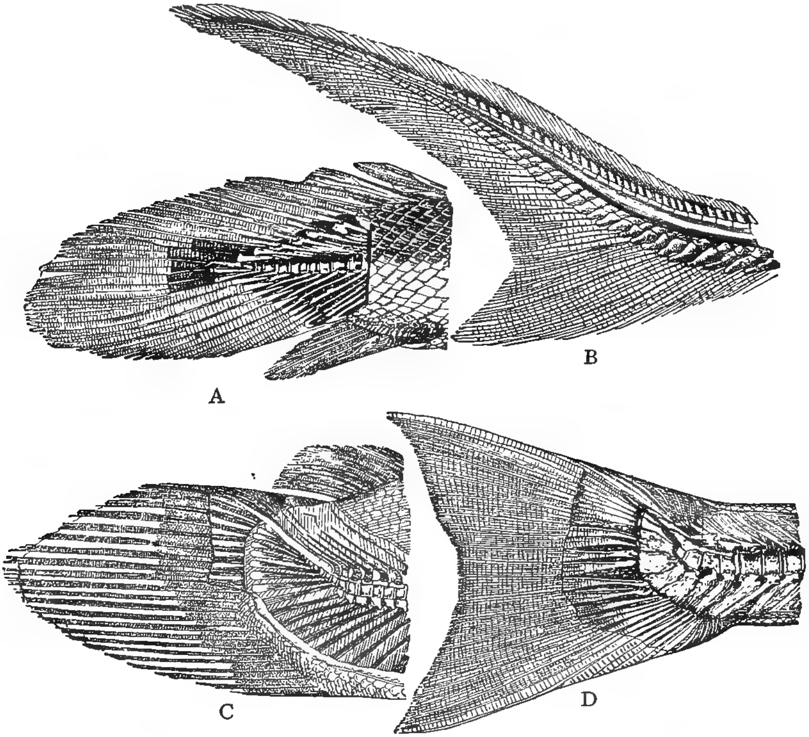

FIG. 234. Different forms of tails of fishes, from Hertwig after Zittel. *A*, diphycercal (*Polypterus*); *B*, heterocercal (*Acipenser*); *C*, homocercal (*Amia*); *D*, homocercal (*Salmo*).

These same figures also illustrate another point. The rays of the ventral side of the fin are supported upon the hæmal arches (Fig. 234, *D*) or upon elements (**interspinalia**) alternating with these (Fig. 234, *A*), while those of the dorsal side (and this applies also to the dorsal and anal fins) are borne on similar interspinalia.[1]

The alimentary canal, though rarely straight (holocephali, dipnoi, and some teleosts), does not present such convolutions as are common in the higher groups. Teeth are almost universally present (except in sturgeon[2] and some lophobranchs), but salivary glands never occur. The stomach is usually not sharply marked off from the œsophagus, and it frequently has a distinct siphon or U-shape.

Gills are always present, the clefts, usually five in number (six or seven in diplospondyli and some fossil forms; four in holocephali). Besides these the hyomandibular cleft persists in most elasmobranchs and ganoids as a much smaller opening, the spiracle, usually placed on the top of the head. In many elasmobranchs, teleosts, and dipnoi the gill arches bear **gill rakers**, — small conical cartilages which extend into the clefts. In the young elasmobranchs, sturgeon, and some teleosts the gills extend outside the clefts as long fringes in the young. Persistent external gills occur in *Polypterus*, and occasionally in *Protopterus*, while they are retained for some time in other forms.

In the adult fish the brain occupies but a part of the cranial cavity. It is characterized by the nearly complete disappearance of flexures in the adult as viewed from the outside, and by the slight development of the cerebral cortex, which in the teleosts is lacking, being represented by a thin epithelial layer, the cerebrum consisting in this group of only the corpora striata of higher forms. The olfactory lobes are distinct, and either lie close to the cerebrum (most teleosts) or are removed some distance, in which case they are con-

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[1] If the median or azygos fins have arisen by the coalescence of pairs of lateral folds (p. 173), these interspinalia would then correspond to the basalia of the paired fins, as maintained by Dohrn and Mayer.

[2] The embryonic sturgeon has teeth.

nected with the brain by an elongate tractus olfactorius. The optic thalamic are small, but the lobi inferiores on the ventral surface of the twixt brain are well marked. The optic lobes are strongly developed (only a single lobe occurs in *Protopterus*), and contain a large ventricle (epicœle). The optic nerves cross in the teleosts; a true chiasma is developed in other groups (p. 61). The eleventh and twelfth nerves are lacking.

The nasal organs only exceptionally have connection with the cavity of the mouth. The eyes are without accessory glands; the lens is strongly convex, and is connected with the wall of the posterior chamber by a structure, the falciform process, the distal end of which is swollen into a bulb, the campanula Halleri, in the walls of which muscles are developed so that this structure plays a part in accommodation. There is no true Eustachian tube in connection with the ear, and a stapes never occurs.

The muscular system shows plainly its division into myotomes, and there is no differentiation of layers of oblique muscles in the abdominal walls. Epiaxial and hypaxial muscles (p. 109) are well differentiated.

The vertebral centres are either incompletely developed or they are of the amphicœlous type; the only exception being found in *Lepidosteus*, where they are opisthocœlous, this condition being brought about in the same way as in amphibia (p. 139). Only trunk and caudal regions are differentiated. Ribs, when present, are, except in elasmobranchs, modified hæmal arches. In *Polypterus* both kinds of ribs occur (p. 144). The skull is noticeable for the great development of the visceral arches and their independence from the other parts. Almost always the hyomandibular acts as a suspensor of the lower jaw. The paired appendages are always fins, pectoral and ventral, but occasionally one or the other of these may be degenerate. As a rule these occupy positions, the pectoral at what would compare to the shoulder, the ventral just in front of the anus; but occasionally the ventral fins may move forward to a position just behind the pectorals (**thoracic**), or even in a line with these (**jugular**). The pelvic girdle never enters into connection with the vertebral column; the shoulder girdle rarely. The latter, however, may become connected (many teleosts) with the otic region by a chain of bones. The skeleton of the fins themselves varies greatly, but there is never anything that approaches the pentadactyle condition found in the higher vertebrates.

The heart always consists of a single atrium and a single ventricle, and a sinus which is undivided except in the dipnoi. Conus and bulbus vary in their development. The aortic arches are always symmetrically developed. No postcava occurs; the blood from the posterior portion of the body being returned by the postcardinals, the portal system, and the hypogastric veins. A spleen is always present.

The functional excretory organ is the mesonephros, the pronephros but rarely persisting. Urinary bladders are frequently present; but these are simply expansions of the urinary duct, and are not comparable to the allantoic bladder of the higher vertebrates. The urinary ducts either empty into the hinder end of the intestine or by separate openings to the exterior. Pori abdominales are almost always present, and these in some cases serve for the extrusion of the reproductive products. Only in elasmobranchs and ganoids do the urogenital ducts serve to carry away the eggs and milt.

SUB-CLASS I. ELASMOBRANCHII (PLAGIOSTOMI, CHONDROPTERYGII).

Cartilaginous fishes without true bones; tail usually heterocercal; gill slits 5–7, no operculum present; skin, with rare exceptions, bearing placoid scales; pelvic fin in males of recent forms bearing a complicated copulatory apparatus ('clasper'); skull, amphi- or hyostylic, never autostylic; upper jaw formed by pterygoquadrate; a true optic chiasma; intestine with a spiral valve; no air-bladder.

The sub-class elasmobranchii includes those fishes popularly known as sharks and skates, all of which, with two or three exceptions, are marine. The body is usually fish-like in shape, but is greatly flattened horizontally in the skates. The caudal fin, when present, is always heterocercal; but in many skates the fin is absent, the tail tapering to a point. In most forms the mouth and nostrils are ventral in position, and are placed some distance behind the tip of the snout. The body is covered with placoid scales, which are usually small, and form shagreen, formerly much used by cabinet-makers in place of sandpaper. The pelvic fins are always abdominal in position.

The jaws are armed with acutely pointed teeth or with flattened crushing-plates. The œsophagus is ciliated; the stomach shaped like the letter J, and no pyloric cæca occur. The intestine is provided with a well-developed spiral valve, and the rectum bears a finger-shaped rectal gland on its dorsal surface. A cloaca is present.

The gill clefts are usually five in number, six or seven in some lower forms. They open freely to the outside, no operculum being developed. The gills are attached their whole length to the interbranchial septum. Usually a spiracle occurs, and this may bear a pseudobranch (p. 23).

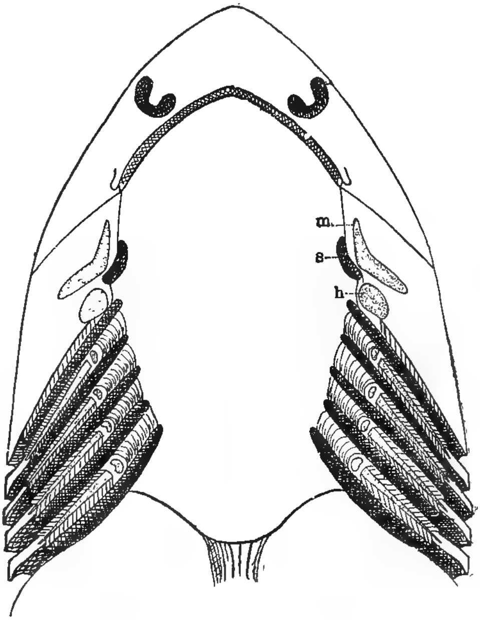

FIG. 235. Relations of gill clefts in the elasmobranchs. *h*, hyoid arch; *m*, mandible; *s*, spiracle.

The hemispheres of the brain are united, and the olfactory lobes are separated from the cerebrum by an elongate olfactory tract. The twixt brain is short, and an optic chiasma occurs. The lateral line system is well developed, and in the skates becomes greatly branched. On the head are numerous sensory ampullæ filled with jelly.

The skeleton is cartilaginous; but in many cases it is rendered more dense by the deposition of lime, which, however, never takes the shape of bone corpuscles, there being a sharp line between calcified cartilage and bone. Membrane bones are absent in all recent forms, but in some fossils the dermal scales united to form an extensive armor. In some the vertebral centra are entirely of cartilage. When lime is deposited in them it may take two shapes, either laid down in concentric areas (**cyclospondylous type**), or in a radial manner (**asterospondylous**). In the diplospondyli and in the tail of some skates an embolomerous condition occurs. In all recent forms the neural arch is converted into a closed canal by the insertion of intercalary pieces betweeen the neural processes and spine.

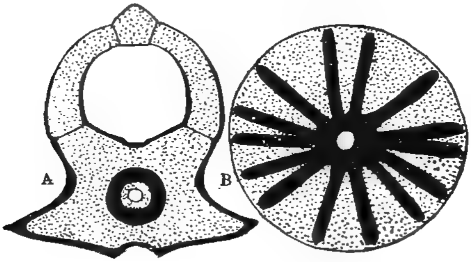

FIG. 236. Diagrams of cyclospondylous (*A*) and asterospondylous (*B*) vertebræ. Calcifications of cartilage black.

The cranium is a solid box without sutures. In its roof there may be one or two gaps (**fontanelles**) closed by membrane. The pterygoquadrate is never firmly united to the cranium, but either articulates directly with it (**amphistylic**, Fig. 237), or is supported by ligaments and by the intervention of the hyomandibular between the hinder end of the pterygoquadrate and the otic region of the cranium (**hyostylic**, Fig. 162), thus forming a suspensor for the jaws. The pterygoquadrate forms the upper jaw, but is reenforced in many species by labial cartilages. In some extinct elasmobranchs girdles are apparently absent, but in all recent forms they are well developed. The pectoral girdle consists of a simple U-shaped

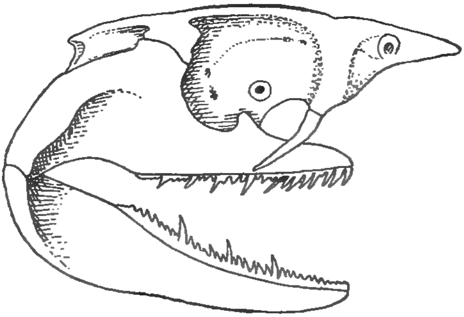

FIG. 237. Skull of *Heptanchus*, after Günther; amphistylic.

arch, usually free, but occasionally (raiæ) connected with the vertebral column, or rarely with the skull. The pelvic girdle consists of a transverse ventral bar without dorsal or iliac processes.

A conus with two or more rows of valves occurs in connection with the heart ; the aortic arches and the chief arteries and veins are of the primitive type, and a cardinal sinus (p. 195) usually occurs.

The eggs are few and large, and in the recent forms undergo internal inpregnation, more or less complicated structures (the 'claspers'), which serve as intromittent organs, being developed in the pectoral fins of the male. The spermatozoa is carried to the exterior by means of the Wolffian duct, while the Müllerian duct serves as oviduct, the fused nephrostomes of the rudimentary pronephros serving as the ostium tubæ. In many sharks and in some of the rays a portion of the oviduct becomes enlarged into a uterus, and in some species of *Carcharias* and *Mustelus*, a placenta is formed, at first sight strikingly similar to that of the mammals, but developed from the yolk sac rather than from an allantois (see mammals). The outer surface of the yolk sac in these forms becomes richly vascular ; and this becomes connected with the uterine walls, so that the growing embryo receives nourishment from the blood of the mother.

The segmentation is restricted to a portion of the upper surface, *i.e.*, is meroblastic. The result of this is the formation of a circular layer of cells, the blastoderm, resting upon the yolk. Inside of these cells is a space corresponding to the segmentation cavity of the typical egg (p. 211). Owing to the great amount of yolk, the process of gastrulation becomes greatly modified. At one end of the blastoderm the cells turn in between the blastoderm and the yolk, and these ingrowing cells become the entoderm. At the place where this ingrowth occurs an arcuate elevation appears, terminating in a pair of swellings, the tail swellings, on the margin of the blastoderm. With growth the distance between the arched elevation (which marks the tip of the head) and the tail swellings increases, forming the rest of the head and the trunk region of the body. At first this embryonic area forms a broad, shallow medullary plate ; but the edges of this rise up and gradually unite, so that the plate becomes converted into the medullary tube.

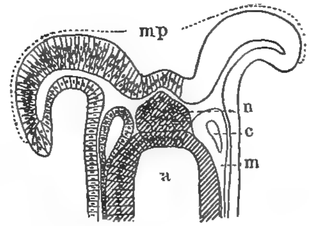

FIG. 238. Section through the broadly expanded medullary plate of a shark (*Acanthias*). *a*, archenteron; *c*, cœlom; *m*, mesothelium; *mp*, medullary plate; *n*, notochord.

Gradually the embryo thus outlined is raised above the yolk, and soon becomes so separated from it that only a slender **yolk stalk** remains connecting the two. This stalk carries blood-vessels (omphalomesaraics), while the yolk itself is connected with the alimentary canal.

The mesothelium arises as ingrowths on either side at the point of differentiation of ectoderm and entoderm, these growing in between the two layers. The gill slits break through the sides of the neck in regular succession from in front backwards, the mouth breaking through after all five gill slits are open. For a time the gill filaments protrude from the gill slits. The spiracle is at first the largest of the clefts, but it soon begins to close at the ventral end so that only the dorsal portion persists. The paired fins start as lateral folds (in some cases continuous, *e.g.*, *Acanthias*), into which grow cells from the myotomes (p. 110).

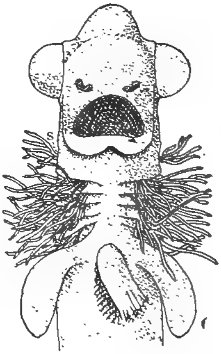

FIG. 239. Head of embryo *Acanthias*, showing the gill filaments protruding from the gill slits.

Elasmobranchs are, on the whole, the most primitive of the jawed vertebrates, although in some respects they seem to stand above the other fish-like forms. The sharks are free-swimming forms, seeking their prey in all parts of the sea, a few species ascending rivers, and one being found in Lake Nicaragua. The skates, on the other hand, are bottom feeders, living on molluscs, crabs, etc., and their teeth are modified into crushing-plates adapted to such food. None of the species are very small; but some of them are of enormous size, among the largest of living fishes; sharks reaching, in the basking shark and blue shark, a length of thirty-five or forty feet; the rays, in *Manta*, a breadth of fifteen feet.

ORDER I. CLADOSELACHII (PLEUROPTERYGII).

Notochord persistent; neural and hæmal arches slender. Paired fins with basalia and radialia arranged much as in the median fins of recent fish (Fig. 188). No claspers yet found.

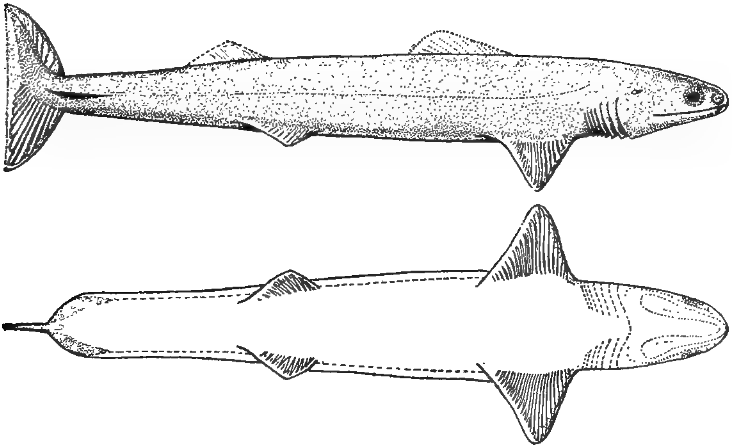

FIG. 240. Lateral and ventral veins of *Cladoselache*, restored by Dr. Dean.

Apparently a flap of skin much like an operculum covered the first of the gill slits which were seven (possibly nine) in number. Jaws apparently hyostylic. Lateral line an open groove. The only known member of the group is *Cladoselache*, from the Waverley group (lower carboniferous) of Ohio. It is probable that some of the fossils with similar teeth (*Cladodus*) belong here.

ORDER II. ICHTHYOTOMI.

Notochord persistent; neural and hæmal arches and intercalary cartilages present. Pectoral fin archipterygial (p. 172). Pelvic fins with claspers, caudal fin diphycercal. No placoid scales, but the head was covered with dermal bones. The best-known genus is *Pleuracanthus* (=*Xenacanthus*, *Didymodus*) from the carboniferous and Permian of Europe and America.

ORDER III. SELACHII.

Elasmobranchs with the notochord more or less completely replaced by vertebral centra. The neural canal completely arched in by neurapophyses and intercalaria. No dermal bones. Paired fins never archipterygial; claspers always developed in the male. To this order belong all recent as well as many fossil elasmobranchs.

SUB-ORDER 1. DIPLOSPONDYLI.

Selachians with embolomerous vertebræ with two neural arches to each myotomic centre; a single dorsal fin; anal fin present; amphistylic skull, and gill slits 6 or 7. Two families are recognized. The CHLAMYDOSELACHIDÆ has an eel-like body, terminal mouth, nostrils on the dorsal surface, *Cladodus*-like teeth, and 6 gill slits. To it belongs the single genus *Chlamydoselachus* of the deeper portions of the northern parts of the Atlantic and Pacific. In the NOTIDANIDÆ the body is shark-like, the spiracle is lateral, the teeth differ in the two jaws. The species are viviparous. *Hexanchus* has six gills, *Heptanchus* (Fig. 237) seven.

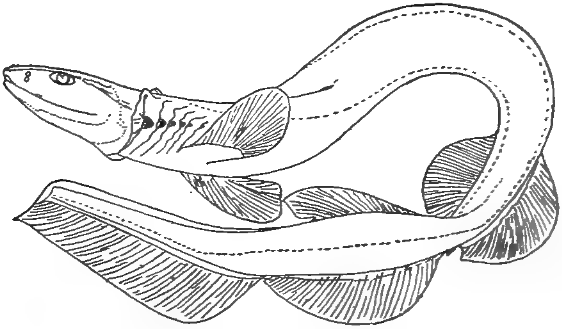

FIG. 241. *Chlamydoselachus anguineus*, after Garman.

SUB-ORDER 2. EUSELACHII.

Vertebræ normal, branchial slits five in number, skull hyostylic.

SECTION *a* — ASTEROSPONDYLI. The vertebræ in this group, which include the typical sharks, are asterospondylous; two dorsals and a single anal fin present. Here belong a large series of forms. In the CESTRACIONTIDÆ, which is represented by a few Pacific species to-day, but which was abundant in past times, the dorsal fins bear spines, while the jaws behind bear transverse rows of pavement-like teeth. In the GALEIDÆ the head is normal, the spiracles are small or lacking, the last gill cleft is above the pectoral, and a nictitating membrane is present. Here belong the dog-sharks, grouped under *Galeus* and *Mustelus*; the largest of all sharks, commonly called *Carcharias* (*Charcharinus*), some of which have man-eating reputations; and the tiger sharks, *Galeocerdo*. In the hammer-head sharks (ZYGÆNIDÆ or SPHRYNIDÆ) the structure is much as in the Galeidæ, except that the sides of the head bearing the eyes are produced into lobes, giving the whole a mallet-like appearance, In the thresher-sharks (ALOPIIDÆ) the spiracle is lacking, the last gill cleft above the pectoral, the nictitating membrane absent, and the tail about as long as the rest of the body. In the LAMNIDÆ, including the mackerel-sharks (*Lamna*) and the great white 'man-eater' shark (*Carcharodon*), the teeth are sharp, the spiracles small or absent, and the gill slits all in front of the pectoral.

SECTION β — CYCLOSPONDYLI. Calcareous deposits of the vertebral centra arranged in one or more concentric rings about the axis. In the SQUALIDÆ, including the common dog-fishes (*Acanthias* or *Squalus*), the fins are normal, the spiracles present, the gill openings in front of pectoral, and the dorsal fins each with a spine in front. In the SQUATINIDÆ the pectoral fins are very large, so that the body has more the shape of a large flattened disk, presenting a close appearance to the skates, except that the pectoral has not grown to the head. Here, too, belongs the family PRISTIOPHORIDÆ, in which the snout is prolonged into a long beak, armed with teeth on either side. These saw-fishes are confined to the southern hemisphere, but may readily be distinguished from the common forms (which are rays) by the position of the gill slits.

SUB-ORDER 3. RAIÆ (BATOIDEA).

Vertebræ normal, cyclospondylous; gill slits ventral in position; spiracles present; body typically flattened and rendered disk-like by the great development of the pectorals. This group is greatly specialized, and is apparently derived from the cyclospondylous Euselachii.

In the PRISTIDÆ there is no sharp distinction between disk and tail; and the rostrum is prolonged into a saw, like that of the Pristiophoridæ, from which, however, these saw-fish, which belong to the northern hemisphere, may be distinguished by the position of the gills. *Pristis pectinatus* occasionally occurs on our southern coasts. The TORPEDINIDÆ, which includes *Torpedo*, the electric skate, have the body without scales, the disk rounded, and the tail thick and fleshy. A single species, known as the 'cramp-fish,' occurs occasionally on our shores south of Cape Cod. The electrical organ has been described (p. 115). In the RAJIDÆ, which includes our common skates, the disk is more or less rhombic in outline, roughened by large placoid scales, two dorsals without serrated spines. Several species of the genus *Raja* occur on the coasts. In the TRYGONIDÆ belong the sting-rays, which have the tail usually whip-like, never two dorsals, and near the base of the tail one or two serrated spines, the 'sting,' which can inflict a severe wound. Our sting-rays belong to the genus *Dasyatis*. In the MYLIOBATIDÆ the anterior ends of the pectorals are free from the head, forming ear-like 'cephalic fins.' On our southern coast and extending into the tropics is the genus *Manta*, the species of which are known as devil-fish. These and allied forms are among the largest of fishes.

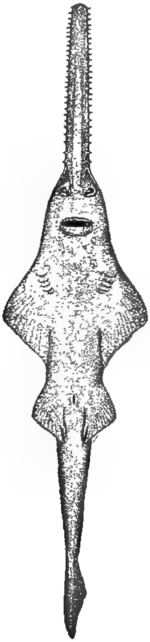

FIG. 242. Saw-fish, *Pristis pectinatus*, ventral view, after Goode.

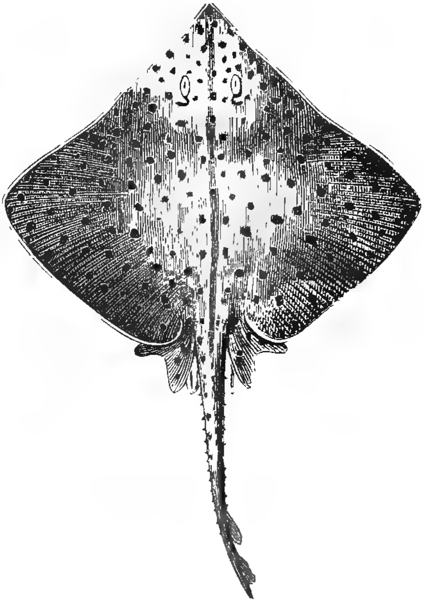

FIG. 243. Common skate, *Raia erinacea*, from Agassiz and Gould.

ORDER IV. HOLOCEPHALI.

Cartilaginous fishes in which no true bone is developed; tail heterocercal; gill slits 4, externally covered by a membranous fold, so that but one opening appears on the outside; skin naked; pelvic fin of male with 'clasper'; skull autostylic; upper jaw formed by pterygoquadrate; optic chiasma present; a spiral valve in the intestine; no air-bladder.

Three genera containing about half a dozen species represent this group to-day. The body is much like that of the sharks; but the four gill slits are not visible from the exterior, since a membranous fold of the skin, the operculum, grows backwards over them, so that but a single aperture is visible exteriorly. The spiracle is closed. The pelvic fins are abdominal in position and bear claspers in the males, while in front of these fins there is a pit containing an **anterior clasper** armed with hook-like spines, the function of which is unknown. In addition there is borne on the head in *Chimæra* and *Callorhynchus* a peculiar **frontal clasper** differing in the sexes. The skin in recent species is naked, and the lateral line on the trunk is an open groove. The tail is heterocercal.

The mouth is terminal, the nostrils dorsal, the latter not communicating with the mouth. The teeth are in the form of strong plates, two pairs in the upper jaw, a single pair in the lower. These have areas (**tritors**) specially hardened by deposits of lime. The alimentary canal is almost straight; the intestine possesses a spiral valve. No cloaca is present, the urogenital ducts opening behind the vent. The gills are related to the septa as in the selachians. No air-bladder is developed.

The brain has the hemispheres distinct from each other, the olfactory lobes being separated from the cerebrum by long olfactory tracts. The twixt brain is extremely long; an optic chiasma occurs. The heart is like that of selachians, three rows of valves being present in the conus.

The skeleton is cartilaginous. The notochordal sheath contains cartilage rings more numerous than the segments; and the neural tube, composed of neural arches and intercalaria, is very high. The cranium is high and narrow, and the pterygoquadrate is indistinguishably fused with the cranium (**autostylic**). The skull is movably articulated to the vertebral column by a (basi) occipital condyle. The shoulder girdle is like that of elasmobranchs; but the pelvic girdle consists of right and left halves, connected by ligament. The excretory organs and female reproductive organs are much as in other elasmobranchs; the male organs are noticeable for the large size of the epididymes and the seminal vesicles developed from the posterior portions of the vasa deferentia. The Müllerian ducts also retain their lumen in the male, and connect with the cœlom by a common ostium tubæ. Of the development almost nothing is known. The eggs are very large, six and one-half inches long in *Chimæra*, ten inches long in *Callorhynchus*. According to the unpublished studies of Dr. Dean, in the early stages these forms are decidedly shark-like, and the elevation of the division to the rank of a sub-class is not warranted. The pterygoquadrate is free as in other elasmobranchs; the gills are not covered, and external gill filaments are present.

Only three genera — *Chimæra*, *Callorhynchus*, and *Harriotta* — are known from existing seas. The first is represented on our east coast by *Chimæra monstrosa* and *C. affinis*, and on the Pacific by *C. collei*. *Harriotta* has been found in the North Atlantic and in Japan. The third genus is from the southern seas, and also occurs fossil in New Zealand. Several fossil genera — *Ischyodus*, *Eumylodus*, *Rhynchodes*, *Edaphodon*, etc. — range from the Devonian to the cretaceous. The fossil *Squaloraia* from the lias of England also appears to belong here. Less certain is the group PTYCTODONTIDÆ (*Ptyctodus*, *Rhynchodus*) from the Devonian, known only from the dental plates, a pair in each jaw.

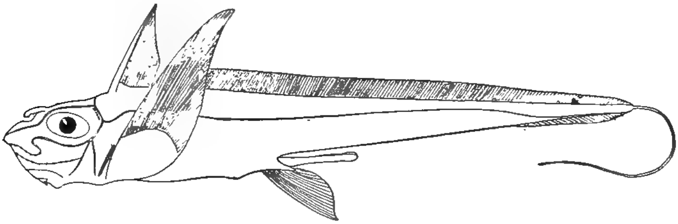

FIG. 244. *Chimæra monstrosa*, 'king of the herrings.'

SUB-CLASS II. TELEOSTOMI.

Fishes in which bones are developed; gill slits 5, externally covered with a bony operculum; scales, when present, ganoid, ctenoid, or cycloid; no claspers; skull hyostylic; upper jaw formed by membrane bones; skull with sutures; air-bladder frequently present.

Here belong all the common fishes, — trout, cod, herring, shad, eels, etc., — as well as a series of forms not so familiar, which are frequently grouped together as ganoids. All these agree in a number of particulars of considerable importance.

The gill slits do not open directly to the external world, but into a gill chamber formed by an operculum or fold, which extends backwards on either side from the hyoid arch; and this operculum is strengthened by bone. The body may be naked or scaled, but placoid scales never occur, and claspers are never developed in connection with the pelvic fins.

The most marked characters are presented by the skeleton. In this the cartilage may be partially or almost completely replaced by bone, and besides, there is always an extensive formation of membrane bones, unknown in the recent members of the other groups of fishes. In all except the sturgeons the vertebral centra are ossified, and in all except the sturgeons and the garpikes the vertebræ are amphicœlous. More or less extensive ossifications occur in the chondrocranium, and besides, a large number of dermal bones are developed, which roof in the cranium above and build it out in other places. Excepting the dipnoi, the cranial structures of which will be described later, the most constant and most characteristic of these bones are the following: The upper jaw is formed by a pair each of maxillaries and premaxillaries, while the roof of the mouth is formed by a pair each of vomers and palatines and a parasphenoid, all of which may bear teeth. Thus the pterygoquadrate no longer forms the upper jaw as in the lower groups, but becomes deeper in position, and undergoes more or less extensive ossification, sometimes developing but two bones, — pterygoid

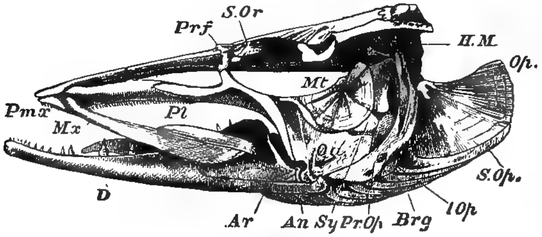

FIG. 245. Skull of pike, *Esox lucius*, from Huxley. *An*, angulare; *Ar*, articulare; *Brg*, branchiostegals; *D*, dentary; *HM*, hyomandibular; *IOp*, interopercle; *Mt*, metapterygoid; *Mx*, maxillary; *Op*, operculum; *Pl*, palatine; *Pmx*, premaxilla; *Prf*, prefrontal; *Pr Op*, preoperculum; *Qu*, quadrate; *SOp*, subopercle; *SOr*, suborbital; *Sy*, symplectic.

and quadrate; or again, the pterygoid may be differentiated into several elements (ento-, ecto-, meso-, and metapterygoid); but in all cases the quadrate furnishes the support for the lower jaw. The quadrate, in turn, is attached to the skull by a suspensor apparatus formed of the hyomandibular alone; or a membrane bone, the sympletic, may intervene between quadrate and hyomandibular. Thus this skull is hyostylic. The primitive lower jaw (Meckel's cartilage) becomes incased in membrane bones, of which a pair of dentaries in front are always present, while an articulare and an angulare may be added on either side. The roofing bones of the cranium may be a pair each of parietals (small), frontals, and nasals. Beneath these is a large fontanelle in the chondrocranium. In the chondrocranium itself the following ossifications may occur: At the base of the skull the four occipitals (basi-, ex-, and supraoccipital); in the ear region five otic bones, the sphen-, pter-, and epiotic above, the pro- and opisthotic below. Occasionally the opisthotic may be absent. Basi- and presphenoid never occur, their place being supplied by the parasphenoid. Ali- and orbitosphenoid are sometimes well developed, sometimes inconspicuous or absent, while the ethmoid region bears three ossifications, — a mesethmoid, and a pair of ectethmoids.

The operculum is supported by the hyoid arch, the lower portion of which, the hyoid proper, is connected with the hyomandibular by a small **interhyal** bone. The operculum consists of two portions, — a dorsal, containing several flattened bones: above, a preoperculum and an operculum proper; below and behind, a suboperculum and an interoperculum, all of which may be regarded as modified branchiostegals of the hyomandibular; the ventral part of the operculum is supported by the long and slender branchiostegals of the hyoid. The branchial arches are united below by a copula composed of the fused basibranchials, which extends forward, connecting the series with the hyoid. Frequently the fifth arch is modified into a tooth-bearing accessory jaw, the so-called **pharyngeal bones.**

The shoulder girdle is well developed. In the cartilaginous arch two ossifications — scapula and coracoid — appear on either side, and besides these a large membrane bone, the cleithrum (clavicle of authors), the cleithra of the two sides frequently uniting below. Other smaller membrane bones, some of them less constant, are the supra-, post-, and infraclavicles; and the arch is usually articulated to the otic region of the skull, either by the supraclavicle, or by the intervention of a post-temporal bone between the supraclavicle and the epiotic. The pelvic arch is either greatly reduced (ganoids) or entirely absent (teleosts), its place being supplied by the greatly enlarged basalia (see, however, p. 173). The dorsal and anal fins are supported upon small interspinous bones embedded in the flesh and usually alternating with the neural and hæmal spines, or they may be more numerous than these. The caudal fin is either heterocercal, or the lower lobe may be so well developed that the homocercal condition occurs (p. 229). The ribs, except in *Polypterus*, where both types occur (p. 145), are modified hæmal arches; and the flesh is further supported by intermuscular

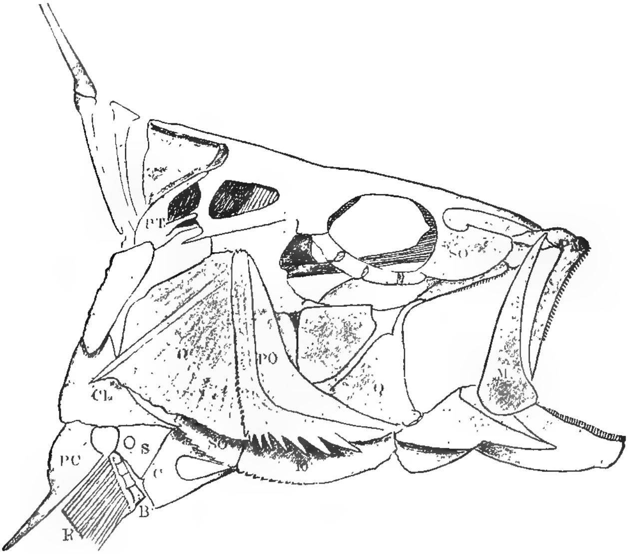

FIG. 246. Skull of perch. *B*, basalia of fin; *C*, coracoid; *CL*, cleithrum; *IO*, infraopercular; *M*, maxillary; *O*, opercular; *PC*, postclavicula; *PO*, preopercular; *PM*, premaxilla; *PT*, post-temporal; *Q*, quadrate; *R*, radialia of fin; *SO*, subocular chain of bones, also suboperculum; *S*, scapula.

bones, called **epineurals, epicentrals,** or **epipleurals,** accordingly as they are articulated to neural arch, centrum, or ribs.

The mouth is usually armed with teeth; and these may occur not only on the bones which form the edge of the jaws (premaxillary, maxillary, dentary), but on those which form the roof of the mouth (palatine, vomer, pterygoid), and also on the pharyngeal bones. The alimentary canal usually has the regions well differentiated, and in the ganoids a spiral valve occurs in the intestine. Pyloric cæca, from a single one to two hundred in number, are common. There is no cloaca, as the urogenital ducts always open behind the vent.

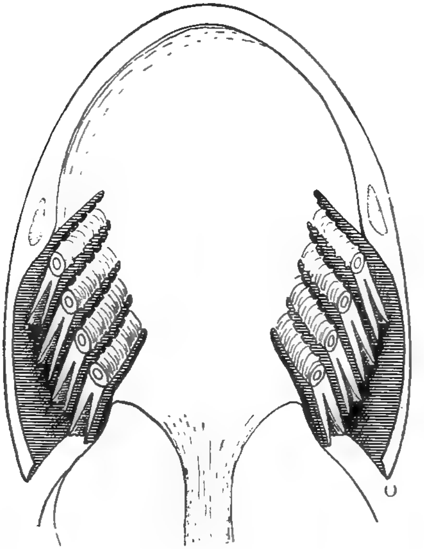

Fig. 247. Relations of gill clefts in a teleost. *O*, operculum, enclosing a branchial chamber.

A spiracle occurs only in some ganoids. The gills differ from those of the lower fishes in the reduction of the interbranchial septum, so that the gills themselves project beyond the arch into the opercular cavity like the teeth of a comb. In the lophobranchs the gill filaments are replaced by curious tufts. An air-bladder or swim-bladder is usually present. It arises as an outgrowth from the dorsal side of the œsophagus (except in *Polypterus*), which soon becomes differentiated into bladder and duct. In the lower forms the duct remains open throughout life (ganoids and physostomi), but in the physoclisti it closes later, and the bladder loses all connection with the exterior. In many ganoids and some teleosts the inner surface becomes plicated. In most forms it receives its blood-supply from the aorta direct, or by way of the cœliac axis; but in *Polypterus* it comes from the radix aortæ, and therefore it receives only arterial blood. The bladder serves as a hydrostatic apparatus, but there is also evidence to show that at least in some fishes it is to some extent respiratory as well. For the relations of the bladder to the ear, see p. 255.

The brain is noticeable for the large size of the optic lobes and the cerebellum. The cerebrum is rudimentary, and consists of merely corpora striata and a non-nervous pallium in the teleosts, but in the ganoids larger hemispheres occur. In the ganoids there is a true optic chiasma, but in the teleosts the optic nerves cross (p. 61). The twixt brain is short. The olfactory lobes in most teleosts and in the ganoids are joined to the cerebrum; but in a few forms a long olfactory tract intervenes.

The urogenital organs of the teleostomes will repay further study, for there are many points as yet in doubt. The permanent excretory organ is the mesonephros; only in *Fierasfer* and *Dactylopterus* does the pronephros retain its excretory functions. In all others, while it may be of large size, it degenerates into a lymphatic or adenoid structure. The pronephric ducts never divide into Müllerian and Wolffian ducts, but serve solely as ureters. Usually the two unite behind and form a urinary bladder of some size, the common opening being, except in a few teleosts, behind the vent.[1] The usually paired gonads vary in the way in which their products reach the exterior. In the female salmonids and eels, the eggs are discharged directly into the cœlom, from which they escape into a urogenital sinus by means of a pair of slit-like openings, often called pori abdominales, but which are apparently not homologous with the similarly named openings in the elasmobranchs. In most ganoids and in a few teleosts, two longitudinal folds arise in the peritoneum, the edges of which unite so that a tube, the oviduct, results, which opens freely into the cœlom. In most teleosts, however, these folds are continued to the ovary, so that the eggs do not pass into the general body cavity, but fall at once into these tubes, the lumen of which is, as is readily seen, a part

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[1] In Pediculati and some symbranchs and plectognaths the urinary opening is in the hinder end of the intestine.

of the cœlom. In the males there is either a simple tube which connects each testis with the urogenital sinus, or there may intervene between tube and testis a system of smaller canals, the vasa efferentia.

Legion I. Ganoidea.

Teleostomes in which the body is either naked or covered with ganoid or cycloid scales, or bears bony plates; the skeleton either largely cartilaginous or well ossified; the tail diphy-, hetero- or homocercal; ventral fins always abdominal in position; fulcra present in most recent and in fossil forms; swim-bladder with duct; intestine with a spiral valve; an optic chiasma present; heart with a conus arteriosus; eggs with a total segmentation.

The group of ganoids contains but a few recent forms, the remnants of a much larger fauna in past times. Its members are widely distributed over the globe, North America, however, having the greater proportion of the species, most of which are inhabitants of fresh water. In the definition above **fulcra** are mentioned. These are spine-like scales upon the anterior surfaces of the fins.

So far as they have been studied, the eggs of the ganoids undergo a total segmentation; but, owing to the presence of a large amount of yolk, the resulting cells are very unequal in size, the large cells being at one pole of the egg, the smaller at the other. In the sturgeon the central nervous system develops as a tube; but in the other forms it is at first a solid keel, and only later does a lumen appear by splitting. The larvæ of

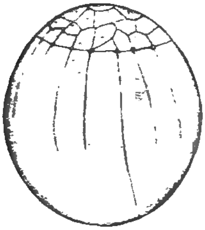

FIG. 248. Segmenting egg of *Amia*, showing the unequal cleavage, after Dean.

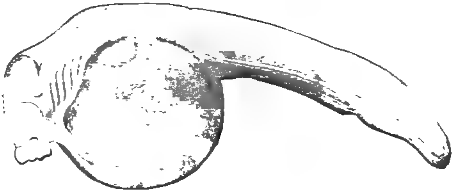

FIG. 249. Larva of *Amia*, about the time of hatching, showing the sucking disk at the tip of the snout, after Dean.

Amia and *Lepidosteus* are noticeable for the sucking disk developed on the front of the head; the larva of the sturgeon has balancer-like structures between the mouth and nose.

ORDER I. CROSSOPTERYGII.

Ganoids with diphy- or heterocercal tails; pectoral fins with a large basal portion covered with scales, the ventral fins usually much like the pectorals, the former abdominal in position; body covered with rhombic or circular ganoid scales; a pair of gular (or 'jugal') plates in place of branchiostegals; no fulcra; dorsal fins two, or a single one divided into many finlets. The crossopterygians are largely extinct, but two genera persisting to-day. The group first appears in the Devonian.

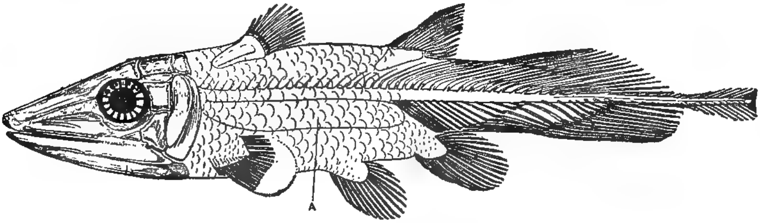

FIG. 250. *Diplurus longicaudatus*, from Dean. *A*, position of the calcified air-bladder.

The CŒLACANTHIDÆ (ACTINISTIA) have unossified centra and cycloid scales, two dorsal fins, diphycercal caudal, and ossified swim-bladder. *Cœlacanthus*, carboniferous of Europe and Ohio; *Diplurus*, trias of New Jersey. CYCLODIPTERINI (RHIPIDISTIA) have the vertebræ partially ossified; tail heterocercal; scales enamelled and rounded behind; a third gular plate between the other two. *Holoptychius*, Devonian of Europe and America; *Onychodus* and *Eusthenopteron*, Devonian of America. RHOM-

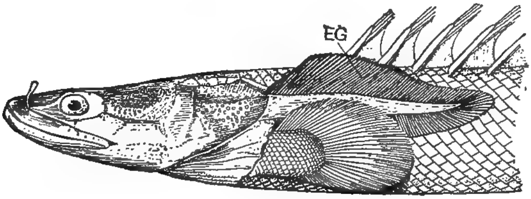

FIG. 251. Head of larval *Polypterus*, after Steindachner, from Dean. *EG*, external gill.

BODIPTERINI, with two dorsals, partially ossified vertebral centra; diphy- or heterocercal tail; two large and several smaller gular plates. *Osteolepis*, Devonian, Europe. The POLYPTERIDÆ (CLADISTIA) with two living genera (*Polypterus* from the Nile, *Calamoichthys*, greatly elongate and lacking ventral fins, from Old Calabar) are most closely allied to the last. The vertebræ are ossified, the caudal diphycercal; the dorsal fin elongate and divided into finlets; pectorals with a short, scaled basal axis; the body covered with rhomboid ganoid scales. No fulcra exist. In the skull epi- and opisthotics are not distinct; there are two sphenoidals and ectethmoids; the parietals and frontals are paired, and the gular plate is double.

ORDER II. CHONDROSTEI.

In the sturgeons and paddle-fish there is but slight ossification of the cartilage, the vertebral centra being unossified, while in the chondrocranium only otic and ectethmoid ossifications appear. The skull is covered with membrane bones, the parietals and frontals being paired, while the large parasphenoid extends back beneath the anterior vertebræ. A premaxilla is absent, and only a dentary is present in the lower jaw. The jaw itself is suspended by sympletic and hyomandibular cartilages, both partially ossified, the mouth itself being ventral as in elasmobranchs. The operculum is large, but its elements are poorly developed; the branchiostegals are weak or wanting. The body is either naked or covered with rows of bony plates, which are continued upon the upper lobe of the heterocercal tail, upon which fulcra are also strongly developed. The ventral fins have a row of cartilaginous basalia.

Two recent families are recognized. In the ACIPENSERIDÆ or sturgeons the body is covered with five rows of keeled bony plates, the skin between the rows bearing small granules. The mouth is toothless in the adult, and in front of it are four barbels. The gill slits are four in number, and the operculum, which does not completely cover the slits, bears an accessory gill. The air-bladder is large and simple, and the stomach has pyloric

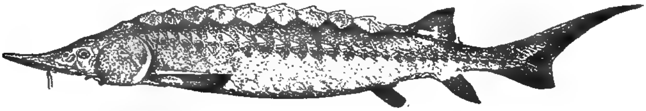

FIG. 252. Common sturgeon, *Acipenser sturio*, after Goode.

appendages. The dorsal and anal fins are posterior in position, the anal being anterior to the dorsal. In *Acipenser* there is a spiracle, and the naked skin between the plates extends to the tail. About twenty living species are known, half a dozen from North America. From the ovaries caviare is made, while the air-bladders furnish isinglass. The genus appear in the London clay (eocene). The shovel-nose sturgeons (*Scaphirhynchus*), one species of which is American, lack the spiracle, have the plates forming a complete armor on the depressed tail, while the caudal fin ends in a filament. In the POLYODONTIDÆ (SELACHOSTOMI), represented to-day by *Polyodon spathula* in the U.S., and *Psephurus* in China, the skin is smooth, the snout is prolonged into a long blade (whence the name paddle-fish), the maxillary is obsolete, a spiracle (lacking pseudobranchs) occurs. The PALÆONISCIDÆ, which range from the Devonian to the lias, have small conical or styliform teeth, simple dorsal and heterocercal tail, and rhombic scales. *Palæoniscus*, Europe, U. S.; *Eurylepis*, U. S. Allied is *Platysomus* from the carboniferous of Europe and Illinois.[1]

ORDER III. HOLOSTEI.

Ganoids with well-ossified skeletons; tail heterocercal; body with ganoid or cycloid scales; fulcra frequently present; branchiostegals and operculum well developed, and frequently a median gular plate; mouth terminal, with teeth; fins without a scaled basal region; the ventrals with the proximal skeletal elements reduced, much as in teleosts.

The garpikes, LEPIDOSTEIDÆ (GINGLYMODI) are closely related, structurally, to the palæoniscid forms of the chondrostei. They have opisthocœlous vertebræ, the body covered with rhombic scales, greatly elongate jaws, these, like the vomers and palatines, with sharp teeth; and numerous pyloric cæca. The living species of the only existing genus *Lepidosteus* are all American. The common garpike, *L. osseus*, is widely distributed;

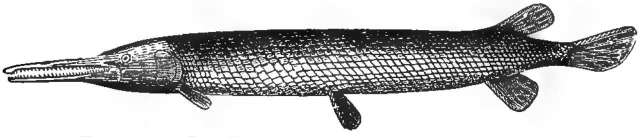

FIG. 253. Garpike, *Lepidosteus osseus*, from Tenney.

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[1] The group ACANTHODIDÆ, which combines ganoid and elasmobranch characters, may be mentioned here. The cartilaginous skeleton, spine in front of the dorsal, absence of opercular elements, are elasmobranch characters, while the presence of spines in the pectorals, and especially of bones in the orbital region and in the roof of the cranium, and the absence of claspers, recall the teleostomes. These forms occur in palæozoic rocks. *Acanthodes* occurs in U. S.

the alligator gar, *L. tristœchus* of the southern states, reaches a length of ten feet. Allied fossil forms are numerous. *Catopterus* being represented in the triassic rocks of the Connecticut valley. *Lepidotus* ranges from the trias to the Jura of Europe. *Aspidorhynchus* had a snout something like that of the sword-fish. In the AMIIDÆ (HALECOMORPHI) the vertebræ are amphicœlous, the scales cycloid. teeth on pterygoids as well as on vomers and palatines, no pyloric cæca. *Amia calva*, the bow fin of the eastern U. S., is the only living species. The genus dates from the eocene. Allied fossil forms are *Eurycormus*, *Callopterus*, *Caturus*, and *Pachycormus*, ranging from the lias to the Jurassic.

Legion II. Teleostei.

Fishes with the bony skeleton well developed, the cranium and the vertebral centra ossified, the latter amphicœlous; tail diphy- or homocercal; spiral valve and conus arteriosus not developed; no optic chiasma; scales, when present, cycloid or ctenoid.

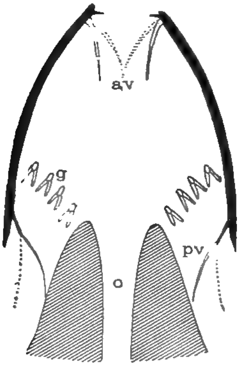

FIG. 254. Breathing valves of teleosts, after Dahlgren. *av*, anterior or oral valves open; *g*, gills; *o*, œsophagus; *pv*, posterior valves. At expiration the anterior valves close, the posterior open; the enlargement and contraction of the oral cavity being brought about by motion of the oral walls (black).

The group of teleosts or bony fishes so closely follows the ganoids that some students do not distinguish between them. There are, however, some distinctions between the two groups, while the matter of convenience warrants their recognition.

In a few teleosts the skin is naked or covered with bony plates, but usually the body is covered with scales of the cycloid or ctenoid type. In a few the tail is diphycercal, but usually it is homocercal. The fulcra, so characteristic of most ganoids, never occur. The skeleton is well ossified, this being especially true of the skull, where the cartilages are almost entirely replaced by bone. The operculum and its skeleton are well developed, branchiostegals are present, and gular plates rarely occur. The paired fins never have a basal lobe; and the ventrals, when present, may either be near the vent or far forward, beneath the throat. A spiral valve is absent except in the single genus *Cheirocentrus*, while the conus arteriosus is represented only in the genus *Butrinus* (see, however, p. 227). The bulbus aortæ is large. The pallium of the cerebrum is non-nervous in character (Fig. 53), and the optic nerves cross (Fig. 63) and never unite in a chiasma.

An interesting discovery has recently been made, that in many if not in all teleosts breathing-valves exist, one pair at the mouth, the other behind the gills, so arranged that when the mouth cavity is enlarged water can only flow in through the mouth; when contracted, it can only escape through the gills.

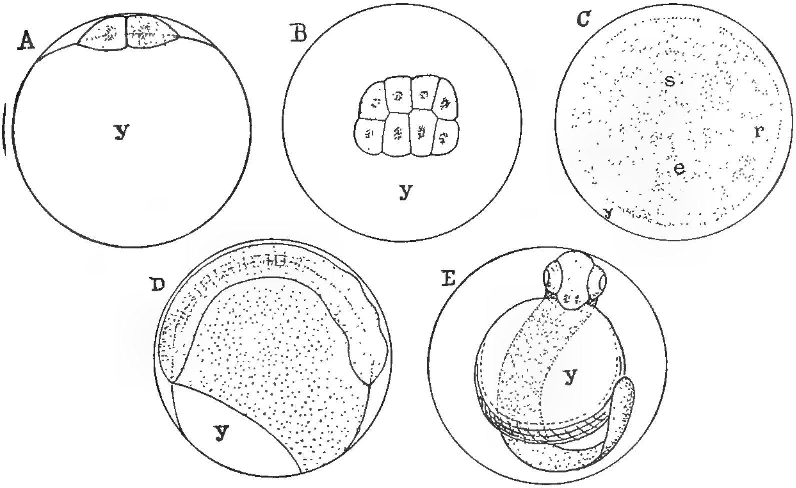

FIG. 255. Five stages in the development of the cunner (*Ctenolabrus*). *A*, two cells, resting upon the yolk; *B*, surface view of the eight-celled stage; *C*, the blastoderm covers about one-third of the yolk, the segmentation cavity (*s*) showing through; the embryo (*e*) is outlined, while the blastoderm is margined by a thicker rim (*r*) of inturned entoderm; *D*, the blastoderm has covered three-quarters of the yolk; the three primary brain regions are differentiated, and myotomes have appeared; *E*, a stage shortly before hatching, the yolk having been largely absorbed, and the tail having grown out.

