CHORDATE MORPHOLOGY

Malcolm Jollie

REINHOLD BOOKS
IN THE
BIOLOGICAL SCIENCES

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Consulting Editor:

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CONSULTING EDITOR'S STATEMENT

All of us who teach comparative anatomy have regretted the passing, many years ago, of that grand old classic Kingsley. Here, at last, comes a book to fill the void. Malcolm Jollie's modern, superbly illustrated, account of the structure of the chordates was worth waiting for. This book is written with impeccable scholarship and draws not only from the literature of the world but from long and painstaking original dissections. No single illustration in this book has been "borrowed" from another book. Each has been drawn, and redrawn, until it shows with startling clarity just what the reader wants to know about almost any conceivable structure of the whole wide range of chordates. Histological and embryological details are also given wherever they serve to illuminate the point under discussion.

The theme of the book is evolution but this is not shoved down the student's throat as a cause. Malcolm Jollie, as any other good teacher, believes that an intelligent student, presented with logically arranged and clearly explained facts, can reach correct conclusions. In this case, these conclusions are that the process of evolution, imperfectly understood though it is, serves to link together the glorious diversity and complexity of the forms called chordates.

Pittsburgh, Pennsylvania
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Preface

New textbooks are usually viewed as revisions of those that preceded them—although they may be abridgments or expansions. It would be presumptive to propose to present comparative morphology in an entirely new way; yet there should be some justification for another text. Justification is based on the answers to several questions: Do current texts document, in terms of actual observed structures, and phylogenetic history they describe or do they demand acceptance of an authoritative view? Do current texts serve as an introduction to research in this area, so that the student can read with comprehension the current literature?

With such questions in mind, it was apparent that what was needed was a text enriched in vocabulary and concept, both in terms of anatomy and of systematics. The text should in some ways be a report on current research. It should demonstrate the method of approach and present a transection of existing views on the many facets of structural history. Although the whole of comparative morphology cannot be reviewed in a single volume, a practical sample can. It was with this in mind that this volume was planned.

As a part of this fresh approach, many of the illustrations are originals, drawn by the author from his dissections. Like the illustrations, many of the basic facts have been personally investigated. However, there is still a vast debt to the previous works in this field. In the selection of descriptive materials, discussion is restricted to as few kinds of animals as possible. Ranging over the entire chordate series would only have resulted in a presentation of anatomical vignettes. In each account, or chapter, a balance has been sought between a knowledge of facts and an understanding of their phylogenetic contribution. Each chapter looks at the whole area concerned rather than at a few spotlighted parts of it, which is usually done because of presumed practicality or student interest.

The plan of study seeks to develop analytic ability in the student. The customary procedure is to classify vertebrates and then to consider anatomical variations within such a framework as if there were no interrelationships between classes of vertebrates. Although it is necessary to introduce the various chordates at the beginning, a formal classification should actually stem from the morphological information presented during the course of study.

Traditionally the study of chordate morphology is identified by the title "comparative anatomy." By definition though, morphology is a broader term than anatomy since it includes not only the study of anatomical structure but also the origin of structure in terms of its embryology and evolution. Thus morphogenesis adds another dimension to anatomy.

The content of courses in this area of zoology varies, but generally it consists of summaries of anatomical variations observed in vertebrates, or chordates, set in a phylogenetic background. An extreme presentation deals with the anatomical details of a single animal, such as the cat; occasionally this is interspersed with remarks on functional or comparative aspects, but little or no information is given on phylogenetic history. If a course is based only on summaries of anatomy and statements about phylogeny, it tends to present the subject as stereotyped and colorless. If a course is based only on anatomical facts deemed useful, it ignores another important value, which is to reveal to the student something of his nature, and his place in the cosmos. Historically one of the goals of man's intellectual efforts in the field of the natural sciences has been to understand himself and his environment, an environment of harsh and rigorous ideology as well as physical surroundings.

As a field of study, comparative morphology is always in a state of some confusion because of its vast scope and because of the many aspects of structure or systematics from which it seeks clews. Information is pouring in from all sides and the task of creating greater order becomes larger every year. Disorder is, in part, an evidence of growth, as well as an indication of changes in viewpoint. Fossil discoveries are continually filling in gaps and smoothing the sequences between fossil and living species, and studies of the phylogeny of many groups of animals can and are being made. No one has more than a hazy notion of what the first vertebrates looked like or even how the jawed and jawless groups are related to each other. Almost any vertebrate can be investigated as an experience in discovery.

It has recently been pointed out that whereas comparative morphology since 1859 has been documenting the phylogenetic history of structural elements, which is a purely descriptive operation, its proper goal as a science is to explain the structural stages which organisms have passed through in the course of time in terms of their genetic origin and environmental selection. It is the author's opinion that comparative morphologists can for some time yet legitimately confine themselves to phylogenetic studies and interpretations. This is by no means a "purely descriptive" activity nor a matter of documenting a preconceived pattern of evolution, but rather the discovery of the actual, or most probable, pathways that have been followed. Thus, this area of scholarly endeavor is not in competition with genetics or ecology but complements these by supplying phylogenetic sequences for analysis.

Comparative morphology is not an experimental study; it is primarily a descriptive and interpretive realm. This does not preclude the possibility of experimental work; it implies that the usual activity is one of determining taxonomic groups and revealing the morphological time series behind them. Thus the comparative morphologist is either a taxonomist dealing with some living group or a palaeontologist using the phylogeny of fossil animals to reveal the ages of rock strata. The geneticist, ecologist, or physiologist may use comparative morphology as a part of his research background, just as the comparative morphologist utilizes knowledge of embryology, genetics, physiology, and ecology in pursuit of the history of a structure.

The basic prerequisite for study in this field is a patient, meticulous, detail-seeking nature. All ideas must be carefully screened and tested both in terms of direct observations and of historical retrospect. Yet one must, like a detective, continually re-sort the evidence with the hope of discovering its hidden significance. One cannot expect simple, direct, or quantitatively expressed answers, but only the most indirect "revelations." Technological skills may also be important in a study involving dissection and the preparation of many kinds of specimens from serial sections of embryos to the uncovering of a fossil from its stony shroud. There are many pitfalls and temptations inherent in the methods of this study and one should continually return to the instructions of Louis Agassiz —study nature and not books.

In the preparation of this text, I have received help from a number of sources. I wish to express my thanks to Dr. Peter Gray, the consulting editor for Reinhold Books in the Biological Sciences, for his advice and encouragement. Miss Joan Thomas assisted with the illustrations, along with several student assistants. Mr.

and Mrs. Eric Meadows were indispensable in labeling the illustrations and in indexing. I am indeed grateful to all these persons and many others who helped with the multitudinous tasks required for a text.

MALCOLM JOLLIE

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Contents

Introduction: An Historical Sketch

Although knowledge of a subject's historical background is not essential, a good grounding in any field is based on knowledge of its past and some conception of the human contribution it represents. The history of comparative anatomy might be likened to a vast and fascinating labyrinth into which one can easily wander and never return. Within the biological sciences, the contributions to this field exceed in bulk and number those of any other, and its bibliography contains some of the earliest writings on biology. Even today, when the peak of production has probably been passed, there is still a large volume of work appearing in various periodicals and reference books.

The absolute value of comparative morphology's contribution to man's present intellectual status is difficult to assess. The history of the natural sciences in general is the history of man's emancipation from controlled and regimented thinking or from environmental situations that preclude thought beyond mere survival. Comparative morphology, by providing man with a better understanding of the nature and evolution of living things, has given him a sound basis for contemplating the more meaningful questions of existence: man's origin, his place in nature, and perhaps his ultimate fate. In this lies its contribution.

Since the beginnings of natural history are shrouded in the past, much must be inferred. Certainly, early man was aware of the multiplicity of animals and plants, with which he lived in closer harmony than we do today, and also of their structural complexities. He knew much about the life histories of the more conspicuous organisms, many of which he used for food, and had names for those that figured importantly in his life. He also realized that the parts of the body had different functions. The heart, for example, was conceived of as the organ of life and the center of the soul. Man became familiar with the gross aspects of anatomy through hunting, warfare, and daily social life, and thus, by seeing similar gross structures in other animals, he might also have formed some conception of "comparative anatomy." In this primitive period, the similarity between man and the apes probably did not go unnoticed although gradually the concept of man as a unique creature, specially endowed, emerged.

During the early period of the ancients, the accumulation of knowledge began to be recorded in writing, but not in a permanent or indestructible form. Since few people had the leisure or the opportunity to dedicate themselves to learning, the growth of the fund of knowledge was slow and at times the losses exceeded the gains. Growth of an information pool means little if it is revised without reference to fact, simply to conform to current beliefs. Knowledge, like many radioactive substances, has been described as having a "half-life" of about ten years. "Facts" must be continually rediscovered, reviewed, discussed, and critically analyzed if they are to contribute to the working knowledge of succeeding generations.

The nature of the information to be recorded is also an important factor in the survival and accumulation of knowledge. Anatomy, like so many other subjects in natural history, requires illustrations. The art of anatomical drawing was not perfected until the sixteenth century, and developments before that time were extremely crude. A systematic study of anatomy also requires a special vocabulary. This is developed after careful dissection of specimens and studies of accurate, detailed drawings. Any discussion of anatomy, morphology, and evolution must be based on this special vocabulary and the extensive knowledge gained from careful dissection recorded in accurate drawings.

Although the primary interest of the ancients was in the anatomy of man because of the pertinence of medical practicality, comparative morphology has long been practiced—certainly since the Greek period. It was not, however, sharply defined. A structural *scala naturae,* the arrangement of organisms from the simplest to the most complex (man), was already in existence by the time of Aristotle, as were concepts of spontaneous generation and a god-directed evolution from lower to higher forms. Aristotles' anatomical diagnoses of taxonomic groups involved the comparative method and were as precise as those made several hundred years later.

With the appearance of Belon's *L'Histoire des Oyseaux* (1555), in which the skeletons of the bird and man are illustrated and compared, comparative morphology can be said to have really begun. This early stage involved only the crudest illustrations and superficial descriptions of the anatomy of various animals; yet even here could be found a hint of the emerging concept of homology. The similarities in the structure of man and the lower animals invited comparisons, some of which were extremely improbable in terms of our present understanding. The study of the anatomy of man, reinstituted by Vesalius (1543), now became comparative both in terms of structural variations and in terms of the function of the various parts of the body.

An important anatomical and physiological milepost was Harvey's (1628) description and proof of the circulation of the blood, based upon the structure and functioning of the heart, and the direction of flow in the larger blood channels. What was lacking was observation of the capillaries which connect the arteries and veins. The significance of this work lies in its mechanistic interpretation of what had been considered the seat of vitalism in man. The paradox is that in other respects Harvey was quite loath to break with tradition.

The first compendium of "Comparative Anatomy," that of Samuel Collins (1685), was based on the functional approach. "The structure of one animal throws light on, and explains, that of another, for comparative anatomy is the most liberal and accurate guide. Parts which are dark and incomprehensible in one animal may often be understood very clearly in another." (Swammerdam, 1737)

Daubenton (*c.* 1750) collaborated with Buffon in an extensive comparative study of mammals, and as a result Buffon developed ideas of homology of structure. Homology implies that a structure in one organism is the *same* or nearly the same, however specialized in form or function, as that in another organism. The problem is one of defining what is meant by *same*. In the minds of these early biologists, homology merely involved a fundamental plan of structure. All vertebrates were assumed to be built on a common plan with each species showing certain divergences from this plan as specializations for its way of life. This idea of a fundamental plan was carried to the extreme of assuming a basic one for all animals.

Richard Owen (1843) was the first to define the terms "homology" and "analogy," and discussion as to their meaning has continued right down to the present time. Whether a structure is truly homologous (the same) or analogous (similar only in function) depends now on our concept of evolution. Homologous structures trace back to the same part, more or less, of a common ancestor; analogous structures do not.

Following Daubenton, many individuals (Goethe, Vicq d'Azyr, Geoffroy Saint-Hilaire, and Cuvier) helped expand our knowledge of vertebrate structure and systematized it so as to realize the "greater truths" demanded of it by Buffon. These "greater truths," in some instances, turned out to be wild speculations. Many of these are fascinating, such as Goethe's (or Oken's) theory that the skull is made up of several modified vertebrae or the view held by many that nature is an organism which shows a single graded series of forms from matter to man. The amateur status of some of these philosophers as well as the general metaphysical atmosphere in which they lived accounts for some of these hypotheses.

In the hands of Cuvier (1829) anatomical facts were conservatively interpreted in terms of specializations for different ways of life. He thought they represented several taxonomic hierarchies rather than one "great chain of being," although he did not believe in the mutability of species or evolution. His interest in fossil forms gave the subject a new dimension, one largely relegated to paleontology at the present time. His work with fossils produced a catastrophe theory which involved only local exterminations of life followed by invasions of animals from other regions of the world. This view could not stand up under close examination—new species had to come from somewhere; they were not all present from the beginnings of the earth.

The study of fossil forms and geology continually demanded a greater and greater age for the earth—Bishop Ussher's estimate of about 6000 years simply did not allow enough time. Studies of fossil faunas showed that gradual changes were the rule and that so-called catastrophes were largely the result of gaps in the geological sequences of the rocks. The many observations of the continuum of life demanded acceptance of the law of uniformitarianism, which declared that the conditions and forces operating today are like those that operated in the past.

The "great chain of being" had now become involved with the past as well as the present, and it was apparent that many kinds of animals had become extinct whereas others had appeared relatively late in the history of the earth—certainly man was a late-comer. The idea of the "great chain of being," as the handiwork of God, now demanded new creations for each geological period as old members became extinct. The possibility of new creations did not agree with uniformitarianism; so a concept of the evolution of simpler forms into more complex ones was necessary to fill the gaps. In addition, it was observed that species showed adaptation to various climates and habitat situations by morphological differentiation, as, for example, the races of man. Buffon's, Lamark's, and Saint-Hilaire's views on the mutability of species could account for the origin of replacement species without special creation.

The concept of the fixity of the created species had now become quite shaky. There were several possible interpretations to the observations of the schools of the "great chain of being" and the mutability of species as an adaptive mechanism. One extreme was the idea that only one species had been created at the beginning and that from this all animals had evolved through adaptation for various niches. Another was the proposal of Darwin, which assumed a continuing change and modification of life with time, great periods of time, and a struggle for existence—with success going to that individual or population most suited to the specific environment. This theory involved not just a seeking of a niche, but a continual adjustment to changing niches. This theory can account better for the sequence and replacements of faunas known to have lived in any given area. It differs from the former concept only in its explanation of method and perhaps in its starting point.

The theory of evolution, based on natural selection (Darwin, 1858, 1859),.did not materially change the direction of study in comparative morphology. With the general acceptance of this *modus operandi* of life, comparative morphologists switched easily from the documentation of the numerous and minutely different steps in a chain, or chains of being, to the study of the phylogeny of the various evolutionary lines.