The eggs of the teleosts are peculiar in the almost complete separation between yolk and protoplasmic portions; the latter alone dividing in the early stages of development, and giving rise to the blastoderm, which gradually extends over the yolk. A peculiarity in development is the formation of the central nervous system as a solid cord or 'keel,' in which a lumen appears later by splitting. In many teleosts a peculiar saccular structure, known as **Kupffer's vesicle,** occurs near the hinder end of the alimentary tract. It disappears before hatching, and its significance is not yet understood.

The teleosts first appear in the triassic, and in the cretaceous they exceed the ganoids in number, while to-day the group includes the vast majority of the forms — some fifteen thousand in all — commonly known as fishes.

The classification of the group is in a very unsatisfactory condition, especially as regards the vast order acanthopteri, where as yet it is almost impossible to frame sub-orders, owing to the extent to which the different families intergrade, and the limited degree to which we can ascertain the lines of descent. The trouble is largely based upon the fact that many lines have persisted, so that our artificial systems cannot easily be applied. The teleosts have apparently had two lines of descent, one leading from sturgeon-like ancestors to the Ostariophysi (for it is difficult to believe that the peculiar Weberian apparatus has been evolved twice in the history of the fishes), and the other from some *Amia*-like form to the isospondyli, and these to the apodes on the one hand, and to the acanthopteri and other orders. For convenience the division Physostomi is retained for all those fishes, the ostariophysi excepted, in which the duct of the air-bladder remains open permanently; the term Physoclisti is frequently employed for the remaining groups in which the duct is closed, as well as for those in which the bladder itself has disappeared.

ORDER I. OSTARIOPHYSI.

Teleosts with the anterior vertebræ modified into a 'Weberian apparatus' connecting the inner ear with the large swim-bladder. Fins without spiny rays, or at most with a single spine in front of pectorals and dorsals; ventrals abdominal in position; duct to air-bladder persisting.

SILURIDÆ (upwards of 1,000 species), skin without scales, naked, or covered with bony plates; premaxilla toothed and forming upper jaw; maxilla with barbels. Mostly fresh-water forms from South America and Africa. *Amiurus* contains our smaller cat-fish (bull-heads or horned pout); closely allied is the nearly blind *Gronias* from caves in Pennsylvania. *Ictalurus*, larger river cat-fish. *Loricaria* and *Clarias* are armored; *Malapterurus* of Africa is electric. Fossil siluroids appear in the eocene of Wyoming.

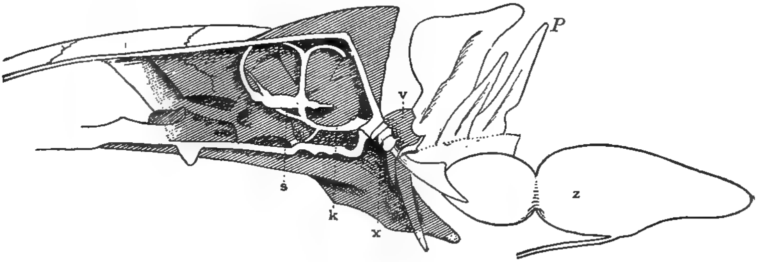

FIG. 256. Weberian apparatus of the carp, *Cyprinus*, after Weber. *k*, sinus impar of ear; *r*, pneumatic duct; *s*, utriculus of ear; *p*, spinous processes of anterior vertebræ; *x*, Weberian chain, leading to *z*, the air-bladder.

CYPRINIDÆ, narrow mouths, frequently with barbels; the jaws toothless, but with teeth on the pharyngeals, scales cycloid, fins without spines. About 1,000 species in fresh water. *Cyprinus*, the carp, and *Carassius* the gold-fish, come from China. *Leucisus* and *Notropis*, numerous. *Ptychochrilus* of the Pacific coast, 4 feet long. *Barbus Cobitis*. The Cyprindæ appear in eocene. The suckers (CATOSTOMIDÆ) have sucker-like toothless mouths. About 60 species, mostly from North America. *Ictobius*, *Catostomus*. *Amyzon*, from American eocene. The CHARACINIDÆ (*Erythrinus*, *Characinus*) are tropical.

The GYMNONOTI of South America are eel-like, the dorsal fin reduced or absent. *Gymnotus electricus*, the electric eel. MORMYRIDÆ, fresh-water, Africa.

ORDER II. PHYSOSTOMI.

A duct to the air-bladder, fins without spines, ventral fins abdominal in position; no Weberian apparatus; gills comb-like; scales, when present, usually cycloid

SUB–ORDER 1. ISOSPONDYLI.

Mostly marine fishes with distinct opercular bones; shoulder girdle connected with the cranium by a post-temporal; maxillary and premaxillary distinct, no barbels; ventral fins sometimes wanting, pharyngeal bones simple.

CLUPEIDÆ (herrings), head naked; lateral line lacking; no adipose dorsal; weak teeth or none. The species number about 125, but are very numerous as individuals. *Clupea* (dates from the cretaceous), shad, alewife, and herring, *Brevoortia*, the menhaden. Allied are *Albulia*, *Dorosoma*, and *Engraulis*. *Arapaima* from South America reaches a length of 15 feet. The ancestral *Leptolepis* from the Jurassic shows marked ganoid features. ALEPOCEPHALIDÆ, deep-sea forms. SAUROCEPHALIDÆ, extinct; *Xiphactinus* (*Portheus*) from American cretaceous.

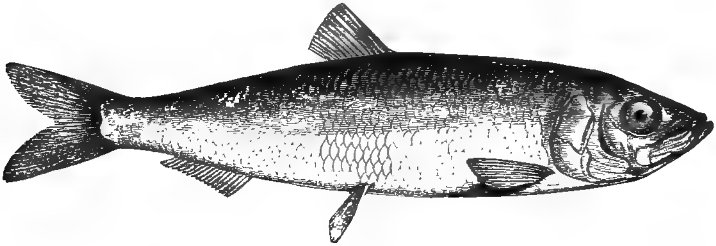

FIG. 257. Herring, *Clupea harengus*.

The SALMONIDÆ, containing the salmon, trout, etc., are among the most valuable of food fishes. They have an adipose fin; teeth variable; lateral line present; no oviducts, the eggs passing out by the pori abdominales. *Coregonus*, the white fishes; *Salmo*, the salmon and trout (the Pacific salmon sometimes placed in sub-genus *Oncorhynchus*). Closely allied is the smelt, *Osmerus*. The fossils not readily distinguished from the Clupeidæ.

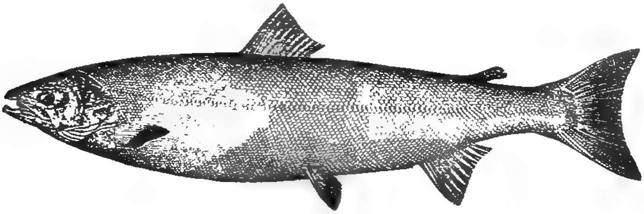

FIG. 258. Atlantic salmon, *Salmo salar*, after Goode.

A number of forms, mostly from the deep sea, are grouped as INIOMI, many of which are furnished with phosphorescent organs. In *Ipnops* the eyes are absent, but the head is covered with a luminous plate. *Scopelus* *Chauliodus*. Scopelid-like forms occur in the cretaceous.

SUB–ORDER 2. APODES.

Degenerate eel-like physostomi without ventral fins, mouth and operculum reduced, scales minute or lacking; scapular arch free from the skull. The true eels (ANGUILLIDÆ) have the gill openings well developed; pectoral fins present. *Anguilla vulgaris*, the common eel of Europe and America. *Conger vulgaris*, conger eel, almost cosmopolitan. The name *Leptocephalus* was given to the young of both *Anguilla* and *Conger*. MURÆNIDÆ, gill slits small and rounded, pectorals lacking. *Muræna*, the murrys of warmer seas. The Apodes are an old group, *Anguilla* dating from the cretaceous. They have possibly descended from the Isospondyli.

SUB-ORDER 3. LYOMERI.

Deep sea physostomes with eel-shaped bodies, large heads, 5–6 simple gill arches; skull imperfectly ossified. In some features they appear degenerate, in some primitive. But few specimens known. *Eurypharynx*, *Gastrostomus*.

SUB-ORDER 4. HAPLOMI.

Physostomes with the head usually scaly, scales cycloid; shoulder girdle attached to the cranium; teeth present; no adipose dorsal. UMBRIDÆ (mud-minnows), teeth villiform; maxillaries forming the lateral part of the jaw. *Umbra*. ESOCIDÆ, pikes, maxilla similar to the last; teeth are card-like and unequal. *Esox*, pickerel, pike, muskalunge. *Esox* dates from the miocene, *Ischyrhiza* from the cretaceous of the United States. CYPRINODONTIDÆ, premaxilla forms the entire upper jaw; vent normal. *Fundulus*, the mummichogs or killifishes, *Anableps*. *Cyprinodon*. *Lebias* from the miocene. AMBLYOPSIDÆ (Heteropygii); jaws as in cyprinodonts; vent in the branchial region; species mostly cave inhabitants (American) and have greatly degenerate eyes. *Amblyopsis*, *Chologaster*. The STRATIODONTIDÆ are extinct. *Cimolichthys*, upper cretaceous.

ORDER III. SYNENTOGNATHI.

Large physoclistous bladder; fins without spines; lower pharyngeals united into a single bone; shoulder girdle connected to cranium; a row of keeled scales on the belly; marine. These forms are allied to the percesoces and the spine-finned fishes.

EXOCŒTIDÆ or SCOMBRESOCIDÆ, gill openings wide; jaws more or less prolonged; maxillary and premaxillary free; and the third upper pharyngeal greatly enlarged. *Scomberesox*, bill-fish, *Exocœtus*, flying-fish. *Isteus*, etc., cretaceous. BELONIDÆ, jaws greatly elongate, the lower the longer; maxillaries and premaxillaries closely united, third upper pharyngeal not enlarged. *Tylosurus*, needle-fish; *Belone*, bony gars, appears in the miocene.

ORDER IV. HEMIBRANCHII.

Teleosts with the pharyngeals reduced in number, the lower not united; gills pectinate; mouth bounded by premaxilla above; scapular arch connected to cranium; ventrals sub-abdominal.

GASTEROSTEIDÆ: body naked or with bony plates: dorsal with spines: teeth sharp, in jaws alone; anal with one spine: fresh and brackish water. *Gasterosteus*, *Apeltes*, sticklebacks. CENTRISCIDÆ, two dorsals, the first spiny: marine. FISTULARIIDÆ, bony plates are present: the dorsal is without spines: snout produced into a tube: the species are marine. *Fistularia* has persisted since the eocene. The extinct DERCETIDÆ (*Belonorhynchus*, *Saurorhamphus* from the cretaceous) show relations towards *Belone*.

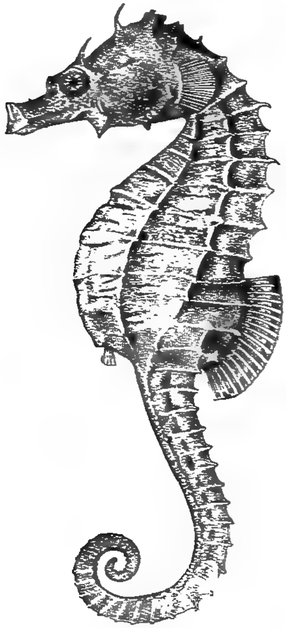

FIG. 259. Sea-horse, *Hippocampus heptagonus*, after Goode.

ORDER V. LOPHOBRANCHII.

Teleosts with hemibranch ancestry: body armored with segmented bony armor: snout elongate; toothless: operculum a single plate; gills composed of small rounded tufts: air-bladder simple, physoclistous; shoulder girdle connected with the cranium.

SOLENOSTOMIDÆ, large gill openings: two dorsals and ventral fins. *Solenorhynchus*, eocene: *Solenostoma*, eocene of Europe and Pacific Ocean to-day. The females carry the eggs and young in a brood pouch formed by the ventral fins and the abdominal or caudal surface. SYGNATHIDÆ, appears in the middle tertiary; gill opening very small: a single dorsal fin and the ventrals absent. *Sygnathus* and *Siphostoma*, pipe-fish, have a caudal fin. In *Hippocampus*, sea-horses, the tail is prehensile and the caudal absent.

ORDER VI. ACANTHOPTERYGII (ACANTHOPTERI).

Gills laminate; ctenoid or cycloid scales; premaxillaries forming the border of the mouth; shoulder girdle connected to the cranium by a (usually forked) post-temporal; ventrals generally far forward, usually attached to the shoulder girdle by means of the pelvis; the anterior rays of pectorals, ventrals, dorsal or anal fins, usually osseous spines. Here belong the great majority of marine teleosts. Judging from vertebral characters and the suspension of the pectoral girdle, they have probably developed from isospondylous ancestors, possibly by way of two or more lines, one of them apparently being the Haplomi. Among the more primitive stocks are percesoces and the salmopercæ, and from these and possibly other groups, the others have descended. In order that the various families may be arranged in some accordance with their affinities these two sub-orders have been somewhat widely separated.

SUB-ORDER 1. SALMOPERCÆ.

Acanthopteri with adipose fin, dorsals and anals spined; ventrals abdominal, ctenoid scales; duct of air-bladder persistent.

A structurally primitive group but no fossils known. Only genus *Percopsis*, with its centre in the great lakes. From this sub-order we follow out first what may be called a percoid line.

SUB-ORDER 2. XENARCHI.

Acanthopteri with a single dorsal fin, ventrals thoracic, air-bladder large, anus at the throat. Contains only the family of pirate perches with one species (*Aphredoderus sayanus*) of the U. S. *Erismatopterus* and *Amphiplaga* from the eocene of Wyoming.

SUB-ORDER 3. PERCOIDEA.

Ventrals with one spine and five rays; lower pharyngeals separate; nostrils double, scales ctenoid. PERCIDÆ, scales extending but a short distance on the vertical fins; lateral line continuous; palatines with teeth; fresh water. *Elassoma*, *Lepomis*, (sunfish), *Micropterus* (black bass), *Etheostoma* (darters), *Perca* (perch). Closely allied are the marine SERRANNIDÆ; *Hæmulon*, *Priacanthus*, etc. *Perca* dates from the oligocene, *Serranus* from the miocene, *Erismatopterus*, eocene. SPARIDÆ, salt-water perches, teeth of the jaws either for cutting, or molars, the palate usually toothless. *Sargus*, represented by the American sheepshead, dates from the miocene. *Lutjanus*. SCIÆNIDÆ, *Cynoscion*, weak fish.

SUB-ORDER 4. LORICATI (CATAPHRACTI).

Body frequently armored with bony keeled scales or plates; a bony process — the suborbital stay — extends across the cheek from the infraorbital ring to the preoperculum. The SCORPÆNIDÆ, or rock-fishes, are the most perch-like; *Scorpæna*, European; *Sebastes*, the Norway haddock. The living species are marine, *Scorpæna* appearing in the miocene, *Petalopteryx* in the cretaceous. COTTIDÆ, sculpins, body naked or covered with irregularly arranged scales; usually two dorsals, anal without spines. A few, like *Uranidea* and *Cottus*, occur in fresh water; but the larger forms, *Hemitripterus*, *Platycephalus*, etc., are marine. *Lepidocottus*, oligocene. The closely allied AGONIDÆ are armored. DISCOBOLI, the skin naked; bases of the ventral fins forming a sucker on the lower surface. *Cyclopterus*, lump-fish; *Liparis*; TRIGLIDÆ, covered with scales or bony plates; anal without spines; two or three rays of the pectoral separate from the rest. *Trigla* (appears in the miocene), the gurnards, European; *Prionotus*, sea-robins, on our coasts. The finger-like free rays of the pectoral are sensory. The DACTYLOPTERIDÆ share with the Exocœtidæ (*supra*) the common name, flying-fishes; they have armored bodies, lack a lateral line, have pectorals enormously developed, and no palatine teeth. *Dactylopterus*. Allied is *Pegasus*, with smaller pectorals and elongate snout, from the East Indies.

SUB-ORDER 5. XENOPTERYGII.

No scales, no spinous dorsal, gill arches reduced, a ventral sucker between the pectorals but not formed by them. The only family GOBIESOCIDÆ is somewhat closely related to the Batrachidæ and Cottidæ. *Gobiesox*, American.

SUB-ORDER 6. HOLCONOTI.

Anal fin very long, scales cycloid, lower pharyngeals united, young brought forth alive. The surf perches (EMBIOTOCIDÆ) of the Pacific coast form the only members of this group, which finds its nearest relatives in the percoid fishes and in the pharyngognaths (*infra*). *Cymatogaster*, *Embiotoca*, *Holconotus*, U. S.; *Ditrema*, Japan.

SUB-ORDER 7. PHARYNGOGNATHI.

Nostrils double, lower pharyngeals united, scales cycloid; oviparous. A single family, LABRIDÆ, of percoid affinities, most of the species being tropical or sub-tropical shore feeders. *Labrus*, European wrasses; *Ctenolabrus*, cunners; *Tautoga*; *Scarus*, parrot-fish. Allied are the tropical

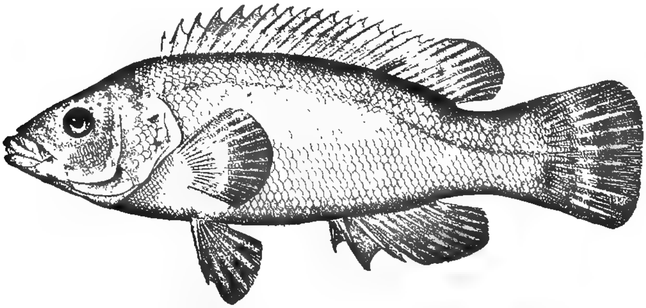

FIG. 260. Cunner, *Ctenolabrus cæruleus*, after Goode.

families, CHROMIDÆ, from fresh water, POMACENTRIDÆ, marine, in which the nostrils are single.

The three sub-orders following form a blennoid series which have sprung from a percoid stem.

SUB-ORDER 8. TRACHINOIDEA.

Ventrals thoracic or jugular, nostrils single, dorsal spines few, soft dorsal and anal long, body scaled or naked. This sub-order is best developed in the south temperate zone. In the deep-sea CHIASMODONTIDÆ the body is naked, the mouth very large, and two dorsals are present. The species are noted for their sharp teeth and enormous stomach, swallowing fishes several times their own size. The MALACANTHIDÆ are represented off our shores by the tile-fish, *Lopholatilus*, of interesting history. TRACHINIDÆ; mouth oblique, small conical teeth, lateral line distinct. *Trachinus*, weevers; *Uranoscopus*, *Dactyloscopus*, star-gazers; *Trachinus* appears in the eocene.

SUB-ORDER 9. BLENNIOIDEA.

Body naked or with ctenoid or cycloid scales; ventrals thoracic or jugular, sometimes wanting, the soft rays few in number; dorsal fin long, the spiny rays numerous; anal long; tail homocercal. BLENNIDÆ, gill openings normal, teeth not molariform; *Blennius*, *Gunnellus*, *Cryptacanthodes*. ANARRHICHIDÆ, posterior teeth are molariform; *Anarrhichas*, wolf-fishes.

SUB-ORDER 10. OPHIDIOIDEA.

Closely related to the last, but without spines, except sometimes in the posterior part of the dorsal; tail diphycercal. The eel-pouts are all marine, and occur in all seas. ZOARCIDÆ, ventral fins never filamentous, sometimes wanting. *Zoarces*. OPHIDIIDÆ, ventrals slender filaments, a little behind the eye. *Ophidium*. FIERASFERIDÆ, ventrals lacking; vent at the throat. Several species of *Fierasfer* live as commensals with pearl oysters or in the cloaca of holothurians.

SUB-ORDER 11. BERYCOIDEA.

Ventrals thoracic, soft rays of pectorals more than 5; tail diphycercal; duct of air-bladder, in some cases at least, persistent; body naked or scaly. The berycoids are an archaic group, the genera *Beryx*, *Platycormus*, *Holocentrum*, etc., appearing in the eocene. The nearest relatives are to be sought in the percoids. The living species are marine, and some belong to the deep seas. BERYCIDÆ, no barbels on the chin; dorsal is single. HOLOCENTRIDÆ, two dorsals. MULLIDÆ, two dorsals and two chin barbels. *Mullus*, the surmullets; *Upeneus*, the goat-fishes. Less certain in its position is the family ZEIDÆ which has some berycoid affinities, while it also shows relationships to the squamipinnes.

SUB-ORDER 12. SQUAMIPINNES.

Ventrals thoracic, tail diphycercal; scales small, ctenoid; dorsal fin long, scales upon the soft portion; postorbital usually ossified to the skull. The squamipinnes have left the main stem somewhere near the point of differentiation of percoid and scombroid groups. In turn they have given rise to the plectognaths. The order is introduced by *Pomacanthus*, and *Asineops* in the eocene. In the CHÆTODONTIDÆ the teeth are bristle-like and thick set. *Chætodon*, butterfly-fishes; *Holacanthus*, emperor-fishes; *Toxodon*, the archer fish, has the palatines with teeth. All the forms are tropical or subtropical. TEUTHIDÆ, doctor-fishes, teeth incisor-like; caudal peduncle is armed with spines or plates, and frequently becomes an important weapon of defence. *Teuthis*, tropical seas.

SUB-ORDER 13. PERCESOCES.

Ventrals abdominal, spined; dorsal spines few, usually forming a separate fin, tail diphycercal, third superior pharyngeal enlarged, scales cycloid. The percesoces form another stem, arising probably from the ancestors of the hemibranchs and lophobranchs, and close to the synentognaths. In turn the scombroids have descended from some percesocid form. ATHERINIDÆ, or silver sides, lateral line lacking, teeth small or wanting; head and body elongate; species carnivorous, mostly marine; *Atherina* (appears in eocene) *Menidia*. MUGILIDÆ, mullets, herbivorous; differ from last in the short and broad head. *Mugil* dates from oligocene. SPHYRÆNIDÆ, lateral line distinct; teeth strong. *Sphyræna*, the barracudas of warmer seas. *Scyllæmus*, cretaceous. The OPHIOCEPHALIDÆ of the rivers of India belong near the percesoces, but differ in absence of spines from all fins. They are capable of aerial respiration, and lead to the labyrinthici. The tropical POLYNEMIDÆ show some relationships to the mugilidæ. *Polydactylus*.

SUB-ORDER 14. LABYRINTHICI.

Dorsal and anal spines present, ventrals thoracic, lateral line interrupted or absent; a complicated apparatus of bony laminæ supporting a respiratory membrane in the accessory branchial chamber, by means of which the animal can breathe air. All are tropical. *Anabas* is said to climb trees. *Osphromenus*, the gouramy.

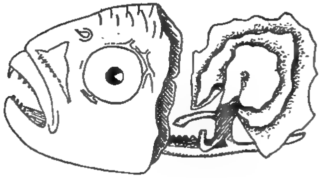

FIG. 261. Head of *Anabas*, showing the labyrinthicine apparatus, after Zograff.

SUB-ORDER 15. AMMODYTOIDEA.

Ventrals absent, no spines in any fins, in other respects much as in the percesoces. A group of uncertain relations, placed here for want of a better place. A single family, AMMODYTIDÆ, with cycloid scales, no teeth, lateral line along the side of the back. *Ammodytes*, sand-launces, common on sandy shores.

SUB-ORDER 16. SCOMBROIDEA.

Tail diphycercal, caudal usually strongly forked; ventrals thoracic; scales usually small, cycloid, sometimes absent; dorsal fin usually long. A heterogeneous group, not easily defined; developing in three main lines. SCOMBRIDÆ, head normal; spinous dorsal well developed; the dorsal divided up into finlets. *Scomber*, mackerels, first appear in miocene; *Thynnus*, horse-mackerel, tunnies (eocene); *Auxis* (miocene), frigate-mackerel. TRICHIURIDÆ, body very long, tapering to a point; no caudal; ventrals rudimentary or absent; tropical. *Trichiurus*, cutlas-fishes. The allied *Lepidopus* appears in the eocene. PALÆORHYNCHIDÆ, extinct. XIPHIIDÆ, bones of upper jaw prolonged into a sword. *Histiophorus*, sail-fish, possesses scales and teeth; *Xiphias*, sword-fish, lacks both. Xiphiidids date from the upper cretaceous.

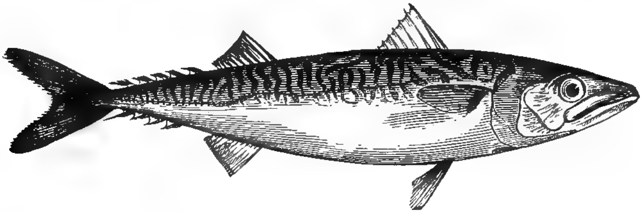

FIG. 262. Mackerel, *Scomber scombrus*.

CARANGIDÆ, pompanos of warmer seas; caudal forked; dorsal not divided into finlets; jaws normal. *Naucrates*, pilot-fish; *Seriola*, amber-fish (date from the eocene); *Caranx*, crevallés (miocene); *Vomer* and *Selene*, moon-fishes, with greatly compressed bodies. *Trachinotus*, *Platax*, cretaceous. POMATOMIDÆ, blue-fish. CORYPHÆNIDÆ, dolphins; date from eocene. STROMATEIDÆ, with teeth-like processes in the œsophagus; *Rhombus*, butter-fish; *Palinurichthys*, rudder-fish. BRAMIDÆ.

SUB-ORDER 17. GOBIOIDEA.

Dorsal spines few and weak; ventrals thoracic, usually close together; soft dorsal and anal long; tail diphycercal. Over 600 species, mostly marine, and of small size. *Callionymus* first appears in the miocene; *Gobius* (from eocene onwards); *Clevelandia*. *Typhlogobius* of Californian shores is blind.

SUB-ORDER 18. DISCOCEPHALI.

With the dorsal fin modified into a flat, transversly laminated oval sucker on the top of the head; ventrals thoracic. Introduced by *Opisthomyzon* in the eocene of Switzerland with a smaller sucker than in recent forms. Living genera, *Echineis* and *Remora*, suck-fishes, which attach themselves by their suckers to fish, ships, etc.

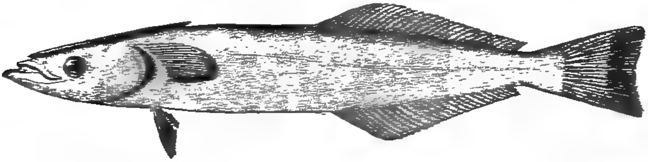

FIG. 263. Suck-fish or remora. *Remora brachyptera*, after Goode.

SUB-ORDER 19. ANACANTHINI.

No spines in any fins, ventrals jugular in position. GADIDÆ, one of the most important families of fishes: caudal fin present, scales cycloid, chin with barbels except in *Merlucius*. *Gadus*, cod and haddock: *Pollachius*, pollock: *Microgadus*, tomcod; *Lota*, burbot, fresh water: *Phycis*; *Merlucius*, hake. MACRURIDÆ, tail tapering to a point, without caudal. *Macrurus*. The Anacanthini are represented by *Nemopteryx* in the oligocene, while *Gadus* and *Phycis* appear in the miocene.

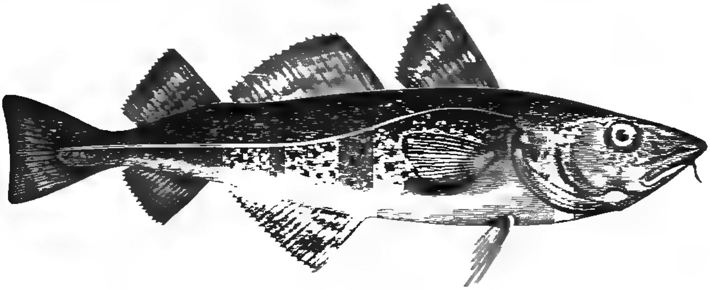

FIG. 264. Cod. *Gadus morrhua*, after Storer.

SUB-ORDER 20. TÆNIOSOMI.

Body elongate and ribbon shaped; ventrals thoracic; dorsal high, and running the length of the back: mouth small, teeth weak: caudal, when present, directed upwards. The ribbon-fishes are deep-sea forms, reaching a length of 15 or 20 feet. REGALECIDÆ, ventrals reduced to a single filament. *Regalecus*. TRACHYPTERIDÆ, ventrals normal or wanting. *Trachypterus*; *Stylephorus*.

SUB-ORDER 21. HETEROSOMATA.

Fins without spines: dorsal and anals very long: ventrals thoracic: tail diphycercal: head twisted so that both eyes appear on the same side. The flat fishes are among the most remarkable of fishes from the torsion of the head. In early life they are symmetrical; but very soon, in some species before reaching the length of an inch, they turn over upon one side, and the eye of the lower surface gradually works around to the upper side, twisting the bones of the skull in its passage. The group is nearest the gadoids, and probably these have both descended from some common ancestor. Many of the species are valuable as food. All are bottom feeders, and some come from the deeper seas. PLEURONECTIDÆ, preopercular margin distinct; mouth large or moderate. *Hippoglossus*, halibut of northern seas; *Paralichthys; Pseudopleuronectes*, winter flounders; *Pleuronectes*, plaice; *Lophopsetta*, window pane. *Psetta* (*Rhombus*), turbot (dates from the eocene). SOLEIDÆ, preopercular covered by skin and scales in front; mouth small and twisted. *Achirus*, American soles; *Solea* (dating from the oligocene), European sole.

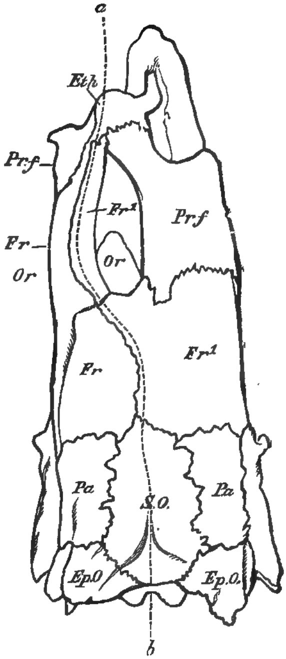

FIG. 265. Cranium of a plaice (*Platessa*), from Huxley, showing the distortion of the bones; the dotted line, *ab*, being the middle line. *Ep O*, epiotics; *Fr*, frontals; *Eth*, ethmoid; *Pa*, parietal; *Prf*, prefrontal; *SO*, supraoccipital; *Cr*, position of eyes.

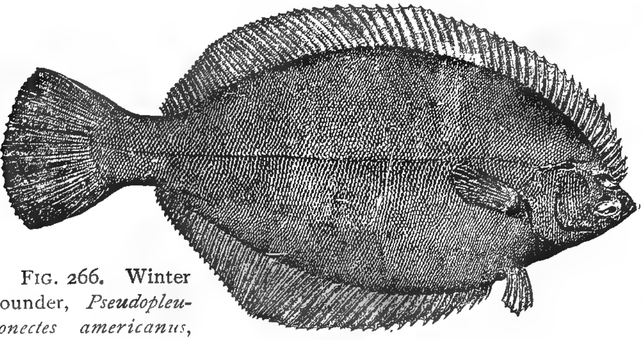

FIG. 266. Winter flounder, *Pseudopleuronectes americanus*, after Goode.

SUB-ORDER 22. HAPLODOCI.

Gill arches reduced to three; head large; post-temporal undivided; dorsal fins two, the dorsals, pectorals, and ventrals spined in front, the ventrals jugular; scales cycloid or wanting. A single family, **Batrachidæ**, mostly from warmer seas. *Batrachus*, toad-fish; *Thalassophryne*, poison toad-fish. *Porichthys*, midshipman, of Pacific coast, with numerous dermal organs, in structure resembling phosphorescent organs, but not luminous.

ORDER VII. PEDICULATI.

Pectorals broad, suspended by an 'arm' formed by the elongation of the basilar bones; head and anterior part of body very large, without scales; spinous dorsal far forward, the spines often like tentacles; gill opening a small foramen in or near the axilla; ventrals jugular. The most specialized of fishes, with possibly an haplodocan ancestry.

Lophiidæ, large mouth; strong teeth; ventrals present. *Lophius*, angler or goose-fish; the genus dates from the eocene. **Antennariidæ**, pectorals bent at an elbow-like angle; ventrals jugular; *Pterophryne*, in gulf-weed. *Antennarius*. **Malthidæ**, mouth small, usually inferior. *Malthe*, sea-bats.

ORDER VIII. PLECTOGNATHI.

Bones of upper and lower jaws each co-ossified; post-temporal simple; ventrals reduced or wanting; gills pectinate; gill opening narrow, just in front of pectorals; spinous dorsal small or wanting. The plectognaths have arisen from near the squamipinnes (above), the teuthids being very near the trigger fishes.

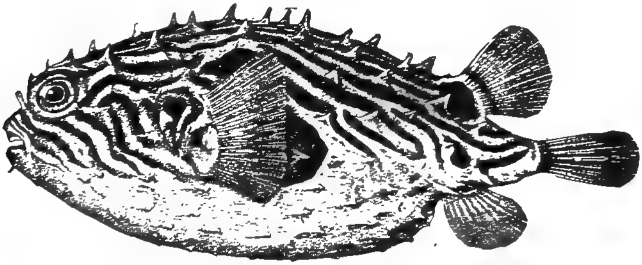

FIG. 267. Swell-fish, *Chilomycterus geometricus*, after Goode.

Sclerodermi, jaws with distinct teeth; spinous dorsal present; body with scales or movable plates. *Balistes*, file-fish or trigger-fish; *Monacanthus*, file-fishes; *Acanthoderma*, eocene; *Alutera*, unicorn-fish. **Ostracodermi**, jaws with distinct teeth; body enclosed in a three, four, or five angled box composed of polygonal body plates, firmly united. *Ostracion Lactophrys*, trunk-fishes. *Ostracion* first appear in the eocene. GYMNODONTI, spinous dorsal lacking; scales spiniform or absent; jaws with enamelled plates, but without distinct teeth. *Tetrodon*, *Diodon*, *Chilomycterus*, etc., swell-fishes or globe-fishes, etc., the common names arising from the powers of inflation possessed by them. *Mola* (*Orthagoriscus*), sun-fish, the most bizarre of fishes, seemingly but a large head with fins attached. Fossils doubtfully referred to *Mola* occur in the British cretaceous; *Diodon* appears in the eocene.

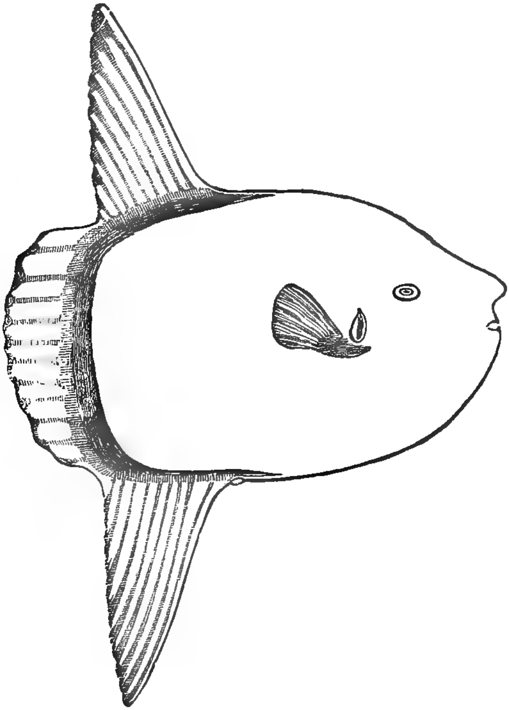

FIG. 268. Sun-fish, *Mola rotunda*, after Putnam.

SUB-CLASS III. DIPNOI (DIPNEUSTES).

Fishes with partially ossified cartilage, numerous membrane bones, and persistent notochord; skull autostylic; a membranous operculum; tail diphycercal; paired fins archiptergial or reduced; heart with multivalvular conus, a spiral valve in intestine; a cloaca present, air-bladder single or paired, functioning as a lung.

The dipnoi, or lung-fishes, are frequently regarded as belonging to the ganoids, and have attracted great attention from the fact that they are often considered as intermediate in position between the lower fishes and the amphibia. In past time the group was richly represented; but in the existing fauna of the earth but four species are known, these having that wide and discontinuous distribution so frequently characteristic of the survivors of an ancient group.

They all have an elongate fish-like or eel-like body, covered in the recent species with overlapping cycloid scales; while in the fossils ganoid scales frequently occurred. The fins are supported by horny dermal rays. The axial skeleton consists of the persistent notochord, around which (except in the tail region of some forms) vertebral centra are not developed, segmentation being shown only in the neural arches and ribs.

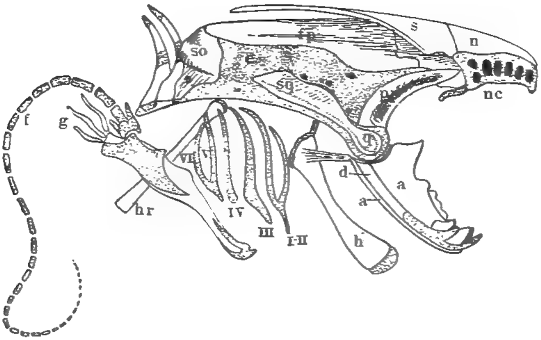

FIG. 269. Skull of *Protopterus*, after Wiedersheim. *a*, angulare; *d*, dentary; *e*, otic capsule; *f*, skeleton of fore limb; *fp*, frontoparietal; *g*, external gills; *h*, hyoid; *hr*, head rib; *n*, nasal; *nc*, nasal capsule: *pp*, palatopterygoid; *q*, quadrate; *s*, supracranial bone; *sq*, squamosal; *so*, supraoccipital; *I–VI*, branchial arches.

The skull consists of the largely persistent chondrocranium plus a number of membrane bones not easily homologized with those of other vertebrates. In the chondrocranium exoccipitals alone are developed. In the lower groups the membrane bones are very numerous; but in existing forms, as in the extinct arthrodira, they are few. In the existing species parasphenoid, vomers, palatoquadrate and squamosal, as well as dentary, angular and opercular in the lower jaw, are more or less certainly to be recognized; but beside these there are several bones in the cranial roof which are not to be homologized with those in other groups.

The operculum is supported by bones (operculum, interoperculum), and the hyoid and (four or five) branchial arches are cartilaginous. The pectoral and pelvic arches are cartilaginous, the former with membrane bones of the fish-type (p. 174) weakly developed. The pelvis consists of a median plate with (in recent forms) three anterior horns. The fins themselves are very primitive, and consist of an axial portion, from which, in *Ceratodus*, biserial cartilaginous fin rays arise. In many fossils the anterior part of the body is enclosed in a strong armor of bony dermal plates, there being a hinge between the dorsal plates and the base of the skull.

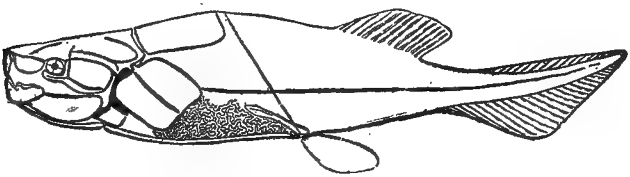

FIG. 270. Restoration of *Dinichthys*, from Dean.

The brain differs from that of the teleostomes in the nervous character of the cerebral mantle. The two hemispheres are united in *Ceratodus*, but in *Protopterus* they are distinct back to the anterior commissure. The mid brain is paired in *Ceratodus*, simple in *Protopterus;* the cerebellum is but a small transverse fold. The pineal structures have a long stalk, while the envelopes of the brain are richly developed, and in *Protopterus* these enter above the fossa rhomboidalis into close connection with the endolymphatic system of the ear. An optic chiasma is present.

The teeth are few in number, and are apparently formed by the fusion of several primitive teeth. Of these there is a pair of larger grinding plates borne on the palatopterygoids, a much smaller pair on the vomerine region, while the lower jaw has a pair on the splenial region. The alimentary canal is nearly straight, and is characterized by the presence of a well-developed spiral valve (Fig. 40) in the intestine. Behind, the intestine empties into a cloaca, which also receives, besides the urogenital ducts, median or paired pori abdominales. There are three (*Protopterus*) or four (*Ceratodus*)[1] pairs of internal gills, and besides, in the former, external gills (Fig. 269). Besides these, there are present in each swim-bladders which also have respiratory functions. In *Ceratodus* this lung is single, in *Protopterus* it is paired; but in both its duct or ducts arise from the ventral surface of the pharynx. Internally these organs are sacculated, while the blood comes to it by true pulmonary arteries, which arise either (*Ceratodus*) from the posterior branchial, or (*Protopterus*) from the radices aortæ.

FIG. 271. Tooth of ceratodan, *Sagenodus*, after Woodward.

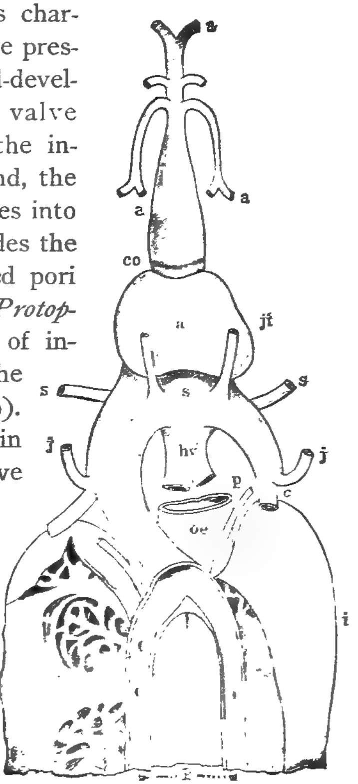

FIG. 272. Heart and anterior part of the lungs of *Ceratodus*, after Röse. *a*, aortic arches and auricle; *c*, postcardinal vein; *co*, conus; *hv*, hepatic veins; *i*, lung; *j*, jugular vein; *ji*, inferior jugular vein; *oe*, œsophagus; *p*, pulmonary arteries; *s*, subclavian vein and sinus venosus.

The heart has both the sinus and the atrium partially divided into right and left halves by an incomplete septum, thus foreshadowing the conditions found in the amphibia, while a true atrio-ventricular valve is lacking. The conus is spirally twisted, and contains several rows of valves, and in *Ceratodus* is partially, in *Protopterus* completely, divided into venous and arterial halves.

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[1] *Ceratodus* also has a hyoid pseudobranch (p. 23).

In the venous system the most marked advance is the presence of a postcava, while but a single (left) postcardinal comes to complete development. A renal portal system is present.

The mesonephros is elongate in *Protopterus*, short in *Ceratodus;* and nephrostomes are lacking in the adult. Its duct is thick walled, and is apparently a Wolffian duct, although embryological evidence is as yet lacking. The gonads are elongate, and attached to the lateral parts of the mesonephros. The oviducts are elongate and contorted, and open into the cœlom far forward by narrow ostia. Posteriorly they unite just in front of the cloaca. In *Ceratodus* no vasa deferentia occur, the spermatozoa apparently passing out through the pori abdominales. In *Protopterus* a well-developed duct occurs in connection with either testis, each passing behind into the rudimentary Müllerian duct, and thence by a common trunk into the cloaca. The cloaca also bears an azygos diverticulum (Fig. 40), usually regarded as an urinary bladder (*cf.* however, the rectal gland of elasmobranchs).

Of the development of *Protopterus* nothing is known. The segmentation and external development of *Ceratodus* have been studied, and show striking similarities to that of *Petromyzon*, and especially to the amphibia. The egg undergoes a total but unequal segmentation, while gastrulation is effected by overgrowth as in the amphibia, the result being, as in that group — the formation of an elongate primitive groove, on either side of which the medullary folds arise. These close in, and gradually the embryo arises as a ridge above the yolk. So far as is known no metamorphosis occurs.

ORDER I. ARTHRODIRA.

Body in front covered with large bony plates, a dorsal pair articulating by a hinge joint with the cranium; paired fins rudimentary or absent; pelvis represented by a pair of club-shaped plates.

The relationship of the arthrodira to the other dipnoi is not beyond question. The group is restricted to the palæozoic rocks, and remains are abundant in Europe and in America.

Coccosteus appears in the Silurian of Europe, and occurs in the Devonian of Ohio. In the Devonian and carboniferous of Ohio

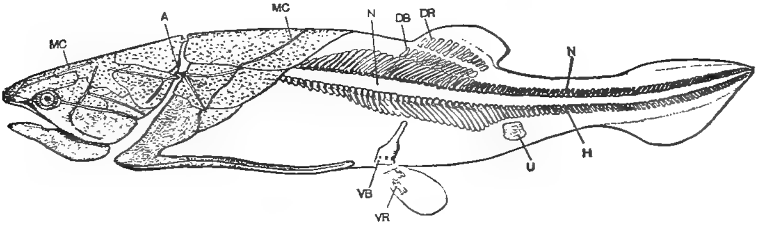

FIG. 273. *Coccosteus*, restored, after Woodward, from Dean. *A*, articulation of head with trunk; *DB*, basalia; *DR*, radialia of dorsal fin; *H*, hæmal arch and spine; *MC*, lateral line canals; *N*, neural arch and notochord; *U*, unpaired plate; *VB*, *VR*, basalia and radialia of ventral fin.

also occur some gigantic forms belonging to the genera *Dinichthys*, *Titanichthys*, and *Macropetalichthys*, the latter genus occurring in Germany as well.

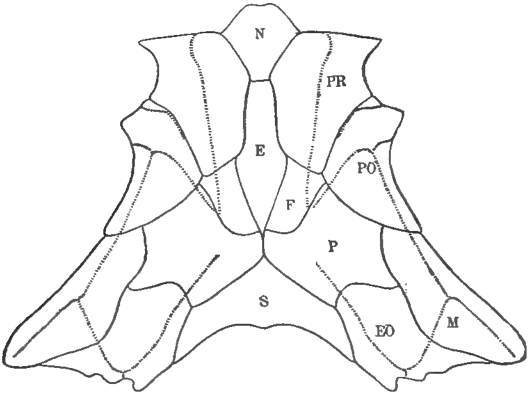

FIG. 274. Dorsal wall of skull of *Dinichthys*, after Claypole. *E*, ethmoid; *EO*, exoccipital; *F*, frontal; *M*, marginal; *N*, nasal; *P*, parietal; *PO*, postorbital; *PR*, preorbital; *S*, supraoccipital; sensory canals dotted. (The homologies of some of the bones with the similarly named elements in other groups is doubtful.)

ORDER II. SIRENOIDEA.

Body never with bony plates, usually covered with cycloid scales; paired fins archipterygial; pelvis a single median plate. The recent forms are subdivided into Monopneumonia and

DIPNEUMONIA. In the first, typified by the Australian genus *Ceratodus*, there is but a single air-bladder (lung), and the fins have the secondary rays of the archipterygium (Fig. 185) well developed. *Ceratodus forsteri* of Australia attains a length of five feet; it lives in fresh water in places where it is apt to become stagnant, and at such times calls its lung into function.

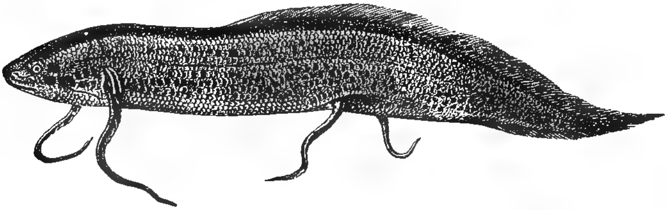

FIG. 275. Lung-fish, *Protopterus annectans*, from Boas.

The genus *Ceratodus* also occurs fossil in the triassic and Jurassic of Europe, India, and Colorado, the peculiar dental plates being very characteristic (Fig. 271). The Dipneumonia have two air-bladders, and the paired fins retain only the axial part of the archipterygial skeleton (Fig. 269). The living genera are *Protopterus* from African rivers, and *Lepidosiren* from South America. At the time of drought the African form burrows into the mud at the bottom of the pools where it lives, and by the aid of the mucus from its body forms the earth into a 'cocoon,' in which it lives in a state of suspended animation until the return of the rainy season.

Allied to these living animals are a number of fossil forms characterized by the presence of numerous plates in the cranial wall. These occur in the palæozoic rocks. In *Dipterus* and *Phaneropleuron* from the Devonian of Europe and America, jugular plates are present; in *Ctenodus* and *Sagenodus*, from the carboniferous of both hemispheres, jugulars are lacking.

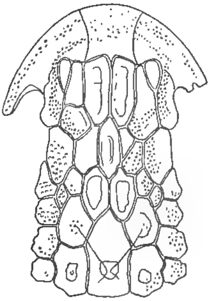

FIG. 276. Dorsal view of skull of *Dipterus*, after Pander.

CLASS II. AMPHIBIA (BATRACHIA).

Ichthyopsida in which lungs are present and the gills are usually lost in the adult. Median fins never supported by dermal rays; paired appendages in the shape of legs; body without scales except in cæcilians and stegocephals; a stapes always present, and an Eustachian tube in the higher forms; nostrils communicating posteriorly with the mouth; a postcava always present.

The amphibia are readily distinguished from the fishes by the absence of paired fins, their place being taken in most forms by legs built upon the pentadactyl type, like those of amniotes. Occasionally, as in *Siren*, one pair of limbs may be absent, or again, as in the gymnophiona and, among the stegocephals, the aistopoda, both pairs are lacking. Median fins, confined to the caudal region, occur in the young of all, and in the adults of many aquatic species, but these are never supported by dermal rays, while the tail is diphycercal in character.

The skin is largely without cuticular structures, but its outer layers become cornified and are periodically shed. The deeper layers contain numerous glands; the secretions of some of these are acrid, and in some cases poisonous; upon these depends the safety of these otherwise unprotected animals. In some cases the skin is smooth, in others it is roughened and covered with warts, in part due to local thickenings, in part to the presence of these defensive glands. Epidermic nails occur on the toes of a few forms.

In a few living species of anura, calcareous deposits occur in the dermis, and occasionally (*Ceratophrys*, etc.) bony dorsal plates may be developed in the same layer. In most gymnophiona semicircular dermal scales envelop the body, giving it a ringed appearance externally. This dermal skeleton was better developed in the extinct stegocephals, where we usually find from one to three large ventral bony plates and a number of smaller ventral scales, but occasionally this armor extended over the back and limbs.

The mouth is always terminal; and teeth, when present, occur on the margins of the jaws (premaxillaries and maxillaries), and usually upon the vomers. In the urodeles teeth may also occur upon the palatines, and occasionally upon the parasphenoid. In all cases they are firmly anchylosed to the supporting bones. In the anuran tadpoles the jaws are covered with horny plates. In the urodeles the tongue is rudimentary. It is lacking in one division (aglossa) of the anura; but in the rest it is fixed in front, the bifid free end being turned back in the mouth. It is capable of extension beyond the jaws, and, covered with adhesive mucus, is used in the capture of food.

The central nervous system has all of its parts lying in one plane. The cerebrum is larger, and differs from that of all fishes, even of the dipnoi, in the greater development of the pallium. The olfactory lobes are in close connection with the cerebral hemispheres. The cerebellum, on the other hand, is reduced to a small transverse fold. The Gasserian and acustico-facialis ganglia are distinct in urodeles and gymnophiona; but in the anura they are closely united, and the roots of the corresponding nerves are not distinguishable by ordinary dissection. There is a similar union of the glossopharyngeal and vagus ganglia, and the common trunk of the ninth and tenth nerves passes from the skull by a single foramen. In all aquatic forms and larvæ the lateralis branches of the seventh and tenth nerves is well developed; but with the assumption of a terrestrial life these are lost, together with the lateral line system which they supply (p. 67).

The nasal passages form complete tubes, opening into the oral or pharyngeal cavities by internal nares or choana in its roof. Connected with the olfactory organs are well-developed organs of Jacobson (p. 77). The epiphysial structures do not extend beyond the skull in urodeles or gymnophiona; but in the anura the parietal eye lies between the skull and the skin, all connection between it and the brain being lost. In the stegocephals there is a large parietal foramen in the skull, which is interpreted as having contained a functional parietal eye. The ears show an advance upon those of the fishes in the development of a distinct lagena,[1] while the spiracular cleft,

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[1] The lagena is the seat of audition, and recent experiments show that hearing first appears in the amphibia.

in the anura, enters into the accessory auditory structures, forming an Eustachian tube leading from the tympanic cavity to the pharynx. A stapes is also developed, and in the anura this is joined to a columella (possibly derived from the hyomandibular) which stretches across the middle ear to the tympanic membrane. In the urodeles and cæcilians the columella and Eustachian tube are absent, and frequently the stapes articulates directly with the quadrate.

The oral and pharyngeal cavities are ciliated; and into them open, in front, the internal nares, and behind, the slit-like glottis, communicating with the more or less elongate trachea. In the young, and in phanerobranchs and derotremes, gill slits occur in the pharyngeal region. Of these, three open to the exterior, while one (or in some cases two) pouches behind these never break through.

The alimentary tract may be nearly straight in the elongate forms, or be greatly convoluted in those with shorter bodies, the convolutions reaching their extreme in the herbivorous tadpoles of the anura. The rectum is short, and opens into the cloaca. The liver is two-lobed, and in the anura the left lobe is more or less completely sub-divided. The pancreas is flattened and lobulated.

In the young of all external gills occur, and these may persist throughout life (perennibranchs). These gills are ectodermal in origin, and arise as outgrowths from the side of the neck before the gill slits break through. Usually they are more or less branched and feathered, but in *Cœcilia compressicauda* they are large sacs. The entodermal gills are a later appearance, and arise from the walls of the gill clefts. These clefts at first open freely to the exterior; but in the adults of most they become closed, remaining permanently open only in the perennibranchs and derotremes. In the anuran tadpole an oper-

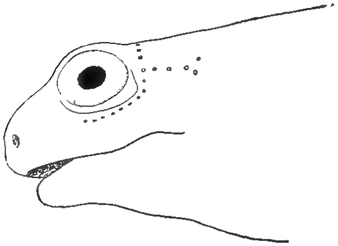

FIG. 277. Head of young *Diemyctylus viridescens*, showing lateral line openings and remains of gill clefts.

cular fold, traces of which are found in some urodeles, grows back over the gill slits in such a way as to enclose them in an extrabranchial or atrial chamber on either side, the two communicating by a passage beneath the throat, and opening to the exterior usually by a single opening upon the left side.[1]

The lungs, which are absent from several salamandars which respire by means of the skin, are thin-walled sacs, which may be either smooth internally or folded into alveoli and infundibula (Fig. 33). The shape is correlated with that of the body, elongate in the longer species, shorter in the more compact forms. Occasionally (gymnophiona, *Amphiuma*) the left lung is small or rudimentary. The trachea may be long or the bronchi may unite just behind the glottis. The glottis is supported by a pair of arytenoid cartilages, and in the anura a ring-like cricoid is added.

In many stegocephals the vertebral column is poorly developed, the centra being sometimes represented by pleuracentra and hypocentra arcale and pleuralia (rhachitomous type, p. 136); or again by an embolomerous condition where centralia and intercentralia alternate. These two conditions, sometimes used as a basis of sub-division, may occur in the same species. In the living species the centra are well developed, and are either amphicœlous (perennibranchs, gymnophiona, and some salamanders), opisthocœlous (most salamanders and aglossate anura), or procœlous (most anura). The number varies from 9, plus the urostyle, in living anura to 250 or more in the gymnophiona. At most but four regions can be recognized, — cervical, trunk, sacral, and caudal; the single cervical is without ribs, but bears in front an odontoid process derived from an anterior vertebra which early fuses with the skull. There is also a single sacral vertebra in all except one group of fossil anura (Palæobatrachidæ), where there are two. In the urodeles the vertebræ bear dia- and parapophyses (p. 141), but in the anura only the diapophysis persists.

The ribs are small, bicipital in urodeles and gymnophiona, anchylosed to the vertebræ in the anura. In the stegocephals they are larger, but in no case do they reach the ventral surface.

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[1] Paired openings occur in the aglossa, a median ventral opening in a few forms.

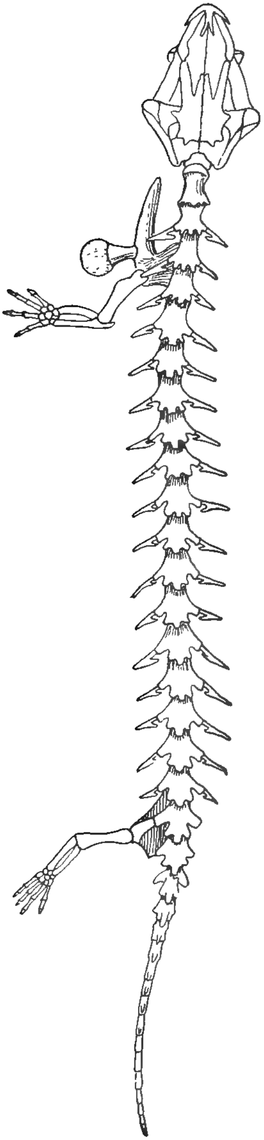

FIG. 278. Skeleton of *Necturus*.

The sternum is lacking in the gymnophiona; in the urodeles and arciferous anura it is a median plate grooved to receive the epicoracoids in front. In the firmisternous anura the sternum expands in front of the procoracoids and clavicles into an omosternum, behind the coracoids to a xiphisternum which may be partially ossified.

The skull is noticeable for the great extent to which the chondrocranium persists, and for the wide interval between the trabeculæ. This persistence of cartilage accounts for the small number of cartilage bones found in all groups except the gymnophiona. Thus in the anura only a prootic occurs in the auditory region; in the urodeles an opisthotic is added. In the occipital region there usually occur but the two exoccipitals, each bearing an occipital condyle. The quadrate forms the sole suspensor of the jaw, and is more or less closely connected with the otic capsule. If a hyomandibular be present, it is modified into the stapes. In the urodeles no ethmoid ossification occurs, while an orbitosphenoid is the only bony element in the trabecular region. In the anura a ring-like sphenethmoid occurs (*os en ceinture*). In the gymnophiona the ethmoid is very large and has large lateral wings.

The membrane bones are more numerous in the gymnophiona, stegocephals, and anura than in the urodeles, the skull being very complete in the first two groups, while in the anura a large gap appears between the cranium and the quadratojugal-malar arch. This latter arch is entirely absent in the urodeles. The roof of the mouth is formed by vomers, palatines, and a parasphenoid, the latter element not reappearing in the higher groups. In the cæcilians the parasphenoid fuses indistinguishably with occipital elements. All of these bones may bear teeth, as may also premaxillaries and maxillaries, the latter element occasionally being absent. The quadrate is overlaid by a squamosal.

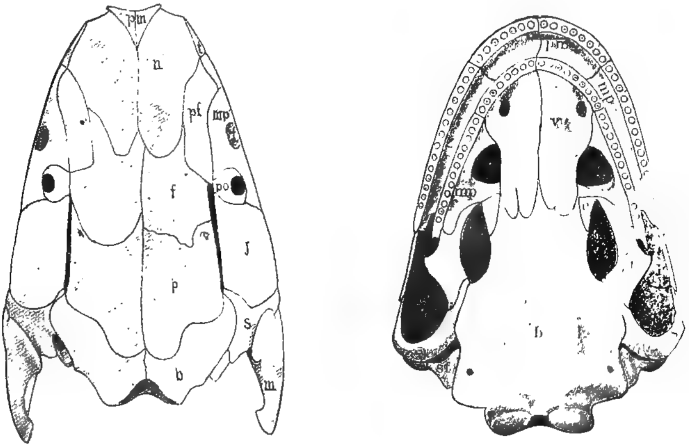

FIG. 279. Skull of *Ichthyophis glutinosus*, after the Sarasins. *b*, basal, composed of the coalesced parasphenoid and the occipitals; *e*, ethmoid; *f*, frontal; *j*, jugal; *mp*, maxillopalatine; *n*, nasal; *p*, parietal; *pf*, prefrontal; *pm*, premaxillary; *po*, postfrontal; *pt*, pterygoid; *s*, suspensorium; *st*, stapes; *t* (in front), turbinal; (behind) tentacular groove.

In the shoulder girdle coracoid, procoracoid, and scapular elements are formed; in the urodeles the procoracoid usually extends directly forward, but in the anura the ventral ends are connected by an epicoracoid, and the procoracoid is more or less completely replaced by a membrane bone, — the clavicle. The amount of ossification varies in different forms. The pelvis is characterized by the development of the ilium, which is very strong in the anura. Ventrally there is frequently a continuous ischiopubic plate in which a distinct pubis rarely ossifies. Epipubic processes are common in the urodeles. The limbs are typically pentadactyl, with primitively a simple carpus and tarsus. In the anura there is a fusion of ulna and radius, while in the hind foot the proximal elements of the tarsus (astragalus and calcaneum) become greatly elongate.

In the heart, which, except in the gymnophiona, is far anterior, there is always a single ventricle. In the perennibranchs and lungless salamanders the auricles are incompletely separated, but in the other amphibia two distinct auricles occur. The right auricle receives venous blood, while, when the lungs are functional, the left receives arterial blood. In the lungless forms the pulmonary vein is absent. In the gymnophiona two rows of valves occur in the conus, but elsewhere this region is reduced to a single circle of semilunar valves. The bulbus is well developed, and in the anura contains a longitudinal valve which, by changes in position, directs the first blood to leave the ventricle (arterial blood) into the carotids and the general circulation, while the venous blood which follows it is sent into the pulmonary artery, and thence to the lungs.

Four pairs of aortic arches appear in the later larvæ, the blood at first passing through them to the gills, and thence to the dorsal aorta. With the metamorphosis the branchial circulation is lost; but in the urodeles all four arches persist, the first supplying the carotids, the second and third forming the radices aortæ, while the fourth go to the lungs. In the gymnophiona and anura the third of these disappears. In the venous system the most marked feature is the appearance of a hepatic-portal system (p. 192) lacking in the other ichthyopsida.

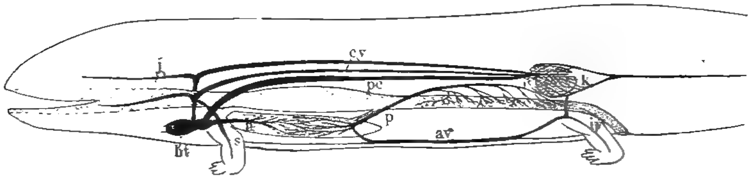

FIG. 280. Diagram of venous circulation in an amphibian. *av*, anterior abdominal vein; *cd*, caudal vein; *cv*, posterior cardinal veins; *h*, hepatic veins; *ht*, heart; *i*, interrenal vein; *iv*, iliac vein; *j*, jugular vein; *k*, mesonephros; *p*, portal vein; *pc*, postcava; *s*, subclavian vein.

The pronephros is a transitory organ. It is confined to two (most urodeles) or three somites (anura) or several segments (gymnophiona, *Amphiuma*.) It is replaced later by the permanent mesonephric kidney, the anterior end of which in the male becomes subsidiary to reproductive purposes (p. 129). In the gymnophiona it is markedly segmental. The ovaries are long bands in the gymnophiona, elongate sacs in the urodeles, and shorter sacs divided by transverse partitions in the anura. The eggs, in their passage through the Müllerian ducts, become enveloped in a gelatine which swells in contact with the water. The Müllerian duct always persists in the male. The sperm passes through the anterior part of the kidney, and thence to the exterior by the way of the urinary duct. In many urodeles it becomes enclosed in packets (spermatophores). Connected with the reproductive organs are branched 'fat bodies' which probably are connected with the nutrition of the reproductive structures (p. 200).

Fertilization by means of the spermatophores is internal in urodeles, external in the anura. The eggs are laid in the water, and left without further care by most forms. A few, however, have interesting breeding habits. Thus *Amphiuma* and *Ichthyophis* wrap the cords of eggs around the body; in *Alytes* the male wraps the cords around his legs. In *Rhinoderma* there is a large gular fold into which the eggs are received, while in *Nototrema* and *Notodelphys* a brood pouch, open behind, is formed by a duplication of the skin of the back. In the Surinam toad, *Pipa*, the eggs are spread upon the back, the skin of which thickens around each egg so that it assumes the character of honeycomb, each cell being occupied by an egg which developes in this position until the adult characters are assumed. A few species (*Salamandra atra*, *S. maculosa*, *Cæcilia compressicauda*) bring forth living young, while *Amblystoma tigrinum* frequently breeds in the larval or 'Siredon' stage.

The eggs contain a large amount of yolk, and undergo a total but unequal segmentation (Fig. 214), the result being the formation of a blastula with small cells on one side and larger (entodermic) cells on the other, and an eccentric segmentation cavity (Fig. 215). The gastrula arises in part as an inpushing, in part as the result of an overgrowth of the ectoderm, and before this process is completed, the differentiation of the central nervous system begins. The medullary plate infolds into a tube, and at the same the egg begins to elongate into the embryo. The head now becomes differentiated, and the outlines of the eyes are seen, while the tail begins to extend behind, the ventral surface of the embryo being swollen by the large amount of yolk. On the sides of the neck appear small swellings, the rudiments of the external gills, two pairs in the anura, three in the urodeles and some cæcilians. Besides these, the anuran develops a pair of suckers beneath the head, while the urodele is characterized by the formation of a pair of slender rod-like 'balancers' in front of the external gills, these balancers being apparently the gills of the hyoid arch. After escape from the egg into the water the gill clefts break through. The limbs make their appearance later than the external gills.

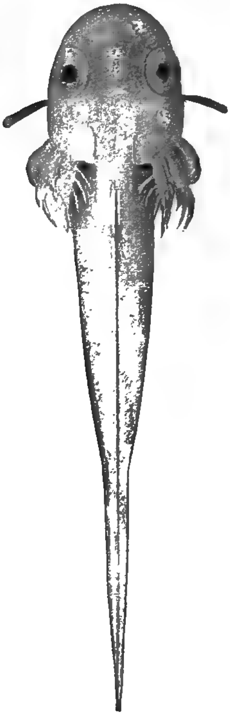

FIG. 281. Larva of *Amblystoma punctata*, enlarged, showing the balancers.

In most amphibia there is a metamorphosis, most marked in the anura where there is a tailed larva, the tadpole, with small toothless mouth. The external gills disappear; the tail is absorbed, its vertebræ being reduced to the urostyle; the internal gills appear, and the gill slits first become enclosed in a gill chamber formed by the backward growth of the opercular fold, and then close up completely. The mouth enlarges, and the tadpole assumes the adult form.

All the facts of structure and development go to show that the amphibia have arisen from the crossopterygian ganoids, and that existing groups have descended from the stegocephali, each by its own line of ancestry. The view that the anura have descended from urodeles has little morphological evidence in its favor, while there is much against it.

SUB-CLASS I. STEGOCEPHALI (LABYRINTHODONTIA).

Extinct amphibia with well-developed tail; skull solid, with numerous dermal bones, including paired supraoccipitals, supratemporals, and postorbitals; the lower surface of the body usually with three large ventral bony shields, and frequently with smaller scales which may extend over the dorsal surface and limbs; a separate pubic ossification. The stegocephali appear in the carboniferous[1] and became extinct in the triassic. Some were of gigantic size, and in some the dentine of the teeth was so folded as to give these animals the name of labyrinthodonts.

ORDER I. LEPOSPONDYLI.

With vertebral centra consisting of bony envelopes surrounding the persistent notochord; teeth simple, with large pulp cavities. *Branchiosaurus* (one species about four feet long) had persistent gills, and the ventral surface of body, limbs, and tail with oval scales. European carboniferous. *Melanerpeton.* The MICROSAURIA, with pointed heads and weak fore limbs, are well represented in the carboniferous of Nova Scotia (*Hylerpeton, Hylonomus*) and Ohio (*Tutidanus, Colosteus*), as well as of Europe (*Keraterpeton*). In the AISTOPODA the body was snakelike and limbless. *Dolichosoma, Ophiderpeton,* European carboniferous; *Phlegethontia* (coal of Ohio) lacked ribs.

ORDER II. TEMNOSPONDYLI.

Vertebræ embolomerous or rhachitomous, dentine of teeth radially folded. RHACHITOMI, with rhachitomous vertebræ. *Archegosaurus,* the best known stegocephalan (European carboniferous), five feet long. *Trimerorhachis* (Texas Permian) had a skull five feet long. *Eryops* from the same beds was half as large. EMBOLOMERI, embolomerous vertebræ. *Cricotus,* Permian of Texas and Illinois.

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[1] Foot-prints, possibly of a stegocephalan, have recently been found in the Devonian of Pennsylvania.

ORDER III. STEREOSPONDYLI.

Vertebræ amphicœlous, occipital region ossified, teeth labyrinthine. GASTROLEPIDOTI. With ventral elongate scales. *Baphetes* (coal, Nova Scotia), *Platyops* (Permian of Europe). LABYRINTHODONTIDÆ, no ventral scales. *Trematosaurus*, *Labyrinthodon*, *Mastodonsaurus*, etc., Europe.

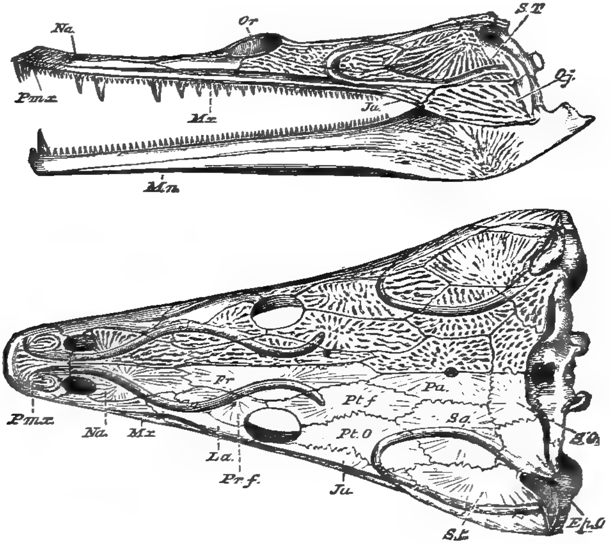

FIG. 282. Skull of stegocephal, *Trematosaurus*, from Huxley. *EpO*, epotic; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mn*, mandible (of several bones); *Mx*, maxilla; *Na*, nasal; *Or*, orbit; *Pa*, parietal; *Pmx*, premaxilla; *Prf*, prefrontal; *Ptf*, postfrontal; *PtO*, postorbital; *Qj*, quadratojugal; *SO*, supraoccipital; *Sq*, squamosal; *St*, supratemporal. The grooves shown were for lateral line organs.

SUB-CLASS II. URODELA. (GRADIENTIA.)

Amphibia with persistent tails; usually two pairs of limbs; skull without ethmoid, supraoccipital, postorbital, or supratemporal; no parietal foramen. Vertebræ amphicœlous, never embolomerous or rhachitomous. Skin naked.

ORDER I. PERENNIBRANCHIATA (PHANEROBRANCHIA).

With persistent, bushy, external gills and gill slits; maxilla usually lacking; teeth on vomers and palatines. SIRENIDÆ, hind limbs lacking; *Siren*, the mud eel of southern United States, has jaws armed with horny sheaths. PROTEIDÆ, hind limbs present; jaws with teeth. *Proteus* of Austrian caves nearly blind; *Necturus* (*Menobranchus*), the mud puppy of the central United States.

ORDER II. DEROTREMATA (CRYPTOBRANCHIA).

External gills lost, a spiracle on the side of the neck, leading to persistent gill slits. AMPHIUMIDÆ, limbs rudimentary; *Amphiuma*, one species, the congo eel from the southern states. CRYPTOBRANCHIDÆ, legs strong; body salamander-like. *Menopoma* (*Cryptobranchus*), hell-bender, from U. S. *Megalobatrachus*, giant salamander from Japan, three feet long. *Andrias scheuchzeri*, European miocene, described over one hundred and fifty years ago as a relic of the legendary Noachian deluge.

ORDER III. SALAMANDRINA (MYCTODERA).

Gill slits and external gills lost in the adult; vertebræ fully ossified. LECHRIODONTA, palatine teeth in a transverse row or posteriorly converging series. *Amblystoma*, toothless parasphenoid, toes four in front, five behind; many species in U. S. *Plethodon*, teeth on parasphenoid; premaxillaries separate. *Spelerpes*, premaxillaries fused; *Desmognathus*, with parasphenoid teeth and opisthocœle vertebræ. The species of *Amblystoma* are remarkable for the length of time that their larvæ (*Siredon*) retain their gills, some species (*A. tigrinum*) and the axolotl of Mexico breeding in the siredon stage. Most of the lungless salamanders (p. 27) belong in this family. MECODONTA, parasphenoid toothless, palatine teeth in two rows diverging behind. *Diemyctylus*, our common newt. In Europe *Triton*,

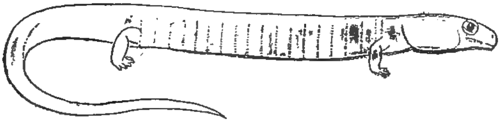

FIG. 283. *Plethodon erythronotus.*

Salamandra, Pleurodeles, etc., the first two genera dating from the European miocene. *Megalotriton,* eocene.

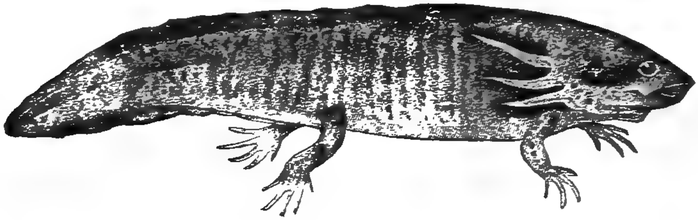

FIG. 284. Siredon lava of *Amblystoma*, from Hertwig, after Dumeril and Bibron.

SUB-CLASS III. ANURA (SALIENTIA).

Tailless in the adult condition, the caudal vertebræ being reduced and fused to a urostyle; vertebræ usually procœlous; frontoparietals fused; sphenethmoid present; hind legs elongate and fitted for leaping, the proximal row of tarsals greatly elongate; a marked metamorphosis, the tadpoles being vegetarians, the adults carnivorous. The anura contains the frogs, toads, tree-toads, etc., the group being best developed in North America and in the tropics. Its origin is uncertain, but probably was from some stegocephalian ancestor.

ORDER I. AGLOSSA.

Tongue lacking; the Eustachian tubes open together into the pharynx; epicoracoids free, but not overlapping. *Xenopus* (*Dactylethra*), from Africa; *Pipa*, the Surinam toad (p. 281), from South America.

ORDER II. ARCIFERA.

Tongue well developed; shoulder girdle arciferous (p. 278), the coracoids of the two sides overlapping; Eustachian tubes widely separate. The BUFONIDÆ includes the toads, in which the jaws are toothless, the toes webbed, but without suckers at the tips; parotid glands prominent. *Bufo*, the common toad. The genus appears in the eocene. The PELOBATIDÆ differ in having teeth. *Pelobates* first appears in the miocene. *Scaphi-*

opus includes the burrowing spade-foot toad which is rarely seen except at the breeding-season. Allied European genera are *Alytes* and *Bombinator.* The Hylidæ have teeth, while the tips of the toes are expanded into sucking-disks. Our tree-toads belong to *Hyla*, *Acris*, and *Chorophilus ; Notodelphys* and *Nototrema*, tropital America. The extinct Palæobatrachidæ (oligocene) are noticeable for two sacral vertebræ.

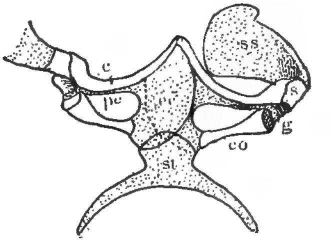

Fig. 285. Shoulder girdle of *Bombinator igneus*, showing the arciferous type, after Wiedersheim. *c*, clavicle ; *co*, coracoid ; *ec*, epicoracoid ; *g*, glenoid fossa ; *pc*, procoracoid ; *s*, scapula ; *ss*, suprascapula ; *st*, sternum.

ORDER III. FIRMISTERNIA.

Tongue well developed ; epicoracoids firmly united in the median line. The Engystomidæ, or toothless frogs, occur in our southern states. *Engystoma.* The Ranidæ, or true frogs, have smooth skin, and teeth in the upper jaw. *Rana* contains our species including the bullfrog (*R. catesbiana*) the largest known frog. *Rana* first appears in the miocene. Numerous other families in the tropics, including the Dendrobatidæ, which have toes like the tree-toads, Hylidæ.

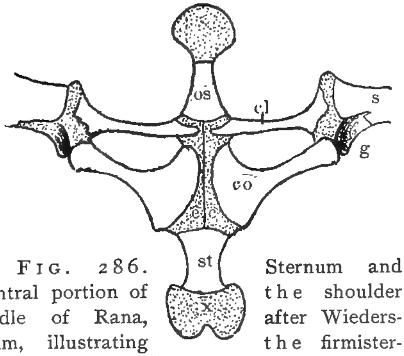

Fig. 286. Sternum and ventral portion of the shoulder girdle of Rana, after Wiedersheim, illustrating the firmisternous type of sternum. *cl*, clavicle ; *co*, coracoid ; *ec*, epicoracoid ; *g*, glenoid fossa ; *os*, omosternum ; *s*, ventral part of scapula ; *st*, sternum ; *x*, xiphisternum.

SUB-CLASS IV. GYMNOPHIONA (CÆCILIÆ).

Limbless amphibia of worm-like shape ; tail lacking ; vertebræ amphicœlous ; skull well ossified, with well-developed ethmoid ; body externally ringed, and bearing semi-circular dermal scales. Frequently a protrusible tentacle in a tentacular sheath between the orbit and nostril. The cæcilians are tropical, occuring in South America, Africa, and Ceylon, where they burrow in the earth, preying upon small invertebrates. The eyes, in consequence of this life, are hidden under the skin. Little is known of the development, except of the Ceylonese species, *Ichthyophis glutinosus*, in which the larva has three pairs of pectinate external gills. In the larval *Typhlonectes* the gills are saccular. Other genera are *Cæcilia*, *Rhinotrema*, and *Hypogeophis*. No fossil species are known, but the distribution as well as the characters of the skeleton point to a great ancestry for the group. Within recent years it has been supposed to be related to *Amphiuma*, but this is clearly not the case. The aistopoda (p. 283) suggest themselves in this connection.

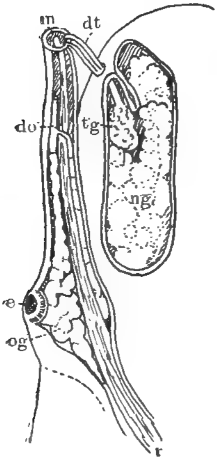

FIG. 287. Tentacle of *Cæcilia oxyura*, after Wiedersheim. *do*, duct of orbital gland; *dt*, duct of tentacular gland; *e*, eye; *m*, mouth of tentacle; *ng*, nasal gland; *og*, orbital gland; *r*, retractor of tentactle; *tg*, tentacular gland.

GRADE II. AMNIOTA (ALLANTOIDEA).

Vertebrates with well-developed amnion and allantois ; no gills, no lateral line system, and no rental portal system in the adult.

The amniotes derive their name from the existence during fœtal life of a peculiar envelope — the **amnion**. This consists of folds of the somatopleure (head, tail, and lateral folds) which grow upwards on all sides of the embryo, meeting and fusing above the back, so that the embryo is enclosed in a cavity bounded by double walls, that nearest the embryo being the amnion, the other being the **chorion**. The amnotic cavity is filled with an amniotic fluid. Both amnion and chorion are composed of ectoderm and the somatic mesothelium of the lateral plates, and the space between them is an extension of the cœlom. With growth, the amniotic structures become connected with the embryo by only a small stalk, the **umbilicus**, on the ventral side, through which, as will be seen from Fig. 288, *D*, pass the stalks of the yolk sac and of the allantois next to be mentioned.

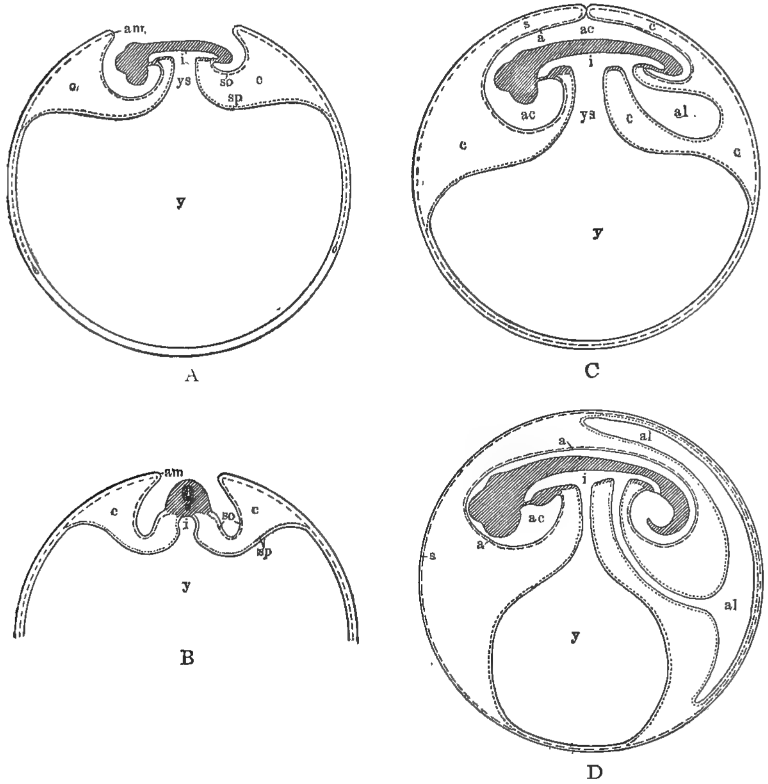

FIG. 288. Diagram of the fœtal envelopes of an amniote. *A*, before the union of the amniotic folds; *B*, transverse section of *A*; *C*, union of amniotic folds; *D*, outgrowth of allantois and reduction of yolk sac. *a*, amnion; *al*, allantois; *am*, amniotic folds; *ac*, cavity of amnion; *c*, cœlom; *i*, alimentary tract; *s*, serosa; *so*, somatopleure; *sp*, splanchnopleure; *y*, yolk sac; *ys*, yolk stalk. The somatic mesoderm by dashes, the splanchnic layer dotted; ectoderm and entoderm a continuous line.

The **allantois** is represented in the amphibia by a ventral outgrowth from the hinder portion of the alimentary canal, which never extends beyond the body walls, but develops in situ into the urinary bladder. In the amniotes, on the other hand, this outgrowth is more extensive, and extends outward behind the yolk stalk into the extra embryonic part of the cœlom (Fig. 288), carrying with it the allantoic artery and the umbilical vein or veins. Distally it expands into a large sac (which receives the excretion of the primitive kidneys), the outer surface of the sac fusing with the chorion. The result of this, in oviparous forms, is that the allantoic structures come to lie close beneath the shell, and hence, with their rich blood-supply, they form efficient organs of fœtal respiration. In the higher mammals this allantois enters into close connection with the uterine walls, thus giving rise to a structure both nutrient and indirectly respiratory in character, the **placenta,** the features of which will be described in connection with that group.

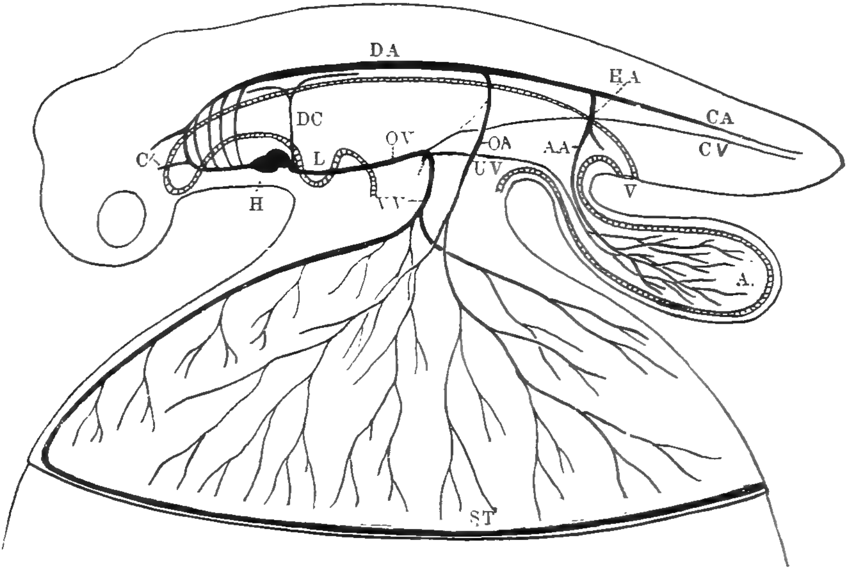

FIG. 289. Diagram of embryonic circulation in an amniote, the amnion omitted for clearness. *A*, allantois ; *AA*, allantoic artery ; *C*, carotids ; *CA*, caudal artery ; *CV*, caudal vein ; *DA*, dorsal aorta ; *DC*, ductus Curvierii : *H*, heart ; *HA*, hypogastric artery ; *L*, liver ; *OA*, *OR*, omphalomesaraic artery and vein ; *UV*, umbilical vein ; *V*, vent ; *VV*, vitelline vein. The outline of the alimentary canal blocked.

Basi- and presphenoid bones are present, and a parasphenoid occurs only in some reptiles (ophidia) as a small plate. The ribs are developed in connection with the transverse processes, and the skeleton of the limbs (when present) is reducible to the pentadactyl type. A sternum is present except in some apodal forms, and is developed in connection with the ribs; and the branchial arches are much reduced and modified.

Gill pouches occur, and some of these may break through to the exterior; but in no case are gills developed in connection with them, and they never serve in connection with respiration. The alimentary canal either terminates in a cloaca, or the vent is behind the urogenital openings. The heart always has two auricles, the sinus venosus becoming included in the right of these, while the ventricle, either partially or completely divided by a longitudinal septum, is at least physiologically divided into arterial and venous halves.

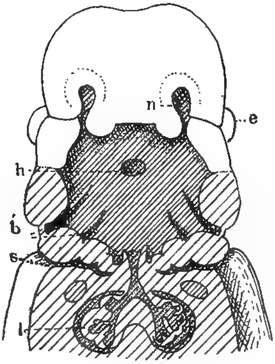

FIG. 290. Human embryo with the floor of the mouth removed, after Hertwig. *b*, branchial clefts; *s*, cervical sinus; *e*, eye; *h*, hypophysial pocket; *l*, lungs; *n*, nostril.

In the adult true kidneys (metanephros) are developed, the renal portal system is reduced or lacking in the higher forms, and the posterior cardinals become greatly reduced (p. 196).

The amniotes are divided into the Sauropsida and the Mammalia.

CLASS I. SAUROPSIDA (MONOCONDYLIA).

Amniote vertebrates with one occipital condyle; lower jaw suspended by the free or fixed quadrate; ankle joint between the first and second rows of carpals or tarsals; coracoid well developed; external surface covered, at least in part, with ectodermic scales; corpus callosum rudimentary; heart three or four chambered, red blood corpuscles small, oval, nucleated; a cloaca present; the eggs are large, and undergo a partial (meroblastic) segmentation; all except a few forms are oviparous, and the eggs are enclosed in a more or less calcareous shell.

Besides the features of the diagnosis, several other points are characteristic of the sauropsida. The skin is remarkably deficient in glands, these, when present, usually occurring upon the legs or upon the tail. The characteristic scales are cornifications of the epidermis, and are occasionally re-enforced by bony plates developed in the dermis. The single occipital condyle is situated on the basioccipital, the exoccipitals contributing to its formation to a varying extent. The mandible consists of a single cartilage bone, the articulare, and at most five membrane bones, — dentary, splenial, coronoid, angulare, and surangulare. The cervical ribs are usually well developed, the neck passing insensibly into the thorax. The ovarian ducts have their inner ends entire as in the ichthyopsida.

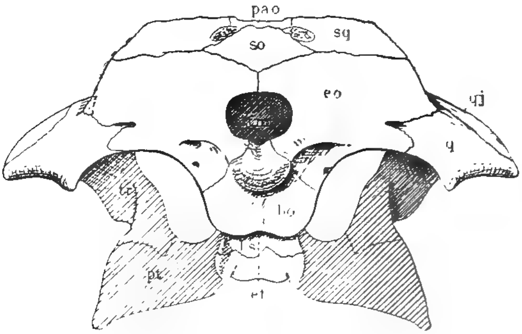

FIG. 291. Base of skull of alligator, showing the single occipital condyle. *bo*, basioccipital; *bs*, basisphenoid; *eo*, exoccipital; *et*, opening of Eustachian tube; *fm*, foramen magnum; *pao*, paroccipital; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *tr*, transversum.

The sauropsida contains the Reptilia and the Aves.

SUB-CLASS I. REPTILIA.

Cold-blooded amniotes; the external surface of the body (except in a few fossil forms) covered with horny epidermal scales or bony dermal plates; anterior appendages, when present, ambulatory (except in pterodactyls), the carpals and metacarpals numerous; sacral vertebræ usually two; pubic and ischiadic bones united by symphysis, except in some dinosaurs; persisting right and left aortic arches.

The living reptiles in their external form present three types: (1), the quadrupedal long-tailed form represented by the lizards and alligators; (2), the cuirassed forms of the turtles; and (3), the apodal forms of the snakes and footless lizards. If the fossil groups also be taken into consideration the range of shape is still greater; for it includes not only the swimming-groups, the plesiosaurs and ichthyosaurus, but the flying reptiles, the pterodactyls.

A few of the fossil forms apparently had naked skins; but in the rest the body is more or less completely covered by scales, which differ from those of the ichthyopsida, in that they are cornifications of the superficial layers of the epidermis. These are re-enforced in many by dermal ossifications, which may be minute as in certain lizards, or larger scutes, as in the crocodiles and in many extinct groups; whereas in some fossil crocodiles (*Teleosaurus*) and dinosaurs, they form a complete armor for the body. In the turtles this formation of armor reaches its extreme, for here the dermal plates are usually united with the ribs to form a firm carapace and plastron. Usually there is no pigment in the epidermis; but the derma contains pigment cells, which in certain lizards (*Anolis*, *Chameleo*) are capable of producing marked color changes under control of the nervous system. Epidermal glands are rare. In some turtles scent glands occur beneath the mandibles or on the side of the plastron; in the snakes and crocodiles similar glands are connected with the cloaca; while in most lizards there is a row of glands on the ventral surface of the femur.

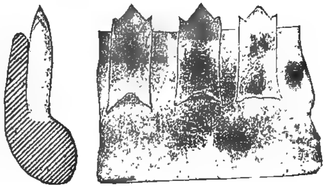

FIG. 292. Section and medial view of jaw of *Anolis*, showing pleurodont dentition.

Teeth (lacking in turtles and some pterodactyls and anomodontia) are usually restricted to the premaxillary, maxillary, and dentary bones; but in snakes and some lizards they may also occur upon the palatines and pterygoids. These teeth are usually simple, without folding of enamel, and only in the theriodontia are they differentiated into incisors, canines, and molars.

In the majority of reptiles the teeth are either anchylosed to the edge of the jaws (**acrodont**), or by their sides to the wall of a groove (**pleurodont**), while in crocodiles and many dinosaurs they are implanted in sockets or alveoli (**thecadont**); usually the teeth are in a single row. In the snakes the teeth are grooved, and in the poisonous species the grooves in one pair may be very deep or completely converted into a canal, which is to convey the poison into the wound made by these fangs. As a rule the teeth are used for the prehension of the prey, and only in the herbivorous orthopoda are they of value in the comminution of food. In the turtles, and apparently in the extinct edentulous forms, the jaws are covered with an epidermal horny beak.

Salivary glands are lacking in the marine chelonians and in the alligator, while in the crocodiles they occur only on the tongue. In other reptiles lingual, sub-lingual, palatine, and labial glands may occur, the poison glands of ophidians being modified labials. The tongue is either spatulate and immobile, as in crocodiles, turtles, and a few lizards, or bifid and extensile in other forms; its variations of shape being of value in the classification of the lacertilia.

In the alimentary canal the most noticeable features are the wide œsophagus, correlated with the swallowing of the food entire, and the large intestine, frequently provided with a cæcum near the ileo-colic valve. In the turtles the œsophagus is armed with numerous papillæ pointing backward. The liver is usually bilobed, but in the snakes and snake-like amphisbænians it is unilobular and elongate.

At no time is there a branchial respiration, the lungs being the sole organs of exchange of gases.[1] The glottis is supported by well-developed cricoids and arytenoids; the trachea is long, and in crocodiles and turtles may be bent into a loop. The tracheal and bronchial rings are better developed than in the amphibia. The lungs show variations in shape and size; and in the elongate reptiles the left lung is the smaller, and may even be reduced to a rudiment (snakes). In these forms the

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[1] Experiments go to show that the pharyngeal epithelium of certain North American and Australian turtles has a respiratory function.

posterior dorsal portion or the right lung is supplied with blood from the dorsal aorta. In the chameleons and geckoes the lungs give off large saccular projections, recalling the air sacs so characteristic of birds. In some dinosaurs the bones exhibit a marked pneumaticity, and it is supposed that in these the air sacs penetrated the bones. In the snakes the chambering of the lung is restricted to the peripheral portion, the centre being occupied by a large air space, and about the same conditions occur in most lizards. In the chameleons, however, each bronchus, on entering the lungs, divides into three parts, and the proximal portion of the lung is sacculated, while distally all three bronchi connect with a common space, without alveoli. In crocodiles and chelonians the sub-division of the lungs is carried farther.

The brain presents advances in several points upon the conditions in the amphibia. Thus there is here developed a cerebral cortex of gray matter containing pyramidal cells. The cerebrum exhibits a tendency to extend backwards, covering in the thalamencephalon. The olfactory lobes may be seated directly on the cerebrum, or an elongate olfactory tract may intervene. The olfactory fibres do not extend back to the corpus striatum, but a distinct olfactory centre is developed in the pallium. Hippocampal lobes occur in a few forms (*Hatteria*, crocodiles, chelonians). The twixt brain is at a lower level than the rest, the infundibular region being well developed. The mid brain is large, and its two halves rarely exhibit a tendency towards division into four. In the cerebellum there is a great range of structure, from forms in which it is merely a transverse fold, up to the crocodiles, where it consists of two lateral lobes and a median portion, recalling the vermis of the mammals. In the medulla occurs the characteristic nuchal flexure.

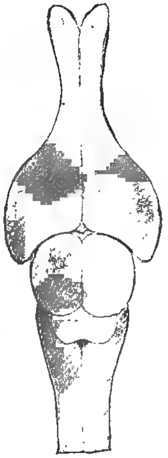

FIG. 293. Brain of garter-snake, *Eutainia sirtalis.*

In the cranial nerves the marked feature is the distinct origin of nerves, the roots of which are closely approximate in the amphibia; thus the facialis is distinct from the trigeminal; the eye-muscle nerves have distinct roots; the glossopharyngeal is distinct from the vagus; the accessorius is a distinct nerve, except in ophidia, and the hypoglossal becomes a cranial nerve, passing through a foramen in the cranial wall.

The nostrils are usually terminal, but are just in front of the orbits in ichthyosaurs and plesiosaurs. In the lizards the nasal passage is divided into an anterior vestibule and a posterior olfactory region, and in these, as in the ophidia, the amount of olfactory surface is increased by the presence of a turbinal bone. In the turtles, and still more in the crocodiles, the nasal passage is divided horizontally into an upper olfactory and a lower respiratory tract. Glands occur in connection with the nose in most reptiles, while in all except crocodiles and turtles an organ of Jacobson occurs.

The eyeball is nearly spherical; the sclerotic which surrounds it is cartilaginous, and in it are frequently developed (as in many birds) a ring of bony sclerotic plates. A tapetum is developed in the lacertilia, but the argentea, so characteristic of lower vertebrates, is lacking. In many there is an internal structure, the pecten, homologous with the process falciformis of the fishes. Eyelids are usually present, the third being frequently developed. In snakes and some lizards the lids are transparent, and their edges are united together so that a lachrymal space is enclosed between them and the conjunctiva. In many lizards and in *Hatteria* the parietal eye (Figs. 90 and 92) is extremely well developed, and is situated in a foramen in the roof of the skull. Many fossil reptiles belonging to different orders have a similar parietal foramen, thus suggesting the former presence of a visual organ in these forms.

In the inner ear the lagena is large, and in the crocodiles shows the beginnings of a spiral coiling, recalling the cochlea of the mammals. With its increase in length the macula lagenæ is correspondingly elongated. The middle ear and Eustachian tube are lacking in adult snakes and amphisbænans, the columella auris in these forms being embedded in the flesh. The stapes is continuous with the columella, and in rhynchocephalia the columella is connected with the hyoid. In many lizards and chelonians the tympanic membrane is exposed; in some lizards it is partially covered by a flap developed from in front, while in the crocodiles the flap is movable and the tympanum is somewhat sunken, the beginnings of the auditory meatus of the higher vertebrates.

In the skeleton the ossifications are far more extensive than in the amphibia. The notochord does not persist, except intervertebrally in a few forms (geckoes and rhynchocephalia). The vertebræ are usually procœlous; but amphicœlous vertebræ occur in some or all theromorpha, ichthyosauria, plesiosaurs, rhynchocephalia, geckoes, theropoda, orthopoda, and ornithopoda, while in a few dinosaurs they are flat (amphiplatyan). In many groups the neural arches are anchylosed to the centra, or again, as in ichthyosaurs, turtles, and crocodiles, they are united by suture. Hæmal arches occur in snakes, lizards, and crocodiles. Transverse processes, when present, are borne on the neural arch (*i.e.*, are diapophyses).

At most five regions can be distinguished in the column; but in the snakes, where no limbs are formed, only trunk and caudal vertebræ can be distinguished. In the plesiosaurs axis and atlas are fused; the proatlas of the crocodilia has been referred to (p. 143). Usually there are two sacral vertebræ.

Ribs are usually present, and may be either with a single head or bicipital. In the snakes they may extend the whole length of the trunk with the exception of the atlas. In the crocodilia and *Hatteria* thoracic and abdominal ribs are distinguished, the latter developing in the myocommata of the ventral surface, and not extending to the vertebræ (see p. 147). Cervical ribs are entirely lacking in the turtles, while in the same group the thoracic ribs are united to the dermal plates forming the carapace.

A sternum is lacking in plesiosaurs, ichthyosaurs, turtles, snakes, and some snake-like lizards, while there is little evidence as to its structure in the theromorphs and dinosaurs, where it was apparently largely cartilaginous. When present it is triangular or rhomboidal in outline, and contains no membrane bone. In the flying reptiles (pterodactyls) it had a strong ventral keel for attachment of the wing muscles. The episternum (lacking in chameleons) is usually well developed, and affords a support for the ventral ends of the clavicles. In many turtles it, together with the clavicles, enters into the formation of the plastron.

FIG. 294. Pectoral girdle and sternum of lizard, *Læmanctus longipes*, after Parker. *c*, coracoid; *cl*, clavicle; *e*, episternum; *g*, glenoid fossa; *p*, procoracoid; *r*, rib; *s*, scapula; *st*, sternum; *x*, xiphisternum. Cartilage dotted.

The skull of recent reptiles differs in many respects from that of existing amphibia; but when the fossil groups are considered, the distinctions largely disappear, the skulls of stegocephalans and theromorphs being strikingly similar. In these lower reptiles the top of the skull forms a continuous roof above the attachment of the jaw muscles; but in other groups gaps or vacuities may occur, so that these muscles are exposed from above. These vacuities or fossæ exhibit the following variations: (1), between the parietals and postorbitals (supratemporal fossa); (2), between postorbitals and squamoso-jugal (infratemporal fossa); (3), between the post-temporal and the exoccipital and opisthotic (post-temporal fossa); (4), the line of bones (arcade) between 1 and 2 may be interrupted, producing one large temporal fossa; (5), the squamosojugal arcade may be discontinuous.

As a rule the cartilage of the primordial cranium is largely replaced by bone, the ethmoid and parts of the sphenoid alone being incompletely ossified. Except in a few theromorphs there is but a single occipital condyle, which is either formed by the basioccipital alone or with the participation of the exoccipitals. Either basi- or supraoccipitals may be excluded from the foramen magnum. In the ear region a fenestra rotunda appears; of the otic bones the prootic is always distinct, the epiotic is fused with the supraoccipital, while the opisthotics (free in turtles) are usually united to the exoccipitals.

While in some the brain extends forwards between the orbits, it frequently does not reach so far forward, and the orbits themselves are separated by a more or less complete interorbital septum. Correlated with this is the frequent absence of ali- and orbitosphenoid ossifications, their places being taken by vertical processes of parietals (turtles) or frontoparietals (snakes); while the frontals frequently take no part in roofing in the cranial cavity, but are placed above the interorbital septum.

The membrane bones of the cranium are numerous, the frontals and parietals of the two sides being frequently fused in the median line. Between the parietals in *Hatteria* and most lizards, as well as in many fossil forms, occurs a well-marked interparietal foramen, connected, at least in the living forms, with a well-developed parietal eye. The ethmoid region is covered by the paired nasals, while in lizards they are covered by paired vomers. In other forms the vomer may be median and unpaired. Prefrontals are almost always present, while postfrontals usually occur; and in lizards, crocodiles, and many extinct forms lachrymals are present. In many fossils and in lizards a supratemporal bone occurs between squamosal and quadrate; while in lizards, snakes, crocodiles, and ichthyosaurs an os transversum connects the maxillary with the pterygoid. In dinosaurs a rostral bone may occur in front of the premaxilla.

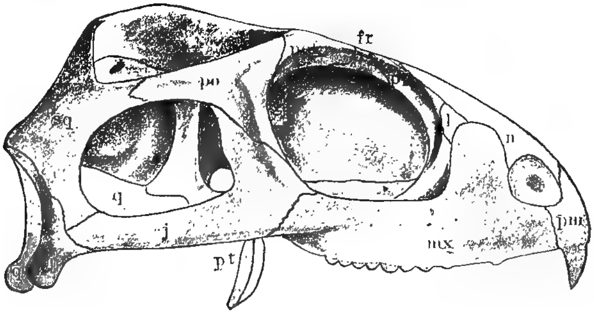

FIG. 295. Lateral view of the skull of *Hatteria* (*Sphenodon*), after Günther. *fr*, frontal; *j*, jugal; *l*, lachrymal; *mx*, maxillare; *n*, nasal; *oo*, opisthotic; *pa*, palatine; *pf*, prefrontal; *pm*, premaxillary; *po*, postorbital; *pof*, postfrontal; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal. The supra- and infratemporal fossæ shown above and below the postorbital-squamosal arch.

The lower jaw is always suspended from the quadrate; and this bone may be either freely movable or firmly united by suture to the adjacent bones, the first condition occurring only in snakes and lizards.[1] The two rami of the lower jaw are usually united by ligament or by suture, but in turtles and pterodactyls the two are fused. Frequently vacuities occur in the jaw, and usually the component bones can be distinguished. In a few dinosaurs a predentary or mento-meckelian bone occurs at the symphysis of the lower jaw (Fig. 310).

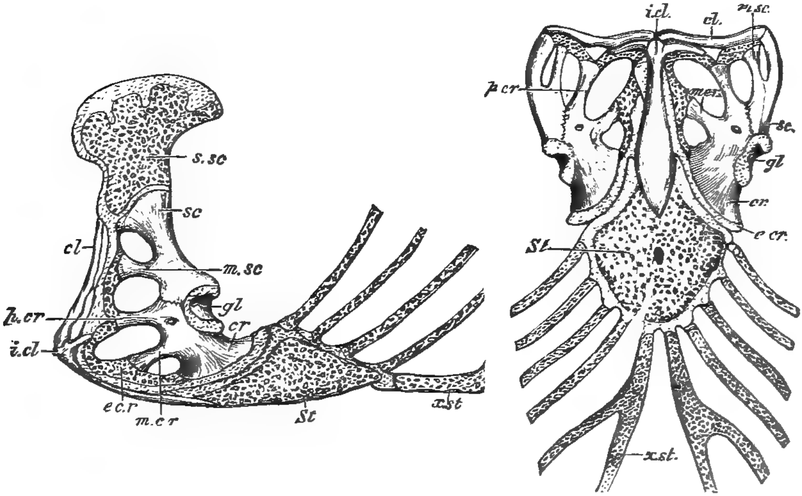

FIG. 296. Sternum and shoulder girdle of lizard, *Iguana*, from Huxley. *cl*, clavicle; *cr*, coracoid; *ecr*, epicoracoid; *gl*, glenoid fossa; *icl*, episternum; *mcr*, mesocoracoid; *msc*, mesoscapula; *sc*, scapula; *St*, sternum; *xst*, xiphisternum.

The hyoid and branchial arches are variously developed, but at no time have they gill-supporting functions. Frequently the first, or first and second, branchial arches are well developed, giving rise to long cornua attached to the well-developed copula.

The pectoral girdle is developed in all reptiles — even the limbless lizards — with the exception of the ophidia. Scapula, coracoid, and precoracoid are almost always present, the latter lacking in ichthyosaurs, plesiosaurs, and dinosaurs, while in

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[1] The fixed or free condition of the quadrate has been employed in dividing the reptilia into monimostylica and streptostylica.

others, except theromorphs, they are represented by processes upon the coracoids. The scapula, except in chelonia, is expanded dorsally, while the coracoids are flattened, and either meet in the middle line as in the ichthyosaurs and plesiosaurs, or they may connect with the sternum. A clavicle is usually present; in the turtles it may enter into the composition of the plastron (Fig. 305). An epicoracoid occurs in some lizards and turtles.

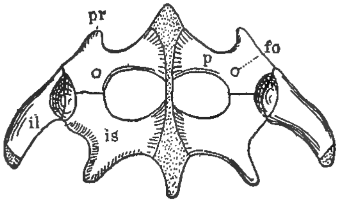

FIG. 297. Pelvis of *Hatteria*, after Wiedersheim. *fo*, obturator foramen; *il*, ilium; *is*, ischium; *p*, pubis; *pr*, prepubic process.

A pelvis is more constant in appearance than is the shoulder girdle, vestiges of it (ischia) appearing in certain snakes. It is characterized by the great development of the ilium and by marked variations in the pubic bone, which in all except crocodiles and pterodactyls participates in the formation of the acetabulum. In many dinosaurs the pubis is differentiated into pre- and postpubic portions (Fig. 298); and traces of the prepubis may be recognized in many other groups, and also in birds, as anteriorly directed processes arising from the pubis.