At this time the biogenetic law (Serres, Haeckel) was being formulated. This law asserted that the embryological stages an organism passed through in its development resembled the adult stages of its ancestry. Haeckel stated this succinctly as "Ontogeny recapitulates phylogeny." A general acceptance of this view made embryology an important part of comparative morphological research. Unfortunately the equating of ontogeny and phylogeny introduced a great deal of confusion as well.

The biogenetic law, like the theory of evolution, was not accepted by everyone and there was considerable debate about its shortcomings and strong points. It was denied from the beginning by some (von Baer), and others sought to discredit it primarily because of its choice of words. Argumentation about this concept has continued until the present, although there is general agreement that it is not a law.

On the one hand, Aulie (1955) affirms that "Recapitulation . . . has turned out to be something quite unlike what it was first thought to be. It is not the mystical expression of some creative force in nature as the Nature-Philosophers lead by Kielmeyer had thought; nor the mechanical pushing back of characters, as Weismann would have it; neither is it a simple expression of heredity, as Haeckel had obscurely maintained The phenomena of recapitulation cannot be deduced from some simple general law, but rather they must be viewed as occurring in an organism developing in the most efficient manner possible, each stage of which is placed with careful reference to future development, as an individual expression of relative growth, and the fitting in of genetic actions into the life of the individual." Needham (1930) also states: "It is the function of the embryo to become an adult without looking backward on ancestral history." In short, recapitulation is only partial and open to short cuts or additions at any stage, as pointed out by von Baer.

On the other hand, Hyman (1940) asserts that "Resemblance to ancestral forms, embryonic or adult, is a common and widespread phenomenon . . . consequently the practice of drawing phylogenetic conclusions from the study of development is to a large extent justifiable." Thus the term *Palingenesis* (or paleogenesis) has been suggested for this inherent, if partial, tendency of descendent ontogenies to recapitulate ancestral ontogenies.

Although Cuvier is usually thought of as the father of comparative anatomy, or at least its first great authority, it is seldom that we refer back to him. Modern comparative anatomy had its real beginnings with Johannes Müller, (*c.* 1840), Carl Gegenbaur (1860–1900), and their students. The documentation of the phylogeny of animals began with Gegenbaur and Haeckel (1864). German biologists were the great contributors at this period and one cannot avoid referring to or using eponyms honoring such names as Meckel, Gaupp, Rathke, Butschli, Fürbringer, Wiederscheim, and Gadow. Of like stature among the English were Owen, Balfour, Huxley, and Parker. More recent are Kerr, Goodrich, and de Beer.

The new comparative morphology did not have easy going. It became embroiled in argumentation over terms. The interpretation of homology was critical since homologs reveal phylogeny, or accepted phylogenies indicate homologs. Gegenbaur related homologs to embryological development. To be homologous, structures must be developed from exactly corresponding rudiments of the embryo. Such a definition resulted in the belief that the pectoral limbs of vertebrates, since they arise at different somite levels, are not homologous but rather parallel developments. This concept was developed and applied to many anatomical details by Fürbringer.

The basis of homology should be the concept of a continuum of living things through time. The pectoral limbs are the *same*, although their somite level may be altered—even within a species or on the two sides of an individual. The concept has become entangled with somite differences, germ layer differences, and reorganizations of body plan affecting general position and interrelationships. Further confusion is adduced by considering serially repeated structures, such as vertebrae. From all of this two real factors emerge. First, the degree of homology between two compared structures can range from complete to nil; an arbitrary cut-off point must be decided upon. Secondly, parallel developments are involved. Recent studies suggest that parallel changes took place in several lines of reptiles, resulting in mammal-like forms. These changes involved conversion of some of the lower jaw bones into middle-ear bones and a concomitant change in the articulation of the lower jaw. This parallelism is revealed against a background of differentiating detail. Technically, parallel structures are not homologous, but one wonders whether "increasing precision of definition," as a scientific goal, is wholly desirable if it increases the number of areas of disagreement.

At the present time, comparative morphology is enjoying a rather pleasant period of productivity traceable to a number of sources. Morphological studies of fossil fishes by Stensiö (1927 to the present), Säve-Söderbergh, Jarvik, Neilsen, and Lehman, along with similar studies of many kinds of vertebrates by D. M. S. Watson, Gregory, Westoll, and Romer, have opened up new vistas as to the ancestry and the nature or direction of evolution of the vertebrates. Renewed interest in the quantitative aspects of the speciation process has focused attention on the species and subspecies in terms of time and geographic distribution. Study of the origin of faunas and their development has helped us to understand the changing aspects of life in time. Studies of the functional importance of anatomical features in terms of internal physiological mechanism or in environmental adjustment and competition also aid in understanding and interpreting the observed stages of the evolution of vertebrates.

The renewed interest in comparative morphology today supports the contention that old disciplines become more interesting with time. Subject matter and its interpretation, like living organisms, undergoes changes with time and must be continually re-examined. Although man has a long intellectual phylogeny behind him, each of us must undergo an educational ontogeny if we are to pick up and proceed from where others have left off. Each individual seeks answers to the riddles of life and culture, answers which in part can be gained from the study of comparative morphology.

1

Chordates, Protochordates, and their Relationships

THE PHYLUM CHORDATA

The Phylum Chordata unites a number of seemingly distinct groups of organisms, one of which is the Subphylum Vertebrata. The student already has some familiarity with the vertebrates and has perhaps been introduced to the other subphyla, at least by name. These subphyla are the Cephalochordata and the Urochordata or Tunicata, which are invertebrates, that is, without vertebrae. The fact that these invertebrates are included with the vertebrates in a common phylum is of special interest, for it suggests the possibility of intergradation between these two extremes and, therefore, the pathway for evolutionary transition from one to the other.

The historical background of this association is pertinent. Lamarck (1809, 1815) and Cuvier (1816) created the schism between the categories of vertebrates and invertebrates on the basis of the uniqueness of the former, the presence of a vertebral column. This subjective evaluation was not revised even after the recognition by Costa in 1834 of *Branchiostoma lanceolatum*, named *Amphioxus* by Yarrel a year later, as a "low vertebrate," and the demonstration by Kowalevski (1869, 1871) of the similarities in basic structure of vertebrates and the larvae of tunicates. Balfour in 1880 destroyed this schism, in theory if not in fact, by establishing the Phylum Chordata for the vertebrates, lancets (Amphioxus), and tunicates. Bateson in 1885 added the hemichordates, containing *Balanoglossus*, to the Phylum Chordata. Fowler (1892) suggested the inclusion of *Rhabdopleura* in the Hemichordata, and Spengel (1932) added *Planctosphaera* to this subphylum. Current opinion removes the Hemichordata as a separate phylum, leaving the Cephalochordata, Urochordata, and Vertebrata as subphyla of the Chordata. Collectively, the cephalochordates, urochordates, and hemichordates are identified as protochordates, thus inferring a transitional nature between the lower invertebrate phyla and the vertebrates.

The Phylum Chordata as now defined unites organisms having a notochord, hollow dorsal nerve cord, and pharyngeal pouches or slits. As a basis for discussion, the anatomy of the various subphyla of the chordates and the hemichordates should be described. From these anatomical facts the interrelationships of the chordate subphyla and the relationships of chordates and hemichordates can be defined and discussed. No specific order will be followed for this description, for all of these early animal forms are equally complex in structure and none can be identified as ancestral or transitional to the others. Furthermore, to avoid anticipating the results of comparative study and indoctrinating the student, no specific order based on the conclusions of "authorities" will be followed. It is recommended that the student work from the raw materials of dissection and observation to conclusions regarding interrelationships of an evolutionary or phylogenetic nature.

Amphioxus is usually described as being most like the vertebrate and is the protochordate that is perhaps best known to the student. It thus constitutes a starting point in working from the familiar toward the unknown.

THE PROTOCHORDATES

Cephalochordata

Branchiostoma (*B. lanceolatus* or Amphioxus) is the usual representative of this group, which has only one other genus in it, *Asymmetron*. The group derives its name from the fact that the notochord extends farther forward than the brain (in the vertebrate the cord ends about midway along the length of the brain).

The body is elongate and fusiform, or lanceolate (Figures 1-1, 1-5). At the anterior end, the mouth lies within an **oral funnel** or **hood**, below the **snout** or **rostrum** (Figure 1-2). The membranous lateral and ventral walls of the oral hood are fringed by **cirri**. These cirri have small lumps or **sensory papillae** on them and, along with the margin of the oral funnel, are supported by a jointed connective tissue skeleton.

The **mouth** is set in the middle of a partition or **velum**, and from the edge of the mouth tentacle-like **languets** extend into the pharynx. In the oral hood there is a **ciliated wheel organ** and in the roof is a **ciliated fossa** (literally "ditch") **of Hatschek**, which lies just to the left of the notochord (Figure 1-3).

The snout is somewhat expanded and into it extends the notochord. The **notochord** extends the entire length of the

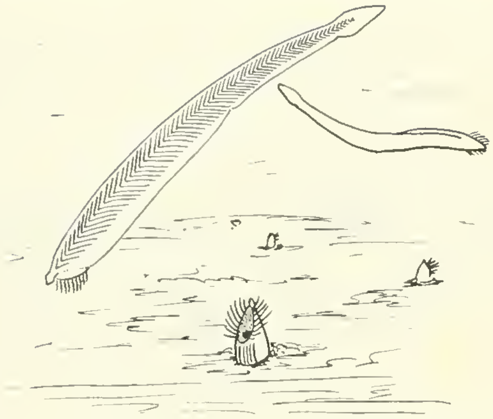


Figure 1-1. Amphioxus swimming (when disturbed) and feeding. (After Newman)

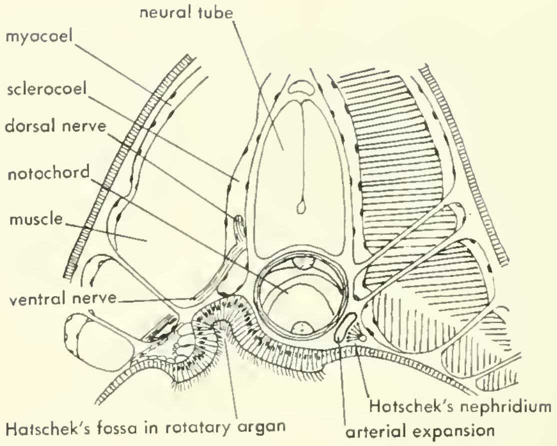


Figure 1-3. Cross section through oral funnel showing Hatschek's fossa in the rotatory organ.

animal, beyond the **neural tube** anteriorly. Above the neural tube is a series of **dorsal rays** supporting the **dorsal fin fold.**

The body wall is smooth and covered by a cuticle. Within the anterior third of the animal, the **slits** of the **pharynx** are observed. These open into an **atrial cavity** (Figure 1-4), which exits to the outside by an **atrial pore** (Figure 1-5) about two-thirds of the way back on the body (Figure 1-4). The atrium is enclosed below by a sheet of tissue in which there are **transverse muscle fibers.** The body wall extends down beyond this plate as **metapleural folds.** The atrial cavity extends posteriorly beyond the atriopore as bilateral sacs, the one on the right side being the larger. There are also anterior digitations into the restricted dorsolateral coelomic spaces above the pharynx.

The <-shaped **muscle segments (myomeres)**, whose points are directed anteriorly, are also visible through the cover of the body. There are about 60 pairs of muscle segments in the body and 180 slits in the pharynx. The difference in number is due to the fact that the slits continue to multiply in the course of development after the number of muscle segments has become fixed.

The digestive tract begins at the posterior end of the pharynx, which tapers to an **esophagus** (Figure 1-5). A short

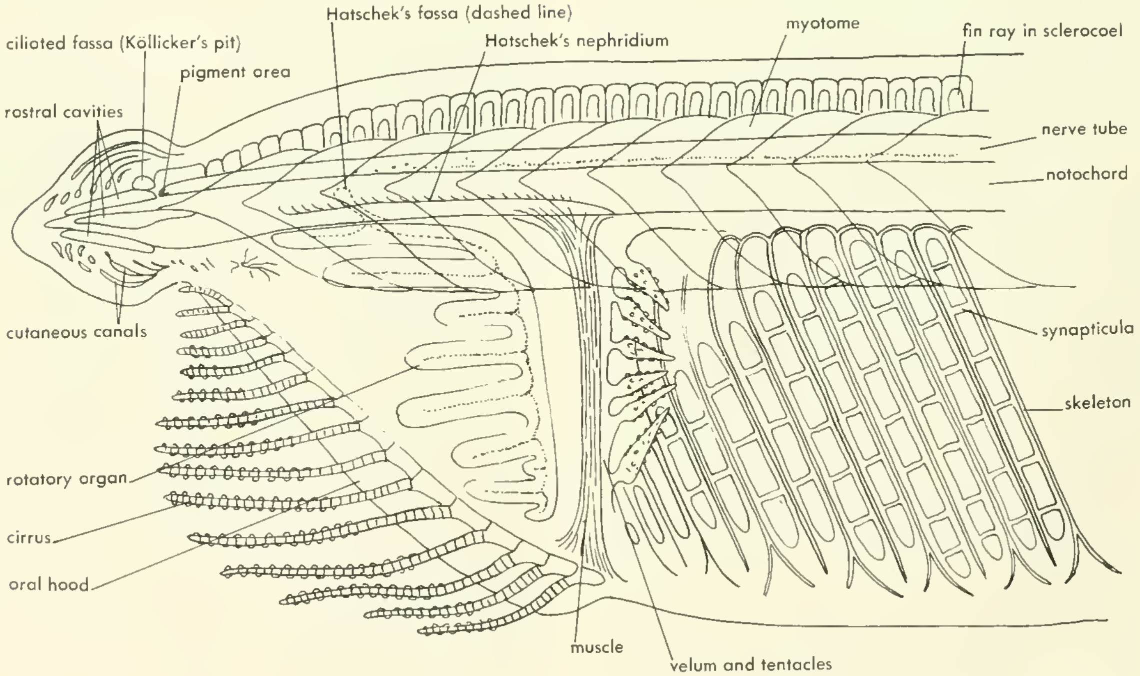


Figure 1-2. Anterior end of Amphioxus. (After Franz, 1927)