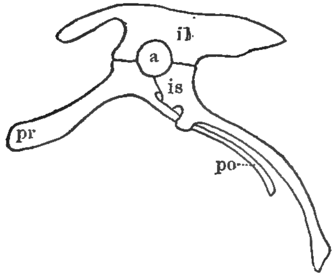

FIG. 298. Pelvis of *Iguanodon*, after Dollo. *a*, acetabulum; *il*, ilium; *is*, ischium; *po*, postpubis; *pr*, prepubis.

The fore and hind limbs are much alike in their general structure, and distinctively reptilian features are most marked in the distal portions. In the lower reptiles, as in chelonians, the carpal bones are much as in amphibia; but elsewhere there is a tendency to fusion, intermedium and centrales uniting with the radiale, while the carpales are similarly reduced in number by fusion. In the hind limbs much the same features can be seen, except that the tarsal bones can fuse to an even greater extent. In both carpus and tarsus there is a tendency for the proximal row to become closely united to the radius and ulna or tibia and fibula, while the carpales and tarsales in the same way become associated with the metacarpals or metatarsals, thus producing an intracarpal or intratarsal joint. The modifications of metacarpals, metatarsals, and phalanges are more varied; and we may have walking-feet, as in most reptiles, swimming-feet or paddles, as in ichthyosaurs, plesiosaurs, pythonomorphs, and some turtles, or, as in the pterodactyls, the anterior pair may be modified into supports for the organs of flight. In the swimming-feet there is frequently a reduction in length of the proximal bones, while the number of phalanges may be indefinitely increased.

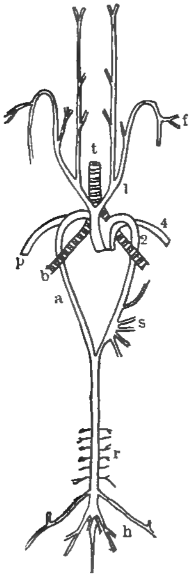

FIG. 299. Arterial trunks of turtle (*Emys*), after Wiedersheim. *a*, left aortic arch; *b*, bronchus; *f*, to fore limbs; *h*, to hind limbs; *r*, renals; *s*, to stomach.

The heart is farther removed from the head than in the ichthyopsida, and the sinus venosus becomes connected with the right auricle. Into the sinus empty the post- and the two precavæ, except in the ophidia, where the left precava opens directly into the auricle. The greatest advance is seen in the development of a partial or complete (crocodiles) septum, dividing the ventricle into right and left halves. Even when the septum is incomplete the ventricle is actually divided in contraction, the right side containing only venous blood, while the left receives that returning from the lungs. Associated with the division of the ventricle is a corresponding division of the ventral aorta of the ichthyopsida into three trunks, two connected with the right and one with the left ventricle. One of those arising from the right ventricle forms the pulmonary artery, blood passing through it, by means of the last aortic arches, to the lungs. The other right ventricular trunk connects by means of the fourth arch of the left side with the left aortic root. Thus, as will be seen, venous blood is forced from the right ventricle of the heart into the lungs and into the dorsal aorta. The aortic trunk arising from the left ventricle connects by means of the fourth aortic arch of the right side with the right radix aortæ, and also, by both of the third arches, with the carotids. This insures the supply of arterial blood to the brain, while a part of the same is carried to the dorsal aorta, which consequently contains both venous and arterial blood. In *Lacerta* and a few other forms the third arch of either side remains in connection with the radices aortæ, but in all other groups this connection is lost.

Among other peculiarities of the circulation are the persistence of a ductus Botalli (p. 187) in some chelonians and crocodilia, and the varying position of the origin of the subclavians, which may arise either from the third (carotid arch) of either side, or from the right radix aortæ. Subclavians are lacking in the ophidia. A renal portal system occurs in all except the chelonia, and in chelonia there are two hypogastric veins; in lacertilia and ophidia but one. In the latter group the hypogastric breaks up into a plexus connected with the 'fat body;' passing thence to the portal vein.

The permanent kidneys of the adult reptile are the metanephridia; they are usually small, compact, or lobulated, but in snakes the lobulation may be carried so far that the lobes are connected only by the ureter. In lizards the metanephridia of the two sides are sometimes united behind. The mesonephros and the Wolffian duct are more or less degenerate, never functioning in the adult. Their remains are more evident in the female than in the male, the mesonephros forming the so-called 'golden yellow body.' A urinary (allantoic) bladder is connected with the cloaca in turtles and lizards, but in other reptiles it is lacking.

The gonads vary in shape with the shape of the body, being broad in the chelonia, long in others. In many forms, and this is especially true of the ophidia, the right gonad is larger and in advance of the left. The ovaries are penetrated with a vascular network of connective tissue. The oviducts are long, folded or contorted, and have smooth margined ostia. The ducts themselves are muscular and glandular, the glandular portion secreting the shell.

Accessory reproductive organs of two types occur. In lizards and snakes there are a pair of eversible sacs (hemipenes) opening into the cloaca, and when in repose retracted under the skin of the tail. In chelonians and crocodiles there is but a single penis, formed by a thickened portion of the ventral wall of the cloaca, which is composed of erectile tissue, and can be protruded from the vent. Both types are grooved for transmission of the seminal fluid. The hemipenes of embryo snakes have often been described as rudimentary hind limbs. *Hatteria* lacks a penis.

The eggs of reptiles are large and undergo a partial (meroblastic) segmentation ; the subsequent phases of development being much like that of birds. Most reptiles are oviparous, the eggs being deposited in sand or soil, and left to hatch by the heat of the sun. Some lizards and many snakes, however, are viviparous.

The following classification of the Reptilia follows most closely that of Lyddeker. The late Professor Cope recognized several more orders, which seem to be but sub-divisions of the theromorpha.

ORDER I. THEROMORPHA.

Extinct reptiles, with amphicœlous vertebræ, the notochord frequently persisting intervertebrally ; with a sacrum composed of from two to six vertebræ ; ribs bicipital, their articulation with the vertebræ as in mammals ; quadrate immovable ; teeth in alveoli, and showing much differentiation (occasionally teeth are lacking) ; no sternum ; girdles solid, the pubic and ischiatic bones fused into a continuous os innominatum ; humerus with a foramen (entepicondylar) above the inner condyle.

The theriomorphs were mostly terrestrial vertebrates, and are especially interesting, since they show features which make many regard them as having been the ancestors of the mammalia. The order appears in the Permian, and dies out in the triassic.

SUB–ORDER 1. PAREIASAURIA (COTYLOSAURIA).

Teeth homodont, numerous, without diastema ; no temporal fossa ; one occipital condyle ; vertebræ with remains of notochord ; two sacral vertebræ. *Pareiasaurus*, South African Permian ; *Empedias*, Permian of

Texas; *Elginia*, triassic of Scotland. *Isodectes*, from the coal of Ohio, is the oldest known reptile. This sub-order is regarded by Cope as ancestral to all other reptiles.

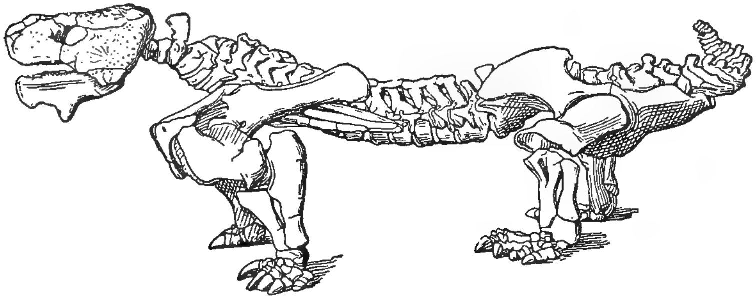

FIG. 300. *Pareiasaurus baini*, after Seeley.

SUB–ORDER 2. ANOMODONTIA.

Large lizard-like, five-toed reptiles; toothless, or with a single pair of canine-like teeth; no intercentra; five or six sacral vertebræ; a single occipital condyle; supratemporal fossa present. *Dicynodon* and *Oudenodon*, South African Permo-trias.

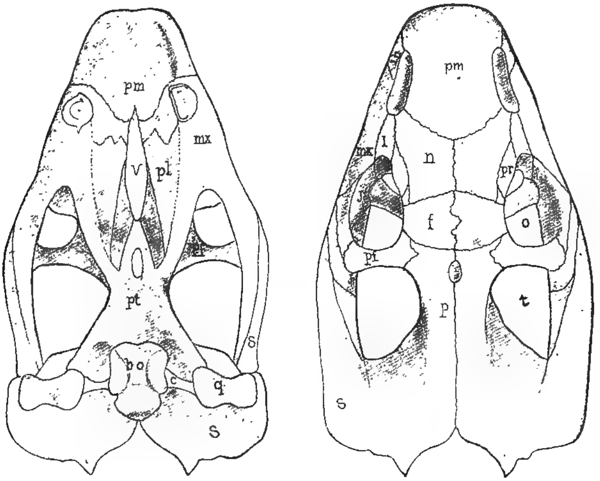

FIG. 301. Skull of *Dicynodon*, after Seeley. *bo*, basioccipital; *c*, columella; *f*, frontal; *in*, infranasal; *j*, jugal; *l*, lachrymal; *mx*, maxilla; *n*, nasal; *o*, orbit; *p*, parietal; *pf*, postfrontal; *pl*, palatine; *pm*, premaxilla; *pr*, prefrontal; *pt*, pterygoid; *q*, quadrate; *s*, squamosal; *t*, temporal fossa; *v*, vomer.

SUB-ORDER 3. PLACODONTIA.

Palatine teeth large, pavement-like; premaxilla with incisors, maxilla with rounded molars; lower jaw with incisors and pavement teeth; one occipital condyle. The rest of the skeleton is unknown. *Placodus*, European trias.

SUB-ORDER 4. THERIODONTIA (PELYCOSAURIA).

Teeth differentiated into incisors, canines, and molars; intercentra frequently present; supra- and infratemporal fossæ developed; two or three sacral vertebræ; carnivorous. *Clepsydrops*, Permian of Texas and Illinois; *Dimetrodon* and *Naosaurus* from the Permian of Texas, both with enormous spinous processes; in the latter these bear several transverse bars; *Galesaurus*, trias of Africa.

ORDER II. PLESIOSAURIA (SAUROPTERYGII).

Extinct aquatic reptiles, apparently with naked skin; the tail short, the neck long; a single occipital condyle; temporal fossa present; teeth in alveoli, quadrate immovable; anterior nares separate, near orbit; a parasphenoid sometimes present; no sclerotic ring in orbit; vertebræ amphicœlous or flat; ribs with a single head; abdominal ribs present; sternum and precoracoid absent, the coracoids meeting in the middle line; feet pentadactyl and usually modified into swimming-organs. The plesiosaurs were large carnivorous reptiles, sometimes reaching a length of forty feet. In *Nothosaurus* and *Lariosaurus* the feet were fitted for creeping, and the animal was lizard-like; triassic of Europe. In *Plesiosaurus* the limbs were flipper-like, the phalanges being greatly increased in number, while the neck was extremely long. Allied genera are *Cimolio-*

FIG. 302. Restoration of *Plesiosaurus*, after Dames.

saurus and *Pliosaurus* from the Jurassic and cretaceous of Europe, America, and New Zealand.

ORDER III. CHELONIA (TESTUDINATA).

Recent and fossil reptilia in which the trunk is enclosed in a bony framework, composed of a dorsal carapace and a ventral plastron, these parts of dermal and partly of endoskeletal origin; the quadrate is fixed; teeth are lacking, the jaws being covered with a horny sheath. The anterior bony nares are united, and open at the tip of the snout. A temporal fossa is frequently present. The scapular and pelvic arches are internal to the ribs. The feet have five digits and, while usually fitted for walking and provided with claws, are occasionally modified into flippers.

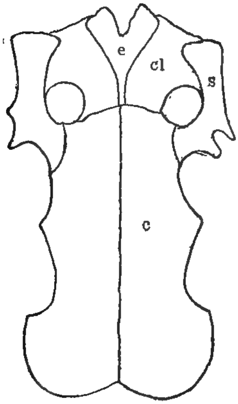

FIG. 303. Pectoral girdle of *Plesiosaurus*, after Zittel. *c*, coracoid; *cl*, clavicle; *e*, episternum; *s*, scapula.

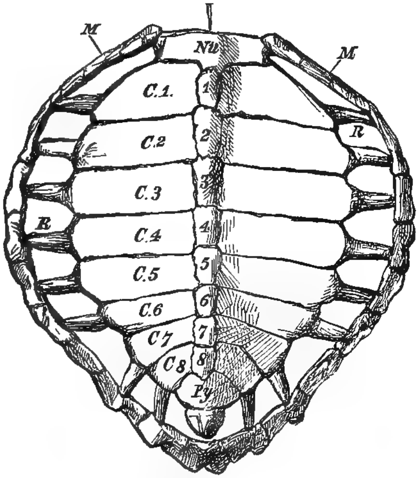

FIG. 304. Dorsal view of carapace of green turtle, *Chelone midas*, showing the ribs, *R*, extending beyond the costal plates, *C*. *M*, marginal plates; *Nu*, nuchal; *Py*, pygal plates. From Huxley.

The turtles and tortoises are strongly marked off from all other reptiles, the armor surrounding the body being especially characteristic. In most cases head, legs, and tail can be retracted into this, and in the box tortoises the plastron is hinged so that it can still further protect these parts. In the atheca the body is covered by a thick leathery skin; but in the others it bears bony epidermal scales or plates, the arrangement of which is of systematic importance. These plates in one species (*Erctmochelys imbricata*) furnish the well-known 'tortoise shell.' There is a median and a pair of lateral rows of plates on the dorsal surface, while around the edge is a series of marginal plates. Beneath these scales comes the dermal skeleton of bony plates ,which, however, do not correspond in position to the epidermal coating. In the atheca this dermal skeleton is free from the ribs and vertebræ, and consists of longitudinal rows of polygonal dermal ossicles. In all others the dorsal portion of the armor, the carapace, consists of a median row of (usually eight) neural plates, each being the expanded end of a neural spine of a vertebra. In front of the first neural is a nuchal plate, while behind the last are two or three pygal plates, these being unconnected with the vertebræ. On either side and corresponding to the neurals are the costal plates, each fused to a rib; around the margin of the carapax is a series of marginal plates, the nuchal and posterior pygal forming parts of the series. The ventral portion of the armor, the **plastron**, usually consists of nine plates, — in front a median episternum (entoplastron) flanked on either side by a clavicle (epiplastron), while behind, on either side, follow hyoplastron, hypoplastron, and xiphiplastron. Occasionally the episterum is lacking. All of these plates, except neurals and costals, are membrane bones.

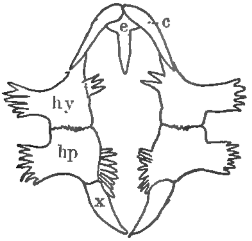

FIG. 305. Plastron of *Chelone midas*, after Zittel. *c*, clavicle; *e*, episternum; *hp*, hypoplastron; *hy*, hyoplastron; *x*, xiphoplastron.

Besides the characters quoted in the diagnosis, the absence of ali-, pre-, or orbitosphenoid ossifications; the distinct pro- and opisthotic bones; and the absence of an os transversum, — are distinctive. The epiotic is fused to the supraoccipital; a temporal fossa is usually present, but as in chelydosauria, it may be absent, or again, as in *Chelone*, it may be arched over by an expansion of the parietal reaching to the squamosal.

The vertebræ are mostly procœlous, but some of them may have plain faces. There are two sacral vertebræ.

The position of the girdles inside the ribs is secondary, and is produced during growth by the forward and backward extension of the carapace. The ribs have but a single head, and extend into the caudal region (Fig. 155). The procoracoid is fused to the scapula, the carpus is primitive, but the tarsus is modified by fusion of its ossicles. Five digits always occur, but the number of phalanges is not constant.

The brain has large hemispheres which cover the twixt and partly the mid brain; the cerebellum is a slightly arcuate transverse fold. The facialis and acusticus nerves are united at their origin. Both Harderian and lachrymal glands occur, the latter being at the posterior angle of the orbit. The tympanum is well developed, the membrane is visible externally, and the Eustachian tube is large.

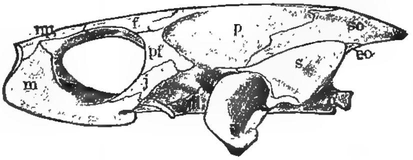

FIG. 306. Skull of turtle, *Chrysemys picta*. *b*, basioccipital; *f*, frontal; *eo*, exoccipital; *j*, jugal; *m*, maxillary; *np*, naso-prefrontal; *p*, parietal; *pf*, postfrontal; *pt*, pterygoid; *q*, quadrate; *s*, squamosal; *so*, supraoccipital.

The ventricular septum is poorly developed; the third aortic arches are not connected with the radices aortæ, and the left radix gives off the cœliac artery before joining with its fellow. A renal portal system is lacking, the caudal vein connecting with the epigastrics. The sexual and urinary ducts empty into the neck of the urinary bladder. The penis is an unpaired structure arising from the dorsal wall of the cloaca, and in it are two canalicular extensions of the cœlom, which open on two papillæ to the exterior.

The eggs are covered with a leathery calcareous shell, and are buried in the sand, being hatched by the heat of the sun.

Some of the chelonia are herbivorous, some feed on insects, molluscs, etc., and some are strictly carnivorous. All are rather slow in their motions; and the group is best represented in the tropics, the colder temperate regions having but few species. In cold climates the species undergo a hibernation, and in the tropics the terrestrial species sleep through the dry season. The group appears in the Permian of North America, and has continued until the present.

SUB-ORDER I. CHELYDOSAURIA.

No temporal fossa; carapace of transverse osseous arches in close contact, extending across the back from side to side. Vertebræ amphicœlous; limbs ambulatory. This sub-order, represented by *Otocœlus* from the Permian of North America, is regarded by Cope as ancestral to the other chelonia and the pseudosuchian crocodilia.

SUB-ORDER 2. ATHECÆ.

Turtles without scales but with a leathery skin, carapace of polygonal dermal bony plates arranged in rows, unconnected with ribs and vertebræ; plastron poorly developed, with large central fontanelle; episternum lacking. Skull without descending process of parietals. Feet flipper-like, claws lacking. *Dermochelys* (*Sphargis*) *coriacea*, the leather-back tortoise, occurs in all warmer seas, extending north to Cape Cod. It weighs occasionally 1,500 lbs. The sub-order appears (*Psephoderma*) in the trias. *Protostega*, cretaceous of Kansas.

SUB-ORDER 3. TRIONYCHIA.

Turtles with the carapace poorly ossified, ribs and vertebræ being connected with it. Scales lacking, the body covered with a leathery skin; marginal bones few or absent. Plastron with episternum and a large median fontanelle; sacral and caudal ribs articulating with neural arches. A descending process of the parietals present. Feet webbed, three claws on each foot. The sub-order appears in the upper cretaceous of New Jersey, and is represented by over thirty species to-day, all inhabitants of fresh water, and best developed in the Oriental regions. All are carnivorous. Four species of leather turtle (*Amyda*) and soft-shell turtles (*Aspidonectes*) in the U. S.

SUB-ORDER 4. CRYPTODIRA.

Turtles with well-ossified carapace, connected with internal skeleton; epidermal scales and marginal ossicles present; an episternum; pelvis free from plastron; caudal ribs articulated to vertebral centra. A descending process to the parietals. The species are numerous, the more important families being the following: CHELONIDÆ, with heart-shaped carapace, and paddle-like feet, bearing at most two claws. The costal plates do not reach the marginals. *Thalassochelys caretta*, the loggerhead turtle, weighs 450 lbs. *Eretmochelys imbricata*, the tortoise-shell turtle, is smaller. The green turtle, *Chelone mydas*, may weigh 850 lbs. It is highly esteemed as food. All of these occur in the warmer Atlantic, the tortoise-shell ranging to the Indian Ocean, and all occasionally occur on our shores. TESTUDINIDÆ, carapace strongly arched; plastron very broad; five toes in front, four behind. Terrestrial, represented in southern U. S. by the gopher turtle, *Xerobates polyphemus*. Here also belong the giant tortoises (*Testudo elephantopus*, etc.) of the Galapagos Islands and Mozambique, and the colossal fossil, *Colossochelys atlas*, of the upper miocene of India, which was 18–20 feet long, the carapace being 8 feet high. KINOSTERNIDÆ with free toes, short tail; 9 or 11 plates on plastron, with our mud-turtle (*Kinosternon pennsylvanicum*) and our musk-turtles (*Aromochelys*). EMYDÆ with 12 plates on plastron, including about 80 species, among them the wood and spotted tortoises (*Chelopus*), the painted turtle (*Chrysemys*), the box-turtles (*Cistudo*) with hinge in plastron, and the various terrapins, including the famous 'diamond back' (*Malaclemmys palustris*). CHELYDRIDÆ with long tail, and 9 plates on the plastron. Embraces three species, two, the snapping-turtle (*Chelydra serpentina*) and the alligator snapper (*Macrochelys lacertina*) being the fiercest of reptiles inhabiting the U. S. The Cryptodira are found in all ages from the Jurassic down.

FIG. 307. Snapping-turtle, *Chelydra serpentina*, from Huxley.

SUB-ORDER 5. PLEURODIRA.

Turtles with epidermal scales; carapace united to skeleton; marginals present; caudal ribs articulated to centrum; descending process of parietals present; neck bending horizontally; pelvis anchylosed to carapace and plastron; plastron always with 13 epidermal plates.[1] Contains over 50 species confined to the southern hemisphere, mostly South American, among them *Podocnemis*, *Chelys*, *Pelomedusa*. *Sternothærus* is African. While the living forms are very distinct, the fossils show intergradations between the Cryptodira and Pleurodira. *Proganochelys*, triassic of Germany; *Bothremys*, upper cretaceous of New Jersey.

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[1] Except in Carettochelydæ, in which epidermal plates are lacking.

ORDER IV. ICHTHYOSAURIA (ICHTHYOPTERYGIA).

Extinct aquatic reptiles with naked skin, large head, short neck, long bilobed tail and flipper-like appendages. Amphicœlous vertebræ; no sacrum; vertebral column extending into lower lobe of tail; no sternum; ribs bicipital, abdominal ribs present; quadrate immovable; jaws long and pointed, the upper jaw composed chiefly of premaxillæ; teeth usually numerous (absent in *Baptanodon*) and seated in a common groove.

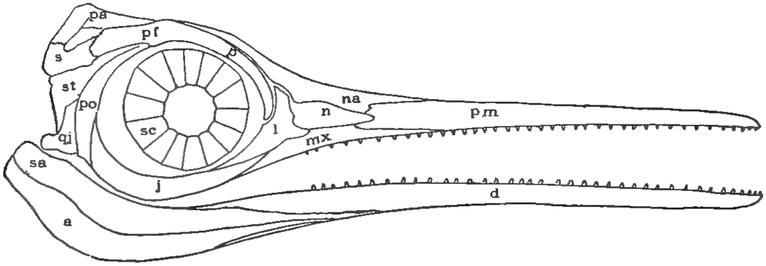

FIG. 308. Skull of *Ichthyosaurus*, after Zittel. *a*, angulare; *d*, dentary; *j*, jugal; *l*, lachrymal; *mx*, maxillary; *n*, nostril; *na*, nasal; *pa*, parietal; *pf*, postfrontal; *pm*, premaxillary; *po*, postorbital; *p*, prefrontal; *qj*, quadratojugal; *s*, squamosal; *sa*, supraangulare; *st*, stapes.

The neural arches of the vertebræ are united by suture to the centra; the caudal vertebræ have chevron bones; supratemporal fossa and parietal foramen are present. The orbits are very large, and contain a ring of sclerotic bones; the external nostrils are just in front of the orbits. The prefrontals are as large as, or larger than, the frontals; the pterygoids extend forward between the palatines to the vomers, and a large parasphenoid is present.

The coracoids meet in the middle line; procoracoids are lacking. The pelvis is entirely free from the vertebral column, and its elements are reduced. The limbs are very short and paddle-shaped, the radius, ulna, tibia, and fibula being reduced to polygonal bones, distinguishable only by position from the metapodial elements. The digits are usually five, but this number is sometimes apparently increased either by fission or by formation of marginal rows; the phalanges are very numerous.

Ichthyosaurian coprolites (Fig. 41) show that these animals possessed a spiral valve, while the finding of embryos within the fossil skeleton shows that at least some species were viviparous.

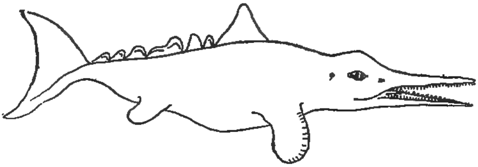

FIG. 309. Restoration of *Ichthyosaurus*, after Fraas.

Ichthyosaurians were widely distributed, fossils having been found in all parts of the globe except South America. In time they ranged from the upper triassic to the upper cretaceous. Some reached a length of 30 or 40 feet. Over 50 species have been described. *Ichthyosaurus*, *Mixosaurus*, and *Baptanodon* (Jurassic of Wyoming) are the best known.

ORDER V. RHYNCHOCEPHALIA.

Lizard-like, scaly reptiles with long tail; amphicœlous vertebræ with frequent intercentra; ribs one-headed, with uncinate processes; abdominal ribs; sternum and episternum present; two sacral vertebræ; quadrate immovable; supra- and infratemporal fossæ present; no procoracoid; limbs pentadactyl, vent transverse; heart, lungs, and brain as in lacertilia.

This order is represented to-day by but a single living species, *Sphenodon* (*Hatteria*) *punctata*, from the New Zealand region. While in general appearance it is lizard-like, it differs much from them in structure, and finds its nearest relatives in fossil forms which range from the trias to the present time. From the fact that all the remaining groups of reptiles have probably sprung from a rhynchocephalian ancestry, the order becomes very important, despite its small size.

The vertebræ are usually amphicœlous, and remains of the notochord occasionally persist intervertebrally. Sometimes they are flat, and in *Proterosaurus* the cervicals are opisthocœlous. Intercentra occur in the caudal and cervical regions, and occasionally in the region of the trunk. A proatlas (p. 143) occurs. The premaxillæ are never anchylosed; the jaws bear acrodont teeth or are toothless, and occasionally teeth occur on the ossified palatines (Fig. 171). The feet are either fitted for walking or for swimming.

SUB-ORDER 1. SPHENODONTINA.

Small terrestrial forms with amphicœlous vertebræ. Here belongs the living *Sphenodon*. The fossil forms, *Homœosaurus*, *Hyperodapedon*, *Proterosaurus*, *Palæohatteria*, *Telerpeton*, etc., have been found only in Europe.

SUB-ORDER 2. CHORISTODERA.

Aquatic reptiles with flattened vertebræ; teeth on the palatines and pterygoids. Large forms from the upper cretaceous of North America (*Champosaurus*) and lower eocene of Europe (*Simœdosaurus*).

ORDER VI. DINOSAURIA.

Extinct, mostly terrestrial reptiles, frequently of enormous size, with long tail, ambulatory feet, and a skin either naked or covered with large dermal spines, plates, and ossicles. Vertebræ solid or hollow; flat, amphicœlous, or opisthocœlous, the latter predominating; sacrum of 3 to 6 vertebræ; ribs bicipital; abdominal ribs occasionally present; quadrate fixed; supra- and infratemporal fossæ present. Teeth in alveoli or alveolar grooves; no episternum or procoracoid; sternum partially ossified; ilium elongate in front of and behind the acetabulum, the acetabulum itself open; pubis with frequently a well-developed postpubic branch; toes with claws or hoofs.

As the name implies, the dinosauria were enormous reptiles, remains of which have been found in all continents except Australia, but which were especially developed in western America. In many respects they resemble the lizards; in others some were decidedly bird-like. In size they varied between forms a yard in length up to giants over a hundred feet long. Some were herbivorous, some carnivorous, and they were largely inhabitants of swampy places: some, like *Amphicœlias* and the Megalosaurs, having bones so hollow and light that it seems as if they could only support the weight of the body when it was immersed in water.

An exoskeleton occurred only in some orthopoda, and possibly in some theropoda. It consisted of separate ossicles or bony plates, some of these upon the back of the stegosaurs measuring a yard across. These forms also had large bony spines on the tail as weapons of offence and defence.

While as a rule the vertebræ were amphicœlous, occasionally those of the neck were opisthocœle, the rest being flat. Rarely procœlous vertebræ occurred in the tail. As a rule, there were 10 cervical, 18 trunk, 3 to 6 sacral, and 30 to 50 caudal vertebræ. A double proatlas occurred in the neck, and occasionally the number of sacrals exceeded 6, there being 10 in *Polyonax*. The caudals frequently bore chevron bones, forked at their free ends. The ribs are without uncinate processes, and abdominal ribs occur only in theropoda. Usually, as in the crocodiles, there is a preorbital fossa between the eyes and the nostrils; teeth occur only on the jaws. Clavicles and an episternum are known only in *Iguanodon*. The scapula is large, the coracoid small and discoid. The anterior limbs are frequently much shorter than the posterior, and these forms must have had bipedal or kangaroo-like habits. The feet are digitigrade or plantigrade; the metapodial bones are variously modified, and the feet are pentadactyl, although in many but three toes were functional.

The brain cavity shows, according to Cope, that the brain was exceedingly small, while the neural canal in the sacral region was much larger than the brain cavity (ten times as large in some stegosaurs), implying a great lumbar enlargement of the cord. At least some of the order (*Compsognathus*) were viviparous. The group is confined to mesozoic rocks, and attained its greatest development in the upper cretaceous.

SUB-ORDER I. SAUROPODA.

Large Dinosaurs with the fore feet little shorter than the hind; anterior vertebræ opisthocœlous, the others amphicœlous or flat, the centra with large lateral cavities. A large preorbital fossa, nares elongate; premaxilla toothed, teeth in alveoli, spatulate, the sharp margins smooth. No post pubis; bones of the extremities massive, femur without inner trochanter, all feet plantigrade, pentadactyl, digits clawed. This sub-order contained the largest land animals known, most or all of them probably being herbivorous. *Amphicœlias* (*Brontosaurus*), *Camarasaurus* (*Atlantosaurus*), and

Diplodocus, from the upper Jurassic of Wyoming and Colorado, are the best-known forms, one species of *Camarasaurus* measuring 115 feet in length. Only fragments are known of the European species.

SUB–ORDER 2. THEROPODA.

Moderate-sized digitigrade carnivorous dinosaurs with short fore limbs and long tail; vertebræ massive or hollow, the anterior ones opistho- or amphicœle; a large preorbital fossa, nares large, lateral; premaxilla toothed, teeth pointed, dagger shaped, with serrate margins, seated in alveoli; no postpubis; bones of extremities hollow; femur with inner trochanter, digits 5 or 3, with claws. The species range in size from that of a cat (*Compsognathus*) to that of an elephant (*Megalosaurus*). In Europe the sub-order was restricted to the triassic and Jurassic; in America from the triassic to the upper cretaceous. *Allosaurus*, *Megalosaurus* (*Lœlaps*), and *Ceratosaurus* are the best-known American genera. Probably some, at least, of the famous footprints of the triassic of the Connecticut Valley and New Jersey were made by forms belonging to this sub-order.

SUB–ORDER 3. ORTHOPODA.

Large herbivorous dinosaurs with solid vertebræ; preorbital fossa small or absent; nares large, anterior; premaxilla toothless, or with teeth behind, lower jaw with an anterior toothless predental bone; teeth flattened, the edges serrate. Fore legs usually very short, the hind feet with three (rarely four) functional toes. The sub-order is divided into three sections:

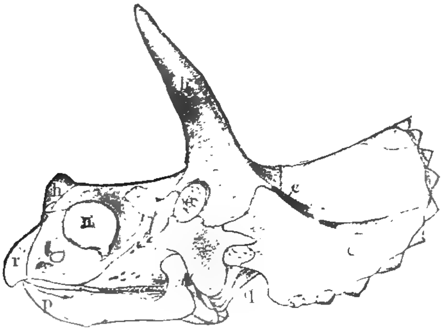

FIG. 310. Skull of *Agathaumas*, after Marsh. *e*, eye; *h*, horn; *p*, predentary; *r*, rostrum.

A. STEGOSAURIA. Plantigrade orthopods with a well-developed exoskeleton; the bones massive, the vertebræ flat or amphicœlian. Prepubes not united in front, postpubes slender and parallel to ischium. Terminal phalanges hoof-like. Best known are *Scelidosaurus*. from the lower lias of England, and *Hypsirhophus* (*Stegosaurus*), from the Jurassic of the western U. S.

B. CERATOPSIA. Plantigrade orthopods with well-developed dermal skeleton. sometimes forming a complete cuirass. Bones massive; vertebræ flat: skull with pointed processes on the frontals and with the parietals broadly expanded posteriorly. A 'rostral bone' in front of the premaxilla. No postpubis; prepubes distally expanded and united by symphysis. Femur without third trochanter. The ceratopsia are best developed in the upper cretaceous of the western U. S., but have also been found in Austria. They were wonderfully protected by their armor and the frontal horns against enemies. *Agathaumas* (*Ceratops*) and *Polyonax* (*Triceratops*), from the Laramie beds, are best known. *C.* ORNITHOPODA. Digitigrade orthopods without exoskeleton. Vertebræ of neck opisthocœle; fore legs very short; prepubes free, postpubes slender and parallel to ischium; bones of extremities hollow; digits with pointed claws. *Iguanodon* from the upper cretaceous of Europe, and *Hadrosaurus* (*Diclonius*) from the green sand of England and America, are best known. *Laosaurus*, upper Jurassic of Wyoming. One species of *Iguanodon* was 33 feet long.

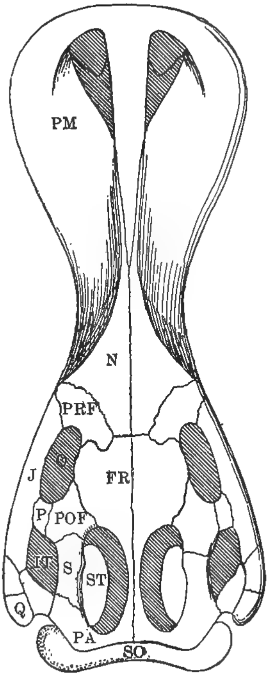

FIG. 311. Skull of *Hadrosaurus*, after Cope (see Fig. 176).

ORDER VII. SQUAMATA (LEPIDOSAURIA, PLAGIOTREMATA).

Scaled reptiles with usually procœlous vertebræ; ribs with a single head, no abdominal ribs; sacrum, when present, consisting of two vertebræ; quadrate free; supratemporal fossa present or postfrontal arch incomplete; jugal arch always incomplete; teeth acrodont or pleurodont; cerebellum very small, optic lobes approximate; ventricles of heart incompletely separated; vent a transverse slit; two hemipenes.

Lizards and snakes are frequently regarded as constituting two distinct orders; but in spite of the absence of feet and some other characters, the two groups (together with the extinct pythonomorphs) have so many points in common that the order here recognized is justified. The body is covered with horny epidermal scales, and frequently these are re-enforced by dermal ossifications. In only rare instances are the vertebræ amphicœlous. The nasal apertures in the skull are separate; the lungs are simple sacs; limbs, when present, are ambulatory or natatory.

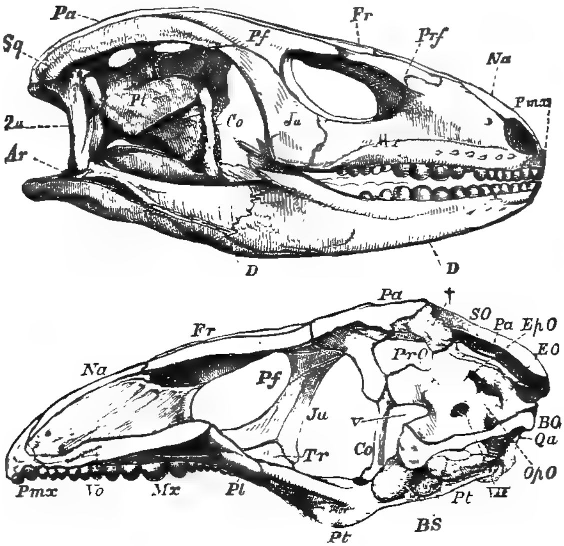

FIG. 312. Side and sectional veins of skull of *Cyclodus*, from Huxley. *Ar*, articulare; *BS*, basisphenoid; *BO*, basioccipital; *Co*, columella; *D*, dentary; *EO*, exoccipital; *Fr*, frontal; *EpO*, epiotic; *Ju*, jugal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pf*, postfrontal; *Pmx*, premaxillary; *Pl*, palatine; *Pt*, pterygoid; *PrO*, prootic; *OpO*, opisthotic; *Prf*, prefrontal; *Qu*, quadrate; *SO*, supraoccipital; *Sq*, squamosal; *Tr*, transversum; *Vo*, vomer; *V*, *VII*, passages for fifth and seventh nerves.

SUB-ORDER I. LACERTILIA (SAURII).

Scaled or plated reptiles usually with two pairs of feet; vertebræ rarely amphicœlous; premaxilla single or paired. Postorbital arcade sometimes entire, jugal arch never complete. Ali- and orbitosphenoids not ossified; shoulder girdle always present. Sternum and episternum usually present. Feet sometimes rudimentary or absent; when present, usually five-toed and ambulatory; the maxilla, palatines, and pterygoids cannot move on the bones of the skull, and the mouth can be opened to but a moderate extent. Movable eyelids, tympanic cavity and membrane usually occur. The arteries supplying the alimentary canal are extremely variable.

The lizards in their outward appearance resemble closely the crocodiles and *Sphenodon*, but in structure they have many and important points of difference. The apodal forms are strikingly snake-like: but these may be distinguished in most cases at a glance by the presence of eyelids and small scales instead of broad abdominal scutes on the ventral surface of the body. The lizards are largely insectivorous, and only one has the reputation of being poison. Most of them lay eggs enclosed in a leathery shell. Most of the 1,200 living species are confined to the warmer regions of the earth. The sub-order appears in cretaceous, but the fossil forms are few. A natural classification of the sub-order is still a desideratum. That adopted here, based primarily upon the tongue, associates together widely diverse forms.

SECTION I. VERMILINGUIA. Old-world lizards with vermiform, highly extensile tongue; tongue papillose, its enlarged tip sheathed; body covered with small chagreen scales; tail coiling vertically, and used as organ of prehension. No anal or femoral pores. Orbits closed behind by process of jugal; teeth acrodont; no teeth on palatines. Feet with the toes in two groups. Only genus, *Chamæleon*, with about 30 species. The chameleons are noted for their color-changes, a feature which is shared to a marked extent by the American genus *Anolis* (*infra*). There are two pigment layers in the skin, an upper bright yellow and a deeper dark brown or black layer. The pigment cells in these layers are under control of the sympathetic system, and according as one or the other becomes prominent the color of the animal changes.

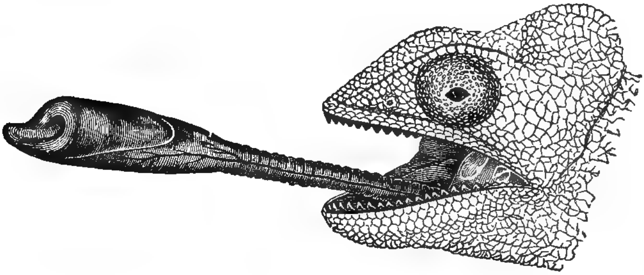

FIG. 313. Head of Chamelon with the tongue extended.

SECTION II. CRASSILINGUIA. Lizards with thick, short, fleshy tongue, usually rounded at the tip (never strongly emarginate), not protrusible, papillose or smooth; tympanic membrane usually free. ASCALABOTÆ or geckoes have the feet with adhesive disks on the underside, and usually granular or spinose scales. Teeth pleurodont; no teeth on palatines or pterygoids; a circular fold in place of eyelids. Vertebræ amphicœlous. The geckoes receive their common name from their cry. They occur in all the warmer regions of the world except the northeastern part of the U. S. Possibly the group should be more strongly marked off from other forms. *Phyllodactylus* occurs in California. Other genera are *Platydactylus*, *Ptychozoon*, and *Ascalabotes*; 200 species known. All are insectivorous and have great powers of climbing. IGUANIDÆ, lizards of considerable size, without adhesive feet; body compressed; limbs long and slender; often a comb of spines on the back; pleurodont teeth;

teeth usually on pterygoids. Usually a large brightly colored sac beneath the throat connected with the hyoid. Over 300 species known, all but a few from the new world. *Anolis* includes the 'chameleon' (*A carolinensis*) of our southern states. *Sceleporus* contains the common lizard or swift (*S. undulatus*) of the eastern states north to Connecticut and Michigan. The various species of 'horned toad' belong to *Phrynosoma.* The AGAMIDÆ replace the Iguanidæ in the eastern hemisphere. One hundred and fifty species are known. These all have acrodont teeth. *Chlamydosaurus* includes the frilled lizard, *C. kingii*, of Australia, with a broad dermal fold or collar about the neck; *Draco volans* of Java has the ribs greatly elongate, supporting a fold of skin which acts as a parachute.

FIG. 314. Green lizard, *Anolis*, from Lütken.

SECTION III. BREVILINGUIA. Tongue short, thick at base, no sheath; tip smaller and more or less emarginate; only slightly protrusible; pleurodont dentition; feet often reduced, two or none, the toes also frequently reduced in number; but in all cases pectoral and pelvic girdles are present. Over 400 species are known, but few of them inhabitants of the U. S. The SCINCIDÆ have a more or less snake-like body, covered with smooth bony scales; tongue two-pointed. *Eumeces*, with teeth on the palate, contains our blue-tailed lizard (*E. fasciatus*); and our weak-legged ground lizard belongs to the genus *Oligosoma.* *Scincus*, with five toes, contains the true skinks. In *Seps* the toes are three in number. *Scelotes* has only hinder extremities, and in *Anguis* and *Typhline* legs are lacking. *Cyclodus.* The ZONURIDÆ may be recognized by a finely scaled groove along the side of the body. All except our 'glass snake,' *Ophisaurus ventralis*, belong to the old world. This species, which is limbless, derives its common name from the brittleness of its tail.

SECTION IV. FISSILINGUIA. Tongue long, slender, protrusible, its tip deeply split; eyelids well developed; tympanic membrane visible; legs well developed. VARANIDÆ, pleurodont, tongue retractile into sheath; *Varanus* (*Monitor*) contains about 30 old-world species. LACERTIDÆ, pleurodont, no tongue sheath; usually femoral pores; *Lacerta*, *Tropido-*

saurus. All the species belong to the old world. HELODERMIDÆ, pleurodont; tongue with papillæ at base; no femoral pores. *Heloderma*, with two species, *horridum* and *suspectum*, from the Mexican region, contains the only poisonous lizards. TEIDÆ, acrodont, tongue two-pointed, covered with imbricate scales; tympanic membrane visible; usually two transverse folds on throat. Limbs present, rarely rudimentary. About 70 American species. *Cnemidophorus*, with rounded tail, eyelids developed, small scales and large ventral plates, includes the six-striped lizard (*C. sexlineatus*) of the eastern U. S. *Tejus teguixin* of Central America reaches a length of 6 or 7 feet.

SECTION V. ANNULATA. Body covered by quadrangular scales, arranged in rings around the body. Body vermiform, limbless, or with small fore limbs. Teeth acrodont or pleurodont, no palatine teeth; tongue short, thick, non-protrusible; eyelids and tympanic membrane lacking. About 50 species, half of them belonging to *Amphisbæna*. All the species tropical or subtropical; they live burrowing in the earth, and feed especially on insects and worms.

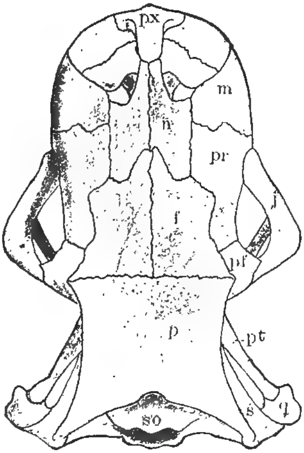

FIG. 315. Skull of *Heloderma*, after Günther. *f*, frontal; *j*, jugal; *m*, maxillary; *n*, nasal; *p*, parietal; *pf*, postfrontal; *pr*, prefrontal; *pt*, pterygoid; *px*, premaxillary; *s*, squamosal; *so*, supraoccipital.

The Lacertilia are poorly represented as fossils, the group appearing in the cretaceous. Most of the fossils are referred to existing families, but the Dolichosauria from the cretaceous of Europe, differ from all recent lizards in having more than nine cervical vertebræ.

SUB–ORDER 2. PYTHONOMORPHA.

Large, extinct, extremely elongate reptiles with four flipper-like extremities; vertebræ procœlous, with or without zygantra and zygosphenes; usually no sacrum; supratemporal fossa present, jugal arch incomplete; teeth large, conic, acrodont, fused to maxillæ and pterygoids; a parietal foramen; both girdles present; feet pentadactyl, without claws.

The Pythonomorpha occur in the upper cretaceous of America, Europe, and New Zealand. The vertebræ number more than a hundred; the cervicals bear strong hypapophyses, the caudals with chevron bones. The skull was lizard-like, the cranial cavity being open in front. The parietals are fused in the middle line, and were connected with the alisphenoids and prootic by lateral processes. The quadrates are large, and are articulated to a supratemporal. The premaxilla unpaired, the rami of the lower jaw united by ligament at the symphysis. Sternum and episternum but rarely occur, the coracoids (which bear a procoracoid process) meeting in the middle line. The pelvis was weak, and in most forms the ilium was without connection with the vertebral column. The bones of the limbs were short. In most forms the skin was naked, or at least lacked dermal ossicles.

Two groups are recognized, — the PLIOPLATECARPIDÆ, with a sacrum of two fused vertebræ and an episternum; and the MOSASAURIDÆ, in which a sacrum was lacking. *Plioplatecarpus* occurs in the rocks of Maestricht. *Mosasaurus* (species of which occur in Holland, England, and the eastern U. S.) was first found over a hundred years ago. *Clidastes* from Alabama, and *Platecarpus* from Kansas, are pretty well known. *Liodon*, from the cretaceous of both continents. Some of the phythonomorphs were over 40 feet in length.

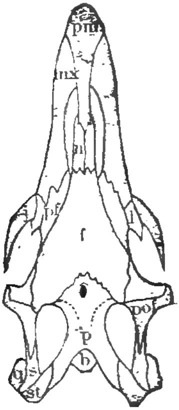

FIG. 316. Skull of *Liodon*, after Owen. *b*, basioccipital; *f*, frontal; *j*, jugal; *l*, lachrymal; *mx*, maxilla; *n*, nasal; *p*, parietal, with large parietal foramen; *pm*, premaxilla; *pf*, prefrontal; *pof*, postfrontal; *q*, quadrate; *s*, squamosal; *st*, supratemporal.

SUB-ORDER 3. OPHIDIA (SERPENTES).

Footless, elongate, scaled reptiles, with procœlous vertebræ; without chevron bones, sacrum, or pectoral girdle; no parietal foramen or temporal arch; sternum and tympanum lacking; no movable eyelids; tongue bifid, protrusible; teeth acrodont; no dermal osseous scutes; no urinary bladder.

Snakes are to be confused only with the footless lizards, from which they differ, however, in many structural features. The body is covered above by imbricate scales, while the lower surface of the body is usually covered by broad plates, — the abdominal scutes. The scuta on the head are regularly arranged, and the characters they present are of value in classification (Fig. 317). These scales are regularly shed, and as regularly reformed by epidermal cornification.

The procœlous vertebræ, which may exceed 400 in number, bear zygantra and zygosphenes, and can only be divided into caudal and precaudal series. The anterior 10 to 30 bear large hypapophyses. The neural arches are fused to the centra, and the ribs, which are frequently hollow, begin with the third vertebræ. Abdominal ribs and all sternal structures are lacking.

The bones of the skull are very solidly ossified, the brain capsule being long, and closed in front. Many of the bones (maxilla, pterygoids, supratemporal) are loosely articulated together. The parietals are laterally elongate, and fused with the prootic, ali- and orbitosphenoid. The opisthotics are fused with the exoccipital, and the basi- and presphenoids are united. Post- and prefrontals and lachrymals are present, and the vomers are paired. There is an os transversum, but jugals and quadratojugals are lacking. The premaxillary is very small, and there is no columella. The quadrate is articulated to the supratemporal (squamosal *auct*), which in most forms has but a loose connection with the other bones of the skull. Teeth occur on the maxillæ and pterygoids, and usually on the palatines, and they may be present on premaxilla. The teeth are usually sharp, conic, and retrorse, and frequently those of the maxilla may be grooved. When the grooved teeth occur on the anterior end of the maxilla (Proteroglypha, Solenoglypha) they are connected with poison glands. The rami

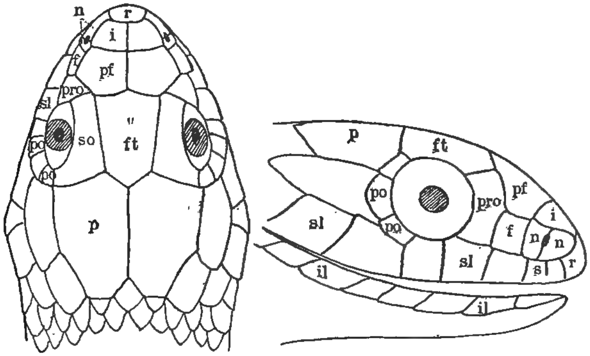

FIG. 317. Diagram of the cephalic plates in a colubrine snake. *f*, frenal; *ft*, frontal; *i*, internasal; *il*, infralabial; *n*, nasal; *p*, parietal; *pf*, prefrontal; *po*, postorbital; *pro*, preorbital; *r*, rostral; *sl*, supralabial.

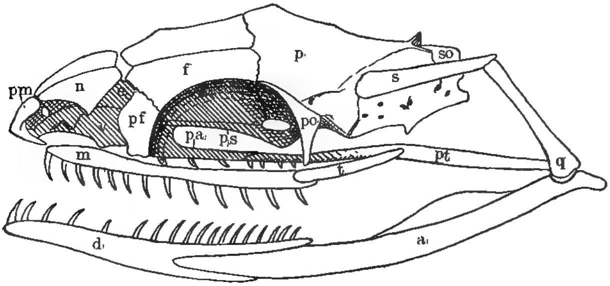

FIG. 318. Skull of garter-snake (*Eutainia sirtalis*). *a*, angulare; *d*, dentary; *e*, ethmoid; *f*, frontal; *m*, maxillary; *n*, nasal; *p*, parietal; *pa*, palatine; *pm*, premaxillary; *pf*, prefrontal; *po*, postfrontal; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, supratemporal; *t*, transversum; *v*, vomer.

of the lower jaw are united by ligament at the symphysis, and are capable of wide separation, which, together with the loosely articulated cranial bones, allows of great increase in the size of the oral opening.

In only the peropoda are rudiments of hind limbs visible as small stumps having small claws on either side of the vent. The pelvic girdle occurs as a rudimentary structure, unconnected with the vertebral column, in the peropoda and *Typhlops*. In the latter but the rudiments of the girdle occur, in the former the pelvis is represented by a slender bone with which two diverging bones are articulated below.

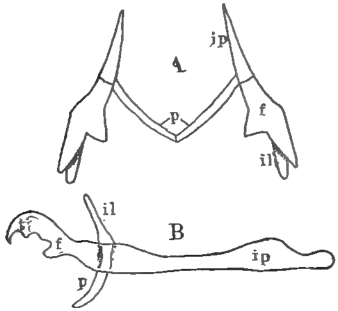

FIG. 319. Rudimentary pelvis and hind limb (*A*) of *Stenostoma macrolepis* and (*B*) of *Boa*, after Fürbringer. *f*, femur; *il*, ilium; *ip*, 'iliopectineum;' *p*, pubis; *t*, tibia.

The tongue of the snakes is deeply forked, and is retractile into a sheath on the floor of the mouth. It can be protruded when the mouth is closed, thanks to a groove in the edge of the lips. The poison glands which occur in certain snakes are modified labial glands. Sometimes they are greatly enlarged, and may extend backwards into the throat. They are so placed that the action of the muscles which close the jaw will force the poison out through a duct into a groove in the modified teeth which serve as poison fangs. In the proteroglyphs these grooves are open; but in the solenoglyphs the edges of the groove meet, so that a poison canal is formed inside the tooth. The stomach is long, and the intestine has few convolutions. The trachea is very long, and often has respiratory chambers in its course. The left lung is rudimentary, the right very long with an air reservoir at the end.

Locomotion is effected by the lateral bending of the vertebral column and by the ribs, which can be moved forward and back; and as these are attached to the abdominal scutes these latter can be moved, and as they catch every irregularity of the surface, the animal is able to propel itself. Snakes are all carnivorous, the majority feeding upon vertebrates, some killing their prey by poison, some by crushing it. It is swallowed whole. Most snakes lay eggs, which are large and enclosed in a leathery shell; but a large number are viviparous. Snakes, of which nearly 2,000 species have been described, have their metropolis in the tropics. In colder climates they undergo a hibernation during the winter. The earliest snakes appear in the cretaceous: but few fossils of the group are known, and these chiefly by vertebræ, skulls being very rare.