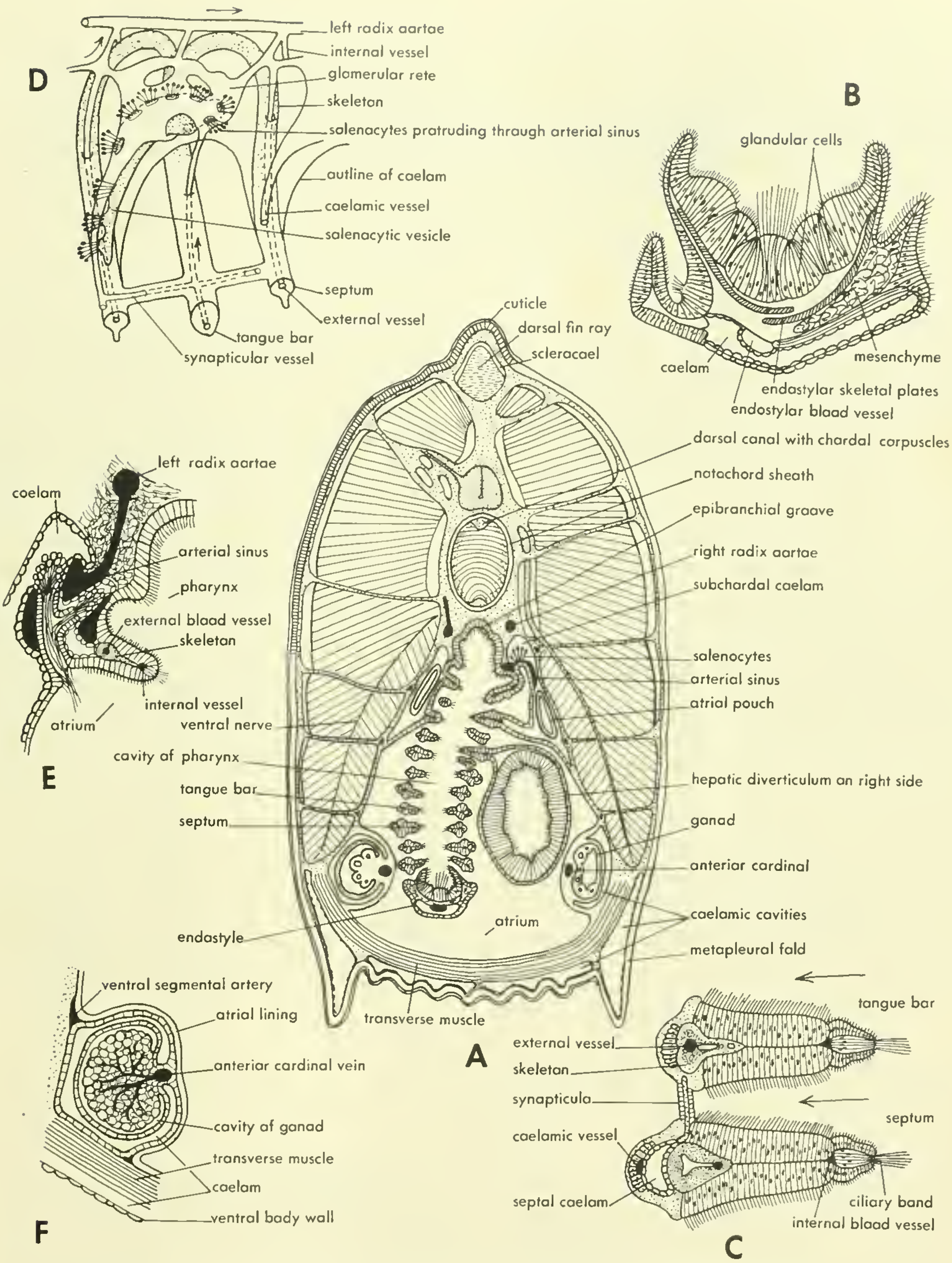


Figure 1-4. Anatomical details of Amphioxus. (After Franz) A, cross section of posterior pharyngeal region; B, cross section of endostyle; C, frontal section of pharyngeal bars; D, lateral view of a solenocytic vesicle (after Goodrich, and Franz); E, cross section of a solenocytic vesicle showing its relationship to the blood, coelom, and pharynx; F, cross section of a gonad.

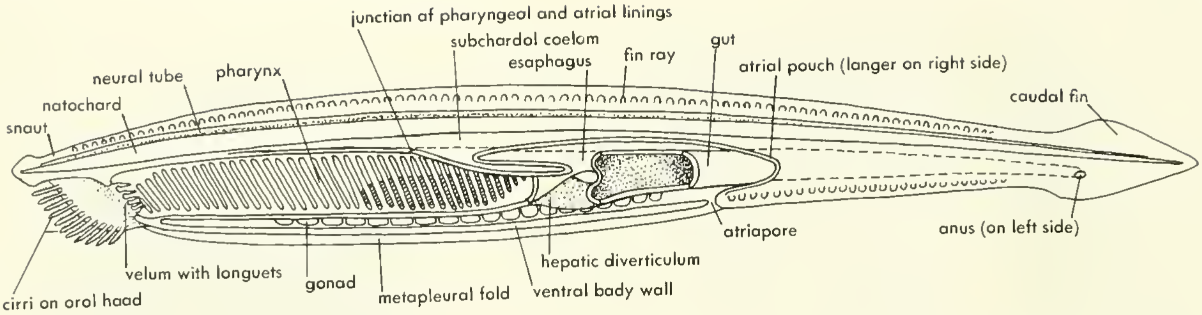


Figure 1-5. Gross internal relationships in Amphioxus.

distance behind the esophagus a diverticulum (blindly ending pouch) of the gut extends forward on the right side for about one-third of the length of the pharynx. This **hepatic** ("liver-like") **diverticulum,** carrying with it a pouch of the coelom, projects into the atrium. Behind the diverticulum the gut tapers toward the **intestine,** which leads to the **anus** near the posterior end of the animal. The anus opens to the left of the caudal fin, which is displaced to the right.

The interior of the pharynx and the intestine is ciliated. The **pharyngeal cilia** drive a **mucous net** from the ventral **endostyle** or **hypobranchial groove** upward to the **epibranchial groove.** Here the net is rolled up and driven back into the esophagus. In the gut the food materials are moved about by the cilia during the process of digestion.

The excretory system consists of a series of segmental **vesicles;** into each of them opens a large number of **solenocytes,** excretory cells containing a flagellum (Figure 1-4 D,E). The vesicles open into the pharynx above the dorsal margin of the slits. In addition to these segmental "nephridia," there is a single tube extending forward to the right of the notochord from just above the mouth; this is the **nephridium of Hatschek.**

In the ventrolateral angles of the pharyngeal region, there are about 26 pairs of **gonads** (reproductive organs) in the adult animal (Figure 1-4 F). These extend back to the atrial pore. The sex cells are shed into the atrium and carried to the exterior through the atrial pore.

Each of the muscle segments lies in a connective tissue sheath. Near the notochord there is a small **sclerocoel,** a term applied to the fluid-filled cavities along the axis of the animal. The sclerocoels also enclose the rays of the dorsal and ventral (posterior to atriopore) fin folds.

The notochord is well developed and has a strong **outer sheath** and **inner elastic membrane** (Figure 1-4 A). Just inside the membrane are the nuclei of the chordal cells. The central cells are discs with a large central vacuole; within the notochord they are stacked from front to rear. There are ventral and dorsal canals just within the sheath which contain small, free cells, the **chordal corpuscles.**

Amphioxus has a well-developed circulatory system (Figure 1-6). There is a ventral blood vessel which collects from the digestive tract and extends forward to the hepatic diverticulum and along the underside of that structure. Here it breaks down into smaller vessels which permeate the wall of this diverticulum and are recollected by a dorsal vessel. This dorsal vessel hooks forward beneath the pharynx and here receives the so-called **posterior and anterior cardinal vessels** draining the ventrolateral body wall. The main channel leads forward below the endostyle sending branches into the gill bars.

The blood is collected dorsally by **paired aortae** which join behind the pharynx to form a midline **dorsal aorta.** This has branches extending through the myosepta both dorsally and ventrally to the body wall (Figure 1-4 A). The myosepta are sheets of connective tissue separating the blocks of muscle, the myomeres, one from another. The dorsal

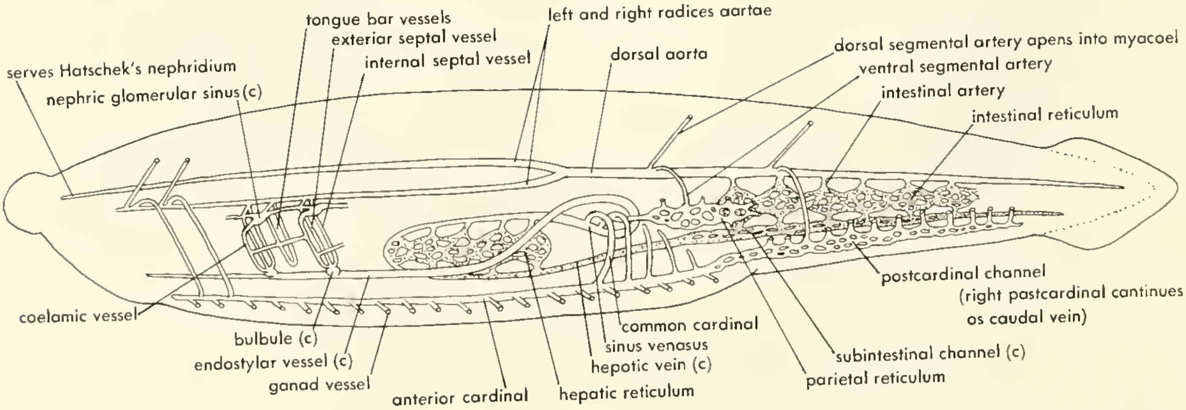


Figure 1-6. Diagrammatic circulatory system of Amphioxus. Contractile vessels are indicated (c).

vessel passes between the myomeres and opens into the myocoel, the cavity between the myomere and the body wall. The ventral vessel passes down on the inner aspect of the body wall and enters the cardinal vessel. Irregular branches from the dorsal aorta also extend to the intestine. The dorsal aorta extends back into the tail as the **caudal artery**, and blood is collected in the tail by a **caudal vein.** The vein extends forward to enter the **subintestinal** vessel and the posterior cardinal of the right side.

The blood of Amphioxus is without cells, and the vessels, with the exception of the dorsal aorta, are without linings. The **subintestinal vein, hepatic vein, endostylar** vessel and its **bulbuli** (tiny expansions), and the **nephric glomerulae** are contractile. The term glomerulus refers to a knot, or in this case a net, of small blood vessels. Such "knots" of small arterial vessels are associated generally with excretory structures (Figure 1-4 D,E).

The nervous system (Figures 1-2 to 1-4) consists of a **dorsal nerve tube** and paired **segmental nerves.** In this tube are scattered **photosensory cells,** the **cells of Hesse** and **Joseph.** Those of Joseph are distributed anteriorly and dorsally, those of Hesse along the inner face of the tube throughout most of its length. The former are cells enclosed by a cup of pigment granules. **Giant cells** (**of Rhodes**) are segmentally arranged for much of the length of the tube, and their fibers run ventrally along the cord, on the side opposite the cell body.

Anteriorly the cord is slightly expanded and its central cavity enlarged to a **ventricle.** The **ventral** and **dorsal nerves** of each segment are separate. The ventral **root** lies opposite the myotome; the dorsal root passes between the myotomes, posterior to the ventral root. The dorsal root of one side is across from the ventral root of the other side. The dorsal root is largely sensory but contains motor fibers for the **nonmyotomic muscles** of the ventral part of the body (the transverse muscle) and fibers for the gut wall (there is a **plexus,** or **nerve net,** in the gut wall). The nerve fibers are not **myelinated,** and **sensory ganglia** are lacking—the sensory cell bodies lie close below the epidermis or are scattered along the course of the nerve.

The two most anterior nerves arise from the expanded "brain." These serve the snout and lack ventral roots. Nerves III to VII have dorsal and ventral roots, the latter serving the myotomes. The dorsal nerve gives rise to superficial and deep branches which, along with the deep branch of the second nerve, give rise to superficial and deep plexuses in the walls of the oral hood. The velum is innervated by branches from the deep plexus of the left side. There is no lateral-line system nor are there special sense organs such as the eye, ear, or nose.

Urachordata (Tunicates)

The adult tunicate is usually an attached (**sessil**) organism; a few species are **planctonic** (floating about), whereas others retain the larval form as adults. They may be solitary, colonial, or compound (Figure 1-7). *Clavelina* or *Ecteinascidia* are solitary types of tubular or sac-like form.

At the free end of the tunicate there is a **mouth** and an **atrial pore.** The animal is enclosed in a **tunic** or secreted

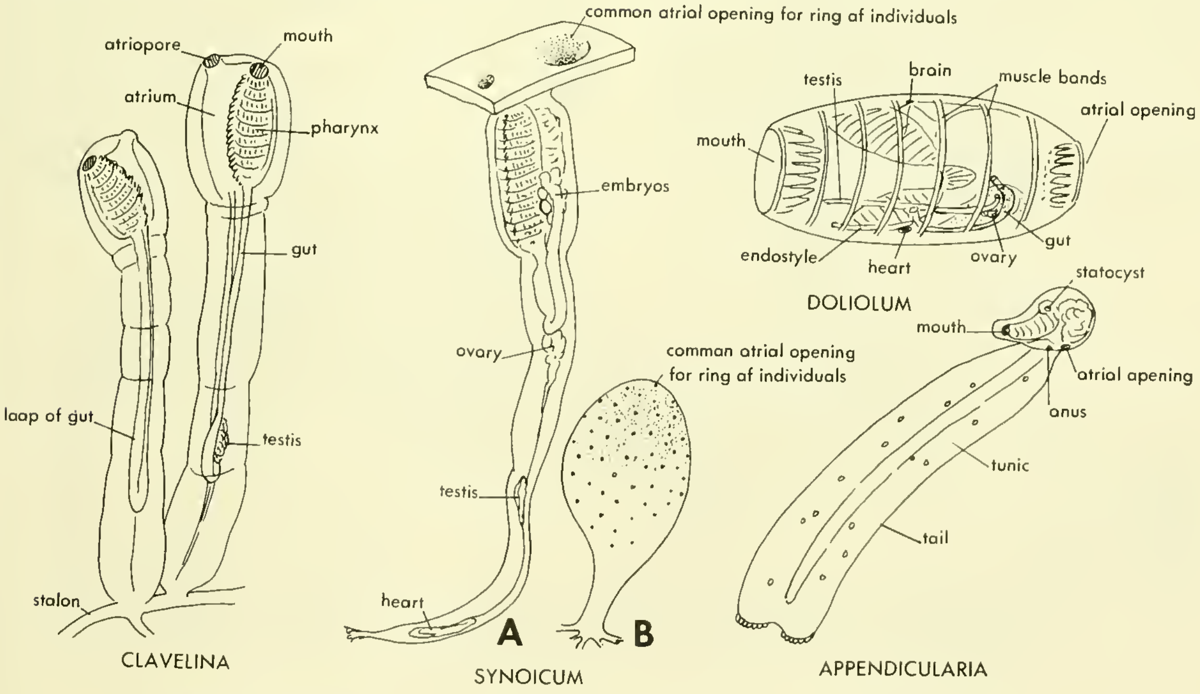


Figure 1-7. Basic kinds of tunicates: solitary (*Clavelina*), colonial (*Synoicum*), and pelagic (*Doliolum, Appendicularia*). A shows individual removed from colony, B.

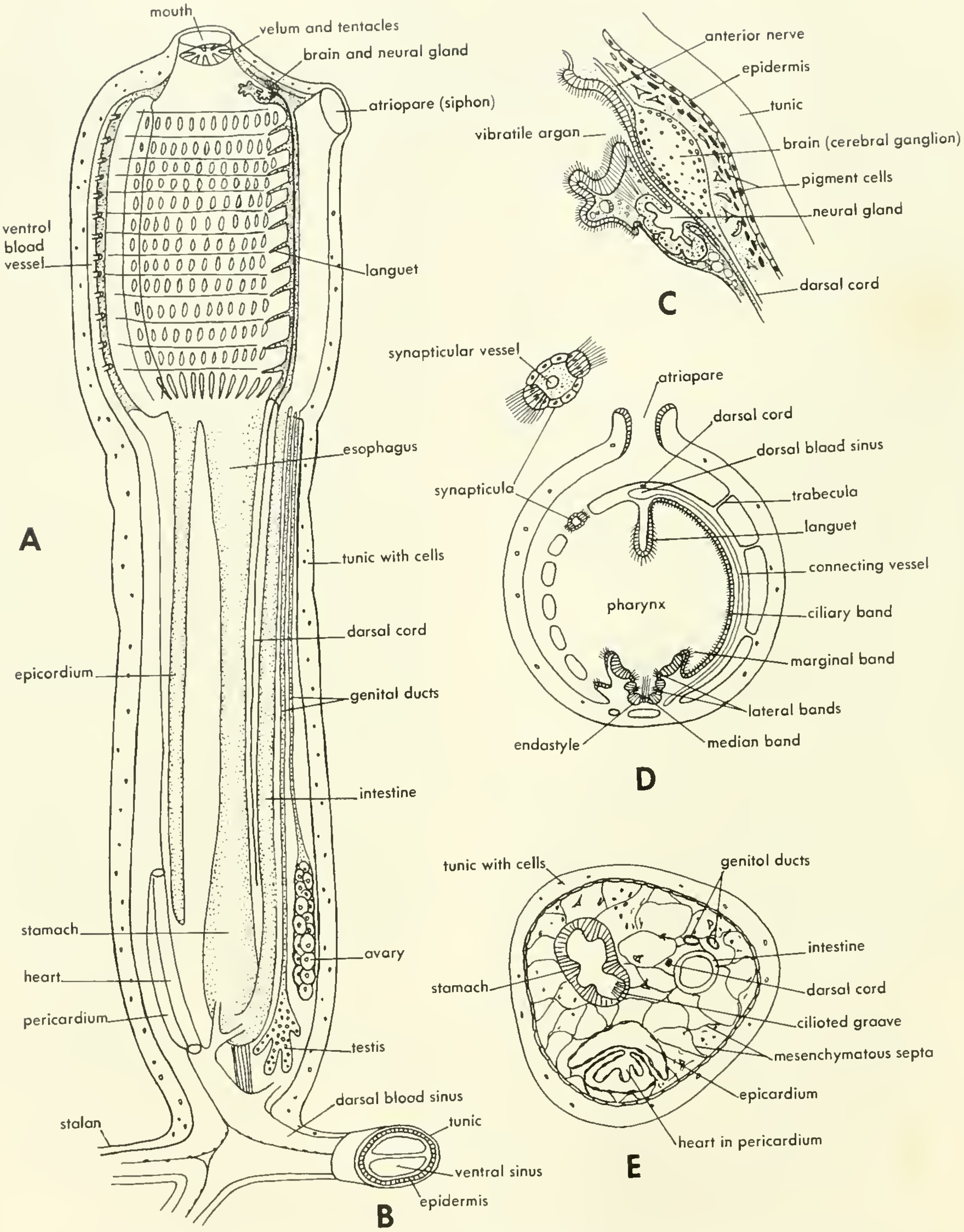


Figure 1-8. Anatomy of *Clavelina lepadiformis.* A, sagittal section of body and stolons; B, cross section of stolon; C, sagittal section of brain and neural gland; D, cross section of pharynx region with enlarged section of a pharyngeal bar at left and above; E, cross section of body near base. (After Brien, 1948)

coat made of **tunicin**, a material which resembles, or is, cellulose. The tunic and tissues are nearly transparent. Free cells occur in the tunic. The **epidermis** underlying the tunic is **simple**, that is, formed of a single layer of cells which are **cuboidal** or **squamous** (flattened) in shape.

The tunicate shows certain similarities to Amphioxus in that it has a complex pharyngeal structure with a **ciliary-mucoid** feeding action. The **pharynx** is enclosed by an **atrium** opening to the exterior through an atrial pore (Figure 1-8). The details of structure of the pharynx and atrium of the two groups are close. The **pharyngeal slits** of the tunicate are subdivided by connecting bars called **synapticulae** but not by **tongue** bars. The tongue bar, as observed in Amphioxus, or the hemichordate, develops as a downgrowth from the dorsal wall of the slit which divides the slit into anterior and posterior openings (Figure 1-12). There is an expanded **stomach** and a simple **intestine** opening at the **anus** into the atrium. The walls of the gut are not ciliated. There is a **pyloric gland** formed of numerous **ampullae** (small sacs) in contact with the intestine. Tubules from the ampullae join to form a duct emptying into the digestive tract just below the stomach.

There is no **coelomic cavity.** The mesoderm consists of the cells of the tunic, which wander out through the epidermis, the **circular** and **longitudinal muscles** of the **subepidermal layer,** mesenchyme cells of the interior, and the tissues of the circulatory and reproductive systems.

The circulatory system consists of a **heart** enclosed in a **pericardial cavity** and connecting channels and sinuses. The direction of blood flow through the heart may be reversed. The blood contains cells but not **erythrocytes** (red blood cells). The **pharyngeal blood vessels** are roughly comparable to those of Amphioxus.

Tunicates, usually **hermaphroditic**, have **ovaries** and **testes** opening into the atrium through long ducts. Eggs and sperm appear at different times in most species. Asexual **reproduction** by means of **budding** is common.

The brain is a solid ganglion between the mouth and the atrial pore, from which several nerves radiate. Associated with the brain is a **neural gland** which has a **ciliated funnel** opening into the atrium.

Embryological development It is in the larva of the tunicate that there is a real resemblance to the vertebrate (Figure 1-9). The tadpole of *Clavelina* has an ovoid body with a long, slim tail attached. The tadpole swims actively for a short period, settles to the bottom, and there **metamorphoses** to the adult stage.

In the body of the tadpole several structures are observed which are asymmetrically placed. The beginnings of a **pharynx** with a distinct **endostyle,** and subdivided **pharyngeal slits** can be seen. The pharyngeal slits open into **bilateral atria,** whose outer openings join to form a single external **atrial pore.** The **mouth** is dorsal as is the atrial pore. The gut ends blindly behind the atrial sac. The **heart** and its **pericardium** arise from the pharynx and come to lie behind the endostyle. A small **epicardial diverticulum** passes back from the pharyngeal cavity to either side of the heart.

In the tail is the **notochord,** made up of a line of **vacuolated cells.** In many tunicates the number of notochord cells is a constant (40 to 42). The notochord has a thin fibrous sheath and is enclosed in three or four bilateral rows of **segmental muscle cells.** These are elongate, fusiform, smooth units with **myofibrils** around the periphery and a central nucleus. The muscle cells overlap adjacent cells of the notochord.

The brain is an expanded vesicle in which there is a ventral unicellular **otolith** (or **statocyst**) set on a patch of **sensory cells;** on the right side is a **simple** eye formed of several **photosensory cells** associated with a few **lens cells.** These sensory organs function in the swimming activity of the larva and guide it to the place of attachment for the metamorphic period. The brain ventricle opens into the mouth cavity and remains in the adult as the opening of the neural gland. The adult brain ganglion develops as a new structure from the cells roofing the larval brain vesicle. The neural

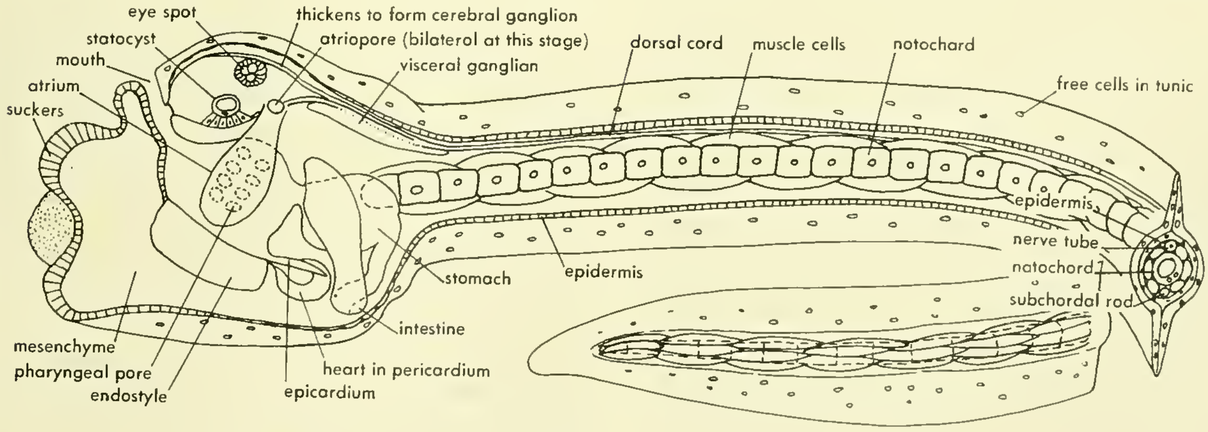


Figure 1-9. Diagrammatic summary of anatomical features of larval *Clavelina*.

tube of the larva is largely non-nervous and there are no segmental fibers extending out to the muscle cells. Innervation appears to be from the **visceral ganglion** next to the brain with transmission from cell to cell. The visceral ganglion disappears with metamorphosis.

The tunicate is peculiar in that it lacks a **coelom**. In the larva the mesoderm (see Chapter 7) is formed as bands from the dorsolateral wall of the gut. The notochord arises from the cells between these two bands. This manner of origin is similar to that in Amphioxus but here the similarity ends. The tail muscles and body mesenchyme produced by these strands develop directly without passing through a pouch stage. The only cavities in the body are the blood channels or hemocoels.

The pericardial cavity evaginates from the posterior floor of the pharynx and the heart forms within this. Bilateral evaginations of the pharynx give rise to the epicardial sacs. These may remain paired and open into the pharynx, or they may separate from the pharynx and fuse to form a single cavity. The epicardium is viewed as having an excretory function since other more obvious structures for this are lacking.

Hemichordata

There are two main divisions of hemichordates, the Enteropneusta and the Pterobranchia. Recently a third group was added—*Planctosphaera.* Its sole genus appears to be only a specialized tornerian larva, whose name stems from the fact that these ciliated animals formerly were identified as belonging to a genus *Tornaria.* They are now recognized as a developmental stage in the life cycle of many species of enteropneusts. A somewhat similar larva also occurs in the pterobranch *Cephalodiscus.*

Enteropneusts *Balanoglossus* (from the Greek words *balanos* meaning acorn and *glossa,* tongue) is the generic name of some, and a common name of many, species belonging to a worm-like group of organisms identified in 1870 by Gegenbaur as the Enteropneusti (intestine breather). There are twelve genera in the group, including *Saccoglossus* (sack tongue), *Glossobalanus,* and *Ptychodera* (split neck). In size these animals are small, or at least slender; they range in length from 10 cm to as much as 2 m. They are bilaterally symmetrical. The body is ciliated and divided into three distinct anteroposterior divisions (Figure 1-10). The most anterior part is the **protosome** (or proboscis), which may be long and slender *(Saccoglossus)* or short and acorn-like, *Ptychodera* or *Glandiceps.* The second segment is the collar or **mesosome.** The **mouth** opens below the thin or tapered connection of the **proboscis** with the **collar.** Behind the collar is the **metasome.** On the dorsal surface of the metasome are bilateral lines of small **pharyngeal openings,** which lie to either side of the slight ridge formed by the **dorsal nerve cord.** In some of the enteropneusts, **genital ridges,** or wings, extend up on either side and may meet above the dorsal body wall (*Balanoglossus* or *Ptychodera*). Posterior to the pharyngeal openings the lateral body wall has many, serially repeated, sacculations produced by the hepatic outpocketings of the gut. There are **mid-dorsal** and **ventral ridges,** or grooves, marking the main nerve cords. The **anus** is at the extreme posterior end of the body.