SECTION I. COLUBRIFORMIA. Snakes with the supratemporal overlapping the cranium; maxillary bone horizontal, not erectile; teeth not grooved or channelled, or only the hinder teeth grooved; not poisonous. The PEROPODA, with rudimentary hinder limbs, includes the *Pythons*, giant snakes of Africa, and *Boa* and *Eunectes* (the anaconda), equally large forms, from South America. The AGLYPHODONTA resemble the Peropoda in the absence of grooved teeth, but differ in the absence of limbs. The species are numerous; our species mostly belong to the COLUBRIDÆ, in which the head is distinct from the trunk; the teeth are numerous on maxillaries and palatines. Over 700 species described; about 50 in northeastern U. S. *Tropidonotus* includes our water-snakes; our garter-snakes belong to *Eutainia*. *Bascanion* contains the black snakes; *Heterodon*, the choleric but harmless spreading vipers. *Rachiodon* of Africa has the vertebral hypapophyses tipped with enamel, forming a series of teeth which penetrate the œsophagus, and are of use in cutting open the eggs on which these animals feed. The OPISTHOGLYPHA have some of the posterior maxillary teeth grooved. *Dipsas* and its allies are tropical arboreal forms, with nocturnal habits.

SECTION II. PROTEROGLYPHA. Snakes with large, permanently erect, grooved poison fangs on the anterior end of the maxillaries. A poison gland is always present. They live in warm countries, and are usually brightly colored (warning colors). The ELAPIDÆ contains the coral-snake or bead-snake, *Elaps fulvus*, of our southern states; *Naja tripudians*, the cobra of India; and *N. haje*, the asp, traditionally connected with Cleopatra. The HYDROPHIDÆ embraces the sea-snakes of the Indian Ocean, one species ranging to Panama. These are pelagic throughout life, feeding upon invertebrates and small fishes. They bring forth their young alive.

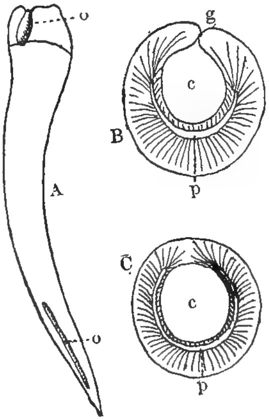

FIG. 320. *A*, poison tooth of rattlesnake; *C*, the same in section (solenoglyphic); *B*, section of poison tooth of the cobra (proteroglyphic), showing the groove (*g*) of closure in formation of the poison canal, *c*; *o*, openings of poison canal; *p*, pulp cavity; after Boas.

SECTION III. SOLENOGLYPHA. Maxilla vertical, in front armed with large erectile poison fangs in which the groove has been converted by folding into a tube. In the VIPERIDÆ there is no pit or groove between nostril and eye. The species, about 20 in number, all belong to the old world, two species of vipers (*Vipera*) and one adder (*Pelias*) occurring in Europe. In the CROTALIDÆ, the 40 species of which occur in America and Asia, there is a deep pit, partly occupying a cavity in the maxillary bone, between nostril and orbit. *Crotalus*, in which the tail ends in a rattle formed by the remains of exuviated skin, contains the rattlesnakes, of which three species, *C. horridus*, *C. adamanteus*, and *C. catenatus* occur in our eastern states. *Agkistrodon contortrix*, the copperhead, and *A. piscivorus*, the moccasin, lack the rattle, as does *Bothrops lanceotatus*, the *fer-de-lance* of the Antilles, possibly the most deadly snake.

SECTION IV. TORTRICINA. Colubriform snakes with supratemporal articulated with bones of skull; mouth incapable of distention; a horizontal maxillary bone, rudiments of pelvis and anal claw. The species, belonging to *Tortrix*, *Rhinophis*, *Uropeltes*, etc., are all tropical.

SECTION V. OPODERODONTA. With articulated supratemporal, rudimentary pelvis, head and eyes small; bones of skull immovable; mouth incapable of distention, teeth in only upper or under jaw, body worm-like, tail very short. Seventy species in the tropics, where they live a burrowing life like earthworms. *Typhlops*; *Stenostoma*.

ORDER VIII. CROCODILIA (LORICATA, CATAPHRACTA).

Lizard-shaped reptiles with bony, dermal scutes; bicipital ribs; a supra- and usually an infratemporal fossa; teeth in alveoli in the edges of the jaws only; quadrate immovable; sternum and episternum present; four, usually clawed, ambulatory limbs; tail long, keeled; lungs compound sacs; vent longitudinal; penis unpaired; heart with ventricles completely separated.

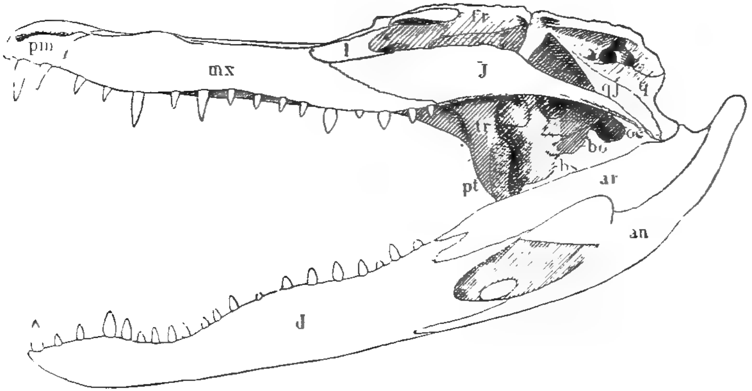

FIG. 321. Skull of alligator. *an*, angulare; *ar*, articulare; *bo*, basioccipital; *bs*, basisphenoid; *d*, dentary; *fr*, frontal; *j*, jugal; *l*, lachrymal; *mx*, maxillary; *pm*, premaxillary; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *tr*, os transversum.

The crocodiles, alligators, and caimans, and their extinct relatives, are sharply marked off from all other reptilian groups, except the theromorphs, by structural characters, although in external appearance they are closely similar to the lizards. They have the vertebræ pro- or amphicœlous or amphiplatyan, the atlas peculiar in consisting of four parts; cervical ribs are present, and the sternum is largely cartilaginous. The skull has usually a corroded appearance, an interorbital septum occurs, the premaxillæ are paired, and there is no parietal foramen. Ventral ribs are present; the procoracoid is a process of the coracoid. The acetabulum is closed. All of the bones are solid.

Dermal plates are best developed on the back, but may occur on the ventral surface as well. They consist of dermal ossifications overlaid with epidermal scales. The eyes have a vertical pupil, and both lids and nictitating membrane are present. The nostrils and ears are provided with valves. The teeth are confined to the edges of the jaws, and are never found on palatines or pterygoids. Salivary and lachrymal glands are lacking; the stomach is muscular and resembles somewhat that of birds. There is no cæcum. A peculiarity is the existence of peritoneal canals connecting the cœlom with the exterior.

The crocodiles and alligators are among the largest of living reptiles, the giant tortoises alone rivalling them. They are aquatic and mostly fluviatile. They capture their prey by lying in wait for it, usually with but the eyes and the tip of the nose above water. In their motions they are very quick. The smaller forms live chiefly upon fishes, but the larger prey on mammals when the chance comes. The eggs are laid either in sand or in rough nests, and vary in size from those of a hen to those of a goose. The group to-day is exclusively tropical, and has recently been greatly reduced in numbers, owing to the desire for the skins. The crocodiles appear in the trias (Parasuchia and Pseudosuchia).

SUB-ORDER I. PSEUDOSUCHIA.

Extinct crocodilia in which the back is covered with two rows of oblong bony plates. Vertebræ unknown; premaxilla small and thin; nostrils anterior; postorbitals present; no infratemporal fossa; teeth few; hinder feet pentadactyl, fifth toe reduced. *Ætosaurus*, the best-known genus, comes from the triassic of Würtemberg. *Typothorax*, triassic, New Mexico.

SUB-ORDER 2. PARASUCHIA.

Extinct crocodilia with amphicœlous or flat vertebræ; premaxilla very long; external nostrils separate and near orbits; inner choana at anterior end of palatines. Palatines and pterygoids not meeting in the middle line. Supratemporal fossa small, infratemporal large; parietals and frontals paired; post orbitals present; coracoid short, discoidal; clavicle present; toes unknown. The species come from the trias of Europe, America, and the East Indies. *Belodon* is found in Würtemberg, Pennsylvania, North Carolina, and New Mexico.

SUB-ORDER 3. EUSUCHIA.

Crocodilia with amphi- or procœlous vertebræ; premaxilla short; external nares united and at front of snout; palatines and usually pterygoids touching in the middle line, the choanæ thus being carried far back. Parietals and usually the frontals unpaired. Coracoid elongate; no clavicle. Pubis taking no part in the formation of the acetabulum.[1] Anterior feet pentadactyl, posterior four-toed, the fifth toe being represented only by a metatarsal. First three digits clawed.

SECTION I. LONGIROSTRES. Snout very long, nasals never entering wall of anterior nares; homodont dentition. The GAVIALIDÆ, of the rivers of the Orient, is the only existing family. *Rhamphostoma* (*Gavialis*) *gangeticus* comes from India. *Rhynchosuchus* is Australian. The earlier longirostres have amphicœlous, the later procœlous, vertebræ; the group first appears in the lias. *Telosaurus* and *Thoracosaurus* are fossil.

SECTION II. BREVIROSTRES. Snout shorter, rounded in front; nasals forming part of wall of anterior nares or close to them; heterodont dentition. The ATOPOSAURIDÆ were small lizard-like marine forms from the upper Jurassic. *Goniopholis* (*Diplosaurus*), of the family GONIOPHOLIDÆ, comes from the upper Jurassic of Belgium and Colorado. The ALLIGATORIDÆ have existed since the cretaceous. *Alligator* contains our North American species, *A. lucius*, as well as other species from South America. These have the edge of the upper jaw without excavation for fourth tooth of the lower jaw. In the CROCODILIDÆ such an excavation occurs. The crocodiles occur in the tropics of both hemispheres, *Crocodilus americanus* occuring in our southern states.

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[1] This is the statement usually made; but there is some evidence to show that the bone usually called pubis is in reality the prepubis, the true pubis fusing after a time with the ischium.

ORDER IX. PTERODACTYLIA (PTEROSAURIA, ORNITHOSAURIA).

Extinct reptiles adapted for flight. Skin naked, bones of limbs and vertebræ hollow; the caudal vertebræ amphicœlous, the others procœlous; three to five vertebræ fused to form a sacrum. Skull bird-like in shape and in obliteration of sutures; supra- and infratemporal and preorbital fossæ present; a bony sclerotic ring; premaxilla large; teeth, when present, in alveoli; quadrate immovable. Ribs two headed, sternal and abdominal rib present; sternum keeled; episternum and clavicles absent. The fore limbs have the fifth digit greatly elongate, supporting a membranous wing extending from the side of the body as in the bats. The other digits are normal, except the first, which is vestigial or absent. The pelvis is weak, the hind limbs reduced, the feet five-toed. The tail may be long or short.

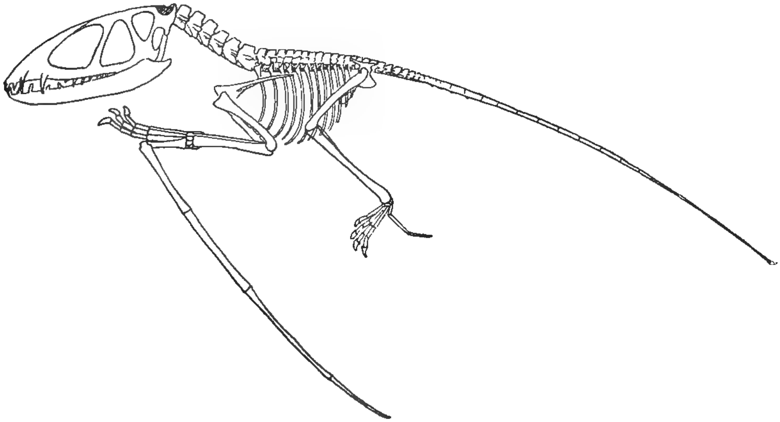

FIG. 322. Restoration of *Dimorphodon*, after Woodward.

The pterodactyls were confined to the Jurassic and cretaceous periods of Europe and North America. In habits they were bird-like or bat-like. Some of them were sparrow-like in size, while in others (*Pteranodon*) the skull was three feet in length, and the wings had an expanse of twenty feet. Casts of the brain cavity show that the brain was more like that of birds than of other reptiles, especially in the shortness of the hemispheres, the widely separated optic lobes, and the presence of a lateral projection (flocculus) from either side of the cerebellum.

In the PTERODACTYLIDÆ teeth were present; in the PTERANODONTIDÆ they were lacking. The pterodactyls proper had a short tail; in others of the family it was longer. *Pteranodon* has been found only in the middle cretaceous of Kansas, *Dimorphodon* from the lower lias of Dorsetshire.

SUB-CLASS II. AVES.

Sauropsida with the body covered with feathers; anterior appendages modified for flight; warm blooded; heart completely divided; only one (right) pertistent aortic arch; oviparous.

The group of birds is strongly marked off from all other vertebrates by the feathers. No other animals, recent or extinct, are known which had this protective envelope, and no birds lack them. The structure and development of these characteristically avian features have been described (p. 94), but their arrangement is of considerable importance in classification.

Except in a few birds the feathers are not distributed evenly over the body, but are in distinct tracts or pterylæ, these being separated by spaces (apteria) with no feathers or with only down-feathers. The feather tracts of the wings bear the feathers of flight which, according to the part on which they are supported, receive different names. Those attached to the hand are the **primaries,** to the fore arm **secondaries,** the three proximal of the fore arm feathers being the **tertiaries.** Primaries, secondaries, and tertiaries together are called the **remiges.** These remiges are overlaid above and below by shorter feathers, the upper or under **wing coverts.** The principal tail-feathers are the **rectrices,** and these are similarly overlaid by the **tail coverts.** The feathers attached to the first digit form the **ala spuria** or **alula.** Some birds are completely naked when hatched, and are called **gymnopædes.** Others (**dasypædes**) are covered with down upon their escape from the egg, while a few (**pteropædes**) have the contour-feathers developed before hatching. All of the gymnopædes and some of the dasypædes are fed by the adult, and are consequently called **altrices**; but most of the latter group can run about at once (**præcoces**).

A marked sauropsidan feature is found in the scales, which more or less completely cover the feet and tarso-metatarsal region. These may be small and numerous (**reticulate** tarsus) or in larger plates extending across the tarsus from side to side (**scutellate**), or the scutes on either side may fuse into a continuous plate (**booted** tarsus). Various modifications and combinations of these conditions may occur. Dermal ossifications are entirely lacking.

The skeleton of birds is usually characterized by lightness and strength, the former being attained by the hollow condition of most of the bones, while strength is the result of frequent fusion of parts which remain distinct in other vertebrates.

In most birds the centra have saddle-shaped extremities. Only in the odontormæ were they amphicœlous, while in a few water-birds the thoracic vertebræ are amphicœlous. The number of vertebræ varies greatly, the variations in number being most noteworthy in neck and tail. The cervical region is long and flexible, but in the rest of the column extensive fusions of vertebræ take place; the result being that usually the anterior thoracic vertebræ are coalesced, while the posterior thoracics, lumbars, sacral (one to five in number), and some of the caudals unite to form a **synsacrum** more or less intimately united with the pelvis. The remaining caudals in existing birds are fused to form a **pygostyle** or ploughshare bone; but in the extinct saururæ the caudals were distinct and decidedly reptilian in character.

The ribs have two heads. Cervical ribs are usually present, but are frequently fused with the vertebræ. The thoracic ribs are divisible into vertebral and sternal portions, the two parts being articulated to each other without the intervention of a cartilaginous portion. The sternal ribs join the sternum directly. Each vertebral rib bears on its posterior margin an uncinate process which overlies the rib behind, thus giving greater strength to the thoracic box.[1] The sternum is well ossified, and has the shape of a broad plate, from the ventral side of which in flying birds a strong keel or carina arises for the attachment of the muscles of flight. The presence or absence

[1] Uncinate processes are lacking in a few birds (*Chauna*, *Archæopteryx*).

of this keel was formerly used as the basis of division of the birds into ratite and carinate groups. Its hinder edge may be entire or with one or two deep notches, or there may be a foramen on either side. An episternum is apparently present in the embryo.

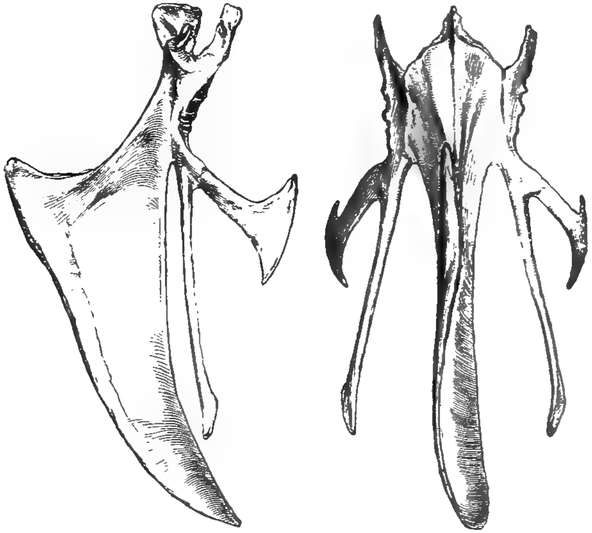

FIG. 323. Front and side views of sternum of common fowl, from Huxley.

The skull of birds is noteworthy for its lightness, and for the great extent to which the fusion of certain of the bones, especially those of the cranial wall, has been carried, in all except the dromæognaths and some fossil forms. A temporal fossa is present, but the supratemporal arcade is not complete. Postfrontals and postorbitals are lacking. A jugal-quadratojugal arch extends from the quadrate to the maxilla. The maxilla is usually fixed; but in some, as in the parrots, it is movable, and in these cases its motion is transmitted by means of the palato-pterygoid and the jugal-quadratojugal arches to the quadrate. The beak is largely made up of premaxillæ, which are fused and have a long frontal process. The orbits are placed in front of the brain, and except in a few cases are separated by a bony interorbital septum. Frequently there is an osseous sclerotic ring. The external nares are usually near the orbits.

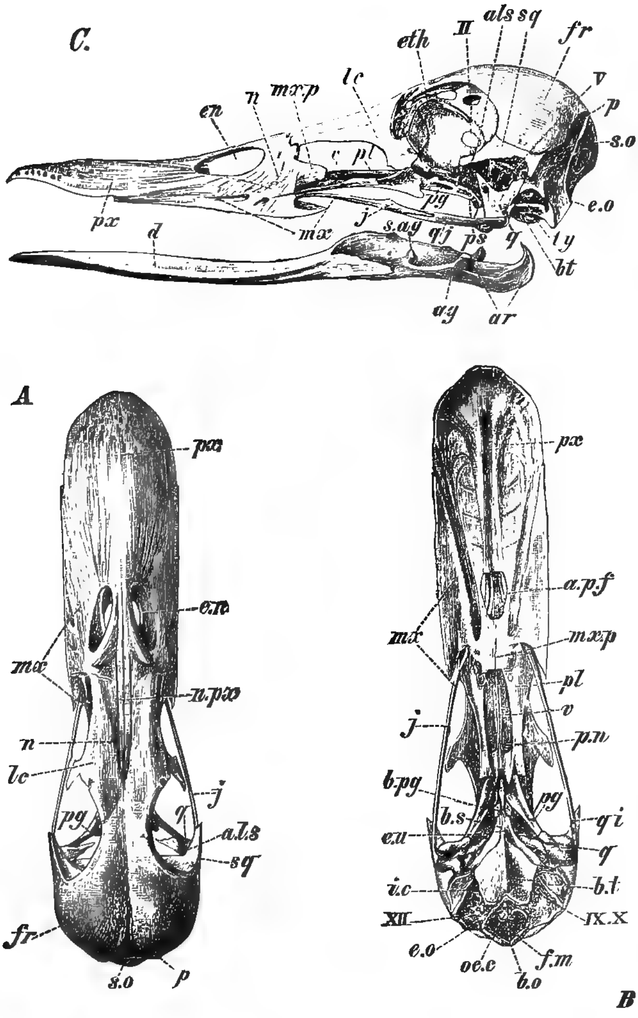

FIG. 324. Skull of duck, from Wiedersheim. *als*, alisphenoid; *ag*, angulare; *apf*, foramen palatinum anterius; *ar*, articulare; *bo*, basioccipital; *bpg*, basipterygoid; *bs*, basisphenoid; *bt*, basitemporal; *d*, dentary; *en*, external nares; *eth*, ethmoid; *eo*, exoccipital; *eu*, Eustachian opening; *fm*, foramen magnum; *fr*, frontal; *ic*, foramen for internal carotid; *j*, jugal; *lc*, lachrymal; *mx*, maxilla; *mxp*, palatine process of maxillary; *n*, nasal; *npx*, nasal process of premaxillary; *p*, parietal; *pg*, pterygoid; *pl*, palatine; *pn*, posterior nares; *ps*, presphenoid; *px*, premaxilla; *q*, quadrate; *qj*, quadratojugal; *so*, supraoccipital; *sq*, squamosal; *ty*, tympanic cavity; *v*, vomer; *II*, *V*, *IX*, *X*, *XII*, openings for corresponding nerves.

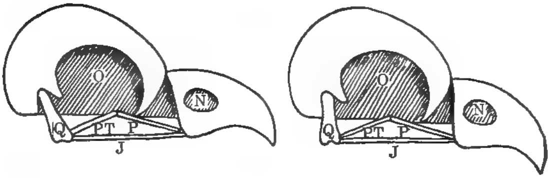

FIG. 325. Illustrating the hinging and movements of the maxilla and other bones in the birds; modified from Boas. *J*, jugal; *N*, nares; *O*, orbit; *P*, palatine; *PT*, pterygoid; *Q*, quadrate.

The quadrate is freely movable. In the floor of the skull appear three bones which in part replace the parasphenoid of the ichthyopsida. These are, behind, a pair of **basitemporals** (fused in the adult), and, in front, a median **rostrum.** The rami of the lower jaw are anchylosed at the symphysis.

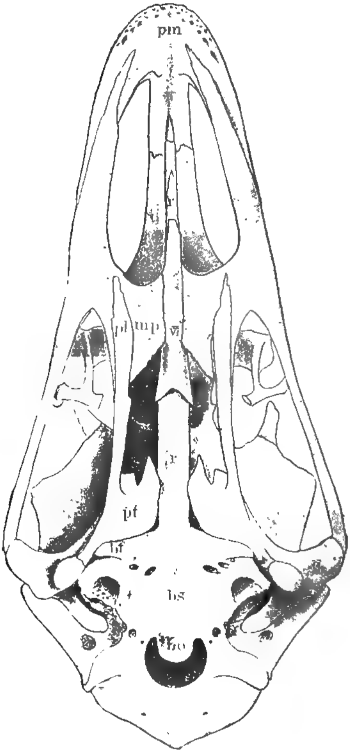

FIG. 326. Skull of ostrich (dromæognathous type). *pl*, palatine; *pt*, pterygoid; *r*, rostrum; *v*, vomer.

The relations of palatines, pterygoids, and vomers show many variations, and have been used as a basis of classification of birds. Although this classification has not obtained acceptance, the conditions are frequently used as characters, and may be described here.

In the **dromæognathous** skulls the vomers form a broad bone separating the rostrum from the palatines (Fig. 326), and occasionally from the pterygoids. In all others the palatines and pterygoids articulate with the rostrum, but they differ in other respects. In the **desmognathous** type the vomer is more or less rudimentary, while the maxillo-palatine processes unite in the median line forming a bony roof across the palate (Fig. 324). In the **schizognathous** skull there is a gap between the maxillopalatine processes, and another between them and the vomer when the latter is present, the latter bone being pointed in front. In the **ægithognathous** forms the vomer is truncate in front and cleft behind, the rostrum being embraced between its forks. In the **saurognathous** skull the vomer is paired.

The hyoid arch is but slightly developed; the first branchials, on the other hand, may be large. These two form a Y-shaped structure, the stem consisting of an anterior os entoglossum (paired in origin and possibly representing the hyoid arches) and a posterior basihyal from which arise a pair of cornua (1st branchials), which are usually made up of several segments. Extending backwards from the basihyal, between the cornua is a 'urohyal,' in reality a basibranchial.

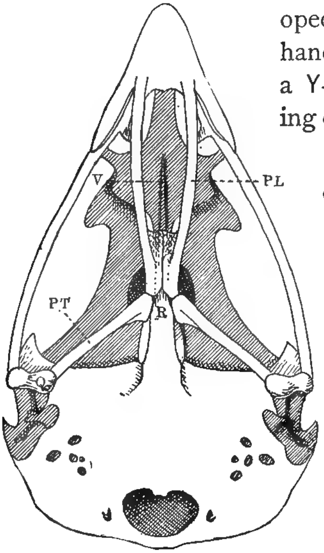

FIG. 327. Skull of quail, schizognathous type. *PL*, maxillopalatines; *PT*, pterygoid; *Q*, quadrate; *R*, rostrum; *V*, vomer.

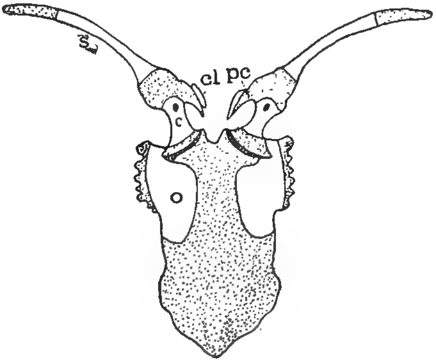

FIG. 328. Sternum and pectoral girdle of *Casuarius*, after Parker. *c*, coracoid; *cl*, clavicle; *pc*, procoracoid; *s*, scapula. Cartilage dotted.

The pectoral girdle is well developed except in the flightless birds, and in some moas apparently it was entirely absent. The coracoids are large, the procoracoids rudimentary or absent. In most ratite forms the clavicles are absent; in all other birds they are well developed, their proximal ends being usually fused, thus giving rise to the furcula or 'wish-bone.' The scapula is either at right angles to the coracoid (carinate birds) or in the same straight line with it (ratite birds).

In the fore limb the distal elements show great reduction, the carpals being reduced by fusion, while the hand has but three digits in the adult (four in the embryo), these apparently 2, 3, and 4 of the normal hand. The metacarpals usually show more or less complete fusion.

The pelvis is large and characteristic. Its bones are fused in all except *Archæopteryx*, and the acetabulum is perforated. The ilium is elongated in front, and is fused with all the vertebræ of the synsacrum (p. 331). The pubis[1] and ischia are directed backwards, and are usually without symphysis. The distal end of the ischium may fuse either with the ilium (most birds) or with the pubis.

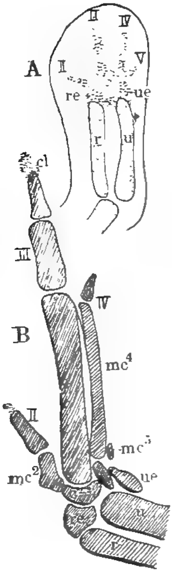

Fig. 329. Development of wing skeleton of tern (*Sterna wilsoni*), after Leighton. *A*, early; *B*, late. *c*, carpales; *cl*, claw; *mc*, metacarpals; *r*, radius; *re*, radiale; *u*, ulna; *ue*, ulnare; *II–V*, digits.

In the hind limb the noticeable features are the great reduction of the fibula, the fusion of the proximal tarsals with the tibia (tibio-tarsus), and the distal tarsals to the metatarsals (tarso-metatarsus), the ankle joint thus being intertarsal. In the foot but four toes occur in the adult (five in certain embryos) these being 1, 2, 3, 4. It is interesting that usually the phalanges increase in number from the first to the fifth toe in the order 2, 3, 4, 5, as in many lizards.

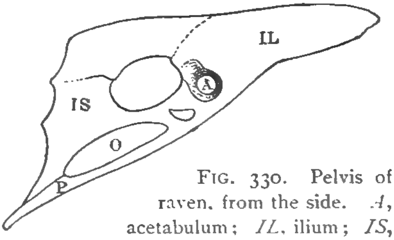

Fig. 330. Pelvis of raven, from the side. *A*, acetabulum; *IL*, ilium; *IS*, ischium; *O*, obturator foramen; *P*, pubis.

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[1] The bone called pubis corresponds to the postpubis of dinosaurs; the prepubis being represented wholly or in part in the pectineal process which occurs in many birds (Fig. 331).

All existing birds are toothless, but the dental ridge (p. 19) is formed in the embryo of at least a few forms. In several fossil birds teeth were present, either in grooves (*Archæopteryx*, *Hesperornis*) or in alveoli (*Ichthyornis*). Many modern birds have the horny sheath of the beak produced into horny tooth-like processes, which in many cases are supported by corresponding elevations of the bone. The tongue is well developed and protrusible, and exhibits many modifications in form. In most birds the œsophagus is of the same size throughout, but in grain-eating birds and birds of prey it has an enlargement or crop which serves as a reservoir of food, and in many cases is glandular, and hence plays a part in digestion. The stomach always consists of two divisions, an anterior glandular stomach or proventriculus and a second muscular stomach or gizzard, the muscles of the latter, which radiate from a tendinous centre on either side, being best developed in the grain-eating forms. A 'pyloric stomach' occurs

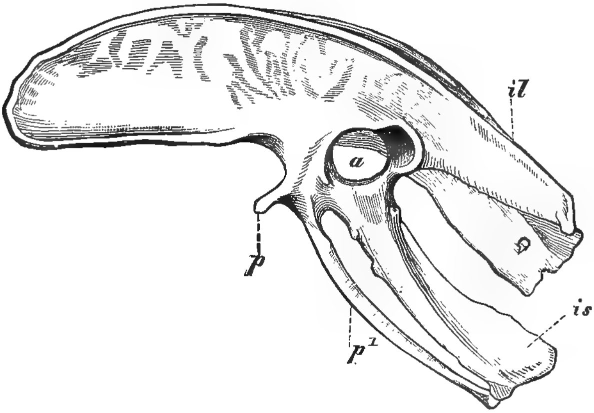

FIG. 331. Pelvis of *Apteryx*, after Marsh, from Wiedersheim. *a*, acetabulum; *il*, ilium; *is*, ischium; p^1, postpubis; *p*, prepubis.

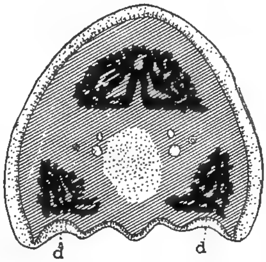

FIG. 332. Transverse section through the beak of an embryo tern, after Röse. *d*, dental ridge; bone, black.

in a few birds between the gizzard and the intestine. The length and coiling of the intestine varies greatly, the large intestine usually being short and straight. There are usually two cæca at the junction of ileum and colon. The cloaca receives on its dorsal wall the urinary and genital ducts, and farther back, in the young of all, there is developed a sac, the bursa Fabricii, of unknown function. It usually degenerates in the adult (Fig. 131).

The liver is usually two lobed, and there are two or three bile ducts. A gall bladder usually occurs. The pancreas is large and compact, and lies in the duodenal loop. The spleen is small.

The trachea is usually straight, but it may be folded or convoluted, the convolutions lying beneath the skin of the abdomen or inside the keel of the breast bone. The tracheal rings are ossified. The syrinx (p. 29) is usually formed by trachea and bronchi, but it may be purely bronchal or entirely tracheal in character. The lungs do not lie free in the cœlom, but are bound to its dorsal wall by cellular tissue. The air sacs are usually large, and it is by changes in the size of these more than by alterations in the volume of the lungs themselves that inspiration and expiration are effected.

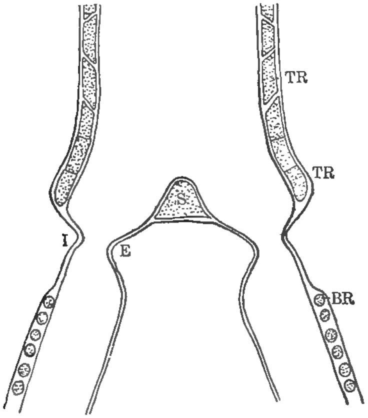

FIG. 333. Diagrammatic section of syrinx, after Boas. *IE*, walls of drum; *S*, bridge; *BR*, bronchus; *TR*, trachea.

The brain is characterized by its compact form and the large size of the non-convoluted cerebrum, which reaches back to meet the cerebellum, thus forcing apart the optic lobes. The cerebrum is largely made up of the corpora striata, and a small corpus callosum is present. The olfactory lobes are small (much larger in extinct birds). The cerebellum has a median vermis, showing an arbor-vitæ in section, and a pair of small lateral floccular lobes; a pons is lacking. The twelve cranial

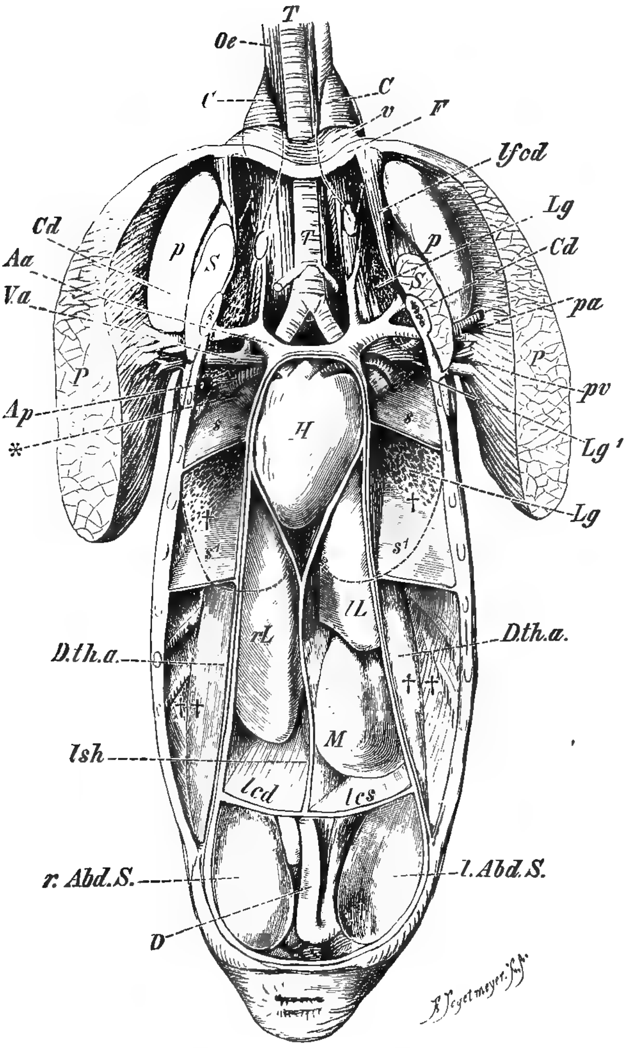

FIG. 334. Air sacs of duck, from Wiedersheim. *Aa*, anonymous, *Ap*, pulmonary artery; *C*, cervical sac; *Cd*, coracoid; *D*, intestine; *Dtha*, diaphragm; *F*, furcula; *H*, heart; *lAbdS*, left abdominal sac; *lcd*, *lcs*, ligamentum coronarium hepatis; *Lg*, lung; *lfcd*, lig. coraco-furcularis; *lL*, liver; *lsh*, suspensor of liver; *M*, stomach; *Oe*, œsophagus; *P*, pectoralis; *p*, pectoral sac; *pa*, artery to, *pv*, vein from, pectoralis; *rL*, liver; *rAbdS*, right abdominal sac; *S*, subclavian; *s*, partition between the anterior diaphragmatic and the supracoracoid sac; s^1, between anterior and posterior diaphragmatic sacs; *T*, trachea; *v*, anterior wall of supracoracoid sac; *Va*, anonymous vein; *, entrance of bronchi into lung; †, anterior, ††, posterior diaphragramatic sac.

nerves are distinct in origin. A characteristic is the double condition of the sympathetic in the region of the neck, one portion following the vertebrarterial canal, the other the carotids.

The nostrils, except in *Apteryx*, are near the orbits. Connected with the olfactory organ is a nasal gland, usually situated in the frontal bone, its duct emptying into the respiratory chamber. The eyes are large and highly developed, and are spherical behind, obtusely conical in front. Except in *Apteryx* there is developed a peculiar fold, the **pecten** or **marsupium,** which is vascular, and projects into the posterior chamber in the line of the choroid fissure. The nictitating membrane is large, transparent, and is moved by two special muscles, the **quadratus** and the **pyramidalis.** The associated Harderian gland is large, the lachrymal, at the external angle of the orbit, being small. The eye muscles proper are small; and the eyeball is somewhat limited in its motions, this being compensated by the flexibility of the neck. The ear has a large semicircular canal; and the lagena is long and slightly coiled, its distal end being somewhat expanded. It recalls the cochlea of the mammals, but a Corti's organ is lacking. The tympanic cavity sends prolongations into the surrounding bones, one, the **siphoneum,** penetrating the lower jaw. The tympanum is crossed by the slender columella, which bears at its membranal end a discoid stapedial plate. The external ear is surrounded by a circle of feathers; and in some birds (*e.g.*, owls) these may be moved, like a valve, by appropriate muscles.

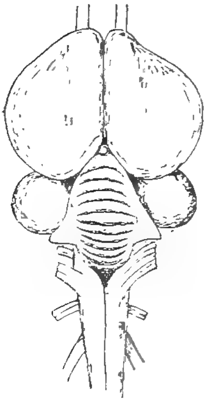

FIG. 335. Brain of bird.

The heart is completely divided into right and left halves; and the dorsal aorta is supplied only by the right aortic arch, the left of the normal pair being converted into the innominate artery. There is no mixture of arterial and venous blood in the heart. The blood returns to the heart usually by two precavæ and a single postcava, these emptying separately into the right auricle in which the sinus has become merged. There is no renal portal system. Characteristic of birds is an arterial plexus beneath the skin of the ventral side, which becomes greatly enlarged at the time of incubation. The red blood corpuscles are oval and nucleated.

The permanent kidneys are metanephridia. Usually they consist of three lobes, each lobe lying in a cavity bounded by the vertebræ and the transverse processes. Frequently the kidneys meet and even fuse posteriorly. The ureters open separately in the cloaca. No urinary bladder occurs. The urine is white and semi-solid.

The left ovary is never functional, and it and its duct are usually aborted. The right ovary is strongly lobulated on account of the large size of the eggs. The corresponding oviduct has a large funnel-shaped opening, and is divided into three regions, the middle of which is glandular and furnishes the white, while the posterior is both muscular and glandular and secretes the egg-shell. From the fact that the egg remains some time in the latter division, this is sometimes spoken of as the uterus. The testes are usually equally developed; they lie in front of the kidneys, and the vasa deferentia have a convoluted course, opening separately into the cloaca. A copulatory organ is usually absent. In the ostrich there is a solid retractile penis like that of alligators and turtles, while a few other ratites and aquatic birds have the ventral wall of the cloaca thickened, with a median groove which serves as a sperm duct. Secondary sexual characters are common. The male may be either larger or (more rarely) smaller than the female. Frequently he is distinguished by brighter colors, by the development of certain feathers, etc.

The eggs are very large, and are incubated by the parents; the period of incubation varying from eleven days to seven weeks (ostrich). The nest-building habits vary greatly.

The development of different birds shows few and unimportant variations, and the history of the common chick is well known. The early phases of segmentation are passed through before the egg is laid. This segmentation affects at first only a small portion of the upper surface of the yolk (*i.e.*, is meroblastic). The resulting blastoderm is several cells in thickness, a layer of superficial ectoderm cells, and beneath this the lower layer cells of undifferentiated mesoderm and entoderm. The blastoderm next exhibits two areas, — a translucent central **area pellucida** and a marginal **area opaca**. At the edge of the blastoderm there now appears an elongate depression, the **primitive streak** (an extremely modified blastopore), the axis of which, corresponding to the future axis of the embryo, lies at right angles to the major axis of the egg. In front of this arise a pair of medullary folds enclosing the medullary groove, the hinder ends of the folds embracing the anterior end of the primitive streak.

While the embryo is thus being outlined the blastoderm increases in size, and soon becomes differentiated into embryonic and extraembryonic portions, the former giving rise to the whole of the embryo, the other to a cellular yolk sac which eventually embraces the whole yolk. At the edge of the embryonic area arises the amniotic fold which closes in over the embryo from all sides, thus enclosing it in a double-walled sac, the inner layer being the amnion, the outer the serosa. While the amnion is being closed in, the embryo begins to be cut off from the yolk, at last only a narrow yolk stalk connecting the two. The allantois grows out from the alimentary tract behind the yolk stalk. At its base it is small, but it expands distally into a large vesicle. Both yolk sac and allantois have blood-vessels developed in them, and form important organs of nutrition in the broader sense. The blood-vessels of the yolk sac appear first as outgrowths from the omphalomesaraic arteries and veins in the area pellucida; but they gradually extend over the area opaca, branching and forming a plexus, the function of which is to take up the yolk and carry it into the circulation. The allantoic circulation is respiratory in character. Its vessels are outgrowths from the anterior abdominal vessels of the non-allantoidan vertebrates. The allantois also serves as a reservoir of urinary waste.

In the general growth of the embryo the most striking feature is the close similarity, until a late stage, with the reptiles. The gill slits — three or four in number — never bear gills, and the appendages in the early stages are distinctly pawor flipper-like. As the yolk is absorbed, the yolk sac is drawn into the body cavity, and the abdominal walls close. Then the shell is broken, in most birds by means of a calcareous or horny growth at the tip of the upper jaw (egg-tooth), and the young begins its free life.

As far as is at present known, birds appeared (*Archæopteryx*, *Laopteryx*) in the Jurassic. In the cretaceous the genera *Ichthyornis* and *Hesperornis* are found, while in the tertiary the forms are more numerous, although at all times fossils belonging to the group are rare.

The order of birds is so uniform in its structural features that it is difficult to find important characters to differentiate the twelve thousand known species into convenient groups. As a result, ornithologists have raised a number of minor groups into so-called orders, which are scarcely of family rank, if we are to accept the rules in vogue in other groups of vertebrates. The group by most authors is sub-divided into Ratitæ and Carinatæ, divisions based upon the presence or absence of a keel to the sternum ; but these divisions are artificial, and do not indicate the phylogeny of the forms concerned.

ORDER I. SAURURÆ (ARCHÆORNITHES).

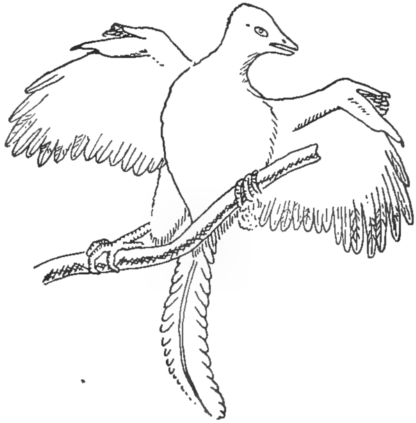

FIG. 336. Restoration of *Archæopteryx*, after Pycraft.

Extinct birds with elongate tail consisting of many vertebræ ; upper jaw with teeth (lower unknown) ; vertebræ amphicœlous ; feathers of the normal type, those of the tail in pairs, a pair to each vertebra. Only two specimens are known, both coming from the lower Jurassic slates of Bavaria. These belong to the genus *Archæopteryx*, but may represent two distinct species. One is about the size of a crow, the other considerably larger. *Laopteryx*, known from a few fragments from the Jurassic of Wyoming, may belong here.

ORDER II. ODONTORMÆ.

Extinct carinate birds with normal avian tail (pygostyle); teeth thecodont; presacral vertebræ amphicœlous; quadrate with a single articular facet; rami of lower jaw united by cartilage.

To this order belong a few birds arranged in the genera *Ichthyornis* and *Apatornis*, pigeon-like in size, found in the middle cretaceous of Kansas and Colorado. They had very large skulls, strong wings, and small legs, while the succession of the teeth was vertical as in the dinosaurs. This and the following order are frequently united as odontornithes or toothed birds.

ORDER III. ODONTOHOLCÆ.

Extinct ratite birds with teeth in alveolar grooves; vertebral centres saddle-shaped; quadrate with one articular facet; skull dromæognathous; rami of lower jaw united by cartilage; wing reduced, only the humerus retained.

The birds belonging to this order occur in the same beds as do the odontormæ. In general appearance they were somewhat like grebes. The cranial bones were firmly united, the premaxillary bone was without teeth, while the teeth of the maxillæ and lower jaw had a lateral succession as in the pythonomorphs. There was no true pygostyle, but the caudal vertebræ were broadly expanded, forming a paddle-like tail, only a few of the distal bones being fused. The clavicles were not united into a wish-bone; the acetabulum resembled that of the crocodiles; ilia, ischia, and pubes were not united posteriorly; and the feet were apparently fitted for swimming only. Here belong *Hesperornis* and *Lestornis*. *H. regalis* was about six feet long; *L. crassipes* considerably larger.

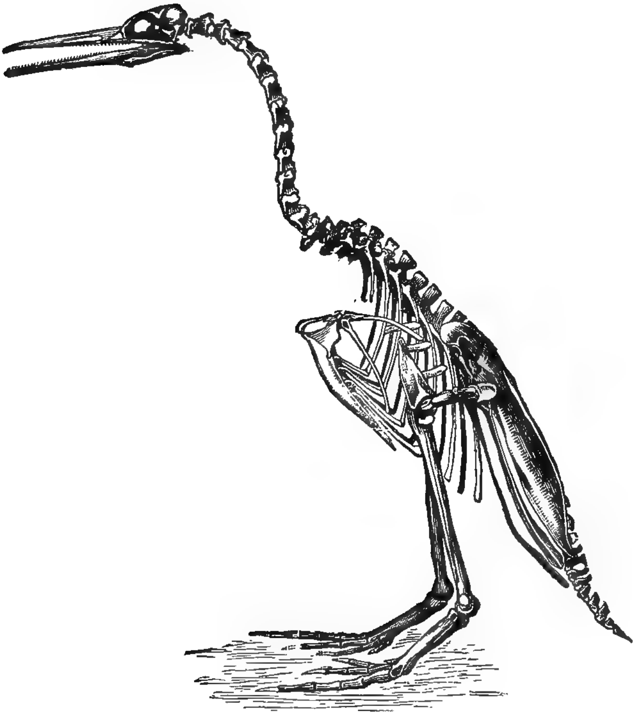

FIG. 337. Restoration of *Hesperornis*, after Marsh.

ORDER IV. EURHIPIDURÆ.

Toothless birds with pygostyle and saddle-shaped centra to the presacral vertebræ. The rami of the lower jaw are firmly united. To this order belong all living and many extinct birds.

SUB-ORDER I. DROMÆOGNATHI.

Eurhipidurine birds with dromæognathous palate; ischium and ilium not united behind; sternum either ratite or carinate; wings rudimentary or of no use in flight.

SECTION I. STRUTHIONES. Large ratite birds with elongate hind legs and neck; bill broad at base; mouth deeply split; toes three or two. Restricted to the southern hemisphere. The STRUTHIONIDÆ, containing the single species *Struthio camelus*, the ostrich of Africa, has but two toes. The South American RHEIDÆ, which have three toes, contain the nandu, *Rhea americana*, the feathers of which are familiar in feather dusters. The CASUARIDÆ of the Oriental region have three toes and a helmet-like development on the head. The family contains the emeus (*Dromaius*) and the cassowaries (*Casuarius*). A fourth family, the DINORNITHIDÆ, the extinct moas of Australia and New Zealand, were birds of gigantic size.

SECTION. II. ÆPIORNITHES. Extinct ratite birds of large size, formerly inhabiting Madagascar. *Æpiornis*.

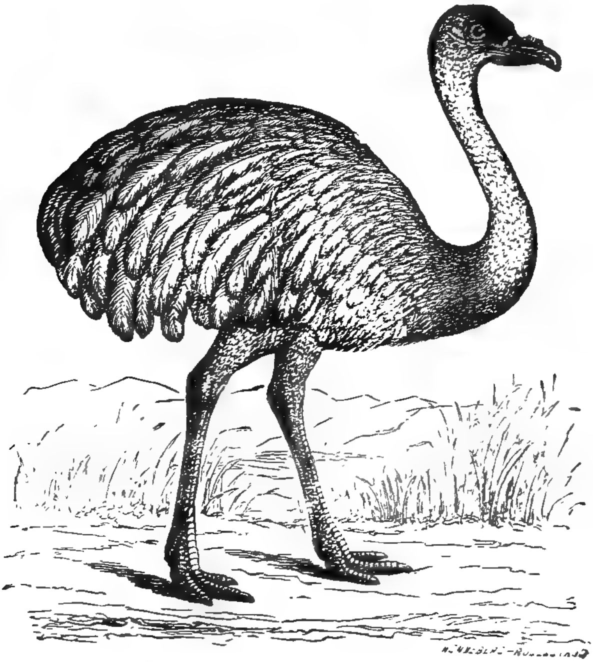

FIG. 338. South American Ostrich, *Rhea americana*, from Lütken.

SECTION III. APTERYGES. Dromæognathous ratite birds with rudimentary wings; no clavicle; four toes; vomer united to palatines and pterygoids; bill long, nostrils near the tip. Four existing species of kiwi, belonging to the genus *Apteryx*, inhabit New Zealand.

SECTION IV. CRYPTURI. Dromæognathous carinate birds with clavicle and functional wings. About 50 species from Central and South America. *Crypturus*, *Rhynchotus*, *Tinamus*.

SECTION V. GASTORNITHES. Extinct carinate birds from the eocene of France and Belgium. *Gastornis*. ? *Diatryma* from New Mexico.

SUB-ORDER 2. IMPENNES.

Aquatic birds with short, paddle-like wings used only for swimming. Pterylæ and apteria not differentiated; no differentiated remiges; dorsal vertebræ opisthocœlous and movable; synsacrum poorly developed; skull schizognathous; uncinate processes not anchylosed to ribs; pollex absent; pubis not united to ischium behind; four toes; feet plantigrade. The penguins, of which there are several genera (*Aptenodytes*, *Spheniscus*, etc.) are confined to the colder portions of the southern hemisphere. They are flightless, but use their wings, which are covered with scale-like feathers, as paddles in swimming. They feed upon fish and shell-fish, and make their nests upon uninhabited islands. *Palæeudyptes* occurs in the eocene of New Zealand.

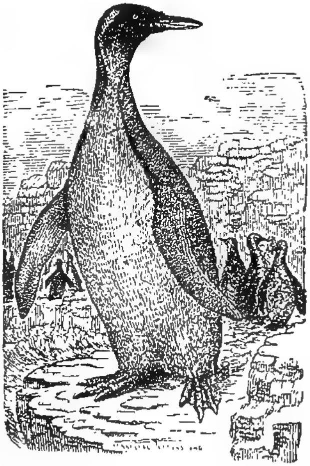

FIG. 339. Penguin, *Aptenodytes longirostris*, after Lütken.

SUB-ORDER 3. EUORNITHES.

Non-dromæognathous birds with (usually) saddle-shaped centra to the dorsal vertebræ; distal caudal vertebræ united to a pygostyle; quadrate with two articular facets; ilium and ischium united behind, enclosing an iliosciatic foramen; pollex free; pterylæ and apteria differentiated.

To this sub-order belong the great majority of living birds, over twelve thousand in number. They are usually sub-divided into a number of groups commonly regarded as 'orders,' but which are only of family rank, the so-called families being equivalent to genera in other groups of vertebrates. Reference must be made to special works on ornithology for details, as space will only allow mention of families here, with such features as will allow of correlation of other works with the system here adopted.

SECTION I. DESMOGNATHÆ. Birds with desmognathous palatine structure (p. 334). The STEGANOPODES are strong flying, web-footed birds, in which all four toes are directed forwards, while basipterygoid processes are lacking. The tropic birds (*Phaëthon*) have all the toes connected by a web, while in the frigate birds (*Fregata*) the web is scarcely developed. The pelicans (*Pelecanus*), with twenty-four tail-feathers, are characterized by the enormous pouch connected with the lower jaw. The gannets (*Sula*), the cormorants (*Phalacrocorax*), and the darters (*Anhinga*) also belong here. The CHENOMORPHÆ have three toes directed forwards, and in most cases, as in the ducks (*Anas*), geese (*Anser*), swans (*Cygnus*), and flamingoes (*Phenicopterus*), webbed and fitted for swimming, while in the screamers (*Anhima*) the web is lacking. The young when hatched are feathered, and able to feed themselves. The HERODII includes altrical forms (p. 330), in which the legs are very long, the toes, of which three are directed forwards, are usually without webs, and these birds, like the grallæ of the schizognathous section, are wading forms. The various species of *Ibis*, the spoonbills (*Platalea*), storks (*Ciconia*), herons (*Ardea*, *Herodias*), and bitterns (*Botaurus*), are familiar examples. The ACCIPITRES (Raptores) are recognized by their hooked bill and claws, the toes, three of which are directed forwards, being without webs. There is no basipterygoid process, and the young are altrical in character. The hooked beak is shared by the parrots, but the toes at once distinguish the two groups. The birds of prey include the vultures and buzzards (*Cathartes*, *Gyps*. *Sarcorhamphus*), the eagles (*Aquila*), hawks (*Buteo*, *Accipiter*), and falcons (*Falco*). forms which are closely alike in structure and differ considerably from the nocturnal owls[1] (*Strix*, *Bubo*, *Scops*, etc.), which compose the rest of the family. The COCCYGOMORPHÆ, as a rule, have three toes directed forwards, but in the cuckoos and toucans the first and fourth toes are turned backwards, while in the colies (*Colius*) all four toes are directed forwards. In all the rostrum is movable. Typical genera are the plantain-eaters (*Musophaga*), the cuckoos (*Cuculus*, *Geococcyx*). the night-hawks (*Caprimulga*, *Chordediles*), the rollers (*Coracias*), bee-eaters (*Merops*). motmots (*Momotus*), todies (*Todus*), kingfishers (*Halcyon* and *Alcedo*), the hornbills (*Buceros*), hoopoes (*Upupa*), puffbirds (*Monasa*. *Bucco*), toucans (*Rhamphastos*), and honey guides (*Indicator*). The TROGONIDÆ are characterized by having toes one and two directed backwards. The STEATORNITHIDÆ resemble the rollers in many of their characters. but they differ from them, as from all desmognaths except the parrots, in the opisthocœle character of the vertebræ. Three toes are directed forward. The oilbird (*Steatornis caripensis*) of South America is the

FIG. 340. Wood-duck, *Aix sponsa*, from Tenney, after Audubon.

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[1] The owls may be more nearly related to *Coracias* than to the Accipitres.

only species. The parrots or PSITTACI agree with the last-mentioned family in the vertebral centra and movable rostrum, but have the first and fourth toes turned backwards, while the beak is hooked. *Conurus*, *Psittacus*, *Cacatua*, *Trichoglossus* are typical genera.

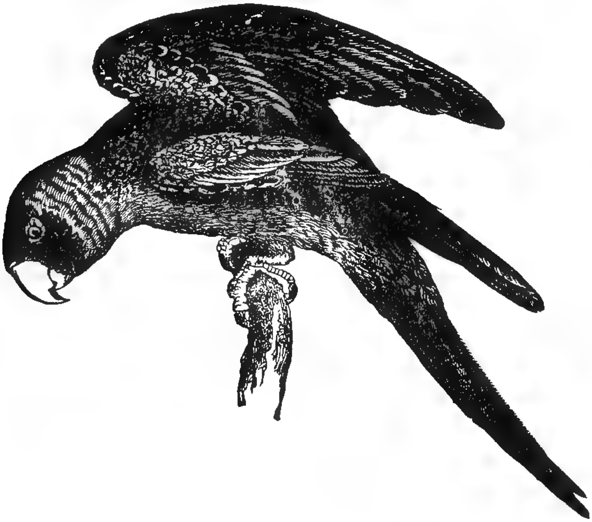

FIG. 341. Carolina paroquet, *Conurus carolinensis*, from Tenney, after Wilson.

SECTION II. SCHIZOGNATHÆ. Birds in which there is a schizognathous palatal structure (p. 355), and the vomer is narrowed and acute in front. The families to some extent parallel those of the desmognathæ in appearance and habits. The CECOMORPHÆ are swimming-birds, in which the feet are webbed, three toes pointing forwards, and the external nostrils are prolonged backwards as a fissure. The family includes the grebes (*Colymbus* and *Podiceps*), loons (*Urinator*), sun-grebes (*Heliornis*), auks (*Alca*), guillemots (*Uria*), gulls (*Larus*), terns (*Sterna*), and skuas (*Stercorarius*). The TUBINARES, including the albatrosses (*Diomedea*), petrels (*Procellaria*), and fulmars (*Fulmarus*), closely resemble the cecomorphæ, except in the tubular nostrils. They are oceanic in their habitat. The GRALLÆ are long-legged wading birds in which the toes (three directed forwards) are not usually webbed. The nostrils are either as in the cecomorphæ, or they are closed behind by a rounded edge. The pratincoles, plovers (*Charadrius*), *Jacana*, snipes (*Scolopax*), cranes (*Grus*), and rails (*Rallus*), and their allies, are littoral forms, while the bustards (*Otis*) have lost their wading habits and are truly terrestrial. The OPISTHOCOMI of South America, like all the remaining schizognathous families have three toes directed forwards. In general appearance the single species recalls the Gallinæ, but differs in the absence of the basipterygoids, the union of lachrymals to the rostrum, etc. The GALLINÆ (Rasores, Alectoromorphæ) includes the quail (*Coturnix*), partridge (*Perdix*), grouse (*Tetrao, Bonasa*), jungle-fowl, including our domestic fowl (*Gallus*), pheasants (*Phasianus, Thaumalea*), turkeys (*Meleagris*), peafowl (*Pavo*). These have the hallux rudimentary and elevated above the other toes and two carotid arteries. The COLUMBÆ (Pullastræ) have usually two carotids and the hallux well developed and near the ground. The group is hardly to be distinguished as a family from the Gallinæ. It contains the doves and pigeons (*Columba, Goura, Didunculus*), as typical members, while the mound-birds (*Megapodius*), the curassows (*Crax*), and the sand-grouse (*Pterocles*), are more aberrant. The dodo (*Didus*), exterminated about two centuries ago, was an aberrant pigeon. The humming-birds form the family TROCHILIDÆ, which has relations with the picarian birds. The toes, however, are three, directed forwards as in the preceding groups.

FIG. 342. Wilson's snipe, *Gallinago wilsoni*, from Tenney, after Wilson.

FIG. 343. Bird of Paradise (*Paradisea apoda*), female, from Hertwig, after Levaillant.

Other characters are the presence of basipterygoid processes and the existence of a single carotid. In the PICARIÆ the first and fourth toes are directed backwards, while the palate is of the saurognathous type

(p. 335). Here belong the woodpeckers (*Picus*, *Colaptes*) and the wrynecks (*Iynx*).

SECTION III. ÆGITOGNATHÆ. Birds with the maxillopalatines not united, the vomer single, broad, and notched in front. In the family PASSERES, which embraces over half the known species of birds, three toes are directed forwards. These birds group themselves in five divisions, typified by the following forms: The lyre-bird (*Menura*), the broad-bills (*Eurylamia*), the tyrant-birds and king-birds (*Tyrannus*), the ant-shrikes (*Formicaria*), and the sparrows (*Passer*), those allied to the last being frequently known as Oscines or singing-birds. Of these the number is legion; no attempt can be made here to even enumerate their names.

FIG. 344. Bird of Paradise (*Paradisea apoda*), male, from Hertwig, after Levaillant.

The Euornithes date back no farther than the eocene, in which period representatives of the cormorants, pelicans, flamingoes, falcons, kingfishers, and pheasants appear. The colies, oilbirds, and opisthocomi are not known as fossils, while the other groups appear with the miocene.

CLASS II. MAMMALIA.

Hair-bearing amniotes with two occipital condyles; lower jaw suspended directly from the cranium without the intervention of the quadrate; ankle joint between the tibia and fibula and the first row of tarsal bones; brain with well-developed corpus callosum; a complete diaphragm; heart four-chambered; only one (left) aortic arch persisting; red blood corpuscles non-nucleate, usually circular in outline; eggs (except in monotremes) minute, and undergoing a total segmentation, the embryonic development taking place inside the mother; the young, when born, nourished by milk secreted by the mammary glands of the mother.

The skin in the mammals has a well-developed stratum corneum (p. 88), which is never molted as a whole, as in the reptiles and lower vertebrates, but comes away piecemeal. The skin is as a rule pigmented, and the pigment may occur in either the deeper (dermal), or more superficial (epidermal) portions. The epidermis gives rise to various structures, the most noticeable and most characteristic of which is hair, the structure and development of which is described elsewhere (p. 97). The hair is usually abundant, and covers most of the body. The other extreme is reached in the cetacea, where it may be reduced to from two to eight pairs of bristles in the mouth region, these occurring in some cases only in fœtal life. Frequently one can distinguish two kinds of hair, one straight and stiff, covering a deeper woolly hair. Hair can undergo considerable modifications. It may be straight or curly; it may develop into bristles, or even into strong protective spines, as in the porcupines, etc. Frequently certain hairs about the mouth (vibrissæ) have tactile functions, their roots being enveloped in a rich plexus of nerve fibres. In some cases the hair seems to persist throughout life (tail and mane of horses), but usually it falls out and is replaced by new hair, this molting occurring gradually, or, as in the case of many inhabitants of colder climates, before and after the winter season. In the case of some arctic species this molting is accompanied by color changes, the winter pelage being white.

Frequently the epidermal layers of the skin becomes greatly thickened and cornified, producing callosities, or thickened, hairless surfaces like those found on the soles of the feet. Cornification of the epidermis also results in the formation of horn, such as that found in the cavicornia (cattle, etc.), and in the rhinoceros, as well as nails, claws, and hoofs.

Some of the relations between the epidermis of the appendages and the claws are interesting. In the human finger (Fig. 345 *A*), there exists beneath the nail a peculiarly modified epidermis, SU, the subungual portion, while the usual epidermis, S, covers the ball of the finger. In the unguiculates (*B*) the subungual portion is more developed, and forms the lower surface, SU, of the claw. In the ungulates (*C*), the unguis becomes much wider, and is rolled into a hoof, on the lower surface of which is still to be recognized the subungual epidermis, forming, for instance, in the case of the horse, the sole, into which there projects behind the frog of the foot, which, in reality, corresponds to the ball of the finger in man.

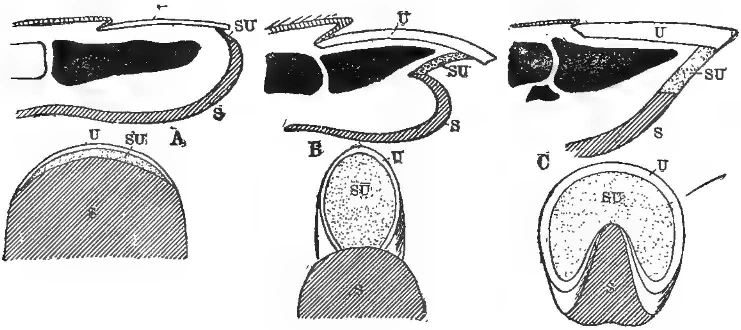

FIG. 345. Diagrams of the relations of nails, claws, and hoofs, after Boas. *A*, in man; *B*, in unguiculates; *C*, in ungulates. *S*, unmodified epidermis; *SU*, subungual epidermis (Sohlenhorn); *U*, nail.

Scales are not frequent in the mammals. They occur upon the tails of certain rodents, and upon the feet of these and some other forms (insectivores, marsupials, etc.). More rarely the whole body may be encased in them as in the pangolins. Again, as in the armadillos, dermal bones are developed in connection with the scales, while in some embryonic cetaceans similar features are seen.

Glands are far more abundant than in the sauropsida, and include, besides the common sebaceous and sweat glands, numerous modifications, usually in the line of scent glands. These are mostly modifications of sebaceous glands, and in many carnivores, rodents, and edentates, are most abundant in the anal or inguinal regions. In other groups they may have widely diverse positions; in the occipital region (camel), in the lachrymal bone (many ruminants), upon the face (bats), on the legs (swine), in the temporal region (elephants), etc. Here, too, belong the problematical glands connected with the spur on the hind legs of the monotremes.

The mammary or milk glands of the mammals are also modified dermal glands, those of the monotremes most closely resembling sweat glands, those of other mammals sebaceous glands. In their development a marked ridge, the 'milk line,' appears along the side of the body, certain portions of which become developed into the glands, the intervening portions aborting. Connected with the glands are the teats or nipples, which are of two kinds; the one produced by a protrusion of that part of the surface upon which the lacteal glands open; or (ungulates) by a similar elevation of the surrounding surface, the openings of the ducts remaining at the bottom of the tube thus formed (Fig. 97). The number of teats varies between one and eleven pairs (*Centetes*). These may be distributed along the length of the trunk, or may be restricted to either thoracic or abdominal region.

Except in a very few forms (hares) there is a layer of fat (**panniculus adiposus**) between the skin and the muscles. Besides, there is usually a layer of skin muscles (**panniculus carnosus**, p. 115). This is distinct from the isolated smooth muscles connected with the hair follicles.

In the skeleton there never occurs that pneumaticity found in birds and some extinct reptiles, the cavities of the bones being filled with marrow. All of the bones except those of the skull, the elements of the sternum, and some of those of the carpus and tarsus, are provided with **epiphyses,** — separate portions which unite later in life with the rest of the bone.

As a rule five regions — cervical, thoracic, lumbar, sacral, and caudal — are differentiated in the vertebral column, but in the cetacea, where the sacrum is lacking, the line cannot be drawn between lumbars and caudals. The cervicals, which are almost constantly seven[1] in number, are free, except in most cetacea and some edentates, where they are greatly flattened and fused. In some rare cases they bear movable cervical ribs, but usually these are firmly fused to dia- and parapophyses, leaving the vertebrarterial canal to betray their true nature. Usually the faces of the centra are flat, but opisthocœle vertebræ are common in the necks of ungulates.

The trunk or dorso-lumbar vertebræ usually number nineteen or twenty, and as a rule, increase in the number of thoracics is correlated with a reduction of the number of lumbar vertebræ. The extremes in the region are found in the armadillo, which has fourteen, and *Hyrax*, which has thirty dorso-lumbar vertebræ. The number of thoracic vertebræ is usually thirteen, but it is lower in bats and armadillos, and reaches eighteen in the horse, nineteen or twenty in the rhinoceros and elephant, and twenty-three or four in the three-toed sloth. The lumbars vary from two in the monotremes, manatee, and two-toed ant-eaters, to nine in *Stenops*, the usual number being six or seven.

The sacral vertebræ are primitively two in number, but others taken from the lumbar and caudal regions may unite by synostosis with the ilium, giving a total number of sacral vertebræ of eight or nine in the sloths and armadillos. The caudals are extremely variable in number and are usually numerous, the number being greatly reduced only in the anthropoid apes and man.

The ribs (corresponding in number to the thoracic vertebræ) are bicipital, being furnished with tubercular and capitular heads, the former articulating with the diapophysis (the transverse

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[1] *Manatus australis* and *Cholœpus hoffmanni* have six, *Bradypus torquatus* has eight, and *B. tridactylus* nine cervicals.

process of human anatomy) the latter with articular facets (reduced parapophyses) on the centra. The ribs usually present bony and cartilaginous portions, the latter reaching the sternum. In floating ribs the union with the sternum is lacking, while false ribs are without vertebral connections.

The sternum frequently retains throughout life the separate elements or sternebræ of which it is composed; but these may fuse into an elongate plate, the corpus sterni or mesosternum, with an anterior portion, the manubrium or presternum, and a posterior xiphisternum or ensiform process with which no ribs articulate. The episternum (p. 149), which is laid down in cartilage, is placed in front of the sternum, but retains its distinctness only in the monotremes and some edentates and rodents. In other forms it fuses with the sternum.

In the mammalian skull there is a more intimate relationship between the cranial and facial elements than is the case in the lower vertebrates. There is also a marked tendency to the fusion of bones which are distinct in the lower vertebrates, but usually the process of co-ossification is not complete except in the hyoid and lower jaw, many of the bones being suturally united throughout life.[1] The floor of the skull is preformed in cartilage, its roof of membrane bones. No interorbital septum occurs, its remnants being found in the crista galli process of the ethmoid, while the lateral walls continue forward to the ethmoid region. Basi- and presphenoids frequently fuse, and from the **sphenoid** thus formed a greater and a lesser wing arises on either side, these being the ali and orbitosphenoids respectively of the lower forms. The pterygoids also unite with the sphenoids, forming the pterygoid processes.

Basi-, ex-, and supraoccipitals may remain distinct, or they may fuse, sometimes late in life, into a single occipital bone which bears a pair of occipital condyles arising from the exoccipitals, the basioccipital but rarely contributing to their formation.

The sides of the skull are formed in part by the sphenoidal alæ, in part by the temporal bones, each of which is a complex of several elements, — the **petrosal** (fused pro-, epi-, and opi-

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[1] The obliteration of sutures has progressed the farthest in monotremes, the weasel and some apes.

sthotics) squamosal, mastoid, and tympanic. These are frequently fused. The tympanic, surrounding the external auditory meatus may develop into a saccular auditory bulla. In front the temporal gives off a zygomatic process which extends forward to join the jugal, or, as it is called, the malar bone.

An interparietal may be distinct, as in rodents, or it may fuse with the supraoccipital, or, more rarely, with the parietals. The frontals are usually paired, and in the ungulates they may develop bony horns. Frequently each gives off a postorbital process which, approaching or meeting the jugal, partially or completely separates the orbit from the temporal fossa. Postfrontals are lacking.

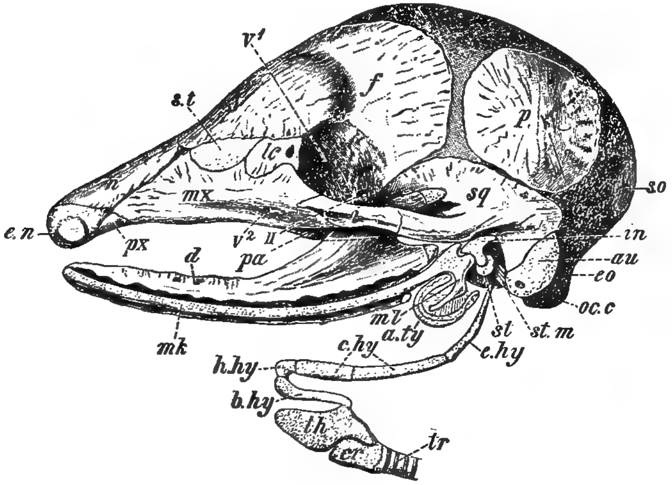

FIG. 346. Skull of young *Tatusia*, from Wiedersheim; cartilage dotted. *aty*, tympanic annulus; *bhy*, basihyal; *chy*, ceratohyal; *cr*, cricoid; *d*, dentary; *ehy*, epihyal; *en*, external nares; *eo*, exoccipital; *f*, frontal; *hhy*, hypohyal; *i*, jugal; *in*, incus; *lc*, lachrymal; *mk*, Meckel's cartilage; *ml*, malleus; *mx*, maxillary; *n*, nasal; *occ*, occipital condyle; *p*, parietal; *pa*, palatine; *px*, premaxilla; *sq*, squamous part of temporal; *st*, stapes; *stm*, stapedial muscle; *so*, supraoccipital; *th*, thyroid cartilage; *tr*, trachea; *II*, *V*, passages of nerves.

The cranium is closed in front by the ethmoid bone in which may be recognized a median (mesethmoid) plate which divides the nasal cavity into right and left halves, and on either side a lamina cribrosa perforated for the passage of the olfactory nerve.

The cribrosa, together with the superior turbinal bones in the nasal passage, apparently represents the prefrontal of lower vertebrates.

The nasal cavity is bounded externally by the nasal bones, which are small in cetacea and fused in the old-world apes. Inside the cavity, besides the superior turbinals already referred to, are the inferior turbinals which, beginning as separate ossifications, fuse with the maxillaries. The septum of the nose, established by the mesethmoid, is continued by the vomer, in which the paired bones of the lower forms are fused, and are entirely cut off from the roof of the mouth.

Among the most characteristic features of the facial skeleton are the close union of the maxillopalatine region with the rest of the skull, and the suspension of the lower jaw direct from the temporal bone without the intervention of a quadrate. The premaxillæ may fuse with the maxillæ, while maxillæ and palatines send off horizontal palatine processes, which, meeting in the middle line, form the hard palate, bound the nasal cavities below, and carry the choana far back. The pterygoids may also contribute to the hard palate (some edentates).

The lower jaw consists of but a single bone, the dentary, on either side, or the two halves may anchylose at the symphysis. In the middle ear are three small bones which form a sound-conducting apparatus leading from the tympanic membrane to the fenestra ovalis. In order from outside in these are the malleus, incus, and stapes. Concerning their homologies the most diverse views are held, both incus and malleus having been regarded as the missing quadrate. The views of the homologies given on p. 159 seem to be in full accord with the results of the studies of most students who have approached the subject from the embryological standpoint.

In the mammals the brain exercises great influence upon the shape of the skull. As it nearly fills the cranial cavity, increase in its size can only be accommodated by an outgrowth of the cranial walls. To measure the extent of this outgrowth and thus approximately to obtain an index of cerebral development, the **facial angle** is employed. According to the system of Camper this is the angle formed by two lines, one passing from the auditory meatus to the base of the nose, the other from the base of the nose to the most prominent part of the frontal bone. Less used is the system in which the lines intersect at the insertion of the teeth in the upper jaw. In man Camper's angle varies from 70° to nearly 90°. In monkeys from 60° (*Chrysothrix*) to 35° or 30°; in other mammals it is 25° or lower.

The hyoid arch is connected dorsally with the otic capsule, ventrally with the first branchial (Fig. 31). In it ossifications take place which proceed to varying extents. The whole arch may ossify, giving the separate elements, basi-, hypo-, cerato-, epi-, and stylohyal, or the median portion on either side may be converted into a stylohyal ligament, the stylohyal element fusing with the skull and forming the styloid process, while the basi- and epihyals fuse to form the body and lesser horn of a single hyoid bone. The first branchial arch also fuses with this, contributing to the body, and forming a greater horn on either side. There is also a ligamentary connection with the second and third branchial arches (thyroid cartilage, p. 28).

The pectoral girdle shows many variations from the typical condition, for while the scapula is always present, the coracoid, except in the monotremes, is reduced to a small element — the coracoid process — fused to the scapula. The presence or absence of a clavicle is correlated with habits; flying, digging, and climbing mammals having it, while it is absent in whales, ungulates, and many others. In rodents and carnivores it is reduced, and has only ligamentary connections. The pelvis, on the other

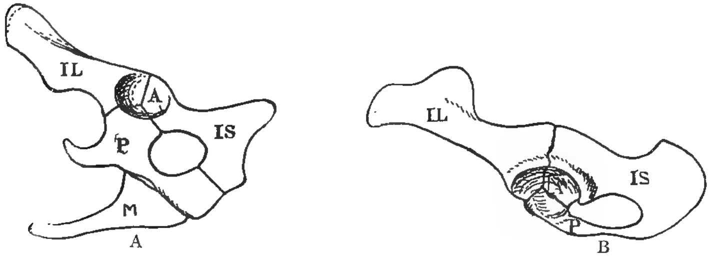

FIG. 347. Pelvis (*A*) of young *Ornithorhynchus*; (*B*) of calf, after Boas. *A*, acetabulum; *IL*, ilium; *IS*, ischium; *M*, marsupial bone; *P*, pubis.

hand, is more normal, except in the cetacea, where it is apparently absent, the one or two rib-like bones which occur imbedded in the muscles free from the vertebral column being usually interpreted as femur and tibia. In all others the ilia are united to the sacral vertebræ, while with rare exceptions the pubes of the two sides, and usually the ischia as well, unite in a symphysis below. In monotremes and marsupials, marsupial bones, probably epipubic in character (p. 171), are developed from the cephalic side of the pelvic girdle.

In the skeleton of the free appendages great variations occur, especially in the direction of reduction of digits, etc.; and for details of these reference must be made to the accounts of the separate orders. In general it may be said that the tendency is towards a reduction in the number of digits, and towards an alternation and interlocking of the carpal and tarsal bones. In the swimming-forms there is also a shortening of the limbs, the reduction going so far that in the case of the sirenia only the elbow joint is functional, while in the whales even this joint is lost. On the other hand, in these forms, as in the ichthyosaurs and plesiosaurs, an increase in the number of phalanges is more or less marked. In the bats, on the other hand, the elongation of most of the digits of the hand, and their utilization as supports of the wing, is noticeable.

In detail: the humerus may be either long or short, the conditions here being usually in reversed correlation to those found in the metacarpus. The ulna and radius are usually longer than the humerus, the ulna being produced beyond the hinge of the elbow as an olecranon process. The radius is more closely related to the carpus, and is capable of turning more or less freely around the ulna in the process of pronation and supination of the manus. Occasionally radius and ulna coalesce.

The femur usually bears two or three enlargements (trochanters) for the attachment of muscles. At the knee joint a patella or knee-pan usually occurs. The tibia and fibula are usually longer than the femur, and in the marsupials are capable of marked rotation. On the other hand, the fibula is frequently reduced, and united more or less closely to the tibia.

The greatest variations occur in the carpus and tarsus and more distal portions. The carpal and tarsal bones are in two or three rows, those of the distal row being opposite or alternate with the others. In the tarsus the os calcis and astragalus are the most prominent, the former being the fibulare, the latter fused tibiale and intermedium (p. 176). The digits are typically five in number, but *Pedetes* presents structures usually interpreted as a sixth toe. The tendency is constantly towards reduction in the number of digits, disappearance being preceded by a reduction in length, in which case the metacarpals are shortened and are occasionally reduced to splint bones. In certain groups there frequently occurs a fusion of the two middle metacarpals. The phalanges in the digits never exceed three, except in the whales. Mammals are spoken of as plantigrade, digitigrade, or unguligrade, accordingly as they walk upon the whole metacarpal or metatarsal region, as in the bear and man; or upon the distal phalanges, as in the cats and dogs; or, again, upon the nails (hoofs), as in the horse and cow.

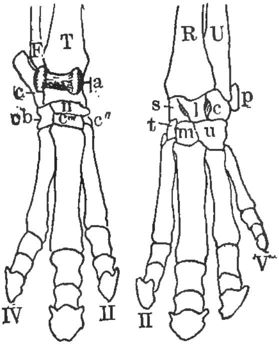

FIG. 348. Fore (right) and hind (left) feet of tapir. *a*, astragalus; *c*, cuneiforme in fore foot, calcaneum in hind foot; *c''*, *c'''*, cuneiforme; *cb*, cuboid; *F*, femur; *l*, lunare; *m*, magnum; *n*, naviculare; *p*, pisiforme; *R*, radius; *s*, scaphoid; *t*, trapezoid; *T*, tibia; *u*, unciforme; *U*, ulna.

The most striking feature of the nervous system of existing mammals is the great size of the brain, and especially of the cerebrum and cerebellum, the former overarching twixt and mid brains and reaching the latter. In the lower mammals the cerebral surface is smooth, but in the higher it is marked by gyri and convolutions, the effect of which is to increase the amount of surface and consequently of gray matter.[1] This great increase of the cerebrum is largely an increase of the pallium, only a small portion of which remains epithelial in character. In

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[1] By some authors the mammals are sub-divided into two groups, — Ineducabilia, with smooth cerebra (Fig. 349), and Educabilia, in which the surface of the cerebrum is convoluted (Fig. 54).

the aplacental mammals the anterior commissure is especially well developed, and forms the chief connection between the two sides of the brain, while the corpus callosum remains more rudimentary, as in sauropsida. In the placentalia, on the other hand, the corpus callosum or commissure between the two hemispheres becomes the most important connection between the right and left sides, the anterior commissure remaining behind. The longitudinal commissures, the fornix, and the cornua ammonii, are also well developed. The lateral ventricles are large, and in them several sub-regions are distinguished,—anterior and descending, and in the higher mammals posterior cornua. The olfactory lobes are comparatively small, and in the whales are absent. In development a diverticulum of the lateral ventricle extends into each olfactory lobe, but except in a few forms, like the horse, this disappears in the adult.

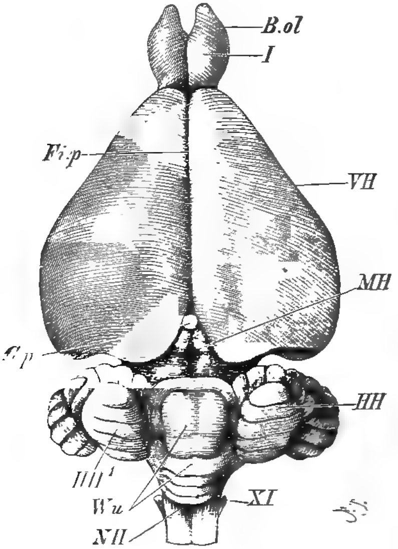

FIG. 349. Brain of rabbit from above, from Wiedersheim. *Bol*, olfactory bulb; *Fip*, pallial fissure; *Gp*, pinealis; *HH*, cerebellar hemispheres; *NH*, medulla; *VH*, cerebral hemispheres; *Wu*, vermis.

The twixt brain and optic lobes (corpora bi- or quadrigemini) are poorly developed, and are covered in by the hinder lobe of the cerebrum. The epiphysis is small and lacks any sensory structures. In the cerebellum the vermis is large in the aplacentals, but in the placentalia the lateral lobes of the cerebellum are in the ascendancy. A corresponding increase from lower to higher is seen in the pons varolii. The spinal cord extends back only to the sacral region, the posterior part of the spinal canal being occupied by a cauda equina formed of the more posterior nerves before their exit.

The olfactory organ is noticeable for the great increase of the olfactory epithelium and the corresponding complexity of the bony labyrinth which supports it. In the formation of this labyrinth small bony processes play the greater part, the upper (superior turbinal) being an outgrowth from the ethmoid, the lower (inferior turbinal) usually uniting with the maxillary. The two cavities are separated behind by the ethmoid and vomer, the partition being continued to the tip of the nose by cartilage. Connected with the nasal cavities are numerous sinuses in the frontal, maxillary, and sphenoid bones. The olfactory nerve breaks up into numerous fibres before leaving the cranial cavity, and these pass through the perforations in the cribiform plate of the ethmoid.

The eyes vary according to the habits, being small in burrowing forms, or even occasionally without muscles and beneath the skin (*Spalax*, *Chrysochloris*). As a rule the eyeball is approximately spherical, except in the whales, where it is flattened. It is placed in orbits, usually incomplete, and these are more or less lateral in position. Sclerotic bones are never developed. Besides the upper and lower lids, a nictitating membrane is usually well developed, but sometimes, as in man, this is reduced to a small muscleless fold, the plica semilunaris, at the inner angle of the eye. In the sirenia the eyelids act as an iris-like diaphragm. Frequently a seventh muscle of the eye, a retractor bulbi, is present, and in the carnivores this is four-divided. In carnivores, dolphins, ungulates, and some marsupials, a metallic lustre is developed in a part of the choroid (tapetum).

The ears are marked externally, except in monotremes, cetacea, and some seals, by the development of a conch, supported by cartilage, and moved by appropriate muscles. From this the external meatus leads inward to the tympanum, which is crossed by the three ossicula auditus — malleus, incus, and stapes — already mentioned (p. 358). From the tympanum the Eustachian tube (p. 73) leads to the pharynx, except in the whales, where it enters the nasal passages. The inner ear is characterized by the great development of the lagena which coils with two or three turns to form the spiral cochlea. The monotremes have the inner ear more on the sauropsidan plan.

Except in the monotremes, which are provided with a horny beak, the mouth of the mammals is bounded by movable lips near the margins of the jaws; between the lips and the jaws on either side are the cheeks, and in many apes and rodents these are developed into large cheek-pouches, sometimes hairy on the inner surface. A tongue is always present. In the cetacea it is immovable, in all others it is mobile and sensory, and in the giraffe it is even prehensile. At its base it bears the papillæ circumvallatæ, special aggregations of taste buds. Beneath the tongue is a single or double under-tongue or **sublingua,** especially developed in the insectivores, which may be the homologue of the tongue of the lower vertebrates, the functional tongue being a new formation. Three pairs of salivary glands are present (parotid, submaxillary, and sublingual) except in the carnivorous cetacea. The secretion is most abundant in the herbivorous mammals. A soft palate is alway present, behind which are the choanæ.

The teeth show a greater range of variation than is found in any other group of vertebrates. They are lacking in but few forms, as *Echidna*, *Manis*, and the baleen whales, while in the adult *Ornithorhynchus* they are replaced by cornified teeth, although true teeth are present in the young. They never have such an extensive distribution as is found in reptilia and ichthyopsida, but are confined to the margins of maxillary, premaxillary, and mandibular (dentary) bones. In all cases they are **thecodont**, *i.e.*, are situated in sockets or alveoli, although, as in the dolphins, the sockets may run together into a continuous groove, while in some shrews the molars in the adult are firmly anchylosed to the jaws.

In a few cases, as in the denticete whales, the teeth are all similar in form (**homodont**), but usually they are differentiated (**heterodont**) into incisors, canines, and molars. The incisors are placed in the premaxilla,[1] and in a corresponding position in the lower jaw. The **canines** are placed behind the suture separating maxillary and premaxillary bones, and never exceed one on a side in either jaw. Behind the canines are the molars. Incisors and canines have single roots, and the crown is usually a

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[1] In some armadillos the premaxillary teeth cannot be incisors.

simple cone or chisel. The molars vary greatly in shape and structure, and may have several roots, a feature not found in other living vertebrates.

The shapes and modifications of the molars are of great value in classification, and a few definitions may prove of use in reading the descriptions of systematic works. In the more primitive teeth, each tooth, no matter where placed, has the shape of a simple cone, as in the denticete whales (**haplodont**), but usually the crowns of the molars present crests, prominences, tubercles, etc. There are two views as to the origin of the more complex condition. According to the one, the typical mammalian molars have arisen by the fusion of several simple teeth, like those of many reptiles. The other view is that accessory prominences have been developed upon the primary tooth, a view which has much in its favor. First to appear of these more complex teeth was the **triconodont,** in which secondary prominences — cones in the upper jaw, conids in the lower — were developed in a straight line, a **paracone** (**paraconid**) in front of the primary or **protocone,** and a **metacone** behind. In the tritubercular tooth, which came next in turn, the three cones are arranged in a triangle, the protocone on the inner side, the protoconid on the outer. This part of the tooth forms the **trigon,** and from this modifications may be developed in different directions. Thus, while retaining its tubercular character, a posterior lower heel or **talon** may be formed, and when this develops a single tubercle it is known as the **hypocone** or **hypoconid,** the former occurring at the postero-internal angle of the upper molars, the latter at the postero-external angle of the lower. **Protoconule** and **metaconule** are smaller intermediate cusps, while the crests which connect the cones and conids are known as **lophs.** Again, peripheral cusps or **styles** may arise outside these from the girdle or cingulum of the tooth.

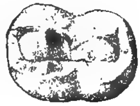

FIG. 350. Bunodont tooth (upper M^3 of baboon).

The tubercles and lophs of the teeth also vary in character. When the surface is calculated for cutting, the tooth is **secodont,** when for crushing, it is **bunodont;** with the development of prominent transverse crests the tooth becomes **lophodont.** When the crests, crescentic in character, have a longitudinal direction, the tooth is **selenodont.** These characteristics may be combined, giving the types called bunolophodont, bunoselenodont, etc.

The teeth first formed may be the only ones to appear during life, when we speak of a **monophyodont** condition as in the monotremes, cetacea, and edentates; or again, we may have a first or milk dentition to be replaced later by a permanent set (**diphyodont**[1]). Milk and permanent dentitions are not exact repetitions of each other, more molars appearing in the permanent than in the milk dentition. This leads to a differentiation of the molars into **premolars** (**bicuspids** of the dentist) which occur in both sets, and molars proper, which appear only with the permanent dentition.

In homodont dentition the number of teeth is very large, and may vary between one and two hundred. In heterodont types this number is greatly reduced. It is greatest in the marsupials, where there may be five incisors and six molars on either side in either jaw. In placental mammals the incisors never exceed three, and the full dentition may be stated as including 44 teeth. Not infrequently, as in rodents and ruminants, the canines may be lacking, producing a gap or diastema between incisors and premolars, while not infrequently the incisors may not be developed in the adult.

To express in concise form the number of teeth present in any mammal — a matter of great importance in classification — a dental formula has been adopted, in which the kinds of teeth are represented by the letters *i*, *c*, *p*, and *m*, while the number of teeth in upper and lower jaws are represented by figures above and below a line. Since the two halves of either jaw are mirror-like repetitions, only the teeth in one side are represented. The dental formula of the adult man is expressed thus: —

$i\,\frac{2}{2},\ c\,\frac{1}{1},\ p\,\frac{2}{2},\ m\,\frac{3}{3} = 32;$

that of the horse, $i\,\frac{3}{3},\ c\,\frac{1}{1},\ p\,\frac{3}{3},\ m\,\frac{3}{3} = 40;$

that of the cow, $i\,\frac{0}{3},\ c\,\frac{0}{0},\ p\,\frac{3}{3},\ m\,\frac{3}{3} = 30.$

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[1] Stirling has described teeth in the marsupial *Myrmecobius*, formed before the milk set, which, taken in connection with the studies of Küchenthal and Röse, show that the marsupials, like most other mammals, are diphyodont, and may lead to the conclusion that the milk dentition must be a second set, and the permanent teeth a third.

A few other facts concerning the teeth may be added. Occasionally, as in rodents and elephants, the incisors may have persistent pulps, and hence may continue to grow throughout life. The enamel is lacking in a few forms, like the edentates and the dugongs. The milk dentition is lacking in some rodents; in the guinea-pig the milk dentition is shed in utero, and in the seal it never cuts the gums. Finally, there is such correlation between the teeth and other structural features, that the dentition affords an index to the classification, and hence becomes of great assistance to the paleontologist.

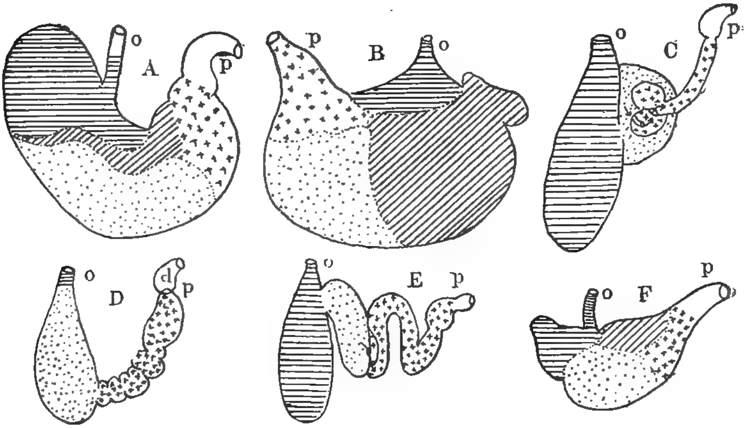

FIG. 351. Diagrams of stomachs of, *A*, horse; *B*, pig; *C*, *Lagenorhynchus*; *D*, ziphioid whale; *E*, seal; *F*, rat. *d*, duodenum; *o*, œsophagus; *p*, pylorus; œsophageal region horizontally lined; cardiac gland region obliquely lined; fundus gland region dotted; pyloric gland region with crosses; after Oppel.

The œsophagus is greatly elongated, extending from the pharynx through the diaphragm to the stomach. Usually the stomach is regarded as the saccular enlargement of the alimentary canal, lying between the œsophagus and the intestine; but when histological and physiological features are taken into account, it is seen that frequently the lower end of the œsophagus expands, and takes part in the formation of the gastric enlargement, and that the stomach proper begins only where the gastric glands appear. Of these glands three kinds are recognized, cardiac, fundus, and pyloric, for the characters of which reference must be made to histological text-books. On the basis of these glands the stomach may be divided into regions, when it is seen that in the monotremes the morphological stomach is entirely lacking, the enlargement which occurs being œsophageal. More frequently the cardiac glands are lacking.

Speaking of the stomach in the more usual sense, it may be said that usually its axis lies at right angles to the axis of the body, and that only exceptionally, as in the seals, is it longitudinal.[1] The stomach may be a simple sac, as in man, but in the cetacea and ruminants it becomes divided into several chambers, the extremes of differentiation being reached in the ruminants, where (the tylopoda and tragulina excepted) four distinct regions, the rumen (paunch), reticulum (honeycomb), psalterium, or omasum (manyplies), and abomasum may be recognized; but of these only the last is a true glandular stomach, the others being œsophageal enlargements.

The intestine is differentiated into small and large divisions, the line between them being marked by the ileocolic valve. The first part of the intestine, the duodenum, is characterized by receiving the ducts of liver and pancreas, and also by the presence of Brunner's glands in its walls. The small intestine is greatly convoluted. The large intestine is of larger diameter than the small, and its walls show outsackings or lobulations. It presents two divisions, a rectum, situated in the pelvis, and comparable to the large intestine of the lower vertebrates, and a much longer colon, which appears for the first time in mammals. Just beyond the ileocolic valve is a blind diverticulum, the cæcum, which undergoes great variations in size. It is largest in the herbivora, where it may equal the body in length, while in the edentates, carnivores, toothed whales, bats, etc., it may be small or even absent. In many rodents, apes, and man, the distal part of the cæcum becomes reduced in size, and forms the appendix vermiformis. The rectum terminates, except in the monotremes, in an anus dorsal to the urogenital opening. In that group it and the urogenital system empty into a cloaca as in the sauropsida.

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[1] In the seals (Fig. 351 *E*), it is only the œsophageal part of the stomach that is longitudinal, the true stomach being transverse.

The liver, often lobed in a complicated manner, is divided into right and left halves by the ligamentum teres, itself a vestige of the earlier umbilical vein. The left half is frequently sub-divided into left and central lobes, while the right also is usually sub-divided, and may have a caudate lobe laterally placed, while a spigelian lobe projects dorsal to the entrance of the portal vein. A gall bladder, which arises as a diverticulum of the hepatic duct, is rarely absent (horse, whales, and some rodents). The pancreas is usually compact, but in some rodents it is diffuse. Its duct, as a rule, unites with the hepatic duct; but occasionally these may empty into the duodenum at points widely remote from each other.

As in the birds, the heart is four-chambered; the divisions occasionally are visible from the outside as in the dugong. Its major axis is horizontal except in the anthropoids and man. The arch of the aorta bends to the left, a condition referable back to the fact that it is the persistent (fourth) primitive arch of the left side. From the proximal portion of the aorta there are given off, first, the coronary arteries (usually paired), which go to the walls of the heart, and then the subclavians and carotids, the arrangement of which shows many variations; the most usual condition being first a right arteria anonyma, dividing later into right subclavian and the two carotids, and then the left subclavian. Other arrangements can be seen from the diagram. In all cases the right subclavian is in part the persistent right fourth arch of the embryo. The internal carotids enter the cavity of the brain either through the periotic (petrosal) bone, or between it and the base of the skull.

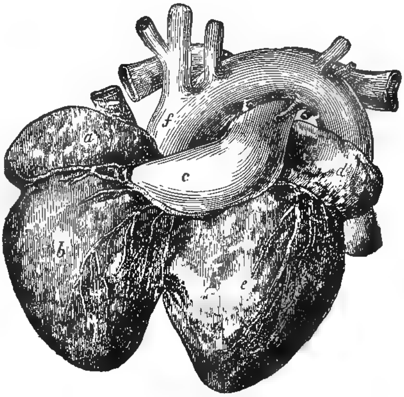

FIG. 352. **Heart of dugong,** after Macalister, showing the double character of the ventricles, *b*, *e*; *a*, *d*, auricles; *c*, pulmonary aorta; *f*, systemic aorta.

In the venous system the most noticeable points are the presence of valves, at least in the veins of the extremities. Both pre- and postcavæ empty directly into the right auricle without the presence of a sinus venosus. In rodents, monotremes, and the elephants, two precavæ occur. Rete mirabilia are frequent in various situations. The red blood corpuscles are anucleate and, except in tylopoda where they are oval, are circular disks.

The lymph vessels, which contain numerous valves, empty by means of a principal or thoracic duct into the precava near the subclavian vein. In their course are numerous lymph glands. Closely related to the lymph system are a couple of masses of adenoid tissue, the tonsils, peculiar to the mammalia, placed at the entrance of the pharynx.

The entrance to the trachea (glottis) is covered by a fleshy fold, the epiglottis. The larynx is well developed, with arytenoid, cricoid, and thyroid cartilages (p. 28), and these, moved by appropriate muscles, put various tensions, etc., upon the vocal cords. The cartilaginous tracheal rings are usually incomplete behind; the trachea itself is never convoluted, and it divides behind into two bronchi, with occasionally a secondary bronchus on the right side. Inside the lung the rule is a single eparterial bronchus arising above the entrance of the pulmonary artery, and nine hyparterial bronchi on either side. Air sacs never occur.

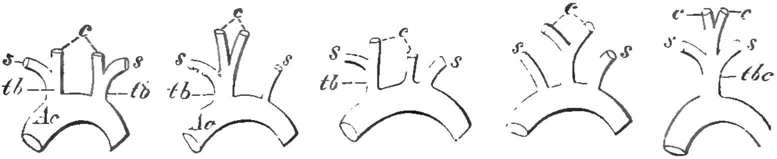

FIG. 353. Modifications of the aortic arch and its vessels in mammals, from Wiedersheim. *Ao*, aorta; *c*, carotid; *s*, subclavian; *tb*, truncus brachiocephalicus (anonyma); *tbc*, truncus brachiocephalicus communis.

The inspiration and expiration of air is effected in part by the intercostal muscles, which by their action alter the size of the thoracic cavity, and in part by a transverse muscular partition, the diaphragm, which divides the abdominal cavity of the lower vertebrates into an anterior or pleural cavity containing the lungs, and a peritonial cavity containing the other viscera (see p. 106). This diaphragm, while foreshadowed in some sauropsida, is only developed in the mammals.

The functional kidneys (metanephridia, p. 122) are small compact organs, only occasionally, as in some seals and whales, showing lobulations. The ureters leading from them empty into the dorsal part of the urinary bladder. The urethra leading from the bladder either empties into the cloaca (monotremes) or into the urogenital sinus. No renal portal system occurs.

In the monotremes and whales the testes remain in their primitive position near the kidneys, but in all other mammals they sink into the pelvis. In the elephants they do not proceed farther; in the rodents, bats, and some insectivora, they emerge during the breeding-season into a temporary sac or scrotum, and after this time is passed are retracted again by a cremaster muscle. In the other mammals the testes remain permanently in the scrotum after their descent, and the opening through which they descended closes. The cremaster muscle persists, but with more limited functions. Closely connected with the male genitalia are the prostate and Cowper's glands, the ducts of which empty into the genital duct (vas deferens), the secretion being added to the spermatozoa, rendering the whole more fluid.

The ovaries are relatively small, and are always abdominal in position. The oviducts have their inner ends wide, the internal apertures being usually fimbriate. In each duct three regions occur, (1) a somewhat narrow Fallopian tube leading to (2) a uterus with muscular walls, and (3) an external canal or vagina. In the lower mammals the ducts of the two sides may remain distinct, but in the higher fusion begins at the lower end, resulting in a single vagina and a uterus, which shows more or less clearly traces of its double origin.

In the monotremes the large eggs, covered by a flexible calcareous shell, pass to the exterior, but in all other mammals the embryo passes through a considerable portion of its development in the uterus, and is brought into the world in a more or less perfect condition.

The development of the mammals pursues two distinct types. In the monotremes there are eggs which are laid, and which undergo their development outside the body of the mother, as do those of birds and most reptiles. These eggs are large (about two centimetres in diameter). They have a large yolk, and the segmentation is restricted to a small portion of it, just as is the case in the sauropsida; *i.e.*, they are meroblastic.

In all other mammals the egg is much smaller, even microscopic in size, and the early stages of development are passed inside the mother, the young being born alive. These smaller eggs undergo a total segmentation, all parts dividing; *i.e.*, they are holoblastic. During this process the egg increases greatly in size by the absorption of fluid which fills the central cavity. As a result the egg is converted into a large sphere (blastula) covered by a single layer of cells except at one pole, where there are a number of 'inner cell-mass cells' beneath the others. Concerning these layers there is much difference of opinion, due to the great difficulty surrounding the subject. According to one view the outer cells are ectoderm, the inner entoderm; according to another the inner cell-mass is ectoderm, the outer entoderm, while a third view sees both ectoderm and entoderm in the inner cell-mass. Certain it is that the region of the inner cell-mass eventually becomes two-layered, and later the embryo is outlined here, only a portion of the blastula being utilized in its formation, the rest forming a yolk sac, in the walls of which omphalomeseraic vessels are developed later, although no yolk occurs.

This development of a complete yolk apparatus, as well as several other peculiarities, is to be explained upon the hypothesis that the mammals have descended from forms — like reptiles or amphibia — which were oviparous, and the embryo had to depend upon the food stored up in the yolk. Subsequently, as a result of an internal development and a supply of nourishment from the mother, the yolk was lost; but heredity has caused certain features not incompatible with uterine development to be retained. The mechanism by which this nourishment from maternal sources is transferred to the embryo has now to be outlined.

Like the other amniotes the mammalian embryo forms the fœtal structures amnion, serosa, and allantois (p. 288). Of these the serosa is the outermost, and necessarily comes in contact with the uterine walls. In most marsupials the development goes little farther. From the uterus is secreted nutrient fluid which passes through the serosa by osmosis, and is thence taken up by the embryo, furnishing it with the material for growth, which in oviparous forms is supplied by the yolk.

In *Perameles*, one of the marsupials, and in all the higher mammals, a more intimate union occurs between the embryo and the uterine walls in the following manner. From the surface of the serosa (which from this time on is known as the **chorion**) numerous outgrowths or villi are formed. These villi are variously arranged in different mammals. They may be distributed evenly over the whole chorionic surface (**diffuse**), or they may be collected in tufts scattered over the surface, the intermediate regions of the chorion being smooth (**cotyledonary**); again, they may form a girdle around the chorion, the ends being free from villi (**zonary**); or, lastly, they may be restricted to a more or less circular patch on one side of the chorion (**discoidal**). These villi enter into more or less intimate connection with the uterine walls in ways to be described below.

The allantois (p. 289) grows out from the body, and finally reaches the inner surface of the chorion, carrying with it the allantoic blood-vessels. The union of chorion and allantois is coextensive with the development of the villi upon the outer surface, and the resulting structure forms the embryonic portion of the **placenta**. The blood-vessels of the allantois may be confined to that structure, or they may extend out into the chorion, but in either case they carry away from the embryo waste which passes, by osmosis, to the maternal tissues, and at the same time bring back to the growing young nourishment and oxygen, which pass into the fœtal blood by osmotic action. In no case is there a direct connection between maternal and fœtal blood-vessels; but the exchange is always of the character indicated here.

It must, however, be noted that the relations of the allantois to the chorion follow two types. In the unguiculate mammals the allantois early grows out to join the chorion, and brings with it its blood-vessels, which then ramify through the chorion, which therefore has its own circulation, although this is dependent upon the allantois. In the ungulates the allantois, although well developed, remains for a considerable time distinct from the chorion, and only later, when its expansion brings it in contact with the latter, does the chorion receive its vascular supply. These two types are known respectively as the allantoic and chorionic placenta.

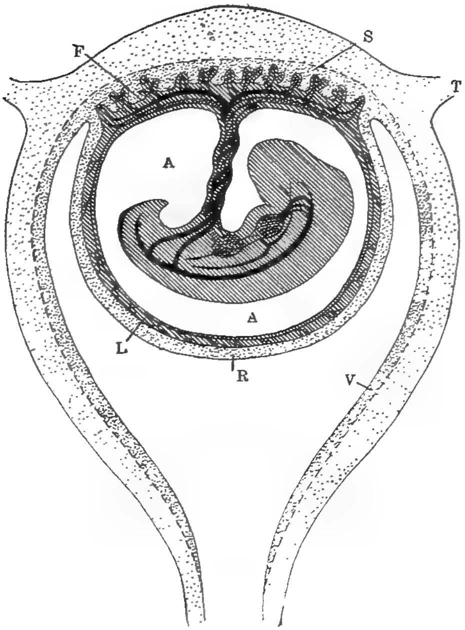

FIG. 354. Diagram of human uterus and placenta, based on Wiedersheim. Fœtal parts lined, uterine dotted, the decidual portions darker. *A*, cavity of the amnion; *F*, fœtal placenta; *L*, chorion læve; *R*, decidua reflexa; *S*, maternal placenta (decidua serotina); *T*, entrance of Fallopian tube; *V*, decidua vera.

In many mammals the union between the villi of the chorion and the uterine walls is slight, and at the time of birth the two separate, only the embryonic placenta being cast off. These forms—including the ungulates, cetacea, sirenia—are called non-deciduata, or indeciduata. In others the union is far more intimate, the branched villi entering into such close connection with the uterus[1] that, at the time of birth, a portion or all the uterine walls (the **decidua**) is cast off with the embryonic, or fœtal, placenta. In some mammals, as in man, the decidua exhibits certain peculiarities. At the time of at-

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[1] This forms the **uterine placenta.**

tachment of the ovum to the walls of the uterus, these walls rise up over and enclose the egg, thus coming in contact with it on all sides. From but one side, however, is the (discoidal) placenta developed, and in this region the decidua is spoken of as the **decidua serotina,** while that which covers the smooth or non-villous portion of the chorion (**chorion læve**) forms the **decidua reflexa.** The rest of the uterine walls, which do not connect with the ovum, are also cast off at birth, and these form the **decidua vera.**

In older books the eutheria of the following pages are frequently divided into the Implacentalia, including the marsupials, and the Placentalia, including the remaining orders; but the recent discovery that at least one genus of marsupials (*Perameles*) has a true allantoic placenta tends to break down this line. Still the distinction is one of convenience, and has been used in these pages, the term placentalia including all the orders from edentates to primates, the implacentalia, the marsupials, and frequently the monotremes, when these have not been specially mentioned.

There are two views as to the origin of the mammals; the one that they have descended from the theromorphous reptiles, the other that they have sprung from the amphibia. The first of these receives its chief support from paleontology. The theromorphs have a heterodont dentition, a triple occipital condyle from which the paired condyles of the mammals can be derived by a suppression of the basioccipital portion, as well as several features in the skeleton of the limbs. The advocates of this view suppose that the quadrate has disappeared in the region of the glenoid fossa.