The mouth or **buccal tube** extends through the collar into the metasome where it becomes the **pharynx** (Figure 1-11). The **stomochord,** or buccal diverticulum, is a simple, anteriorly projecting diverticulum of the buccal tube which projects forward into the **protocoel,** the coelomic cavity of the protosome. The pharynx opens to the exterior by way of a large number of U-shaped slits which lead into sac-like pouches opening to the surface through separate or common pores. The pharynx is frequently divided into a dorsal "slit" passage and a ventral "esophageal" passage by a fold from either side (Figure 1-11 B). These folds do not meet at the midline. Posterior to the pharyngeal region there may be a small dorsal diverticulum in the genus *Glossobalanus.*

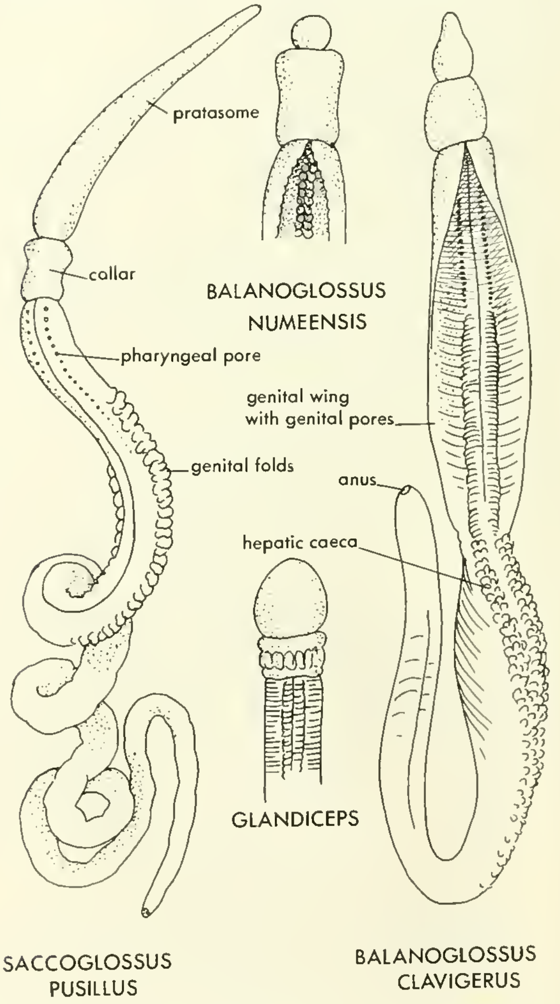


Figure 1-10. External appearance of several enteropneusts. (After Dawydoff, 1948)

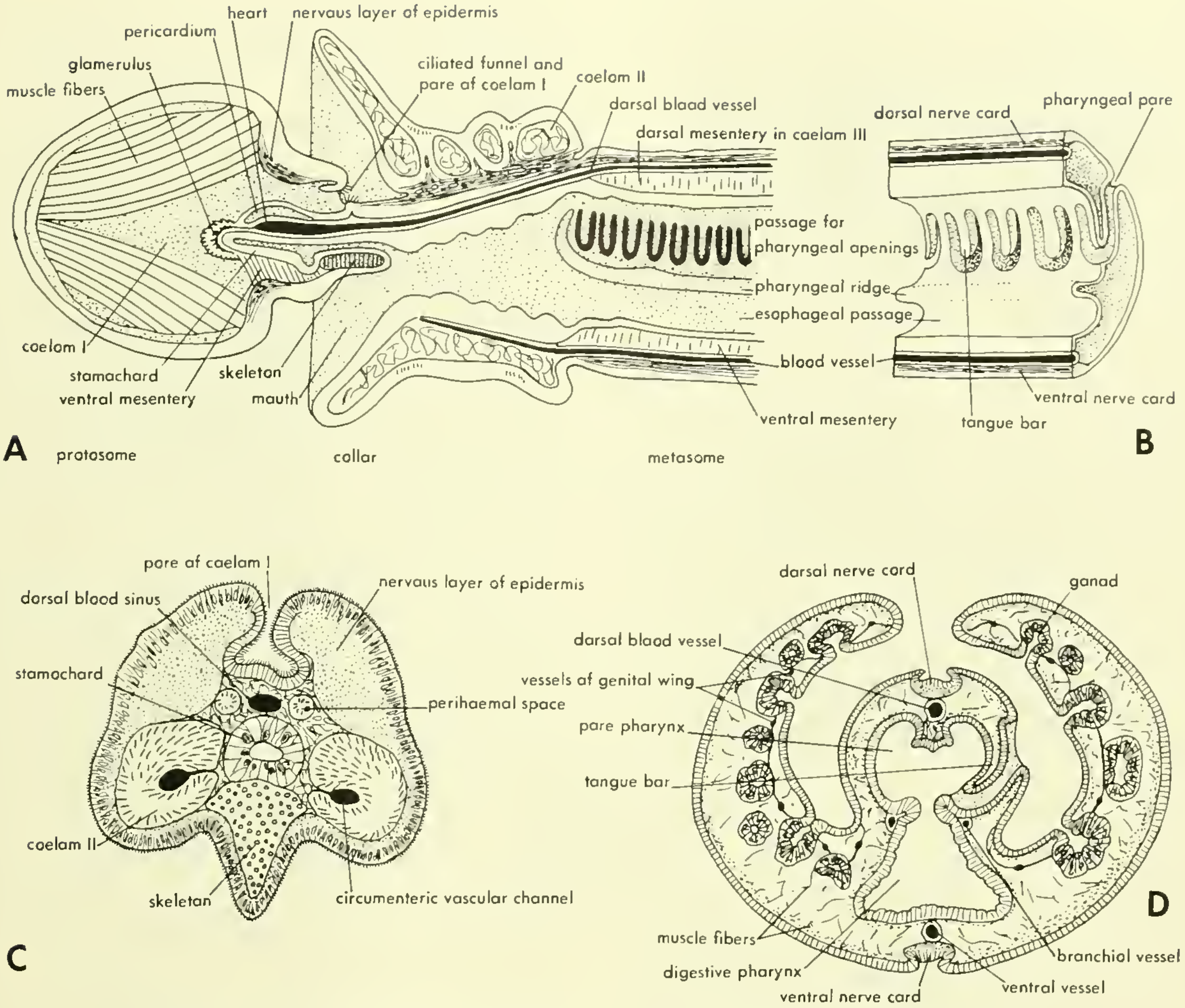


Figure 1-11. Anatomical details of enteropneusts. A, median sagittal section of anterior end of body, not identified as to genus; B, diagrammatic section of body wall showing relationships of pouches to pharynx and the subdivision of the latter by a fold; C, cross section of protosome-mesosome junction area; D, cross section through anterior part of metasome. (After Dawydoff, 1948)

Posterior to the pharynx the **esophagus** may be short and not sharply differentiated; in *Saccoglossus* it opens to the exterior through several pairs of **dorsal canals**. The intestinal walls are ciliated. Anteriorly there are pairs of dorsolateral **hepatic diverticula.** These pouches are richly supplied with blood and have a pigmented, glandular epithelium. Behind the hepatic diverticula, the walls of the **intestine** are folded. There may be **dorsolateral ciliated grooves**, with longer cilia than elsewhere, or a single groove on the left.

Each of the three body segments has **coelomic cavities;** those of the first two segments open to the exterior through ciliated funnels. There is only a single protocoel funnel in some forms (Figure 1-11). The cavities of the collar (mesocoel) and metasome (metacoel) are paired, as indicated by a midline septum. The coelomic spaces are not obviously lined, for much of the mesoderm takes the form of the smooth muscle fibers that criss-cross the cavities or form longitudinal bands. Loose connective tissue (**mesenchyme**) may fill parts of the cavities.

There is no notochord in this group. The buccal diverticulum has been assumed to be a rudimentary notochord because it is an outgrowth from the "gut." However, it lies ventral to the dorsal blood vessel and below it lies a small **skeletogenous plate.** These are not the relationships of a true notochord. From the skeletogenous plate, crura, or processes, extend back to either side of the mouth tube. This skeleton is formed of laminated collagenous material. Skeletal rods are also associated with the U-shaped inner pharyngeal openings (Figure 1-12).

The nervous systems consists of an **epidermal plexus** or network of fibers in which there are main tracts. The **dorsal cord** is invaginated in the collar region to form a tube or a

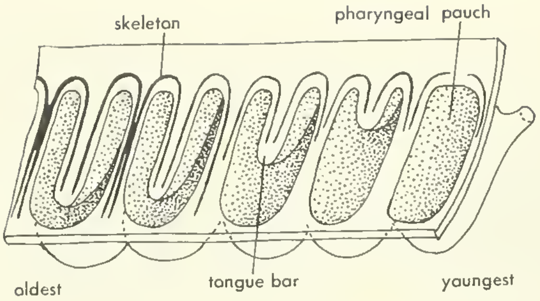


Figure 1-12. Development of tongue bars in the enteropneust. (After Dowydoff, 1948)

strand with several central cavities in it. The dorsal and **ventral cords** are joined by a plexus of connectives around the mouth tube in the posterior part of the collar. There is an anterior nerve ring in the base of the protosome which connects with the dorsal cord and from which the strands of the **proboscis plexus** extend. **Giant cells** are present, particularly in the collar region.

The reproductive system consists of numerous sac-like **gonads,** each of which opens separately to the surface. These are scattered along much of the length of the pharynx or of the metasome in some species. The body wall may be drawn out as lateral wings in which the gonads are located. The pores of the gonads are scattered over the dorsal surface of the wing.

There is a rather elaborate circulatory system of channels, of which only a part are lined. There are **dorsal** and **ventral** lined and **contractile vessels.** The blood moves forward in the dorsal vessel. In the region of the collar, this vessel lies deeper in the body and is enclosed on either side by a **perihemal space**—anterior diverticula of the metacoels. At the anterior end of the collar, the dorsal vessel receives bilateral vessels from the sides of the protosome, then expands as the **central sinus,** or heart.

The central sinus lies dorsal to the stomochord and is overlaid by the **pericardial cavity,** which is contractile. From the central sinus, blood passes forward into a **glomerulus** associated with the tip of the stomochord. Here waste materials are thought to be filtered from the blood into the protocoel, which is filled with sea water. This sea water is exchanged with the exterior water by the action of the **ciliated funnel** or funnels opening dorsally in the constriction between protosome and mesosome.

From the glomerulus (Figure 1-11 A) blood passes into dorsal and ventral protosome vessels and into bilateral **circumenteral channels.** These last pass to either side of the buccal tube to the ventral channel, through which the blood moves posteriorly. There is a plexus of channels in the collar region both in the body wall and the buccal wall. This network drains through a ring vessel in the collar-trunk septum into the dorsal vessel. The ventral vessel supplies the pharyngeal region by way of the branchial vessels, the hepatic diverticula, the gut generally, and the body wall. The region of the gonads may be drained by lateral vessels, which midway along their length connect with the dorsal vessel. The blood is colorless and contains a few epithelial cells.

Pterobranchs *Rhabdopleura* and *Cephalodiscus* are the two genera of this group that are usually described. The third, *Atubaria,* is known from a single collection made in Japanese waters. These small animals, 1 to 5 mm in length, were first collected by the Challenger Expedition in 1876. *Rhabdopleura* is colonial, *Cephalodiscus* social, and *Atubaria* solitary. The first two live in a secreted **coenecium** (not chitinous) consisting of branching tubes or irregular masses with tubular pockets and external decoration in the form of filaments or fibers (Figure 1-13). The tubes of *Rhabdopleura* are formed of small ring-like units (Figure 1-14). All the tubes are joined basally—as all of the individuals in the colony are—by a **black stolon.** In its structure it has been compared to that observed in Graptolites, but this comparison has been rejected by Hyman (1959).

The body of these organisms is covered with a **ciliated epidermis** (some parts may lack cilia) and is divided into the same three segments observed in the enteropneusts: **protosome, collar** (mesosome), and **metasome.** The metasome is divided into a **visceral sac** and a **stalk.** The protosome is a flattened, disc-like structure, and its lateral margins are notched. A pigmented strand of epithelium extends from one notch to the other below the central thickened and glandular area of the ventral surface of the protosome.

The collar bears a lophophore made up of a series of **arms** fused at the base: four to nine pairs in different species of *Cephalodiscus,* four pairs in *Atubaria,* and one pair in *Rhabdopleura.* The arms have two rows of **tentacles** and may be tipped by a **glandular knob.** An **oral lamella** leads from the

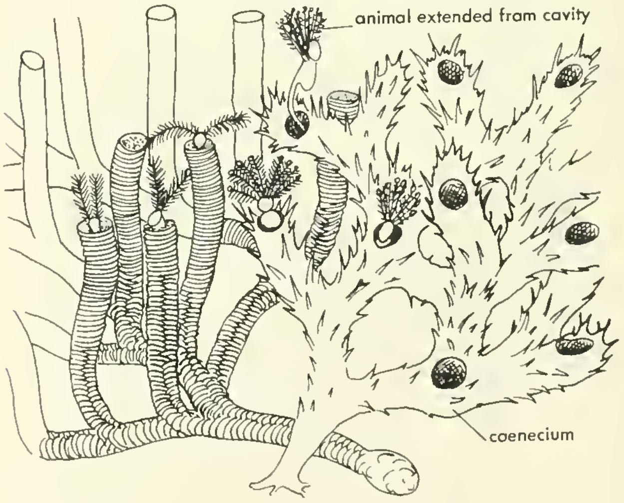


Figure 1-13. General appearance of pterobranchs and their secreted, common, external skeleton or caenecium.

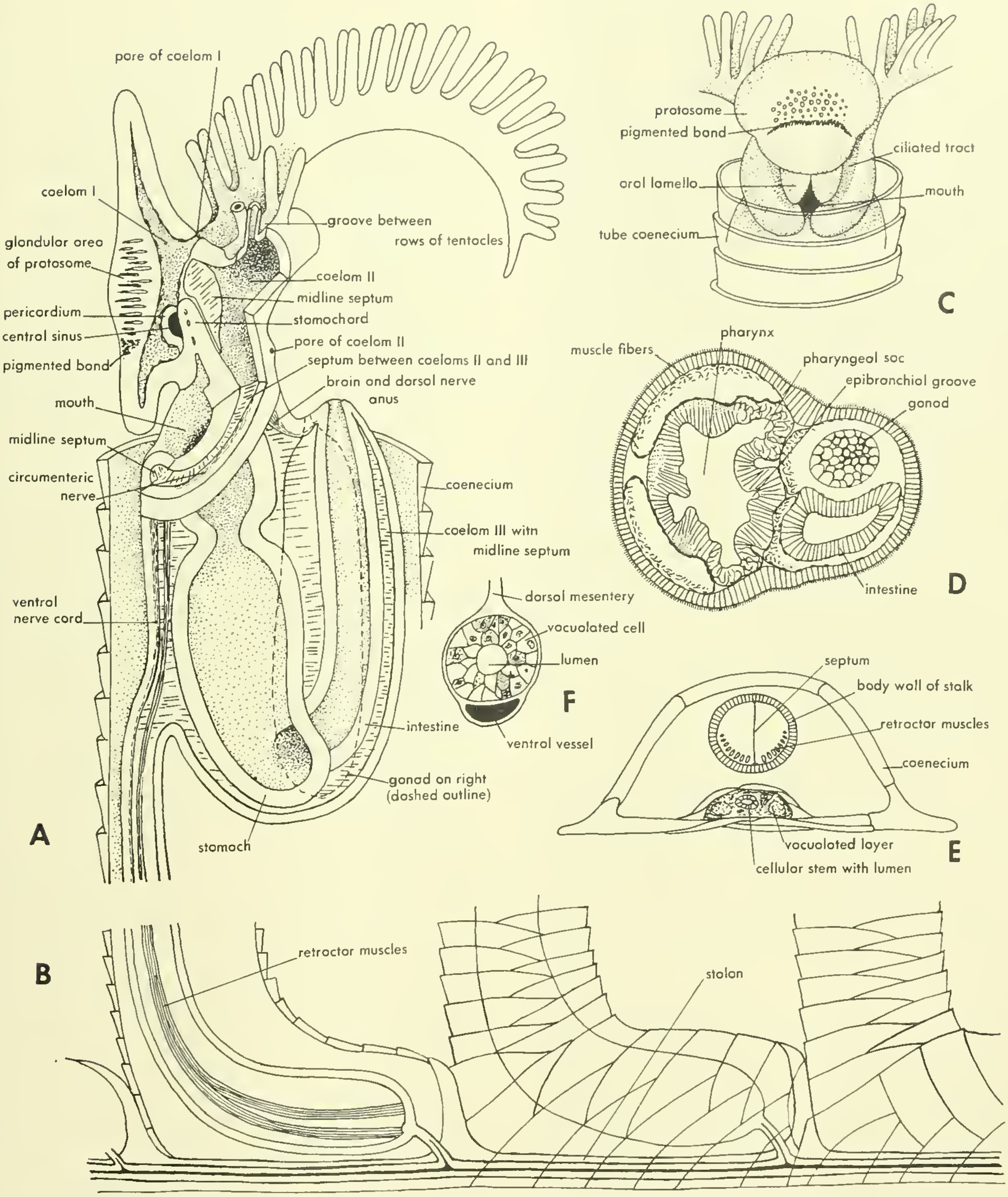


Figure 1-14. Anatomical details of *Rhabdopleura.* A, sagittal section of body and coenecium; B, sagittal section of area of attachment to stolon; C, anterior view of protosome and lophophore; D, cross section through metasome; E, cross section through stolon; F, cross section of stomochord.

base of the arms to below the **mouth.** The whole lophophore is ciliated and food is secured through the secretion of its glandular cells (fibrous mucous) and the action of the cilia.