The amphibian view receives its support in the double occipital condyle, the impossibility of deriving the mammalian ovum from that of any known reptiles, and its easy homology with those of amphibia, and in the relations of the ear bones. This view recognizes the quadrate in the incus, and this articulates with the stapes, a condition repeated in the urodeles, but not derivable from anything known in the reptiles (see p. 159). Another difficulty with the reptilian hypothesis is the impossibility of deriving the mammalian hair from any exoskeletal structures occurring in reptiles; while there are several features which point to the possibility of their origin from the dermal sense organs of the amphibia.

SUB-CLASS I. PROTOTHERIA.

Mammals with a single opening for urogenital system and alimentary canal; sutures of skull obliterated in the adult; a well-developed coracoid and episternum; oviparous.

ORDER I. MONOTREMATA (ORNITHODELPHIA).

Prototheria with small corpus callosum and large anterior commissure; no teeth in the adult; epipubic bones present; ribs with capitular head only; mammary gland without distinct nipple.

The few existing species of monotremes are restricted to the Australasian region, and the only fossils certainly belonging to the order occur in the pleistocene of Australia. These mammals are remarkable for the large number of sauropsidan features which they present. Besides the characters given in the diagnosis the following may be added. The ossicula auditus are of a low grade, the malleus being large and the stapes columelliform. In the embryo of the duckbill multituberculate teeth occur, but these are lost before maturity, and the adults of all species are toothless. Lips are lacking, and the jaws form horny beaks. The brain is smooth in *Ornithorhynchus*, convoluted in *Echidna*. The testes are abdominal in position; the left ovary is reduced as in birds, the right lobular. There is a horny perforated spur developed on the hind legs in connection with a gland. This spur disappears in the adult female duckbill.

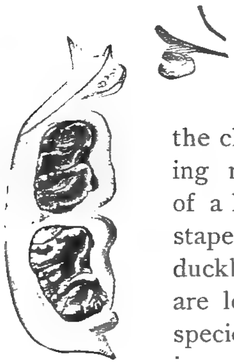

FIG. 355. Embryonic teeth of *Ornithorhynchus*, after Stewart.

Family ORNITHORHYNCHIDÆ. With duck-like bill, two horny teeth in each jaw; feet pentadactyl, webbed; tail flat; soft, close fur. *Ornithorhynchus paradoxus*, the duckbill of Australia and Tasmania, is the only known species. It leads an aquatic, burrowing life, and feeds upon worms and small aquatic animals, using its bill as does a duck.

Family ECHIDNIDÆ. Beak elongate, toothless; tongue elongate, vermiform; body with strong spines among the hair. *Echidna*, with three species from Australia, New Guinea, and Tasmania, has all the toes clawed. In *Acanthoglossus*, from New Guinea, there are claws on but three toes, and the beak is longer. All of these spiny ant-eaters are burrowing animals, feeding chiefly upon ants. *Echidna* occurs as a fossil in the Australian pleistocene.

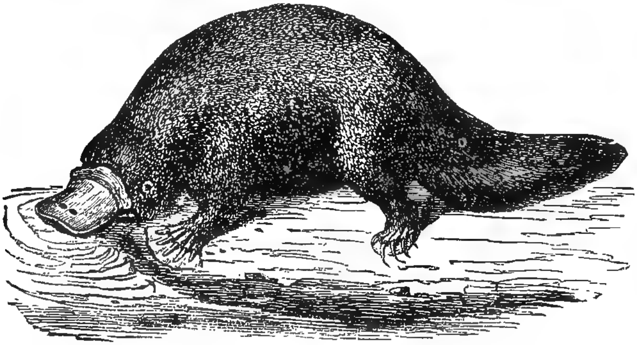

FIG. 356. Duckbill, *Ornithorhynchus paradoxus*, from Lütken.

The earliest fossil mammals yet found occur in the triassic of North Carolina, South Africa, and Germany. Little is known of them except of their jaws and teeth. Allied forms are more abundant in later rocks, and some of them persist until the eocene. From peculiarities of the teeth, which present certain resemblances to the embryonic teeth of *Ornithorhynchus*, these fossils are sometimes placed as members of the Prototheria, an example followed here; although they also present resemblances to the marsupials.

ORDER II. PROTODONTA.

Incisors reduced, molars with compressed cutting crowns and undivided roots. Represented only by lower jaws of *Dromatherium* and *Microconodon* from the American Jurassic.

ORDER III. MULTITUBERCULATA (ALLOTHERIA).

Incisors enlarged, molars tuberculate with distinct roots. In these forms, which are represented by several genera, the teeth are very numerous, ranging from 48 to 68. *Plagiaulax* from the Purbeck beds (upper Jurassic) of England; *Ctenacodon*, American Jurassic; *Chirox* and *Polymastodon* from the Puerco (lower eocene) of America. The Australian quaternary *Thylacoleo*, usually regarded as a marsupial, may belong here.

SUB-CLASS II. EUTHERIA.

Mammals with anus distinct from the urogenital opening; sutures of the skull well marked; episternum reduced; coracoid not articulating with the sternum, but reduced and fused with scapula; viviparous; mammæ with teats.

Legion I. Didelphia.

Eutherian mammals, with small corpus callosum, usually with marsupial bones (except in *Thylacinus*). Vaginæ partially or completely double. As a rule no placenta developed.

ORDER I. MARSUPIALIA.

Teeth always present, only one (p^3) replaced by a second dentition, the number usually different in upper and lower jaws; two precavæ present; mammæ abdominal in position and usually enclosed in a pouch in which the very immature young are placed after birth.

The order marsupialia and the legion didelphia are coextensive. The living species are almost exclusively confined to Australia and the adjacent islands; the only exceptions being the family didelphidæ, which is American. Fossils, however, are found in Europe as well. Forms certainly belonging to the order first occur in the eocene; but others, possibly related, date from the cretaceous. The order receives its name from the pouch (marsupium) in which, in most species, the young are carried after birth; but this pouch is not invariably present, the young in these cases being held in the fur covering the abdominal region. When first born the young are very immature. They are transferred by the mother to the nipples, to which they adhere closely. Milk is forced into their mouths by mammary muscles, and strangulation of the young is prevented by a prolongation of the larynx into the choana, much as in the whales. In development the ova pass into the uterus, from which they absorb nourishment without the intervention of a placenta (except in *Perameles*), no villi being developed on the serosa, and the allantois failing to reach this envelope. An osteological peculiarity, present in all except in *Tarsipes*, is the inflection of the posterior angle of the jaw.

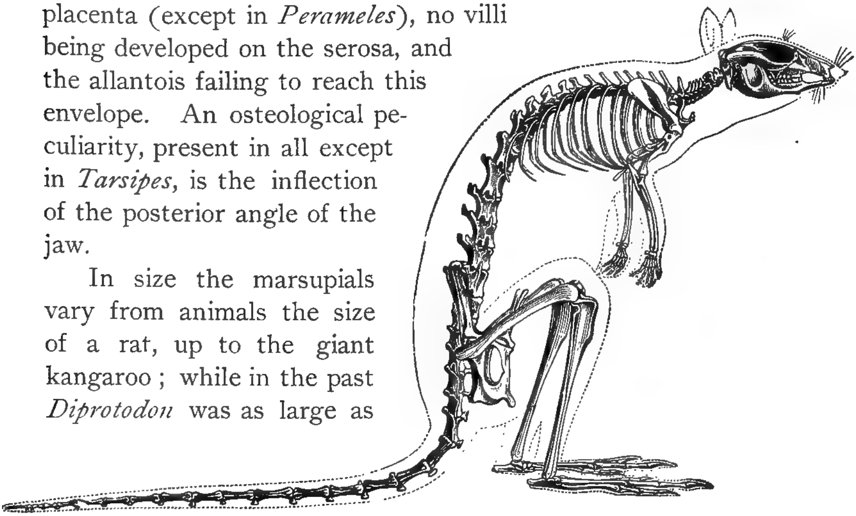

FIG. 357. Skeleton of kangaroo, from Macallister.

In size the marsupials vary from animals the size of a rat, up to the giant kangaroo; while in the past *Diprotodon* was as large as a rhinoceros. In form and habits they show many modifications, usually attributed to the fact that in Australia they have been removed from competition with other mammals, and have developed in every direction, — terrestrial, crawling, leaping, climbing, and soaring forms. The majority are nocturnal.

SUB-ORDER I. POLYPROTODONTIA.

Incisors $\frac{5 \text{ or } 4}{4 \text{ or } 3}$, small, subequal; canines larger; molars acutely tuberculate.

The DIDELPHIDÆ, opossums, American; teeth $i\,\frac{5}{4}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$, $m\,\frac{4}{4}$; feet all five-toed; tail partially naked and usually prehensile. *Didelphys virginiana*, north to New England; other species in the tropics. *Chironectes* has webbed feet. *Didelphys* occurs in the eocene of France and America. DASYURIDÆ $i\,\frac{4}{3}$, $c\,\frac{1}{1}$, $p\,\frac{2 \text{ or } 3}{2 \text{ or } 3}$, $m\,\frac{4\text{–}6}{4\text{–}6}$; hind feet four-toed. *Thylacinus* is dog-like, carnivorous, and occurs in Tasmania. *Myrmecobius* with $m\,\frac{6}{6}$, feeds on ants. *Dasyurus*, *Phascogale*. Allied forms fossil in lower tertiary of South America and later tertiary of Australia. The PERAMELIDÆ, $i\,\frac{5}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$,

$m\ \frac{4}{4}$, include the genera *Perameles*, in which the feet are much alike, and *Chœropus*, in which the hind legs are very long and the fourth toe alone functional. The bandicoots (*Perameles*) are noticeable from the existence of a placenta. Fossils, which in some respects closely resemble the polyprotodonts and in some the insectivores, are the TRICONODONTA and TRITUBERCULATA, with the genera *Amphilestes*, (Jurassic, England and the U. S.), *Dicrocynodon* (Jurassic, Wyoming), *Amphitherim* (English oolite). *Dryolestes* (Jurassic, Wyoming), etc.

FIG. 358. Opossum, *Didelphys virginiana*, after Audubon and Bachman.

SUB-ORDER 2. DIPROTODONTA.

Incisors $\frac{1-3}{1-3}$, the central ones large, the others reduced; canines small or absent; molars with blunt tubercles or transverse ridges.

In the kangaroos and wallabies (MACROPODIDÆ) the hind legs are very large: the feet as in *Perameles*; the teeth $i\ \frac{3}{1}, c\ \frac{0}{0}$ or $\frac{1}{0}, p\ \frac{2 \text{ or } 1}{2 \text{ or } 1}, m\ \frac{4}{4}$: tail very large. The larger kangaroos belong to *Macropus*; the arboreal tree-kangaroos to *Dendrolagus*. *Macropus*, *Palorchestes*, etc., occur in Australian pleistocene. The PHALANGISTIDÆ includes climbing and flying (soaring) forms, with legs of equal size, teeth $i\ \frac{3}{1}, c\ \frac{1}{0}, p\ \frac{2-3}{2-1}, m\ \frac{4}{4}$, tail long. *Tarsipes* is an aberrant form about as large as a mouse. *Petaurus*, *Belidius*, etc., resemble the flying-squirrels in the lateral fold of skin and flying habits. *Cuscus* and *Phalangista* resemble the opossums in their prehensile tail. *Phascolarctos*, the koala, contains but a single climbing species two feet long. The THYLACOLEONIDÆ includes large fossil forms from the Australian pleistocene, with teeth $i\ \frac{3}{1}, c\ \frac{1}{0}, p\ \frac{3}{3}, m\ \frac{1}{2}$. The kangaroo-rats, or HYPSIPRYMNIDÆ, with teeth $i\ \frac{3}{1}, c\ \frac{1}{0}, p\ \frac{1}{1}\ m\ \frac{4}{4}$, resemble the kangaroos in the disproportionate hind legs. *Hypsiprymnus*, *Bettongia*, the last also in the Australian pleistocene. The DIPROTODONTIDÆ includes only fossil forms of large size from the Australian pleistocene, with the teeth $i\ \frac{3}{1}, c\ \frac{0}{0}, p\ \frac{1}{1}, m\ \frac{4}{4}$. *Diprotodon australis* was larger than a rhinoceros; the species of *Nototherium* somewhat smaller. The PHASCOLOMYIDÆ, with a dental formula $i\ \frac{1}{1}, c\ \frac{0}{0}, p\ \frac{1}{1}, m\ \frac{4}{4}$, differ from all other marsupials in the presence of persistent dental pulps. The living wombats all belong to *Phascolomys*, which also occurs in the pleistocene. The extinct *Phascalonus* was as large as a tapir. South America has yielded several fossil diprotodonts of eocene or miocene age, and one recent species, *Cœnolestes obscurus*, has been described from Colombia.

Legion II. Monodelphia (Placentalia).

Eutherian mammals with well-developed corpus callosum and small anterior commissure; no marsupial bones; vagina single; fœtus nourished by an allantoic placenta.

ORDER I. EDENTATA (BRUTA).

Placental mammals with the incisors, and occasionally all the teeth, lacking. Teeth when present, usually prismatic; molars without enamel. Carpals and tarsals usually in linear series (taxeopodous, p. 392); digits armed with long, compressed, and pointed claws.

The Edentata includes a rather heterogeneous assortment of forms, the range of variation being even greater when the fossils are considered. Most of the species are not strictly edentulous, since molars are usually present. These are homodont, and except in *Tatusia* they are monophyodont and have persistent pulps. The skin is covered with hair, horny scales, or bony shields, these sometimes uniting into a more or less complete armor for the body. The mammæ are thoracic or abdominal in position. The cerebral hemispheres are small. The placenta shows great variations; it may be deciduate or not; in shape it may be diffuse, discoidal, or of discoidal lobes, or zonary.

The edentates are given a position here at the base of the placental mammals because of their low grade of structure. In some respects, as in the simple condition of the brain, this low grade is primitive; but in other respects, as in skeleton and teeth, the group is clearly degenerate, although as yet it is uncertain from what group they have sprung. According to Cope they have probably descended from the group of tillodontia of the later cretaceous and eocene. The earliest fossil edentates known occur in the Santa Cruz beds of Patagonia, regarded by Ameghino as eocene, but by some as oligocene; and it is interesting to note that these early forms retained traces of enamel upon the teeth.

The group, as a whole, belongs to the tropics and the southern hemisphere, but few species straying north of the tropic of cancer. In times past they had a greater range; for while the centre even then was in the south, a few species occurred as far north as southern Europe, and to latitude 46° in the new world. The American forms differ from those of the old world in the existence of articular processes, besides the normal zygapophyses on the presacral vertebræ. These have therefore been called Xenarthra in contradistinction to the Nomarthra of the eastern hemisphere. To the Nomarthra belong the sub-orders Fodientia and Squamata; the other sub-orders are xenarthrous.

SUB-ORDER I. FODIENTIA.

Body covered with sparse, bristle-like hairs, five prismatic molars in each jaw; femur with a third trochanter, toes four in front, five behind; placenta zonular. Only the single family, ORYCTEROPODIDÆ, containing the aardvark, *Orycteropus capensis*, of South Africa and a fossil species from the miocene of the island of Samos. The aardvark lives a burrowing life, feeding upon ants and other insects. It is about as large as a pig.

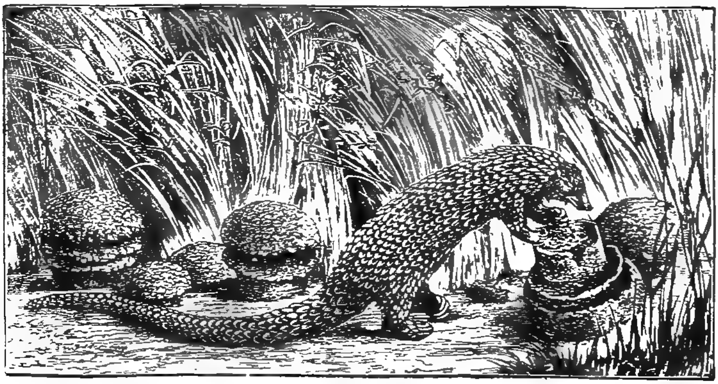

FIG. 359. Pangolin, *Manis longicaudata*, from Monteiro.

SUB-ODER 2. SQUAMATA.

Body covered with overlapping horny scales and scattered hairs; jaws toothless; tongue long, vermiform; feet five-toed; placenta non-deciduate, diffuse. Contains the single family MANIDÆ, the scaly ant-eaters or pangolins of Asia and Africa. Only genus *Manis*, which also occur fossil in the pleistocene of Asia. All the species are arboreal and insectivorous; and have a somewhat reptilian appearance on account of the scaly body and long tail.

SUB–ORDER 3. VERMILINGUIA.

Body hairy; skull very long; no teeth; tongue very long and mobile; tail elongate; hind feet five-toed; placenta deciduate, dome-like or discoidal. The ant-eaters form the family MYRMECOPHAGIDÆ, all of which live in tropical America, where they feed upon ants and other insects; a few are arboreal. *Myrmecophaga jubata*, the great ant-eater, five feet long, lacks a claw on the fifth fore toe. In *Cyclotura* only digits 2 and 3 are clawed. Fossils (*Scotæops*), supposed to belong to this sub-order but with two molar teeth, occur in the Patagonian eocène.

SUB–ORDER 4. TARDIGRADA.

Body haired; head short and rounded; molars $\frac{5 \text{ or } 4}{4 \text{ or } 3}$. The BRADYPODIDÆ, or sloths, have cylindrical teeth; short, weak tail; long, slender limbs; digits armed with long, strong claws; and deciduate, dome-like placenta with numerous discoidal lobes. *Bradypus*, the three-toed sloths; *Cholæpus*, the two-toed sloths. Both genera have the hind feet three-toed, and are noticeable for the number of cervical vertebræ (p. 355). They are arboreal, and live almost entirely in the trees. *Entelops* from the eocene of Patagonia. The extinct MEGATHERIIDÆ includes giant edentates from the pleistocene of both Americas. They had prismatic teeth of peculiar structure; large, long tails and stout limbs; feet 3–5 toed. *Megatherium* from South America, and one doubtful species from the U. S. The largest species equalled an elephant in size. *Megalonyx*, first described by Thomas Jefferson, and *Mylodon* ranged north to Pennsylvania. *Zamicrus*, Patagonian eocene. There is some evidence that a species of *Mylodon* (*Neomylodon*) still persists in Patagonia.

SUB–ORDER 5. LORICATA.

Body with armor of bony plates; teeth prismatic, usually $\frac{8 \text{ to } 10}{7 \text{ to } 9}$. GLYPTODONTIDÆ; trunk plates united into a solid carapace, with other plates on the tail; dorsal vertebræ fused to a continuous tube. Tertiary and pleistocene of South America and north to U. S. *Glyptodon*, *Hoplophorus*, *Parocthus*. These resembled turtles in appearance. One species 12 feet long. DASYPODIDÆ, dermal armor in three or more movable transverse rows, vertebræ free. These armadillos first appear in the Patagonian eocene, and continue until the present. The living species are small, nocturnal, carnivorous forms. *Chlamydophorus;* teeth $\frac{8}{8 \text{ to } 9}$; armor of about 20 transverse bands; body truncate behind. *Dasypus;* teeth $\frac{9 \text{ to } 8}{10 \text{ to } 9}$; armor of two shields upon scapular and pelvic regions, with six or seven bands between. *Xolypeutes* with three bands; *Xenurus* with twelve or thirteen. *Tatusia* has $\frac{8 \text{ to } 7}{8 \text{ to } 7}$ teeth, all except the last preceded by milk dentition;

seven to nine movable armor bands. *Tatusia novemcincta* is the only armadillo entering the U. S. *Chlamydotherium* from the pleistocene of Florida and Patagonia stands nearest the glyptodonts. *Peltephilus*, eocene of Patagonia.

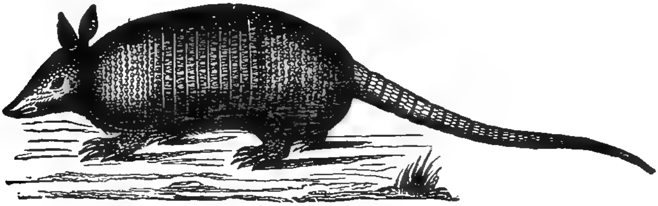

FIG. 360. Nine-banded armadillo, *Tatusia novemcincta*, from Lütken.

ORDER II. INSECTIVORA.

Small plantigrade mammals, usually with five toes armed with claws; carpals and tarsals usually in linear series; dentition complete, the incisors never less than two; canines little differentiated and weak; molars bunodont or lophodont, the cusps acute; clavicles almost invariably present; brain small, cerebrum without convolutions; placenta deciduate, discoidal.

The insectivores owe their name to the fact that the majority feed upon insects or other small invertebrates. They are all small, and the structure points to a low stage of organization. The body is covered with fur, and spines are not infrequently developed. The milk dentition is lost at an early date, and rarely is functional. The canine teeth are not sharply differentiated from the incisors or premolars, and the latter are sharp sectorial. The upper molars have three or four cusps. The testes are internal, and are never enclosed in a scrotum; the uterus is bicornuate. In a few genera vertebral intercentra occur in the dorsal region, a condition not paralleled in other mammalia. Among the more superficial but still very characteristic features is the prolongation of the muzzle far beyond the lower jaw.

Most of the order are nocturnal burrowing animals, only a few being aquatic or arboreal in habits. In external appearance they resemble the smaller rodents; but in structure they are more like the bats, with other resemblances to the polyprotodont marsupials, the creodont carnivores, and the lemurs. They inhabit to-day only the old world and North America; while the fossils occur only in the northern hemisphere, where they date back to the eocene. The order is one of the most primitive of the placental mammals; but as yet the fossils are too few and too imperfectly preserved to allow the complete working out of the lines of descent. As here limited the order includes only the Insectivora Vera. By some writers the galago, *Galeopithecus*, of the East Indies (see p. 415) is included in a second sub-order, Dermaptera.

The ICTOPSIDÆ, from the American eocene and miocene, have skulls much like the hedgehogs, but a simpler dental pattern. The ADAPISORICIDÆ take their place in the eocene of France. The TALPIDÆ, or moles, with $i\,\frac{3}{3}$ to $\frac{2}{1}$, $c\,\frac{1}{1}$, $pm\,\frac{4}{4}$ to $\frac{3}{3}$, $m\,\frac{3}{3}$, snout elongate, tympanic bulla present; fore limbs modified for digging, with a sesamoid bone (os falciforme) on the radial side; tibia and fibula united; are small burrowing animals, of which *Talpa* is the typical genus, with $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$. The species of *Talpa* belong to the temperate part of the old world. In America occur the genera *Scalops*, with 36 teeth, and *Condylura*, the star-nosed mole, with 44 teeth. *Talpa* dates from the miocene, *Talpavus* from the miocene. Allied are the MYOGALIDÆ, in which the falciform bone is absent. *Urotrichus*, the mole shrew, is the only North American genus. In the TUPAIIDÆ, in which the lower incisors are never less than two, the tibia and fibula are distinct, and the orbit is encircled by bone. The species are oriental in their distribution, and have arboreal habits. *Tupaia*. *Galerix*, from the European eocene. The shrews (SORICIDÆ), which appear in the eocene, are distributed through the northern hemisphere. They lack the postorbital process, have tibia and fibula fused, and no zygomatic arch; teeth $i\,\frac{1}{1}$ to $\frac{3}{1}$, $c\,\frac{1}{0}$, $p\,\frac{4-2}{2}$, $m\,\frac{3}{3}$. *Sorex* is represented by many species in both hemispheres. *Blarina* is American. *Crocidura*, *Nectogale*. The DIMYLIDÆ includes miocene species. In the ERINACEIDÆ, or hedgehogs, the dorsal surface is covered with spines or bristles. All of the species belong to the old world, and are terrestrial and nocturnal. The hedgehogs belong to *Erinaceus*, a genus which appears in the miocene. The species of MACROSCELIDÆ from Africa are known as the jumping shrews, from their kangaroo-like gait. The SOLENODONTIDÆ from the West Indies are remarkable for having the mammæ on the buttocks. The tenrecs (CENTETIDÆ) are from Madagascar. The golden moles (CHRYSOCHLORIDÆ) of Africa have the hair of a brilliant metallic lustre, bronze, green, or violet in color; the eyes are covered by the integument, and the external ears are concealed by the fur. The last four families have no fossil representatives, but are nearest in structure to the Ictopsidæ.

ORDER III. CHIROPTERA.

Flying mammals, in which the anterior limbs are modified into supports for the membranous wings ; dentition complete, the canines strong, the molars buno-lophodont ; the total teeth never exceeding $i\ \frac{2}{3}$, $c\ \frac{1}{1}$, $p\ \frac{3}{3}$, $m\ \frac{3}{3}$; mammæ pectoral ; testes abdominal or inguinal ; placenta discoidal, deciduate.

The bats must be regarded as highly specialized offshoots from the insectivores, with which they closely agree in all essential points except the development of wings. These last are membranous folds, supported upon a bony framework composed of the modified fore limbs and extending back to the hind legs, while an interfemoral membrane may or may not include the tail when this is developed. Muscles to move the wing are attached to the sternum, which develops a keel similar to that of the birds. The modifications in the fore limbs consist in an enormous lengthening of the digits with the exception of the pollex, which remains more normal, and may terminate with a claw.

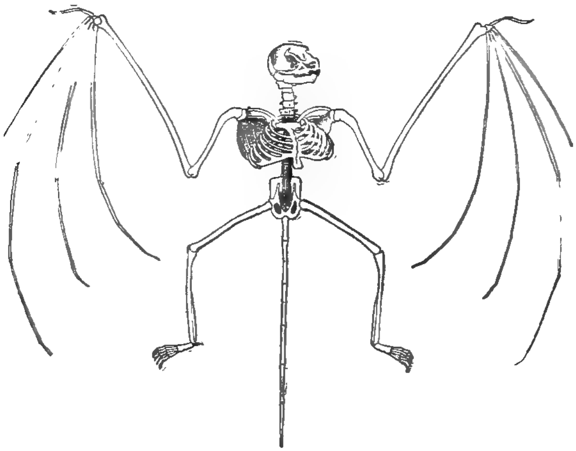

FIG. 361. Skeleton of bat, after Brehm.

The bones are very light, being slender, with large marrow cavities ; the skull varies considerably, and usually possesses a complete zygomatic arch, while as generally there are no frontal-postorbital processes. The clavicle is present, and the ulna is rudimentary. The brain is small and smooth. The sense of touch is highly developed, the wings being important in this respect, while in many species a peculiar dermal sensory apparatus, the 'nose-leaf,' is developed upon the snout. The shape of this, as well as that of the ears, is very variable, and is utilized in classification. The teeth are closely similar to those of the insectivores; the milk dentition is poorly developed, and in some instances is lost before birth. The intestine is short — shortest in the insectivorous species; a cæcum rarely occurs. The left lateral lobe of the liver is very large, and a gall bladder is present.

About four hundred species of bats are known, all nocturnal, and usually gregarious in their habits. Frequently the colonies are found to be composed of individuals of one sex, the sexes only coming together at the breeding-season. There is some evidence to show that the males, at least in certain species, take part in nursing the young. Fossils are rare; they first appear in the eocene. No fossil frugivora are known.

SUB-ORDER I. ANIMALIVORA (MICROCHIROPTERA).

Small bats with acutely cuspidate molars, index finger reduced, usually with a single phalanx, no claw; stomach simple, intestine short; outer and inner edges of ear not meeting below; tail, when present, connected with the interfemoral membrane.

The old-world RHINOLOPHIDÆ, with a nose-leaf, $i\ \frac{1}{2}$, $p\ \frac{2}{3}$ or $\frac{2}{2}$, and a long tail, includes about fifty species. *Rhinolophus* occurs in Europe, Asia, and Africa; *Hipposiderus*, Asiatic. *Rhinolophus* occurs in the eocene of France. Closely allied are *Nycteris* and *Megaderma* of Asia, in which a tragus is developed in the ear. The VESPERTILIONIDÆ have a long tail, lack the nose-leaf, and have a tragus to the ear and a variable number of teeth. *Plecotus*, with an American representative, has $i\ \frac{2}{2}$, $c\ \frac{1}{1}$, p, $\frac{2}{3}$ $m\ \frac{3}{3}$; *Antrozous*, from California, $i\ \frac{1}{2}$, $c\ \frac{1}{1}$, $p\ \frac{1}{2}$, $m\ \frac{3}{3}$. *Vesperugo*, the largest genus of bats, is cosmopolitan, one species (*V. serotinus*) inhabiting both continents. The teeth are $i\ \frac{2}{3}$ or $\frac{1}{3}$, $c\ \frac{1}{1}$, $p\ \frac{2}{2}$ to $\frac{1}{3}$, $m\ \frac{3}{3}$. *Atalapha* ($i\ \frac{1}{3}$, $c\ \frac{1}{1}$, $p\ \frac{2}{2}$ or $\frac{1}{2}$, $m\ \frac{3}{3}$), exclusively American. *Vespertilio* ($i\ \frac{2}{3}$, $c\ \frac{1}{1}$, $p\ \frac{3}{3}$, $m\ \frac{3}{3}$), cosmopolitan. *Vesperugo*, eocene, Wyoming. *Thyroptera*, Brazil. EMBALLONURIDÆ, tropical or subtropical, the middle upper incisors large and close together, no nose-leaf; a distinct tragus, and obliquely truncate muzzle. *Emballonura*, old-world tropics; *Noctilio* and *Molossus*, tropical America. PHYLLOSTOMIDÆ, tropical America; have three phalanges to the middle finger, nose-leaf present, tragus well developed. *Chilonycteris*, *Vampyrus*, *Glossophaga*. *Desmodus* includes the blood-sucking or true vampire bats.

SUB-ORDER 2. FRUGIVORA (MEGACHIROPTERA).

Large bats with smooth-crowned quadrituberculate molars, index finger with three phalanges, clawed; sides of the ear connected below; tail, when present, below the interfemoral membrane; fruit-eating.

The only family is the **PTEROPODIDÆ** of the East Indies; the species of which are generally known as flying-foxes. About 70 species, 40 being included in *Pteropus*.

ORDER IV. RODENTIA (GLIRES).

Placental mammals, with the extremities bearing claws, or more rarely hoof-like nails; feet plantigrade or subplantigrade, usually pentadactyl; condyle of lower jaw moving in an elongate glenoid fossa; teeth diphyodont; canines absent; incisors long, $\frac{1}{1}$ or $\frac{2}{1}$, with persistent pulps; molars (including premolars) varying from $\frac{2}{2}$ to $\frac{6}{6}$; placenta discoidal, deciduate.

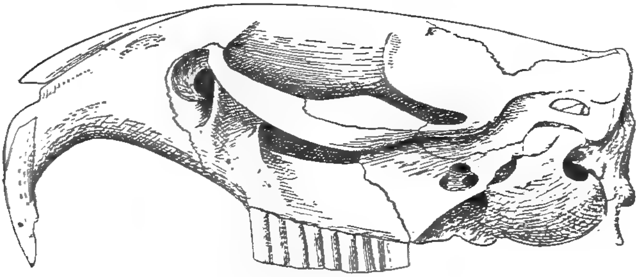

FIG. 362. Skull of muskrat, *Fiber zibithecus*.

The rodents are as sharply marked off from the other mammals as are the sirenians or whales; no forms, living or fossil, serving to connect them with the other orders, unless, possibly, with the tillodontia. Especially characteristic of the group are the gnawing incisors, in which the enamel is on the anterior face, the resulting wear keeping these constantly with a chisel-like edge;[1] the persisting pulp renews all loss by wear. Between the incisors and the molars is a wide gap or diastema. The molars may be lophodont, bunodont, or prismatic. As a whole, the dentition varies between $i\ \frac{2}{1}$, $c\ \frac{0}{0}$, $p\ \frac{3}{2}$, $m\ \frac{3}{3}$ (hares) and $i\ \frac{1}{1}$, $c\ \frac{0}{0}$, $p\ \frac{0}{0}$, $m\ \frac{2}{2}$; the most usual being $i\ \frac{1}{1}$, $c\ \frac{0}{0}$, $p\ \frac{0}{0}$, $m\ \frac{3}{3}$. The milk dentition does not include the incisors as a rule, and in some cases, as the guinea-pigs, is lost before birth.

The skin may be covered with the softest fur (chinchillas), or certain hairs may be developed into enormous spines, as in the porcupines; or again, the spines may be flattened; not infrequently are there scales on the tail. Sternebræ occur in the sternum. The skull usually presents an interparietal bone; the nasal bones are large and long; the orbits and the temporal fossæ are confluent, and especially characteristic is an infra-orbital canal through the zygomatic process of the maxilla. The clavicle may be present or absent; the manus is usually pentadactyl, but the thumb may be reduced, while in the hind foot both hallux and minimus may be lost.

Usually (except myoxidæ) there is a large intestinal cæcum; the brain is small, and the cerebral hemispheres, which never cover the cerebellum, are smooth. The testes are inguinal or abdominal in position, while there is either a uterus bicornis or two distinct uteri. The mammæ vary extremely between the two found in guinea-pigs and the ten in some rats.

About nine hundred living species of rodents are known, and they occur in all regions of the world except the Australian. They are mostly small and are mostly arboreal; although terrestrial, burrowing, and aquatic species occur. All are herbivorous. The order appears in the eocene, but has its greatest development in the present time. The genera are not equivalent to those in the preceding orders.

SUB-ORDER 1. SCIUROMORPHA.

One incisor in the upper jaw, molars $\frac{3}{3}$; clavicle present; tibia and fibula distinct. Mostly belong to the northern hemisphere, where they appeared in the eocene.

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[1] Similar conditions exist among the diprotodont marsupials, in *Typotherium* and in some multituberculates.

SCIURIDÆ; molars $\frac{5}{4}$ or $\frac{4}{4}$, fore feet four-toed, hind pentadactyl; tail covered with fur. To the family belong the woodchucks (*Arctomys*), prairie dogs (*Cynomys*), gophers (*Spermophilus*), chipmunks (*Tamias*), squirrels (*Sciurus*), and flying-squirrels (*Pteromys* and *Sciuropterus*), the latter sailing, rather than flying, through the air by means of an intermembral membrane on either side of the body. *Sciurus* appears in the eocene. The CASTORIDÆ, or beavers, the habits of which are so well known, have the molars $\frac{4}{4}$, the feet webbed, and the tail flattened and scaly. *Castor fiber*, the beaver, formerly ranged over the northern parts of both continents, but has been greatly restricted. The genus dates from the pliocene; the allied *Stenofiber* is miocene. The small families HAPLODONTIDÆ and ANOMALURIDÆ are represented by *Haplodon*, the sewellel of Oregon, and *Anomalurus*, a flying squirrel-like form from Africa. The fossil family, ISCHIROMYIDÆ, occurs in the eocene and miocene of North America.

SUB-ORDER 2. MYOMORPHA.

Incisors $\frac{1}{1}$, molars $\frac{3}{3}$ or $\frac{2}{2}$; clavicle usually present; tibia and fibula fused. The DIPODIDÆ, or jumping mice, including *Zapus* of the United States, *Dipus*, the jerboas of Europe, and *Pedetes* of South Africa, have the hind legs long, the toes being 5, 3, and 4 respectively, in the three genera. A much larger family is the MURIDÆ, in which there are no premolars, the molars are $\frac{2}{2}$ to $\frac{4}{3}$, and the tail generally naked and scaly. Over three hundred living species are known. *Cricetus*, including the hamsters of the old world, and *Hesperomys*, the white-footed mice of the new, have the molars $\frac{3}{3}$. In *Arvicola* and its allies the tail is round, and the molars rootless. These are commonly known as field-mice or voles. The migratory lemmings of northern Europe belong to *Myodes*. *Fiber* includes our muskrat. In *Mus*, which contains our mouse (*M. musculus*), and our rats (*M. decumanus*, the brown rat, and *M. rattus*, the black rat, the latter driven out by the former), the incisors are narrower and the molars rooted. The family dates back to the later pliocene. The MYOXIDÆ of Europe, represented to-day by the seven-sleeper, *Myoxus glis*, dates from the eocene. The GEOMYIDÆ, or pocket gophers, receive their name from the enormous cheek pouches. The legs are fitted for burrowing, and the molars $\frac{4}{4}$. *Geomys* and *Thomomys* occur in our central region. Farther west is *Saccomys* with much more delicate skull. BATHYERGIDÆ: *Spalax*, the blind mole-rat of southeastern Europe, and *Bathyergus*, the strand-rat of South Africa. *Lophiomys*, a peculiar arboreal rat with hairy tail, from northeastern Africa, is nearest to *Cricetus*.

SUB-ORDER 3. HYSTRICOMORPHA.

Skull with very large infraorbital canal; teeth $i\ \frac{1}{1}$, $c\ \frac{0}{0}$, $p\ \frac{1}{1}$, $m\ \frac{3}{3}$; zygomatic process large, clavicles perfect or imperfect; tibia and fibula separate.

The hystricomorphs appear in the eocene of Europe and South America, the latter region containing the majority of the sub-order to-day. Some of the species, both living and fossil, are giants among the rodents. In the tropical OCTODONTIDÆ the clavicles are complete, and the molars have internal and external enamel folds; most of the species are terrestrial. *Ctenodactylus*, from Africa. *Octodon*, from South America. *Myopotamus coypu*, of South America, two feet long. HYSTRICIDÆ; porcupines; stout rodents with spines, molars $\frac{4}{4}$. The species are grouped in two divisions: those of the old world dwell on the ground; those of the new, climb. *Hystrix*, with smooth soles and incomplete clavicles, includes the old-world porcupines; *Erethyzon* and *Synetheres*, with tuberculate soles and complete clavicles, those of the new. The latter genus has a prehensile tail. The CHINCHILLIDÆ, with very soft fur, complete clavicles; toes five or four in front, four or three behind; the molars with simple compressed transverse lamellæ, are confined to South America. *Chinchilla*. *Lagostomus* includes the burrowing vizcacha. *Megamys*, of the miocene of Argentina, was as large as an ox, the largest known rodent. Somewhat closely allied to them was the fossil *Castoroides* of N. Y. and Ohio pleistocene, and the *Amblyrhiza* from the pleistocene of the West Indies. The CAVIIDÆ, also South American, have hoof-like claws on the four toes of the fore feet and the three of the hind; incomplete clavicles, and the molars $\frac{4}{4}$ and rootless. *Cavia* contains the guinea-pigs; *Hydrochœrus*, the capybara, the largest existing rodent. Both these and other genera date from the miocene. The agutis (*Dasyprocta*) and the paca (*Cœlogenys*) are South American forms with hoof-like claws and semi-rooted molars which form the family DASYPROCTIDÆ.

SUB-ORDER 4. LAGOMORPHA (DUPLICIDENTATA).

Infraorbital canal small; dentition $i\,\frac{2}{1}$, $c\,\frac{0}{0}$, $p\,\frac{1}{1}$ to $\frac{3}{2}$, $m\,\frac{3}{0}$; the enamel of the upper incisors extending on to the sides; molars high, prismatic, without roots; tibia and fibula distinct.

The lagomorphs are readily distinguished by the two pairs of incisors in the upper jaw. The seat of the sub-order is in the northern hemisphere, but they extend into South America as well. The LEPORIDÆ, with the premolars $\frac{3}{2}$, long ears and incomplete clavicle, includes the hares and rabbits. *Lepus*, the principal genus, appears in the miocene of Oregon. About 20 living species. In the LAGOMYIDÆ the premolars are $\frac{1}{1}$ or $\frac{2}{2}$, the ears short, and the clavicle complete. The picas (*Lagomys*) inhabit high altitudes, one species occurring in the Rocky Mountains. The genus appears in the miocene of Bavaria.

ORDER V. UNGULATA.

Placental mammals with heterodont, diphyodont dentition; molars with broad tuberculate or ridged crowns; clavicles almost always lacking, digits with broad, blunt nails or more usually with hoofs; digits ranging from five to one, radius and ulna free or united; scaphoid and lunar bones (p. 177) of carpus always free.

If only the living forms were considered the characters of the ungulates and the sub-divisions of the order could be easily given, but the fossil forms, which are especially well developed in our western states, have introduced so many annectent groups that boundary lines tend to disappear, while to almost every character exceptions occur. Were the recent forms alone considered the order would contain only the artiodactyls and perissodactyls of the following pages, but the extinct species connect these so closely with the elephants and *Hyrax* that all must be included under a common heading. The existing forms are all terrestrial and with few exceptions herbivorous, none being distinctly predaceous. For convenience all of these forms may be divided into the true ungulates (Ungulata Vera or Diplarthra) and the Subungulata, the former including the artiodactyls and the perissodactyls, the latter the other sub-orders: Condylarthra, Amblypoda, Proboscidia, Toxodontia, and Hyracoida.

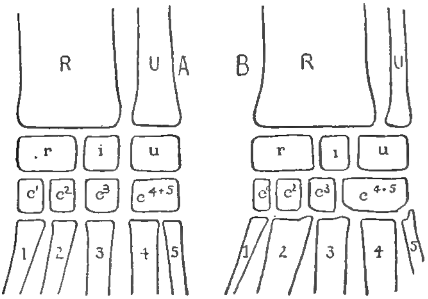

FIG. 363. Types of carpal bones; *A*, in series (taxeopodous); *B*, interlocking (diplarthrous). *R*, radius; *U*, ulna; *c*, carpales; *i*, intermedium; *r*, radiale; *u*, ulnare; 1–5, metacarpals.

In the Ungulata Vera the feet are never plantigrade; the digits never exceed four, the first being suppressed; the molars are quadritubercular. The mammæ are abdominal or inguinal in position, and are usually few in number. The placenta is nondeciduate, and is either diffuse or cotyledonary.

In the Subungulata the feet are frequently five-toed, and they may be plantigrade, and the bones of the first row of the carpus and tarsus are in a direct row with those of the second, while in the ungulata vera they alternate. The subungulata also present considerable differences in the placental arrangements, allusion to which will be made below.

Professor Cope, utilizing the characters presented by the carpal and tarsal bones, has proposed to divide the ungulates into five divisions, — Taxeopoda, Toxodontia, Proboscidia, Amblypoda and Diplarthra, — his Taxeopoda, including not only forms usually recognized as ungulates, but the primates as well.

SUB-ORDER 1. CONDYLARTHRA (MESODACTYLA).

Extinct ungulates with five-toed, plantigrade feet; carpalia in straight rows, not alternating; femur with third trochanter, molars bunodont.

The condylarthra are the most primitive of ungulates. From them have doubtless descended the ungulata vera, and, if the views of Cope be correct, the carnivores and primates as well. The group appears in the lowest eocene, and is especially well developed in the lower tertiaries of the western U. S. Four families, PERIPTYCHIDÆ, PHENACODIDÆ, MENISCOTHERIIDÆ, and PLEURASPIDOTHERIIDÆ recognized, the latter from the eocene of France.

SUB-ORDER 2. PERISSODACTYLA (SOLIDUNGULA).

Unguligrade ungulates with the middle toe well developed, forming the axis of the foot, carpals alternating; astragalus with pulley-like surface for tibial articulation; placenta diffuse.

The perissodactyls, which walk upon the very tips of the toes, have the feet, as a rule, with the toes three or four in front and three behind; but frequently only the third toe on either foot comes to complete development, the others being very rudimentary. The dentition is usually complete, the molars being lophodont or rarely bunodont, while the premolars tend to resemble the molars. The femur (except in *Chalicotherium*) has a third trochanter, and the fibula does not usually reach the calcaneum. The stomach is simple; the intestine has large cæcum, and a gall bladder never occurs. The mammæ, few in number, are inguinal in position. The living perissodactyls present three very distinct types, — horses, tapirs, and rhinoceroses, — but in the tertiary period many other forms occurred

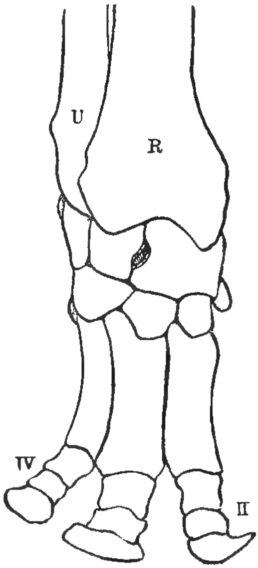

FIG. 364. Fore foot of two-horned rhinoceros, *Atelodus bicornis.*

which intergrade between these, largely obliterating the distinctions. In no group of mammals have the lines of descent been worked out more completely than here.

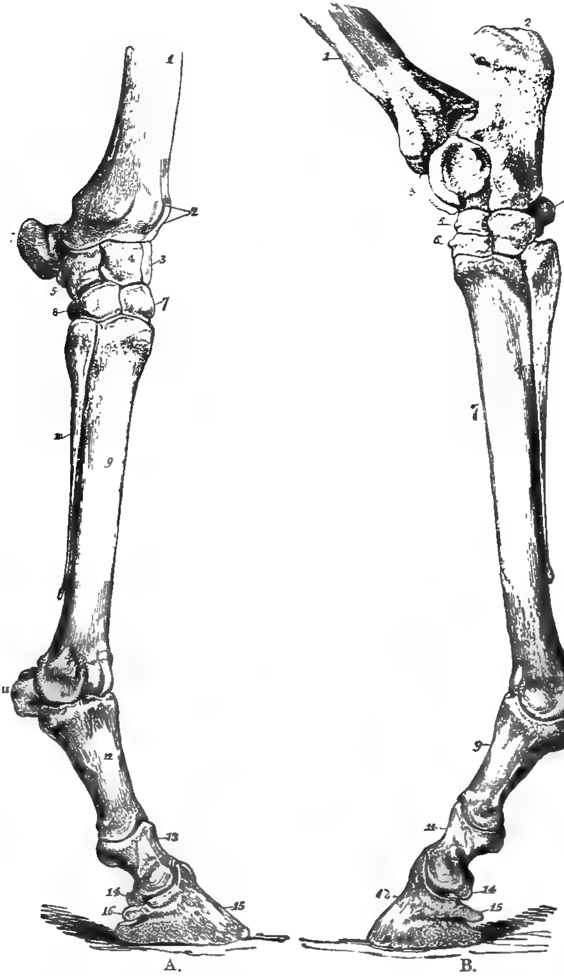

FIG. 365. *A*, right fore foot of horse, from Huxley. 1, radius; 3, scaphoid; 4, lunare; 5, cuneiforme; 6, pisiforme; 7, magnum; 8, unciforme; 9, metacarpal III; 10, splint bone (metacarpal IV); 11, 14, sesamoid bones; 12, proximal phalanx (fetter bone); 13, middle phalanx (coronary bone); 15, distal phalanx (coffin bone). *B*, left hind foot. 1, tibia; 2, calcaneum; 3, astragalus; 4, cuboid; 5, navicular or scaphoid; 6, ectocuneiforme; 7, metatarsal III (cannon bone); 8, metatarsal IV (splint bone); 9, 11, 12, phalanges (see fig. A); 10, 14, sesamoids.

In the horses (EQUIDÆ) the dentition is $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$ to $\frac{4}{4}$, $m\,\frac{3}{3}$; there are from four to one toes on the fore feet, three to one on the hind feet. In *Hyracotherium* (*Eohippus*) the toes are four and three on the fore and hind feet respectively; eocene. *Palæotherium*, eocene and miocene of both hemispheres, with three toes. *Mesohippus*, miocene. In *Hipparion* and *Protohippus* toes 2 and 4 reduced so as not to reach the ground, but furnished with hoofs; pliocene. *Equus*, the existing horses and asses, has toes 2 and 4 reduced to metacarpal splint bones without phalanges. The genus appears in the Indian miocene and a little later in North America. The existing species, including the asses and zebras, all belong to the old world. The PROTOTHERIDÆ, with tridactyl feet and incisors $\frac{1}{2}$, range through South American tertiary, as do the MACRAUCHENIIDÆ with the incisors $\frac{3}{3}$, and with no diastema in the jaws.

TAPIRIDÆ, with four toes on the fore feet, three on the hind (Fig. 348), range from the eocene to the present time. *Lophodon*, *Isectolophus*, eocene. *Tapirus* arises in the pliocene of Europe, from which have differentiated the tapirs of India and tropical America, the genus dying out in Europe in the pliocene. The existing species are of middle size, and live usually in woods or swampy places. The RHINOCERIDÆ, or rhinoceroses, have three or four toes on the fore feet, the hind feet tridactyl, the teeth $i\,\frac{3}{3}$ to $\frac{0}{0}$, $c\,\frac{1}{1}$ or $\frac{0}{0}$, $p\,\frac{4}{4}$ to $\frac{2}{2}$, $m\,\frac{2}{2}$. Some of the extinct forms were without horns, some had one horn and some had two, either one behind the other, as in the existing two-horned species, or as in *Diceratherium*, from the miocene of Oregon, the two horns were placed side by side. *Hyrachius* and *Hyracodon*, from the American eocene and miocene, were hornless, as was *Aceratherium* of the oligocene and miocene, the least differentiated of the true rhinoceroses. The living species are distributed in *Ceratorhinus*, two horns, from Asia; *Atelodus*, two horns, from Africa; and *Rhinoceros*, a single horn.

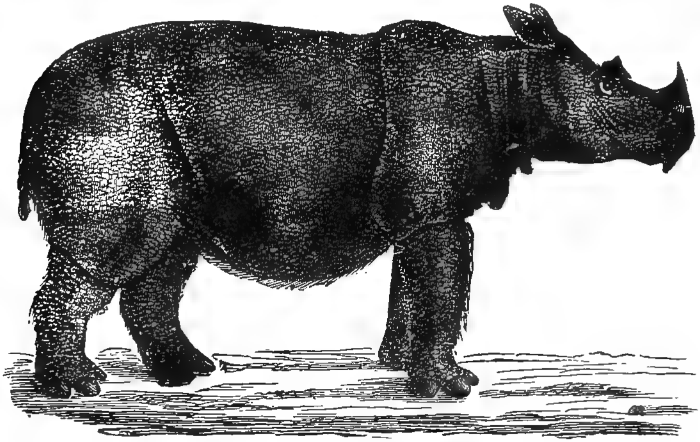

FIG. 366. Sumatran rhinoceros, *Ceratorhinus sumatrensis*, from Lütken.

The TITANOTHERIIDÆ of the eocene and miocene of Europe and America were mostly large animals with toes four and three on the fore and hind feet respectively, and the teeth varying between $i\,\frac{0}{0}$ to $\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{3}$ to $\frac{4}{4}$, $m\,\frac{3}{3}$. *Palæosyops* (*Lymnohyus*). *Titanotherium* (*Brontotherium*) has a pair of large bony processes on the snout, probably covered with horns. One species nearly as large as an elephant.

The position of the CHALICOTHERIIDÆ is uncertain. In the teeth it is distinctly perissodactyl, but its three-toed feet were plantigrade, and terminated with long, curved claws. The family ranges from the eocene to the pliocene, and is best developed in Europe. *Moropus*, *Macrotherium*.

SUB-ORDER 3. ARTIODACTYLA.

Unguligrade or digitigrade ungulates in which the toes are symmetrically developed about an axis passing between the third and fourth digits. Frequently a reduction from the full dentition of 44 teeth: premolars unlike the molars, the former with one lobe, the latter with two, except the last, which has three lobes; femur without third trochanter; fibula articulating with the calcaneum. Stomach complex; cæcum often present, large and convoluted; mammæ 2 or 4, inguinal; placenta diffuse or cotyledonary.

The artiodactyls are mostly large animals, distributed all over the earth, with the exception of the Australian region. The relations of the axis of the foot produce the well-known cloven hoof so characteristic of the group, while in many there is a tendency towards the loss of the incisors and canines in the upper jaw. Another common feature is the development of bony horn cores upon the frontal bones. The recent forms are frequently sub-divided into four series, Suina, Tragulina, Tylopoda, and Ruminantia (Pecora, or Cotylophora), but when the extinct species are taken into account, the divisions break down. For convenience the characters of these groups may be given here.

Suina: with the families Hippopotamidæ and Suidæ, with bunodont molars and distinct or but partially fused third and fourth metatarsals and metacarpals; *i.e.*, without a cannon bone. Tragulina: with the family Tragulidæ, in which a cannon bone usually occurs: and the stomach is three-chambered, the manyplies being absent: fibula complete. Tylopoda: including the Camelidæ: with only digits 3 and 4 developed, their metapodials fused above; manyplies absent, red blood corpuscles oval. Ruminantia: with the families Cervicornia and Cavicornia. In these there are no upper incisors; a cannon bone is present, the stomach four-chambered, and the placenta cotyledonary. The processes concerned in rumination may be described here, although a chewing of the cud occurs also in the camels. When feeding, the food as swallowed passes into the paunch, and thence to the honeycomb. In both of these it is softened, and then is regurgitated into the mouth, and masticated by the teeth. After this comminution it is swallowed again, but at this time it passes directly to the third stomach, or manyplies, and thence to the abomasum, which is the true digestive stomach.

The central stem of the artiodactyls seems to be the PANTOLESTIDÆ of the American eocene, with bunodont molars, and probably four-toed feet.