The digestive tract begins with a **buccal** (mouth) **tube** in the collar region, from which a **stomochord** is evaginated anterodorsally. This lies in contact with the **septum,** between the protosome and collar, and in contact with the dorsal **epidermis** of the collar region in which lies the **brain.** The **lumen** of the stomochord may remain open or be reduced to a series of spaces. Behind the stomochord there may be a **dorsal recess** of the **buccal cavity.** The **pharynx** is short and lined with ciliated epithelium. There is a single pair of **slits** in *Cephalodiscus* and *Atubaria,* but there are none in *Rhabdopleura.* Associated with the undivided slit is a dorsolateral **pharyngeal sac.** The **esophagus** is short and leads into the large sac-like **stomach;** this in turn leads into the **intestine,** which curves anteriorly and dorsally to open at an anus just behind the collar. The stomach and intestine are not lined with cilia.

The **coelom** of the protosome is a single space opening to the exterior by a pair of canals and pores. The mesosome and metasome have bilateral spaces; that of the mesosome opens to the exterior by paired pores behind the oral lamella and just in front of the pharyngeal slits. It extends upward into the arms of the lophophore. These body spaces are not conspicuously lined, for muscle fibers and loose mesenchyme lie within them.

The circulatory system consists of a **dorsal sinus** (unlined), which extends forward along the esophagus and pharynx to terminate in a **central sinus** (heart) on the tip of the stomochord. The heart and its surrounding **pericardium** project into the protocoel. The pericardium is muscular and contractile as in the enteropneust. Blood leaves the glomerulus-like central sinus (there is no apparent glomerulus in terms of a glandular and folded coelomic lining) through a channel ventral to the stomochord, which divides to bypass the mouth. A **ventral vessel** extends back along the body wall and around the posterior end of the stalk to the dorsal side. Here it divides into an **intestinal** and a **dorsal** body wall **vessel.** A plexus enclosing the gonads opens into the dorsal sinus. Cells occur in the blood.

The nervous system consists of an **epidermal plexus** of fibers and cell bodies, in which thickened strands occur. The **collar ganglion** is the main concentration and lies dorsally. From it a midline and bilateral protosome bands extend forward. Behind it there is a mid-**dorsal strand** extending to the anus, and there are also bilateral **circumenteric** bands which pass in front of the pharyngeal slits to the underside of the body where they join the **ventral** midline **cord.** One or two **lateral cords** connect with this circumenteric band. The ventral midline trunk, like the blood vessel, extends around the end of the stalk to the dorsal surface.

Reproduction involves both gametes (sexual) and budding. The **gonads** are bilateral or unilateral (right side in *Rhabdopleura*), opening behind and lateral to the anus. The development of the bud is direct. The buds arise from the tip of the stalk.

One of the most interesting aspects of the hemichordates is their larval development. Some kinds of enteropneusts have a ciliated larva, the tornaria, while others and the pterobranchs develop directly. Both types of development may be observed within a single genus, *Balanoglossus.* The early stages of both types of development are similar and there is much agreement even in the later stages.

In the development of the larva (see Chapter 7), three pairs of mesodermal pouches evaginate from the archenteron (enterocoelous development). These pouches show much variation in their exact mode of origin but in any case agree in most details with the three pairs of pouches observed in the larva of some echinoderms. The resemblance between the tornaria larva and the auricularia or bipinnaria types of larvae of echinoderms has been used to suggest a relationship between these phyla and the chordates.

General observations

In terms of their pharyngeal structure, epidermal nervous system with both dorsal and ventral cords, body musculature, tripartite body, and lack of a notochord (or presence of a stomochord), the hemichordates differ from the tunicates and Amphioxus. Recognition of the hemidiordates as a separate phylum seems reasonable; yet one must assume some kind of relationship to the chordates, perhaps best expressed as common ancestry. If these phyla had a common stem, then the hemichordates would represent an offshoot developed before the appearance of the notochord.

Of the protochordates, Amphioxus seems most like the vertebrate, but the tunicate also shows the multiplication of coelomic and myotomic units, which these organisms share with the vertebrate. To give some meaning to this last statement, the hypothetical primitive vertebrate should be characterized, utilizing some of the anatomical information gained from the description of the protochordates. Such a characterization will necessarily anticipate some of the conclusions regarding the vertebrates. As such it is a preconception and should be so treated. It is hoped that the student will reconsider the problem of an ancestral form, and its relationships to the protochordates, after a detailed study of the vertebrates.

As a generality, the ancestral vertebrate was more complex in every detail of its structure than the invertebrate. The body was covered by a stratified, not simple, epidermis and was divided into a head with branchial pharynx, trunk, and tail. There were segmental myotomes extending through these body divisions. There were at least three myotomes in the head which involved the protosome, mesosome, and a part of the metasome of the ancestral form. To these initial segments new ones were added posteriorly. The caudal somites were without a coelomic space. The tail of the primitive vertebrate is a new structure and does not correspond to the stalk of the hemichordate.

The notochord served as the axial support for this elongate organism and was supplemented by a sheath of fibrous connective tissue which later gave way to cartilage and bone. The notochord extended forward only to the mid part of the brain. The central nervous system lay above the notochord and consisted of a five- (or six-) parted brain associated with well-differentiated sensory organs (nose, eye, ear) and a spinal cord extending most of the length of the body. Spinal and cranial nerves extended out to each of the myotomes. Each nerve had a dorsal and a ventral root, and the dorsal root contained a sensory ganglion. There was a partly separated autonomic system. Some of the ganglia were associated with the viscera, and there were nerve nets within the gut wall. The motor fibers of the nervous system were generally myelinated.

The pharynx had an evaginated thyroid gland that probably retained connection by a duct. The pharyngeal openings were simple slits and few in number. Since new slits were added or subtracted posteriorly, the number was variable. The pharyngeal slits were independent of the myotomes, i.e. not segmental. Each slit had gill filaments associated with it. The mouth was separated from the pharynx by a velum, and in it arose a midline Rathke's pouch and bilateral nasal capsules.

The gut was simple, having an expanded stomach and liver and a pancreatic diverticula, which may not have been well marked. The posterior part of the intestine contained a spiral valve. The gut lay in a large bilateral coelom. Coelomic spaces also occurred in the head and in the branchial arches.

The circulatory system consisted of a ventral vessel, in which the blood passed forward, and a dorsal vessel, close below the notochord, in which it flowed posteriorly. There was a contractile heart, enclosed in a pericardium, which pumped the blood forward and upward through the branchial arches. Anterior and posterior cardinal veins along with jugulars and abdominal vessels returned the blood to the heart. An hepatic portal vein drained the gut into the liver, where it entered a sinusoid reticulum drained into the heart by hepatic veins. The kidney was also associated with some sort of portal system. Erythrocytes containing hemoglobin were in the blood.

Kidneys were present in the anterior part of the body cavity. They were formed of nephric tubules opening into the pericardial space or the coelom at one end and into a common drainage duct at the other. These tubules lay within a blood sinus. The reproductive organs were masses of cells that ruptured into the coelom. The coelomic spaces opened to the exterior by abdominal pores near the cloaca (the common opening of digestive and excretory systems).

Much more could be hypothesized but the general picture has been presented. The origin and development of the vertebrate from the invertebrate host can now be imagined without resort to impossible morphological saltations. A fuller appreciation of this transition, however, is dependent upon a fairly detailed knowledge of the vertebrates. The evolutionary radiation of vertebrates should now be investigated in terms of the morphology of living forms and the historical record.

2

The Vertebrates and their External Anatomy

A SURVEY OF THE MATERIALS

It is useful, before beginning the study of vertebrates, to make a preliminary survey of the kinds of animals making up this group. There must be some order of arrangement of these organisms, some scheme of classification associating similar species together and separating these by means of a graded series of hierarchies which classify species from the similar to the dissimilar. A classification thus reflects observable morphological differences and is presumed to reflect, at least partially, the evolutionary history or phylogeny of the entire group.

The preliminary grouping of organisms in Table 2-1 should not be viewed as a formal classification but rather as an introduction to some of the views regarding the natural grouping of species and the interrelationships of such groups. These views are to be studied in the following chapters in more detail and evaluated in terms of the morphological facts. No conclusions, as expressed by a formal classification, can be reached until all possible information has been accumulated and reviewed, and even then the student may wish to reserve judgment. Discussing anatomical or developmental information within a preconceived taxonomic system robs it of much of its meaning. Working toward an understanding of taxonomy through a study of the many kinds of vertebrates adds a new dimension.

The preliminary system of Table 2-1 is, therefore, not to be memorized nor treated as a formal classification by equating its major divisions with the classes, orders, or families, of other systems. It is intended only as a reference framework, a starting point for a study of the phylogeny of the vertebrates as revealed by their morphology. The names in the right-hand column are, with a few exceptions, genera. Those preceded by an asterisk are of fossil forms. The names in the other columns are of increasingly more inclusive categories from right to left.

LIVING REPRESENTATIVE VERTEBRATES

A description of the more important external features of a few of the animals in this list will reveal some of the diversity of the vertebrates and serve as an introduction to the terminology of comparative morphology. Animals with which the student is already familiar (e.g. the rat) are noted only briefly, whereas more detailed descriptions are used to supplement the illustrations of forms likely to be new to him.

No attempt will be made at this time to discuss the interrelations of these vertebrates since such features as agnath ("jawless") versus gnathostome ("jawed mouth") are more properly discussed under the anatomical structure on which the separation is based. By careful attention to the details of the external anatomy of the following animals, along with comparisons where this is possible, an introductory familiarity with some of the generic and larger group names will be achieved. These names will figure importantly in the following chapters and in the laboratory work.

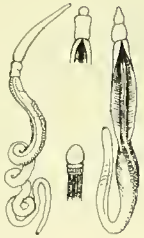
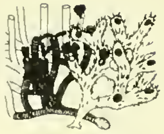
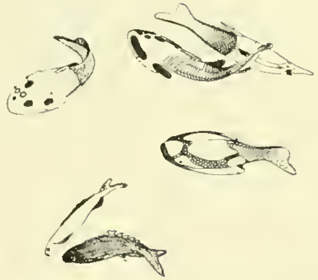
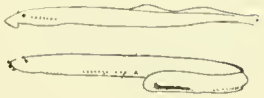
Cyclostomes

The two kinds of living agnath fishes are grouped together as the cyclostomes or "round mouths." The lamprey eels (Figure 2-1), which include the genera *Petromyzon, Lampetra,* and *Entosphenus,* are fairly large fish with a smooth skin. Anteriorly there is a funnel-shaped mouth (buccal funnel) armed with circlets and rows of cornified or horny teeth, as is also the "tongue" or **rasping organ.** The "tongue" is moved back and forth to rasp a hole in the prey animal. The **eyes** are high on the sides of the head and are covered with a whitish skin, the **cornea** (in preserved specimens). There are small bumps on the head, mainly in front of the eye, which indicate the positions of the **sensory organs** of the **lateral-line system.**

Behind the eye is a row of seven **branchial** (gill) **pouch openings,** each having a small papilla and leaf-like valves. There are two **dorsal fins** far back on the body. The posterior dorsal fin is continuous with the caudal fin, which extends around the posterior end of the body and forward to the cloacal aperture, through which extends the urinary papilla. In the female a small anal fin is present just behind the cloaca. There are no lateral fins.

The hagfishes (*Myxine* and *Eptatretus*) are much like the lampreys in their general shape. The **nosahypophyseal** duct opening, seen high on the top of the head in the lamprey

TABLE 2-1 A PARTIAL CHECK-LIST OF STUDY MATERIALS ARRANGED INTO HIERARCHIES SUGGESTING THEIR CLASSIFICATION

PHYLUM HEMICHORDATA		Enteropneusta	*Balanoglossus* *Saccoglossus* *Ptychodera*
			*Planctosphaera*
		Pterobranchia	*Cephalodiscus* *Rhabdopleura*
PHYLUM CHORDATA ACRANIA UROCHORDATA			*Ecteinascidia* *Clavelina*
CEPHALOCHORDATA			*Branchiostoma*
CRANIATA VERTEBRATA AGNATHA		Osteostraci	Tremataspids **Trematapsis* Cephalaspids **Cephalaspis*
		Heterostraci	Pteraspids **Pterospis* Drepanospids **Drepanaspis* Astraspids **Astraspis*
		Anaspids	**Birkenia* **Lasanius*
		Thelodontii	**Thelodus*
		Cyclostomes	Petromyzontids *Petromyzon*

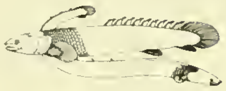
(Continued)

TABLE 2-1 CONTINUED

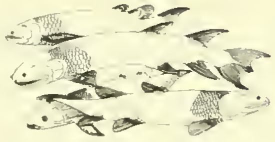
PHYLUM CHORDATA	AGNATHA (Cont'd)			*Entosphenus*
				Lampetra
			Myxinids	
				Myxine
				Eptatretus
	GNATHOSTOMATA			
		Placoderms	Arthrodires	
				**Dunkelosteus*
			Antiarchs	
				**Bothriolepis*
		Elasmobranchs	Selachians	
				Squalus
			Rays	
				Raja
		Holocephalans	Chimaerids	
				Hydrolagus
		Acanthodians		**Acanthodes*
				**Nostolepis*
			Palaeoniscoids	
				**Cheirolepis*
				**Pteronisculus*
				**Boreosomus*
				**Perleidus*
			Chondrosteans	
				Acipenser
				Scaphirhynchus
				Polyodon
			Subholosteans	
				**Broughia*
				**Watsonulus*
			Holosteans	
				Acentrophorus
				Amia
				Lepisosteus
			Teleosts	
				Salmo
				Perca
				Gadus

(Continued)

TABLE 2-1 CONTINUED



- Brachiopterygians
    - *Polypterus*
    - *Calamoichthys*
- Choanates
    - Crossopterygians
        - Rhipidistia
            - Porolepiforms
                - Porolepids
                    - **Porolepis*
                - Holoptychiids
                    - **Holoptychius*
                    - **Glyptolepis*



-
    -
        -
            - Osteolepiforms
                - Osteolepids
                    - **Osteolepis*
                - Rhizodontids
                    - **Eusthenopteron*
        - Actinistia
            - Coelacanths
                - **Diplocercides*
                - *Latimeria*

-
    - Dipnoans
        - **Dipnorhynchus*
        - **Dipterus*
        - **Chirodipterus*
        - *Neoceratodus*
        - *Lepidosiren*
        - *Protopterus*
    - Tetrapods
        - Amphibians
            - Ichthyostegids
                - **Ichthyostega*
            - Labyrinthodonts
                - **Edops*
                - **Eryops*
            - Salamanders
                - *Necturus*
                - *Cryptobranchus*
            - Frogs
                - *Rana*

(Continued)

TABLE 2-1 CONTINUED

- Amniotes
  - Reptiles
    - Cotylosaurs
      - *_Seymouria_
    - Turtles
      - _Caretta_
      - _Macroclemmys_
      - _Chelydra_
    - Crocodiles
      - _Alligator_
    - Rhynchocephalians
      - _Sphenodon_
    - Lizards
      - _Tupinambis_
      - _Iguana_
    - Therapsids
      - *_Diarthrognathus_
  - Birds
    - *_Archaeopteryx_
    - _Gallus_
    - _Columba_
  - Mammals
    - Monotremes
      - _Ornithorhynchus_
      - _Tachyglossus_
    - Marsupials
      - _Didelphis_
    - Placentals
      - Insectivores
        - mole, shrew
      - Primates
        - _Homo_
      - Carnivores
        - _Canis_
        - _Felis_
      - Perissodactyles
        - horse
      - Artiodactyles
        - pig, cow, camel
      - Rodents
        - _Rattus_
      - Lagomorphs
        - _Lepus_

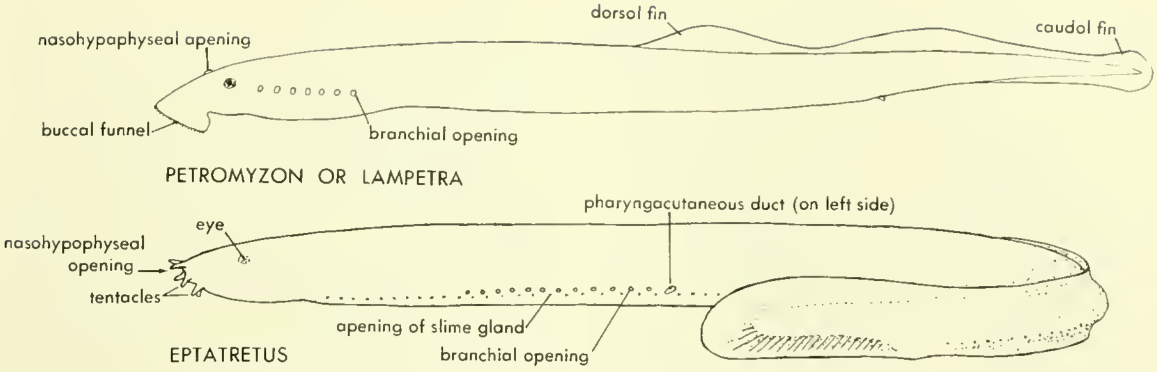


Figure 2-1. Some external features of the lamprey, top, and hagfish, bottom.

(Figure 2-1), is at the tip of the snout in the hagfish. There are three pairs of **tentacles** around the nasohypophyseal opening and the mouth. The mouth is circular, but not distinctly funnel-shaped, and it lacks horny teeth. The body is smooth and in life is covered with slime produced in part by the **slime glands**, whose openings can be seen forming a line along the ventrolateral aspect of the body.

The eyes are indistinct in the case of *Eptatretus*, and they cannot be seen in *Myxine*. There are 10 to 15 pairs of branchial openings in *Eptatretus*, the last on the left side serving also as an opening for a passage from the pharynx known as the **pharyngocutaneous duct**. Next to the branchial openings are pores of slime glands. *Myxine* has only a single pair of openings since all of the gill pouches (5 to 7 pairs) open together. The left opening also serves the pharyngocutaneous duct. The **caudal** (tail) **fin** extends anteriorly above and below the **caudal lobe** of the body. The **cloaca** is a slit-like opening, splitting the anterior margin of the caudal fin (or anal part of the caudal fin). Anterior to the cloacal aperture, a median fin extends to the posterior branchial openings.

Chondrichthyes

The sharks and their relatives are placed in this group of gnathostomes on the basis of their cartilaginous skeletons. In terms of their external anatomy, this group has a skin covered by small, spine-bearing scales (placoid scales); sometimes there are larger spine-bearing plates scattered over the body (ray); in some the skin is naked. The holocephalan differs most markedly from the elasmobranchs in having the gill openings covered by a flap or operculum rather than having each pouch opening separately.

Elasmobranchs (selachians and rays) The Dogfish Shark (*Squalus*) has a long fusiform body with two **dorsal fins**, and two pairs of **lateral fins** (Figure 2-2). The tapered posterior end of the body, the **caudal peduncle**, is turned upward, supporting the upper division of the tail fin. This type of tail is described as **heterocercal**, or "unequal tail." The dorsal fins are preceded by strong **spines**. The **pelvic fins**, the posterior pair of lateral fins, are partly modified into **claspers** in the adult male.

The **mouth** is a crescent-shaped opening, armed with rows of teeth, and it lies on the underside of the head. In front of the mouth are the openings of the **nasal capsules**. These openings are subdivided by a small flap into two parts. The eyes are dorsal to the mouth and large. Behind the eye is a vestigial gill slit, the **spiracle**, and further back are five pairs of gill openings.

The anterior part of the body of *Raja* (Figure 2-2), one of the rays, is flat and triangular in shape; the margins are extended out to form the thick **pectoral fins** (the anterior pair of lateral fins). Close behind the pectoral fins are the pelvic fins; the anterior part of the basal **lobes** of these may be thick and fleshy. The tail is long and slim and ends in a very small fin. There are two small dorsal fins just in front of the caudal. Along the dorsal midline there is a row of large pointed spines. The rest of the body is covered by tooth-like placoid scales, irregular in size but generally larger than those of *Squalus*.

The eyes are dorsal and just in front of the spiracles. The snout or **rostrum** is pointed. The mouth is a transverse ventral slit, and the nasal capsules lie in front of it. The opening of the nasal capsule is divided by a fold that extends back to the margin of the mouth. Behind the mouth are five pairs of gill openings.

Holocephalans *Chimaera* (or *Hydrolagus*) has a large head; from this the body tapers to the tip of the tail (Figure 2-2). The eye is large and there is a soft bulbous snout. The body is naked and grooved by the lateral-line system. The large openings of the **ampullae of Lorenzini**, sensory organs, can be observed on the cheeks and snout. The mouth is ventral and armed with sharp-edged **tooth plates.** The gills are covered by a fleshy **operculum**, which is fused ventrally to the **isthmus**, the midline bar joining lower jaw and body. The margins of the opercula appear to join across the isthmus.

A strong spine lies in front of the anterior dorsal fin. Well

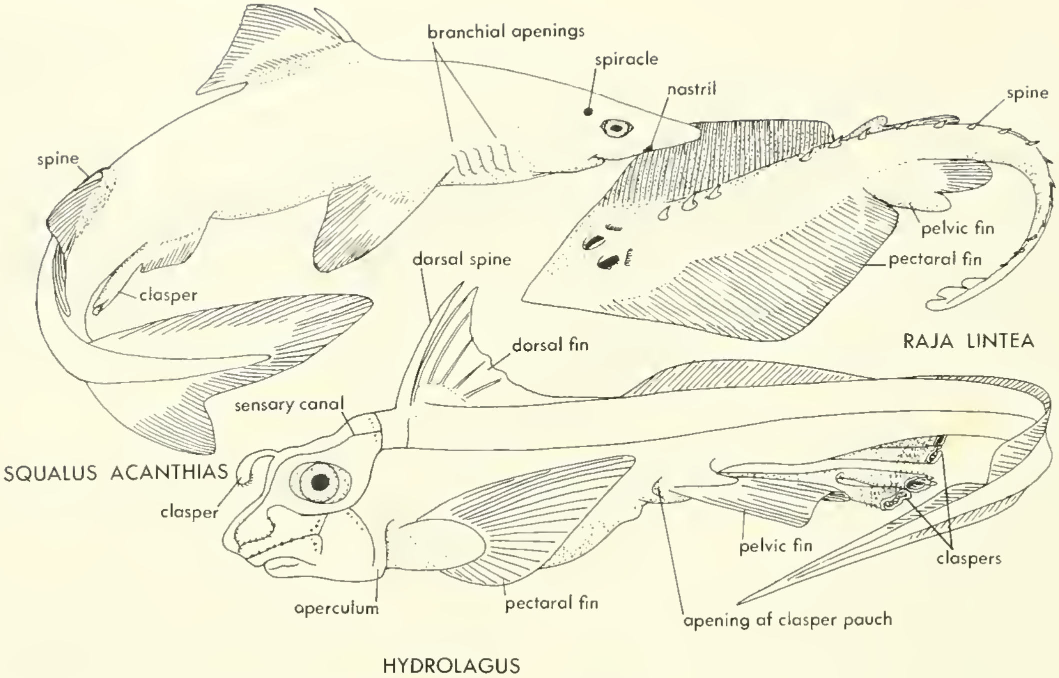


Figure 2-2. External features of the chondrichthions: shark, ray, and chimaerid.

behind this are two more low dorsals and a caudal fin that tapers to a point. It has equally developed dorsal and ventral fin lobes and is thus of a type called **isocercal.** The pectoral fins are large and wing-like; the pelvics lie anterolateral to the anal opening. The pectoral and pelvic fins both have distinct fleshy basal lobes. In the adult male the pelvics have **anterior and posterior claspers.** The anterior clasper is sheathed in a pouch below the anterior margin of the base of the fin; the posterior one extends straight back from the inner margin of the fin. These claspers and that on the head are armed with sharp, hooked denticles.

Actinopterygians

The chondrosteans, holosteans, and teleosts lack a distinct fleshy lobe at the base of the fins. The fin is membranous with supporting, jointed rays radiating from the base. The rays branch as they extend outward and the tips taper at the fin margin. From this kind of fin, this association of fishes gets its name, the ray-finned fishes.

Chondrosteans *Acipenser*, the sturgeon, *Scaphirhynchus*, the Shovel-Nosed Sturgeon, and *Polyodon*, the Paddlefish, are all representatives of this group. (Figure 2-3). These fishes resemble the sharks in the development of a rostrum. The top of the head is covered by bony plates, and a large plate lies in the **operculum** of either side. The eye is dorsolateral, and in front of it are the two openings of the nasal capsule—a small dorsal opening and a larger posterior ventral one. Behind the eye but in front of the opening of the operculum is a small spiracle (lacking in *Scaphirhynchus*).

The mouth is far back on the underside of the rostrum. In the sturgeons there are four sensory feelers (**barbels**) in front of it, two in *Polyodon*. The lips of the sturgeons also have clumps of small **sensory papillae** on them. The **branchial** (gill) **chambers** open by a slit behind the operculum.

The body of the sturgeons has dorsal, lateral, and ventrolateral rows of large, spine-bearing plates (scutes). Between these are small, bony **rhomboid scales,** each of which has a spine. These scales are named for their shape. There is a band of articulated rhomboid scales on the fleshy lobe of the caudal fin. The caudal peduncle of *Scaphirhynchus* is armored with scutes.

There is a single dorsal and anal fin, and there are two pairs of lateral fins with fleshy basal lobes. The tail is heterocercal; its front margin is formed of spines called **fulcra.** The anterior margin of the dorsal fin may also be formed partly of fulcra.

Polyodon differs from the sturgeons in that it lacks the rows of scutes on its body; the caudal fin has fulcra and there are rhomboid scales on the caudal lobe. The body is naked except for minute elements enclosing the lateral-line canal. This canal has short canals leading dorsally and ventrally to pores. The spatulate rostrum is the most noteworthy feature. The eye is at the base of this bill, the mouth is large and toothless, and there is a spiracle midway between the eye and the dorsal margin of the opercular fold. The operculum extends far back on the body as a pointed flap.

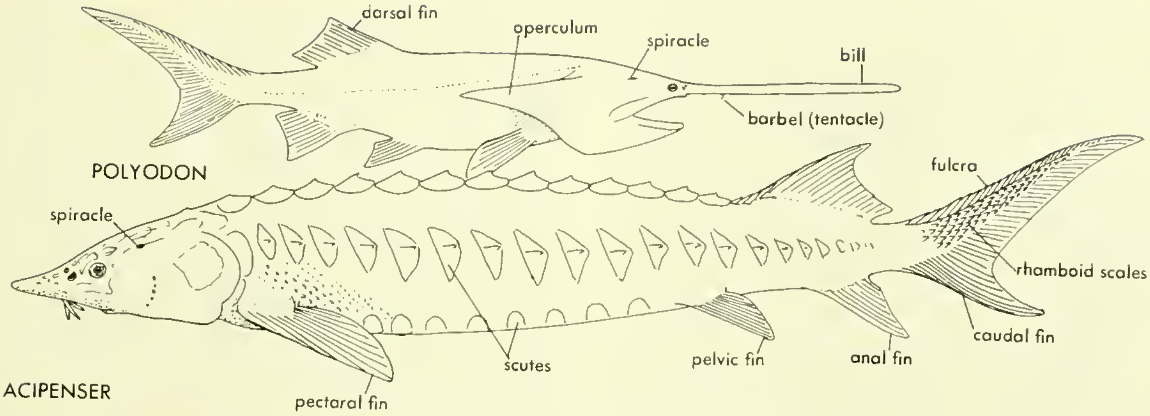


Figure 2-3. External features of two chondrosteans.

Holosteans and teleosts The Bowfin, *Amia,* a representative holostean, is a thick-bodied fish with a large head and mouth (Figure 2-4). The head is covered with thick bones but is without scales on the cheek. There is a long dorsal fin, an anal fin, and two pairs of lateral fins. The caudal fin is rounded in outline. The scales of the body are large and **cycloid,** that is, round in shape and overlapping. The lateral-line system is indicated by rows of **pores** on the head. The eyes are large and lateral. The anterior nasal opening is at the tip of a **nasal tube** extending from the upper lip; the posterior opening is high on the snout in front of the eye. The opercular covers are free to a point far forward between the halves (**rami**) of the lower jaw. These margins end at a median plate (**gular plate**). There is no spiracle.

The gar, *Lepisosteus,* is a very elongated fish with a toothed snout. The nasal capsule with its two openings is at the tip of the snout; the eye lies behind the angle of the mouth. The dermal bones of the head are visible through the skin, and the cheek is covered with an intricate and variable pattern of small plates. The opercula are joined across the throat. The body is covered with imbricated **rhomboid scales** with a glassy surface of an enamel-like material (**ganoin**). The dorsal fin is far back, and there are two pairs of lateral fins and an anal fin. The tail is heterocercal but the fin is not subdivided.