The ANTHRACOTHERIIDÆ, best developed in the European upper eocene, have the teeth $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, the metapodials distinct, and four toes on each foot, the outer ones in process of reduction. *Anthracotherium*, eocene. *Hyopotamus*, miocene of the U. S. and Europe. The SUIDÆ, or swine, apparently derivatives of the last family, appear in the eocene of both continents, and continue to the present time. They have the teeth $i\,\frac{3}{3}$ or $\frac{2}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$ to $\frac{3}{3}$, $m\,\frac{3}{3}$, the molars bunodont. The feet are four-toed, rarely three-toed, toes 2 and 5 smaller than the others, and the metapodials distinct. The stomach has a pouch developed near the cardiac opening; the colon is spirally coiled, and a cæcum is present. The earlier history of the family is less certain than that of some others, and some of the earlier genera seem to have a carnivorous facies. The family to-day belongs to the old world, only the peccaries (frequently set aside as a distinct family, DICOTYLIDÆ) occurring in the western hemisphere. In *Achænodon*, from the eocene, there are already developed the tusk-like canines so characteristic of modern swine; in *Elotherium* they are less conspicuous, while in *Chœropotamus* (eocene, Europe) and *Leptochœrus* (miocene, U. S.) these teeth are smaller. The peccaries (*Dicotyles*) appear in the American pleistocene, and two or three species persist in warmer America to-day. They have the teeth $i\,\frac{2}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$; the fifth toe of the hind feet lacking, and the stomach more complex than in the typical swines. The species are gregarious and omnivorous. The allied *Platygonus* is pliocene. In the pigs proper — *Sus*, *Babirusa*, *Phacochœrus* — the canines are greatly developed and triangular in section, and a large diastema exists between these and the premolars. All are old-world forms, and are distinguished by the dentition: *Sus*, $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$; *Babirusa*, $i\,\frac{2}{3}$, $c\,\frac{1}{1}$, $p\,\frac{2}{2}$, $m\,\frac{3}{3}$; *Phacochœrus*, $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{2}$, $m\,\frac{3}{1}$. The true swine, *Sus*, appear in the pliocene and continue as our domestic hogs, descended from the wild boar and other Asiatic species. The single species of *Babirusa* (*Porcus*) of the Malay Islands is remarkable in that the upper canines of the male grow upward through the skin of the snout. The wart-hogs of Africa (*Phacochœrus*) receive their common name from the projections on the face. In the adults many of the teeth are lost, but the canines form enormous tusks, both pairs curving upwards and outwards.

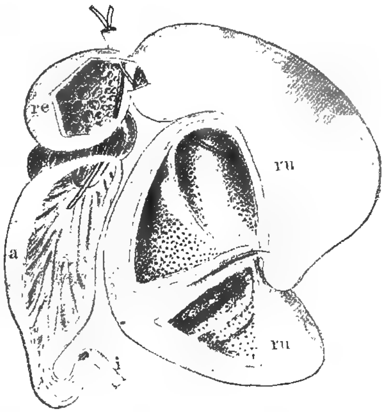

FIG. 367. Stomach of sheep, after Carus and Otto (Oppel). *a*, abomasum; *o*, omasum; *re*, reticulum; *ru*, rumen.

The HIPPOPOTAMIDÆ are large, amphibious, bunodont forms, with teeth $i\,\frac{3}{3}$ to $\frac{2}{1}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$, the lower incisors very long and rootless. The metapodials are distinct, the feet four-toed, the lateral toes being nearly equal to the others; the digits bear nail-like hoofs. Restricted to the eastern hemisphere, where they occur fossil in Europe and Asia since the pliocene, the living species are all African. Three genera are distinguished by the number of lower incisors: *Hippopotamus* with six, *Tetraprotodon* with four, and *Chœropus* with two. *Hippopotamus* dates back to the pliocene. *Chœropus* is living; *Tetraprotodon* is known only from the African pleistocene. The common species, *H. amphibius*, has an enormous three-chambered stomach, eleven feet in axial length. These animals are gregarious and herbivorous.

The OREODONTIDÆ lived from the eocene to the pliocene of North America. They had the teeth $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$. and the feet four-toed; and in *Protoreodon*, from the eocene, the fore toes were five in number. *Agriochœrus* and *Oreodon* miocene, *Merychius* (*Ticholeptus*) miocene and pliocene. The CAMELIDÆ (Tylopoda), which appear in the eocene. may have descended from either the pantolestidæ or the oreodontidæ. They have the teeth $i\,\frac{3}{3}$ to $\frac{1}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$ to $\frac{2}{1}$, $m\,\frac{3}{3}$, the molars selenodont. with a diastema between the premolars and canines; the feet four- or two-toed, the lateral toes completely lost in the more recent species; and in all except the older forms the metapodials fused to a cannon bone. The stomach lacks the manyplies, while rumen and honeycomb are sub-divided into numerous small cavities on the walls. The placenta is diffuse. The living genera, *Camelus*, which inhabits Asia and Africa, and *Auchenia* of South America, appear in the pliocene. They differ in the premolars, these being $\frac{3}{2}$ and $\frac{2}{1}$ respectively. The camels are two in number, the single-humped dromedary. *C. dromedarius*, and the two-humped bactrian, *C. bactrianus*. *Auchenia* contains four species, the llama, alpaca, viçuna, and guanaco. Among the extinct genera are *Leptotragulus*, eocene; *Poëbrotherium* and *Protolabis*, miocene; *Procamelus*, *Eschatius*, and *Pliauchenia*, pliocene. The ANOPLOTHERIIDÆ of the European eocene and pliocene are noticeable from the fact that it was in this group that Cuvier made many restorations. *Anoplotherium*, *Dichobune*, *Cænotherium*, *Xiphodon*.

The TRAGULIDÆ. or chevrotains, have the teeth $i\,\frac{0}{3}$. $c\,\frac{1}{1}$. $p\,\frac{4}{4}$ or $\frac{3}{3}$, $m\,\frac{3}{3}$; fibula complete, usually a cannon bone; feet four-toed; stomach three-chambered; placenta diffuse. These forms have been closely associated with the musk deer. *Tragulus* of Asia contains the smallest existing ungulates. *Dorcatherium* (*Hyomoschus*) from Africa. *Leptomeryx*, American miocene.

The CERVICORNIA, in which the teeth are $i\,\frac{0}{3}$ to $\frac{0}{1}$, $c\,\frac{1}{1}$. $p\,\frac{3}{3}$ to $\frac{3}{4}$ m, $\frac{3}{3}$, the upper canine being sometimes very large, sometimes small or absent, the molars selenodont, are as a rule characterized by the development of horns or antlers upon the frontal bones of the male, although they are occasionally absent, or. as in the reindeer, they may appear in both sexes. These horns consist of a bony outgrowth from the frontals; and at first this is covered with skin, which may persist through life, as in the giraffe, or, more usually, is soon worn off, leaving the bone alone. Each year this horn is shed, and a new antler takes its place, the later one displaying a greater number of branches or 'tines,' so that these become an index of age. Metapodials 3 and 4 usually form a cannon bone: the lateral metapodials are reduced, and the toes do not reach the ground. The stomach and placenta are of the ruminant type (p. 396). The species are very numerous, but none occur in

Australian regions, and only the giraffes in Africa. The family is not known previous to the lower miocene of Europe, the earliest forms showing relationships to the tragulines and antilopes. The musk deer (*Moshus*, *Hydropotes*) are without horns, the upper canine is long and projecting, and the male has a 'musk gland' situated beneath the skin of the abdomen. The species belong to Central Asia. The living muntjacs are also Asiatic, but their ancestors appeared in the miocene of both hemispheres. Cope and Schlosser regard the group as the ancestors of the true deer and of the antilopes as well. *Cervulus*, muntjacs of Asia. *Blastomeryx*, American miocene. *Cosoryx*, American pliocene. The true deer (*Cervus*) are characterized by the presence of horns. They are usually sub-divided into many subgenera, *Axis*, *Cariacus*, *Elaphus*, etc., upon characters of minor importance; more distinct are the moose (*Alces*) and the reindeer or caribou (*Rangifer*). The deer are largely inhabitants of the northern hemisphere. Considerably different is *Protoceras* from the American miocene, in which there were rudimentary horn cores on the frontals and parietals, and vertical bony plates on the maxillæ, while the canines recall those of *Tragulus*. The giraffes (*Giraffa* or *Camelopardalis*, often grouped as a family, Devexa) have long legs, and short non-deciduous horns. Allied to these in structure, but lacking the characteristic long neck, occur in the European and Asiatic miocene *Helladotherium*, *Samotherium*. *Sivatherium*, with a single large species from the Indian miocene, combines giraffe and antilope characters.

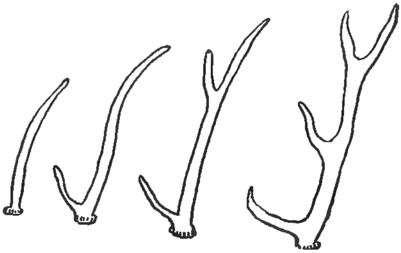

FIG. 368. Successive antlers of the red deer (*Cervus elaphus*), after Gaudry.

In the family CAVICORNIA the horns are almost always borne by both sexes, and, unlike those of the cervicornia, have the bony horn cores covered with true or epidermal horn. With rare exceptions the horns are never shed; the teeth are $i\,\frac{0}{3}$, $c\,\frac{0}{1}$, $p\,\frac{3}{3}$, $m\,\frac{3}{3}$; the median metapodials form a cannon bone; the laterals are greatly reduced or entirely absent. The family, which is richest in species of any of the ungulates, appears to have descended from the muntjacs through the antilopes. The species are usually arranged in antilopine, ovine, and bovine series, the three being distinct in the pliocene. The antilopes, which appear in the miocene, have the round or triangular horns close behind the eyes, the middle incisors largest. *Antilope*, India; *Saiga*, with large inflated nose, Asiatic; *Gazella*, Asiatic, the springbok (*G. euchore*), African; *Oryx*, the gemsboks; *Catoblephas*, gnus; *Rupricapra tragus*, the chamois; closely allied is the Rocky Mountain goat, *Haploceras montanus*. *Antilocapra americana*, the prong-horn of western U. S., is remarkable for its deciduous horns. In all over a hundred living antilopes are known. Among the fossil genera are *Cosoryx*, *Antidorcas*, *Tragelaphus*, etc. The ovine series, which includes the sheep and goats, has the laterally compressed, transversely ribbed horns with hollow cores borne close behind the eyes, and the incisors similar. None are known before the pliocene. *Capra*, ibex, and goats, the domestic goats supposed to descend from *C. ægagrus* of the eastern Mediterranean region. *Ovis*, the sheep, with several European species and one American, the big-horn, *O. montana*. *Ovibos moschatus*, the 'musk ox,' a goat rather than an ox, is confined at present to Arctic America. In pleistocene times it ranged over Siberia and Europe, south to France and England. In the bovine series the horns are strong, some distance behind the eyes, often on the posterior angle of the head; the frontals large, the parietals small. Fossil species first appear in the miocene of India, later, in the pliocene of Europe and America. *Bubalus*, the buffalo of India and Africa; *Bibos*, the domesticated Indian cattle, and the yak and banteng; *Bison*, the aurochs of Europe and the 'buffalo' of America, both near extinction. To *Bos* belong the domestic cattle, and the now extinct 'ur' of Europe, which possibly lived as late as the composition of the Nibilungen tales.[1] There is evidence to show that our domestic cattle are descended from several distinct races.

FIG. 369. Prong-horn antilope. *Antilocapra americana.*

SUB-ORDER 4. AMBLYPODA.

Large, extinct, semiplantigrade ungulates, the pentadactyl feet having the distal phalanges surrounded by hoofs; carpals alternating, molars lophodont, brain very small.

These forms, which begin in the lowest eocene, are regarded by Cope as the ancestors of both artiodactyls and perissodactyls. They also show proboscidian affinities. *Pantolambda*. *Coryphodon*, with complete dentition, feet digitigrade in front, plantigrade behind, ranged through the lower and middle eocene. The species of *Uintatherium* (*Dinoceras*) were elephantine in size, and bore on the head three pairs of large bony processes which may or may not have borne horns.

SUB-ORDER 5. PROBOSCIDEA.

Pentadactyle ungulates with long proboscis (nose), skull increased in size by vacuities in the bone; incisors[2] never exceeding a pair in either jaw, frequently the upper or the lower lacking; no canines, molars lophodont; no clavicles; radius and ulna, tibia and fibula distinct; stomach simple, cæcum

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[1] It is often suggested that the cattle of Chillingham Park, England, are descendants of these wild cattle.

[2] Frequently spoken of as canines; however, they arise in the premaxilla, and only later do the roots extend back into the maxillæ.

large, uterus bicornuate; placenta zonary, non-deciduate; mammæ pectoral, two in number.

The elephants and their extinct relatives form a most interesting group, highly differentiated in some respects, more generalized in others. Most strange is the proboscis with the nostrils at the tip, while the incisors which furnish most of the ivory of commerce are almost solely dentine, the enamel covering the tip being worn off at an early date (elephants), or forming a band on the outer side (*Mastodon*).

The DINOTHERIDÆ, with the single genus *Dinotherium*, occur in the miocene and pliocene of Europe and India. In this only the lower incisors are present, and these grow downwards, the symphysis of the jaw being bent so that the teeth form downward-extending tusks. The succession of molar teeth was normal. The animals were about as large as an elephant.

In the elephants and their near relatives (ELEPHANTIDÆ) the upper incisors form tusks of varying size, the lower are smaller or wanting. The molars bear more than two transverse ridges, and are subject to horizontal replacement. Owing to the shortness of the jaw, and the large size of the molars, not more than two can be in use at the same time. As the more anterior of these becomes worn, it drops out in front, while another takes its place from behind. In some *Mastodons* transitional types of succession occur. *Mastodon* (with several sub-generic divisions) extended from the upper miocene through the pliocene, and may have been contemporaneous with man. Its teeth, characterized by from three to six transverse ridges, or ridges broken into tubercles, are common in the northern hemisphere, Africa, and South America. The skeletons are less perfectly preserved. *Stegodon*, from the later tertiaries of India, etc. *Elephas* (including *Loxodon*) embraces the existing elephants as well as the extinct mammoths. In these the valleys between the transverse enamel folds are filled with cement. The living species, *E. indicus* and *E. africanus* occur in India and Africa, respectively. The genus appears in the miocene, the mammoth, *E. primigenius* of the pleistocene, which became extinct after the appearance of man, being the best known. The discovery in 1799 of frozen mammoth bodies near the Lena delta should be mentioned. The body was covered with close, woolly hair, while a mane on the neck and the hairs on the head were three feet in length.

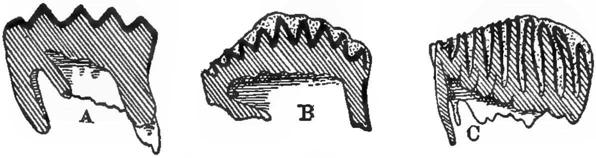


FIG. 370. Evolution of the teeth of elephants after Flower. *A*, *Mastodon*; *B*, *Stegodon*; *C*, *Elephas* (*Loxodon*) *africanus*. Dotted, cement; obliquely lined, dentine; heavy black line, enamel.

SUB-ORDER 6. TOXODONTIA.

Extinct ungulates with tri- or pentadactyl semiplantigrade feet: alternating carpalia; femur without third trochanter; fibula articulating with the calcaneum; third toe the larger. Canines reduced, sometimes to a great extent.

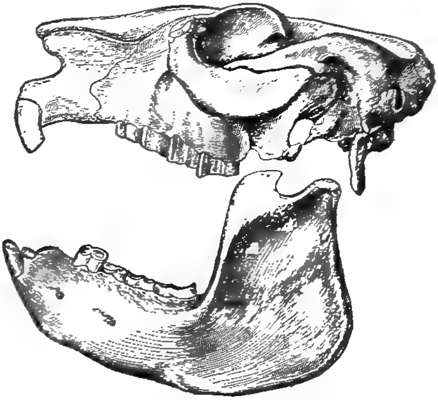


FIG. 371. Skull of *Typotherium cristatum*.

The Toxodons and their allies occur in the tertiary of southern South America, and are as yet imperfectly known. They exhibit a strange association of resemblances to perissodactyls, *Hyrax*, elephants, and rodents. *Toxodon*, which persisted from the older miocene to the pleistocene, was about the size of a rhinoceros. *Nesodon*, from the eocene. Sometimes *Typotherium* and its allies from the same beds are separated as a distinct sub-order Typotheria.

SUB-ORDER 7. HYRACOIDEA.

Small plantigrade ungulates with tridactyl hind feet, fore feet four-toed, the carpalia in series, the digits with nails; femur with third trochanter; teeth $i\,\frac{1}{2}$, $c\,\frac{0}{0}$, $p\,\frac{4}{4}$, $m\,\frac{3}{3}$; placenta zonary. Only a single genus *Hyrax* (with several sub-divisions) known, and this only in the existing fauna. The few species described come from Syria, Arabia, and Africa. They live in holes in the rocks, or in hollow trees, and some of the African species are arboreal. One species, *H. syriacus*, is supposed to be the 'coney' of the Bible.

SUB-ORDER 8. TILLODONTA (INCLUDING TÆNIODONTA).

Extinct plantigrade animals with pentadactyl feet; teeth $i\,\frac{2}{2}$ to $\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{3}{3}$ to $\frac{4}{3}$, $m\,\frac{3}{3}$, the upper molars with three cones, the lower lophodont.

These animals of large or moderate size recall in some respects the carnivores, and in some the rodents. They belong largely to the eocene, and the United States has furnished the greater number of specimens, Europe having but few. Cope has united these forms with the insectivores and creodonts into an order Bunotheria. *Esthonyx*, eocene, New Mexico. *Tillotherium*, eocene, Wyoming. *Calamodon* (*Stylinodon*). *Stagodon*, cretaceous.

ORDER VI. SIRENIA.

Thick skinned, naked or sparsely haired, aquatic, placental mammals, with monophyodont teeth; with fin-like fore limbs; hind limbs lacking; a horizontal caudal fin; a movable elbow joint; small brain with few and shallow convolutions; two pectoral mammæ.

The sirenia contains a few aquatic mammals, which externally resemble the whales in their fusiform bodies, flipper-like fore limbs, absence of hind limbs, and flattened caudal fin. In more important features they are greatly different, and nothing that is known of development or geological history points to their having descended from a common stock. They have the nostrils separate, and opening forward, small eyes with well-developed nictitating membrane, no conch to the ear, no dorsal fin. The paddle-shaped fore limbs have the digits enveloped in the common integument, and only occasionally are nails present. The bones are very dense, and the long bones are without central cavities. Only occasionally are any of the cervical vertebræ anchylosed, and in the recent forms no vertebræ unite to form a sacrum. The anterior caudal vertebræ bear chevron bones. In the skull the chief features are the great development of the zygomatic arch, the reduced nasals, the downward flexure of the jaws in front, and the lower jaw with an ascending ramus. In the fore arm the radius and ulna are usually anchylosed at their extremities; the digits are always five, and there is no such increase in the number of phalanges as occurs in the cetacea. No clavicles are developed. The pelvis is represented by a pair of bones lying at some distance from the vertebral column.

Incisors and molars alone are present in the recent forms, and in one genus (*Rhytina*) no teeth occur, at least in the adult. Many fossil species had a more heterodont dentition, and in *Halitherium* there was a milk dentition not known in

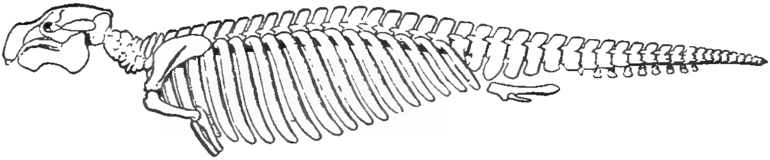


FIG. 372. Restoration of *Halitherium schinzii*, after Miss Woodward.

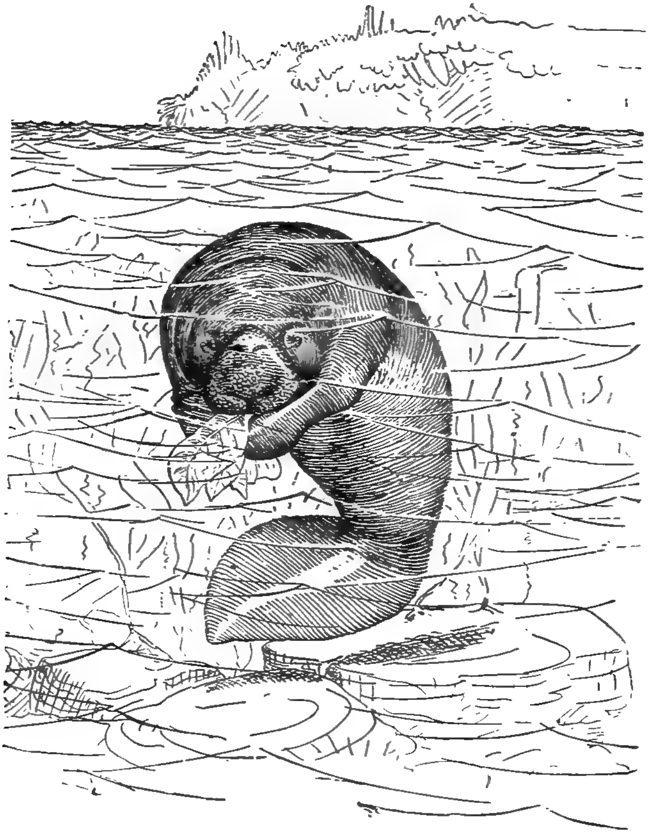


FIG. 373. Manatee, *Manatus americanus*, after Elliott.

recent forms. In place of teeth, horny plates are developed in the palatal region and at the front of the lower jaw, and these are masticatory in function. The stomach is divided into two principal chambers, and these in turn may be sacculated. The diaphragm is oblique, the lungs very long, and the heart is bifid at the tip, the two ventricles being partially separated (Fig. 352). The testes are abdominal in position; the uterus is two-horned. The placentation of the dugong alone is known. This form has a non-deciduate zonary placenta.

The living species of sea-cow are few. All are littoral in their habits, but never leave the water. They feed upon seaweed, or upon the grasses growing in the rivers. They are perfectly harmless, although they attain considerable size. These animals may afford the grain of truth in the mermaid myth.

The PRORASTOMIDÆ (only genus *Prorastoms* from the eocene of Jamaica), is known only from the skull. It is remarkable in having a complete dentition: $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{5}{5}$, $m\,\frac{3}{3}$. The MANATIDÆ have molars 8 to 10, the first single-rooted; incisors and canines never functional. *Manatus* (*Trichechus*) includes the manatees of tropical America and Africa. Fossil in pleistocene of South Carolina. They have but six cervical vertebræ. Here possibly belong the tertiary *Manatherium* and *Ribodon*. HALICORIDÆ with heterodont molars, and either with tusk-like incisors in the upper jaw or these lacking. *Halicore* includes the dugongs of the Indian Ocean. *Halitherium*, from the miocene and pliocene of western Europe, gives evidences of a milk dentition. *Rhytoidus*, *Felsinotherium*, from the tertiary. RHYTINDIÆ, without teeth. The only known species, *Rhytina stelleri*, the northern sea-cow of the northern Pacific, was exterminated in the last century.

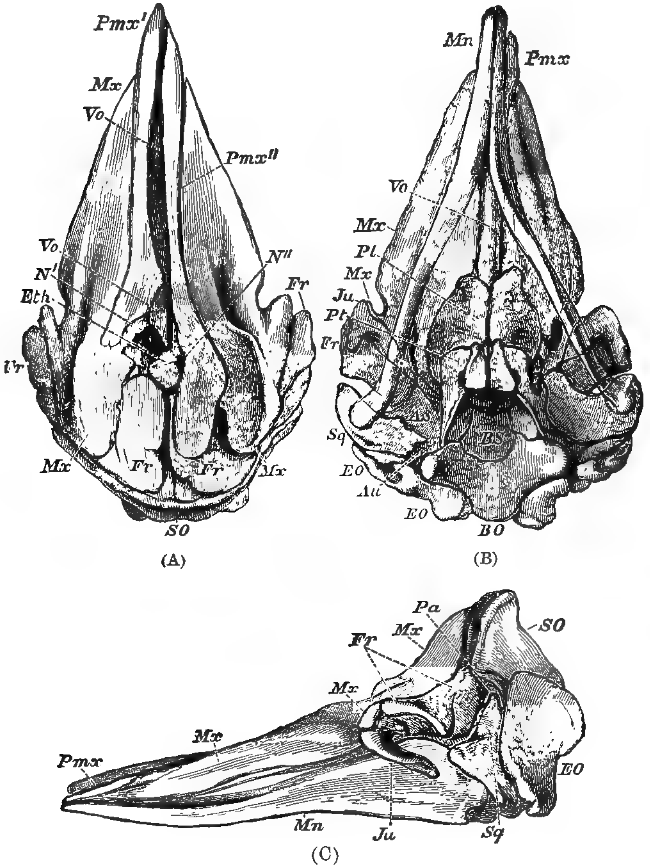
ORDER VII. CETACEA.

Aquatic mammals without distinct neck; fore limbs paddle-like; hind limbs absent; usually a dorsal fin; caudal fin in two lobes or 'flukes,' nostrils on the top of the head; teeth, when present, homodont and monophyodont; no elbow joint; brain large, cerebrum complicately convoluted; placenta non-deciduate, diffuse.

The whales, like the sea-cows, form a distinctly circumscribed group, sharply marked off from all others, so that no clear conclusions can be reached as to their line of descent from other groups, although one is justified in believing that they have come from some more normal quadripedal mammal. More recently the view has been gaining ground that the two living divisions, the toothed and the whalebone whales, may have had diverse origins, and their present resemblance may be due to convergence rather than to community of descent. The best guesses as to their ancestors would trace them either to the carnivores or to some long-tailed ungulate, while the presence of dermal ossicles in one species of *Neomeris*, and possibly in *Zeuglodon*, needs to be taken into account.

The skin is smooth and naked, without hairs; even the bristles around the mouth may disappear in the adult. There is no neck; the head is large, and may form one-third of the total length. The eye is small, and without nictitating membrane; the nostrils, separate or with a common crescentic opening, are on the top of the head; there is no external ear, the small meatus opening close behind the eye. Beneath the skin is the thick layer of fat or 'blubber.' The bones are light and spongy. The cervical vertebræ are more or less completely fused, and have the zygopophyses poorly developed. There is no sacrum, but the caudal vertebræ are distinguished from the lumbar by the presence of chevron bones. The sternum is very variable, and is reached by only one (mystacocetes), or a few ribs. The skull consists of a nearly spherical cranium, from which the facial part projects like a beak. In the cranium the roof is formed by the supraoccipital and interparietal, which extend forward to meet the frontals, excluding the parietals from the middle line. The frontals are expanded laterally to form roofs to the orbits. The maxillæ are very large, the nasals very small. The lower jaw lacks an ascending ramus. Clavicles are lacking, and there is no elbow joint. The bones of the wrist and hand remain almost entirely cartilaginous in the whalebone whales. The digits are four or five, the phalanges of the second and third being increased in number up to fourteen, a condition recalling the ichthyosaurs (p. 312). The pelvis is represented by two bones, free from the vertebral column, which, on account of their muscular relations, are regarded as ischia. In some species rudiments of the skeleton of hind limbs occur, imbedded in the flesh.

The teeth in existing species are homodont and monophyodont, and never pierce the gums in the mystacocetes. In the fossils there is evidence of descent from heterodont ancestors.



(A) (B)

(C)

FIG. 374. Skull of fœtal cachelot whale (*Physeter*), from Huxley. *AS*, alisphenoid; *Au*, auditory region; *BO*, basioccipital; *BS*, basisphenoid; *EO*, exoccipital; *Eth*, ethmoid; *Fr*, frontal; *Ju*, jugal (displaced in the side view from its connection with the squamosal); *Mx*, maxillary; *N*, external nares; *Pa*, parietal; *Pl*, palatine; *Pmx*, premaxillary; *SO*, supraoccipital; *Sq*, squamosal; *Vo*, vomer.

The number varies greatly. The stomach (p. 367) is several chambered, the intestine is comparatively simple, a cæcum being present in some species. The liver has four lobes, and no gall bladder is present. The larynx is prolonged so that it enters the choana, a condition recalling the marsupials. The testes are abdominal, the uterus two-horned, and the two mammæ are in grooves near the vulva. These are provided with constrictor muscles, by which the milk is forced into the mouth of the young. About two hundred existing species are known.

The cetacea are introduced by the zeuglodons in the eocene, the other groups appearing in the miocene.

SUB–ORDER I. ARCHÆOCETI.

External nostrils at the middle of the muzzle; nasals long; temporal fossa elongate; ribs bicipital; anterior teeth with single roots, posterior with two roots, the free edges dentulate. Breast bone of several sternebræ. Cervicle vertebræ free.

Zeuglodon (*Basilosaurus*) the only genus (with several subgenera) comes from the eocene of our southern states, Europe, and New Zealand. One species was 60 feet long.

SUB-ORDER 2. ODONTOCETI (DELPHINOIDEA, DENTICETÆ).

Skull asymmetrical; external nares united at base of snout: nasals very small; temporal fossa short: teeth present in both jaws or only in lower, occasionally reduced to a single pair. Olfactory organs absent or rudimentary; anterior ribs bicipital, others with only a tubercular head; sternum of several sternebrae.

The toothed whales are all carnivorous, but much as they have been pursued by man, many questions concerning the features presented by any species at different ages are still unsettled. The SQUALODONTIDÆ, with teeth in both jaws, and these differentiated into incisors, canines, and two kinds of molars, occur in the miocene and pliocene. In some respects they seem intermediate between the zeuglodons and the toothed whales, but their skeleton is imperfectly known. The PLATANISTIDÆ include the fresh-water dolphins, *Platanista* and *Inia*, from the Ganges and Amazons: allied forms occur in the miocene and pliocene of both continents. The true dolphins (DELPHINIDÆ) have the snout elongate, no premaxillary teeth, the other teeth variable, usually conical, and with a single root. Teeth are numerous in both jaws of the true dolphins and porpoises (*Delphinus*, *Tursiops*, *Phocæna*, *Neomeris*); are fewer in the black fish (*Globiocephalus*) and the killer whales (*Orca*), these latter being the wolves of the sea. The white whale of the Arctic seas is *Delphinapterus*, which in all points of structure except the numerous teeth is closely allied to the narwal (*Monodon*), in which, in the female, all the teeth are functionless, while in the male one left maxillary tooth is developed into an enormous spirally twisted tusk, which sticks straight out from the head. Its functions are unknown. Several of these genera, the narwal included, occur as fossils in the later tertiary and pleistocene. The PHYSETER-

IDÆ includes large and medium-sized whales with toothless upper jaws. *Physeter*, which includes the sperm whales, dates from the pliocene of western Europe and South Carolina. It has numerous (20–25) conical teeth in the lower jaw. The head is high, truncate in front, and in the 'chair' between the cranium and snout occurs a thick waxy oil, the spermaceti. The sperm whale (*P. macrocephalus*) furnishes the ambergris which is really imperfectly digested squid become concretionary in the intestines. *Ziphius* includes the two-toothed whales, so called from the existence of but a pair of teeth in the lower jaw. Allied are *Hyperoodon*, the bottle-nosed whales, *Mesoplodon*, and the pigmy whales, *Kogia*.

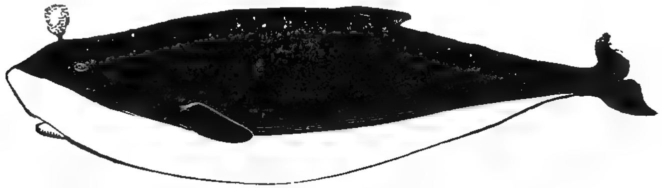


FIG. 375. Pigmy whale, *Kogia floweri*, from Gill.

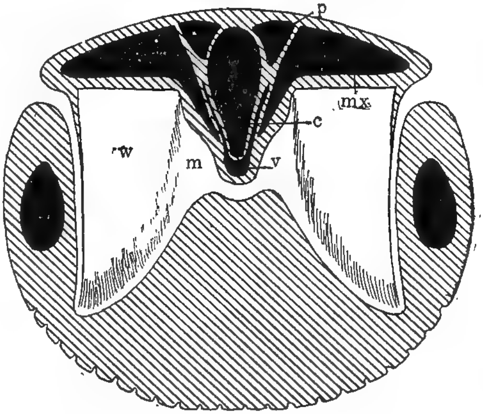


FIG. 376. Cross-section through the jaws of a whalebone whale, after Delage. Bones black; *w*, whalebone, hanging down into the cavity of the mouth, *m*; *c*, ethmoid; *mx*, maxillary; *p*, parietals; *v*, vomer.

SUB-ORDER 3. MYSTACOCETI (BALÆNOIDEA).

Skull symmetrical; two nostrils at the base of the snout; temporal fossæ short; functional teeth lacking, the upper jaw bearing plates of baleen; most of the ribs with a single head; sternum broad, in one piece, and articulating with the first pair of ribs alone.

The whalebone whales have teeth in both jaws in the fœtal stage, but these never pierce the gums, and are absorbed before birth. After birth a series of flattened plates of horny material make their appearance on either side of the upper jaw. These plates, of which there are several hundred pairs, are triangular in shape, with the inner edges fringed out into hair-like fibres, the plates being at right angles to the axis of the body, and the whole forms a very efficient straining-apparatus, by means of which the whales separate the small animals on which they feed from the surrounding water. Morphologically the baleen consists of large numbers of cornified papillæ arising from the ectoderm lining the cavity of the mouth.

In the BALÆNOPTERIDÆ the head is less than a fourth of the total body length, the ventral side of the body is usually marked by longitudinal grooves, a dorsal fin (a tegumentary fold without skeleton) is present, the hands have four digits, and the cervical vertebræ have their large centra free. *Balænoptera*, with the head small and flat, and the grooves extending back as far as the throat region, contains the rorquals, fin-backs, or razor-backs. *B. sibbaldi* is the largest whale, reaching a length of 85 feet. *Megaptera* includes the hump-back whales. The family occurs in all rocks since the miocene. The BALÆNIDÆ or right whales date only from the pliocene; they have a large head, the ventral surface smooth, the hand pentadactyl, the cervical vertebræ fused, and no dorsal fin. *Balæna*, *Neobalæna*, and *Rhachianectes* belong here.

ORDER VIII. CARNIVORA (FERÆ).

Terrestrial or aquatic flesh-eating mammals with unguiculate four- or five-toed feet; incisors usually $\frac{3}{3}$, canines $\frac{1}{1}$, strong, pointed and recurved; molars more or less sectorial; mammæ abdominal; placenta deciduate, almost always zonary.

The carnivora receive their name from their flesh-eating habits, but it must be understood that not every species conforms to this rule, since some live largely upon a vegetable diet. All have diphyodont and heterodont dentition; the first incisor is smallest, the third largest. The canines are especially characteristic; the premolars are compressed and are usually sectorial, while the molars are occasionally broad, but still have cuspidate crowns. The milk dentition is usually functional for a year after birth.

The feet have either four or five toes, and may be either plantigrade, semiplantigrade, digitigrade, or in the seals modified into flippers. The claws are usually compressed, but occasionally may be rudimentary or absent. In the living species the brain is large and richly convoluted, but in the creodonts it was much smaller and nearly smooth. The stomach is a simple pear-shaped sac; the cæcum is small or absent; the uterus two-horned. The radius and ulna are always distinct, the fibula always slender.

Through the extinct group of creodonts the carnivores are closely related to the insectivores, and possibly to the marsupials. In fact Cope has taken the creodonts and united them with insectivores, and certain forms here placed with the ungulates, into an order, Bunotheria, from which he derives the carnivores and rodents. The carnivores appear in the lowest eocene; the creodonts disappear in the miocene, while the pinnipedia are first found in the miocene.

Sub–Order 1. Creodonta.

Extinct digitigrade or semiplantigrade carnivores with small and scarcely convoluted cerebrum; incisors $\frac{3}{3}$ or $\frac{2}{2}$; molars never more than 8; tail long; feet usually five-toed; scaphoid and lunare distinct.

The creodonts present marked resemblances to both marsupials and insectivores in many structural features, but they differ from both in the strong development of the canines, while the presence of a full milk dentition and absence of an inflected angle of the lower jaw serve strongly to mark them off from the former order. Through the miacidæ they seem connected with the canidæ (*infra*), and thus have given rise to the various lines of living fissipedes. From all living carnivores they are marked off by the absence of a carnassial tooth, and by a notch or groove at the tip of the distal phalanges. The Oxyclænidæ from the lowest eocene of New Mexico are known principally by the molar teeth. The Arctocyonidæ occur in the lower eocene of both continents, and have quadritubercular upper molars. *Arctocyon*, France; *Clænodon*, New Mexico. The Mesonychidæ of the American eocene have tritubercular molars; *Mesonyx*. Allied is the family Leptictidæ of Europe and America; *Proviverra*. The Palæonictidæ (*Palæonictis*, *Patriofelis*) occurs in the lower eocene of Europe and America. The Hyænodontidæ were larger animals, much nearer the recent carnivores (fissipedia), but were distinguished by the absence of differentiated carnassial teeth, which however occur in the Miacidæ. The hyænodontidæ range through the eocene to the lower miocene of both continents; the miacidæ have only been found in the eocene of America.

Sub–Order 2. Fissipedia (Carnivora Vera).

Digitigrade or plantigrade carnivores, with incisors $\frac{3}{3}$ (rarely $\frac{2}{2}$), premolar 4 in the upper and molar 1 in the lower jaw sectorial, the other molars tuberculate; feet four- or five-toed; scaphoid and lunare fused.

The carnivores proper are usually terrestrial in habits, only a few being partially aquatic. Most of them are carnivorous in diet, but some are omnivorous. Correlated with this flesh-eating habit is the large size of the canines and the shear-like carnassial or sectorial teeth alluded to in the diagnosis. The brain is convoluted, and the terminal phalanges are never notched at the tip, but they are occasionally retractile along with the claws they bear. The dogs (canidæ) seem to be the central stock from which descent has been in one line through the viverridæ to the cats and hyænas, in another through the ursidæ to the mustelidæ. It must, however, be mentioned that the viverridæ and mustelidæ show intergrading forms. The sub-order appears in the upper eocene, apparently as descendants of the miacidæ or palæonictidæ, and all known families persist at the present time.

The CANIDÆ have typically $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $p\,\frac{4}{4}$, $m\,\frac{2}{2}$ or $\frac{3}{3}$, the upper sectorial with two lobes, the lower with an inner weaker lobe in addition; auditory bulla large, inflated, and undivided; feet digitigrade, the fore feet four- or five-toed, the hind feet usually four-toed, claws not retractile. The majority of the species belong to the genus *Canis* (including *Lupus*, *Vulpes*, etc.) of cosmopolitan range, including the dogs, wolves, foxes, jackals, etc. Other living genera are *Octocyon* and *Lycaon* of South Africa. The fossil genera are numerous in both continents,among them *Temnocyon*, *Amphicyon*. and *Oligobunus*.

The URSIDÆ have plantigrade feet, short and stout body, sectorials scarcely differentiated, some of the premolars lost at an early date, and the auditory bulla flat. *Ursus*, containing the bears, with molars $\frac{2}{3}$, is largely confined to the northern hemisphere. *Melursus* is Asiatic. The fossil genera *Dinocyon*, *Hyænarctus*, and *Arctotherium* form a line uniting the dogs with the bears.

The PROCYONIDÆ with plantigrade feet, molars $\frac{2}{2}$, tuberculate, and with the tail usually ringed, are largely American; but two species, the raccoon (*Procyon lotor*) and the raccoon-fox (*Bassaris astuta*) enter the U. S. The coati (*Nasua*) with long, flexible snout, and *Cercoleptes* occur in Central and South America. The species of MUSTELIDÆ are more numerous; they have the molars $\frac{1}{2}$ ($\frac{1}{1}$ in *Mellivora*). The otters (*Lutra*) and the sea-otter (*Enhydris*) have webbed feet. *Mephitis*, including the skunks, is American. The badgers (*Meles*) belong to the old world, while the same common name is given to the species of the American genus *Taxidea*. The minks, martens, sables, ermines, weasels, and ferrets, belong to *Mustela*, many of the species being valuable for their furs. The genus begins in the miocene of Europe. *Gulo*, the wolverine, occurs in the northern parts of both hemispheres. A peculiarity of many of the mustelidæ is the great development of anal glands which secrete a strong-smelling fluid used as a weapon of defence.

The VIVERRIDÆ, like the remaining fissipedes. have a swollen auditory bulla and digitigrade or sub-plantigrade feet. They have $p\,\frac{3}{3}$ or $\frac{4}{4}$, $m\,\frac{1}{1}$ or $\frac{2}{2}$, and usually five digits on all the feet. The species are all old-world. *Cryptoprocta*; *Viverra*, the civets: *Herpestes*, the mongoose. The family appears in the lower miocene. The HYÆNIDÆ, also an old-world group, is closely related to the viverridæ by its fossil relatives. *Hyæna*, *Proteles*.

The FELIDÆ have retractile claws, stronly developed canines, molars $\frac{1}{1}$ in recent species (never exceeding $\frac{1}{2}$ in fossils); the upper sectorial with a three-lobed blade. *Felis* includes the majority of the living species, — lions, tigers, leopards, panthers, lynxes, pumas, jaguars, and the smaller cats. *Cynælurus*, the only other existing genus, contains the cheetah, or hunting leopard, which ranges from India to Southern Africa. The family appears in the upper eocene of America, while species are found in the miocene of both continents. Among the extinct genera are *Dinictis*, *Hoplophoneus*, and *Machærodus*, the latter characterized by the enormous canines, these being, in one species, seven inches in length.

SUB-ORDER 3. PINNIPEDIA.

Aquatic pentadactyl carnivores, with webbed feet fitted for swimming, incisors always less than $\frac{3}{3}$, *p* typically $\frac{4}{4}$, *m* $\frac{1}{1}$, no differentiated carnassial; tail very short.

The seals and their allies are mostly marine, although some ascend rivers, while one species occurs in Lake Baikal. The body is fitted for an aquatic life; the basal portion of the fore limbs is imbedded in the general integument, while the web of the toes usually extends beyond the extremity of the clawed digits. The seals are true carnivores, feeding upon fish, of which they destroy large numbers. The origin of the group is uncertain. The eared seals show considerable resemblances to the ursidæ, while the true seals suggest an origin from some form like *Lutra*. So it may be that the group is polyphyletic, or again, the pinnipeds may have descended directly from the creodonts. The group first appears with forms allied to *Phoca* in the miocene, while walrus-like forms occur in the pliocene.

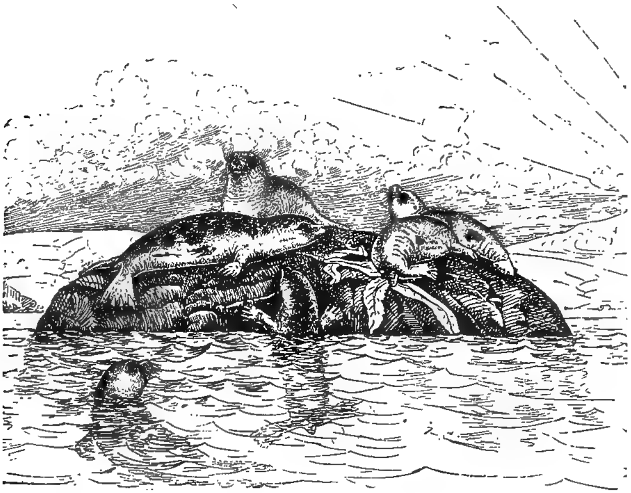


FIG. 377. Harbor seals, *Phoca vitulina*, after Elliott.

The OTARIIDÆ or eared seals have a small external ear, and the soles of the feet naked; teeth *i* $\frac{3}{2}$, *c* $\frac{1}{1}$, *p* $\frac{4}{4}$, *m* $\frac{1}{1}$ or $\frac{2}{1}$. *Otaria* includes sea-lions of the Pacific and South Atlantic; and the fur seals, most familiarly known from the northern Pacific. The TRICHECHIDÆ, or walruses, have the ears without external pinnæ, and the upper incisors developed into immense tusks. The species of *Trichechus*, one or two in number, are confined to the northern parts of both oceans. The PHOCIDÆ lack external ears, have the soles of the feet hairy, the testes abdominal, the teeth *p* $\frac{4}{4}$, *m* $\frac{1}{1}$, and stiff hair without a woolly fur beneath. *Phoca*, with incisors $\frac{3}{2}$, embraces the common seals of the northern Atlantic; *Monachus* ($i\ \frac{2}{2}$). the monk seals of warmer latitudes. *Cystophora* ($i\ \frac{2}{1}$) includes the hooded seals of polar seas with inflatable sac connected with the nostrils.

ORDER IX. PRIMATES.

Diphyodont, heterodont mammals, with typically $i\ \frac{2}{2}$, $m\ \frac{3}{3}$, the molars usually quadritubercular; the orbits separated from the temporal fossa by a postorbital bar; clavicles well developed; ulna and radius always distinct; feet plantigrade, usually pentadactyl; the pollex and (except in man) hallux opposable to the other digits. The placenta deciduate or not; diffuse or discoidal.

The primates, as a group, are not easily defined, especially if the extinct forms be taken into consideration, for these to a great extent bridge over the gap which exists, among recent forms, between the primates and the insectivores and creodonts, while in certain points there are suggestions of marsupial characters. According to one view, the order is polyphyletic, the lemurs having had one line of descent, and the monkeys, apes, and man having had another ancestry. This view is based primarily upon placental structures, but it is largely negatived by the fossil history so far as this is known.

SUB-ORDER I. PROSIMIÆ (LEMUROIDEA).

Arboreal primates with opposable great toe: orbits not completely separated from temporal fossa: mammæ thoracic, or thoracic and abdominal; uterus bicornuate; placenta non-deciduate, the whole surface of the chorion, except one end, being covered with villi.

The lemurs and their allies have their centre to-day in Madagascar, from which outlying species extend to the African continent and to the Indian archipelago, a distribution which has suggested a former continent, 'Lemuria,' in the Indian Ocean. In former times their range was more extensive, since abundant remains have been found in the older tertiaries of Europe and North America. The living species are mostly nocturnal, and many of them have the eyes peculiarly modified in accordance with their habits. In addition to the characters quoted in the diagnosis it may be mentioned that in some all the digits are clawed, while in others only the second and third of the hind toes are provided with claws, the others bearing nails. The upper molars have four or three tubercules, those of the lower jaw having four or five. The brain is but slightly convoluted, and but slightly overlaps the cerebellum.

PACHYLEMURIDÆ, $i\ \frac{3}{3}$ to $\frac{2}{2}$, $c\ \frac{1}{1}$, $p\ \frac{4}{4}$, $m\ \frac{3}{3}$. From the eocene and lowest miocene of Europe and America. *Adapis* of Europe is the best known. *Pelycodus*, *Tomitherium*. This family is regarded by Cope as the ancestor of the true apes. The modern lemurs may have sprung from the ANAPTOMORPHIDÆ, in which the lachrymal foramen lies outside the orbit, while the dentition is $i\ \frac{2}{2}$ to $\frac{2}{0}$, $c\ \frac{1}{1}$, $p\ \frac{3}{3}$ to $\frac{2}{2}$, $m\ \frac{3}{3}$. *Anaptomorphus*, from the lower eocene of Wyoming, resembles *Tarsius* (*infra*). *Necrolemur.*

The TARSIIDÆ of the Indian archipelago, with only a single species, *Tarsius spectrum*, has a dentition $i\ \frac{2}{1}$, $c\ \frac{1}{1}$, $p\ \frac{3}{3}$, $m\ \frac{3}{3}$; digits 2 and 3 of the hind feet with claws. In its placentation *Tarsius* differs from all other prosimiæ and approaches man. The lemurs proper belong to the LEMURIDÆ with $i\ \frac{2}{2}$, $c\ \frac{1}{0}$, $p\ \frac{2}{3}$ *to* $\frac{3}{3}$, $m\ \frac{3}{3}$, the lower incisors and canines directed forward, and the first premolar serving as a canine. *Indris*, *Lemur*, *Galago*, *Loris*, etc. The CHIROMYIDÆ with $i\ \frac{1}{1}$, $c\ \frac{0}{0}$, $p\ \frac{1}{0}$, $m\ \frac{3}{3}$, contains but a single species. the aye-aye, *Chiromys madagascarensis*, which recalls the rodents in its incisors and diastema, and is unique in the greatly elongate middle digit of the hand.

Two aberrant families, exhibiting some relationships to the lemurs, may be mentioned here. The first is NESOPITHECIDÆ, based on the fossil Malagassy genius *Nesopithecus*, which has the premolar dentition of a true lemur, with the orbit of a simian. The second is the GALEOPITHECIDÆ, with a single genus, *Galeopithecus*, from the East Indies. It is frequently referred to the insectivores with which it agrees in its deciduate discoidal placenta. It has the fore and hind limbs connected by membrane forming a parachute like that of the flying-squirrel.

SUB-ORDER 2. SIMIÆ (ANTHROPOIDEA).

Arboreal or terrestrial primates, with the digits (except hapalidæ) all with nails, molars with 4 or 3 tubercles; orbits completely separated from temporal fossa by a plate of bone beneath the postorbital bar; cerebrum greatly convolute, covering or nearly covering the cerebellum; mammæ two, always thoracic; uterus simple; placenta discoidal, deciduate.

The simiæ include the monkeys, apes, and man, and the deeper structural features are re-inforced by characters of less importance. Thus the eyes are directed forwards, the ears are much as in man, and in the young the whole appearance of the face of the lower forms is more like that of the human being than is that of the adult, the change being largely effected by a later forward growth of the jaws. Man excepted, the sub-order is confined to the warmer parts of both hemispheres, but fossils are found in Europe as far north as England. The sub-order has developed in two lines in the two hemispheres, the platyrhine forms belonging to the new world, the catarrhine to the old.

In the PLATYRHINI the nostrils are separated by a wide septum, and are directed outwards. The HAPALIDÆ have $i\ \frac{2}{2}$, $c\ \frac{1}{1}$, $p\ \frac{2}{2}$, $m\ \frac{3}{3}$; all digits, except the great toe, furnished with claws, and the tail non-prehensile. The species belonging to the genera *Hapale* and *Midas* have the common name of marmosets. Apparently this family has descended from the CEBIDÆ, in which the tail is frequently prehensile, and the premolars are $\frac{3}{3}$. *Mycetes* includes the howling monkeys; *Pithecia*, the sakis: *Ateles*, the spider monkeys: *Cebus*, the sapajous, species of which frequently accompany the organ-grinder. *Homunculus* and *Anthropops* occur in the tertiary of Patagonia.

The CATARRHINI have the nasal septum narrow, the nostrils directed forwards, and a dentition $i\,\frac{2}{2}.\ c\,\frac{1}{1}.\ p\,\frac{2}{2}.\ m\,\frac{3}{3}$. In the CERCOPITHECIDÆ (Cynopithecidæ) the tail is usually long, the molars quadrituberculate, and the ischial region presents callosities. All of the tailed apes of the old world belong to this family. *Cynocephalus* contains the baboons of Africa, in which the tail is of moderate size, and the maxillary bones swollen. Here also belong the drill and mandrill. The macaques (*Macacus*), are almost entirely Asiatic, one species entering Europe at Gibraltar. *Cercopithecus*. *Semnopithecus*. The SIMIIDÆ, or ANTHROPOMORPHA, contains apes in which the tail is lacking, the anterior limbs longer than the posterior, and ischial callosities lacking, except in *Hylobates*, which includes the gibbons of Asia, in which the arms are so long that they reach the ground when the animal is in an upright position. *Simia* includes the orang-utan of Sumatra and Borneo, in which the great toe is small, the arms long, and the ribs, 12 pairs. *Gorilla* of Africa has 13 pairs of ribs, and prominent superciliary ridges. *Troglodytes* includes the chimpanzees, of which there are one or two species, in which the ribs are as in gorilla. They come from western Africa.

FIG. 378. Chimpanzee, *Troglodytes niger*, after Brehm.

The HOMINIDÆ, or BIMANA, includes man, who is far less remote from the simiidæ than these are from the new-world monkeys. The chief characters are the upright position, the lack of opposable toe, the enormous size of the brain, correlated with his mental development, and the distribution of hair upon the body, it being best developed in those places where it is most sparse in the allied forms.

Man presents certain features in which he resembles more closely each of the anthropomorphous apes, while in others he differs from them all, so that it is difficult to say which is his nearer relative. Of the genus *Homo* there is, according to accepted tests, but a single species; but the question of arrangement of the races affords far more difficulties. For all such discussions reference must be made to the works on anthropology. The age of man on the earth is another question which can only be alluded to here. That man has been here far longer than the seven or eight thousand years of history is now beyond a doubt. His remains and his handiwork date back to a time far before any records or any traditions; to a time when the mammoth was alive, and when England and continental Europe had a fauna recalling those of the tropics to-day; when the mastodon, *Glyptodon*, and *Megatherium* ranged in South America. But when we attempt to pass back of the pleistocene the evidence is scanty, and not beyond question. The skull of Calaveras and the '*Pithecanthropus erectus*' of Java, like the miocene flint chips of Thenay, need more evidence in their support before they can be accepted as proving the existence of man in tertiary time, no matter how probable such existence may be upon *a priori* grounds.

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