The perch, *Perca,* a typical teleost, has cycloid scales covering the body and cheeks. These scales have fine spines along their anterior margin and are thus identified as ctenoid. The dorsal fin has an anterior spined half and a posterior soft lobe. The lateral fins have slight, fleshy, basal lobes and like the other fins are formed of a skin membrane supported by jointed fin rays. The tail is **homocercal,** that is, it has equal lobes neither of which is supported by an extension of the body.

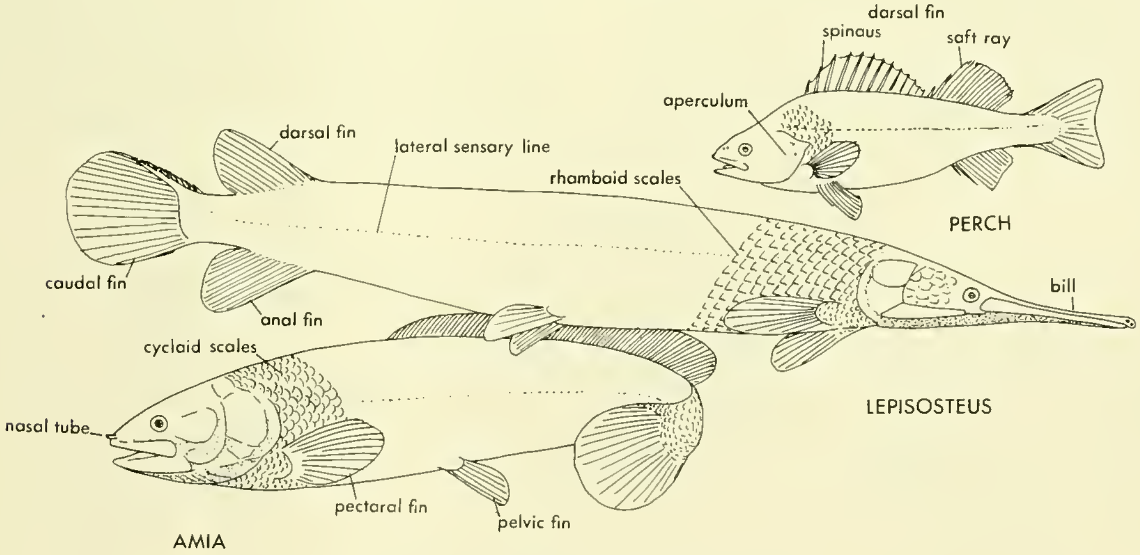


Figure 2-4. Holostean and teleostean bony fishes.

Brachiopterygians *Polypterus* and *Calamoichthys* are the only genera in this peculiar group of African fishes (Figure 2-5). These genera have a distinct lobe at the base of the pectoral fins, from which the name is derived. They differ also in that the throat area, posterior to the opercular margin, is covered by two large gular plates.

The head is fairly large and broad, and the eyes lie far forward. The anterior nasal opening is at the tip of a tube extending forward above the fold of the upper lip; the posterior opening is just anterior to the eye. On the head the openings of the lateral-line canals are apparent. There is a large slit-like spiracle at the anterior end of a fold extending back to the upper margin of the opercular flap. This fold allows lateral movement of the operculum. The opercular opening extends down onto the underside of the head where a transverse membrane joins one side with the other; this transverse membrane lies above the large gular plates of either side. There is a fleshy lip on the lower jaw matching that of the upper jaw.

The body is elongate and slim; that of *Calamoichthys* is eel-like. The dorsal fin is represented by a series of finlets, about nine in number; each finlet is preceded by a spine with a bifurcated tip. The most posterior finlet marks the anterior end of the caudal fin, which extends around to the underside of the caudal peduncle. The tail fin is rounded and without lobes. There is a small anal fin almost touching the anterior margin of the caudal fin. In front of the anal fin is the V-shaped opening of the cloaca. There are two pairs of lateral fins: the pectoral fins have extensive fleshy lobes; the pelvic fins lack such lobes (*Calamoichthys* lacks pelvic fins).

The body is covered by thick rhomboid scales which allow only limited flexion of the body. These scales are covered by a thin layer of shiny enamel (ganoin).

Choanate fishes

This association of fishes is based on their usually having both external and internal nasal openings, which amphibians, reptiles, and mammals also have.

The coelacanth Latimeria The group name, coelacanth, is derived from the hollow neural spines of the vertebral column. *Latimeria,* which sprang into prominence in 1938 as a living fossil, is known from several specimens collected in African waters (Figure 2-6). The head is proportionally large, resembling that of a typical fish. The mouth has thick marginal folds. There is an anterior and a posterior nasal opening; the anterior one is at the tip of a tube. There are also three pairs of openings leading into a midline rostral organ. The eye is large, and there is no spiracle. The body is covered with large cycloid scales with an enameled surface. There are two dorsal fins. The caudal fin is **diphycercal,** with an upper and lower lobe as well as a slightly separated terminal lobule. The anal fin has a fleshy lobe, as do the two pairs of lateral fins and the posterior dorsal fin.

Latimeria is a large species, four to five feet in length and weighing 60 to 180 pounds. Since these fishes have been collected during only a limited part of the year, their full life history is not known.

Dipnoans or lung fishes This group gets its name, Dipnoi, from its two breathing devices, gills and lungs. *Protopterus* is the most easily obtained example of the lungfish (Figure 2-7). It is an elongated fish, round in cross section. The mouth is small and in it the outermost nostril of either side can be observed. Just inside the mouth margin lies the inner narial opening. The fleshy lips extend back on the side of the head, some distance from the mouth. The eye is rather small. The opercular opening is limited to a slit just in front of the pectoral fin, which almost appears to come out of the opercular opening.

The body is covered with large cycloid scales that are very thin and covered by the skin. The scales extend forward onto the head, and thus none of the cranial bones is externally evident. There is a dorsal fin, which is continuous with the caudal fin. The caudal fin and its supporting fleshy lobe taper to a posterior point, i.e. it is **isocercal** or **protocercal.** The caudal fin is continuous with the anal fin. The cloaca opens asymmetrically to the left of the anterior margin of

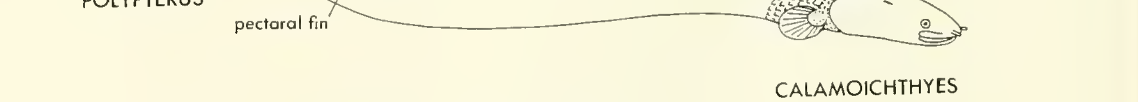


Figure 2-5. The brachiopterygians.

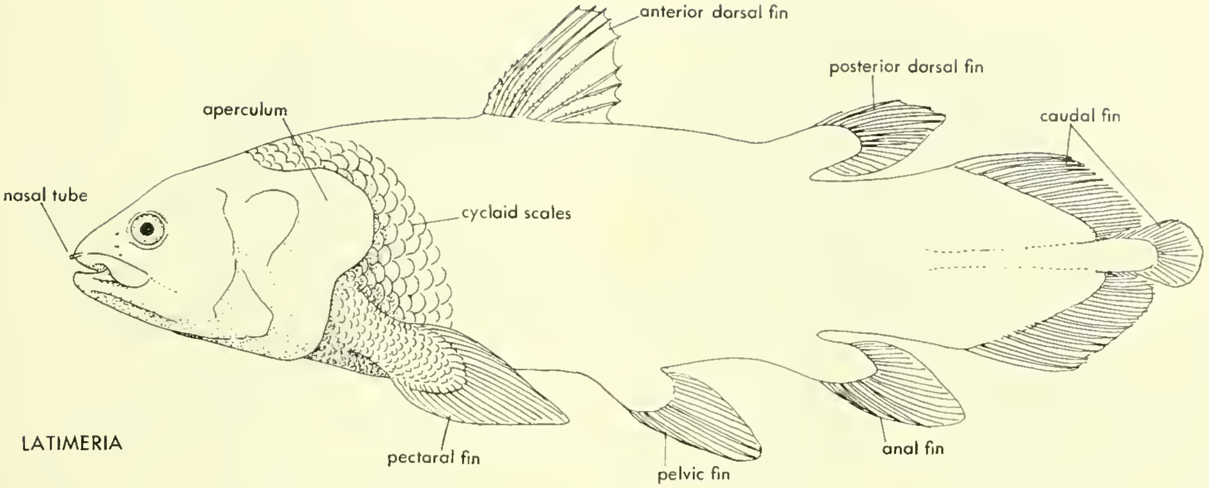


Figure 2-6. The living fossil *Latimeria*, a coelacanth crossopterygian.

the anal fin. There are two pairs of lateral fins. These are long, slim, fleshy structures with slight webbed margins.

The lateral-line system is indicated on the head by grooves or lines of openings. The lateral line of the body is distinct and there is an indistinct ventral line extending back from below the pectoral fin to just in front of the pelvic fin. From here it appears to pass above the pelvic fin.

Neoceratodus resembles *Protopterus* in many details. The cycloid scales covering the body and the back of the head are very large. The fins have much heavier, broader basal lobes. The dorsal, caudal, and anal fins are continuous as in *Protopterus*. The **nasal** or **narial** openings lie inside the margin of the upper jaw; the more posterior one lies inside the mouth.

Amphibians

Necturus and *Cryptobranchus* are large American salamanders, both presumed to be **neotenic** forms; that is, they retain larval features as adults (Figure 2-8). They are dorsoventrally flattened with relatively small limbs. The anterior limb has four fingers, the posterior five; in *Necturus* the posterior limb has only four. Each **digit** has a terminal pad of skin.

The head is broad and flat, the mouth is large with soft fleshy lips. *Necturus* has an extensive **opercular fold** joined across the ventral midline with that of the other side. These folds are also fused to the isthmus. At the upper margin of the opercular fold are the three large **external gills**, and inside of the fold are the two openings between branchial arches. In *Cryptobranchus* there is only a single branchial opening in the fleshy lateral margin of the head.

The body is covered with a smooth skin that has many folds, and with many irregular lumps. The caudal fin extends far forward above and below the fleshy tail. The cloacal opening lies just behind the posterior pair of limbs. The lateral-line organs are apparent as small bumps on the skin, usually with a white tip.

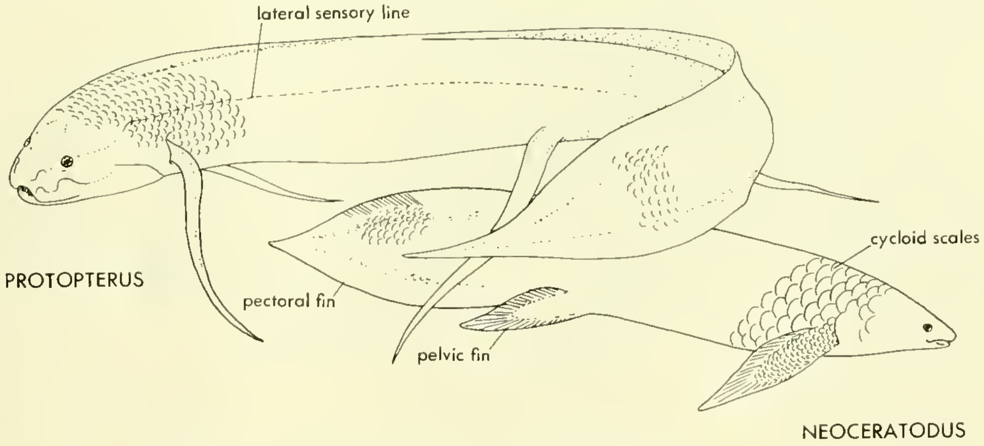


Figure 2-7. General appearance of two of the living lungfishes.

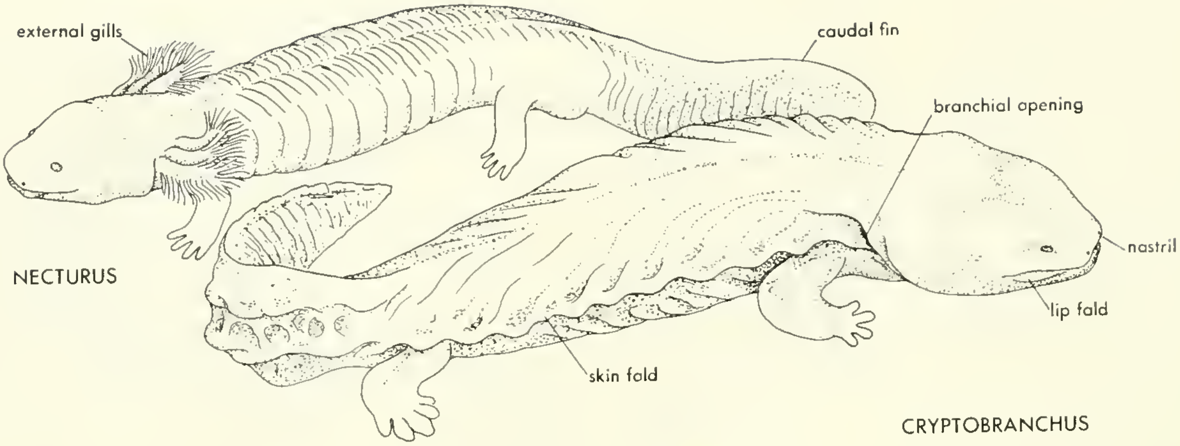


Figure 2-8. Two large American salamanders.

Another group of living amphibians is that of the Anura, the frogs and toads. The last group, the Gymnophiona or Apoda, contains legless, worm-like forms.

Reptiles

Several reptiles are readily available: turtles, alligators, and lizards (Figure 2-9). These show much of this group's range of variation. All have a scaly skin, two pairs of five-digited limbs with claws, and a long, tapered tail, with the exception of the turtle. The turtle has a heavy shell which is quite distinctive of the group. In most reptiles the eye can be covered by eyelids, largely the lower lid, or by a **nictitating membrane,** an inner membrane that can be drawn over the eye. In the snakes the margins of the eyelids fuse, and a clear scale in the lower lid, the **brille,** permits good vision. Such a clear area in the lower eyelid is observed in some lizards of burrowing habit. There is a single external nasal opening lying forward on the snout. The mouth is generally large and armed with teeth. Again the turtle is the exception, for it has horny jaw margins.

Birds

The pigeon or chicken can be used as a representative of this group (Figure 2-10). Feathers cover all of the body except the bill, the lower leg (tarsometatarsus), and toes. The feathers are modified on different parts of the body to serve various functions—protection, insulation, and flight. The bill is covered with a horny sheath and at the base has a soft, fleshy lump, the **cere.** The nostril is in or below the cere. The eye is surrounded by a rim of skin in which hair-

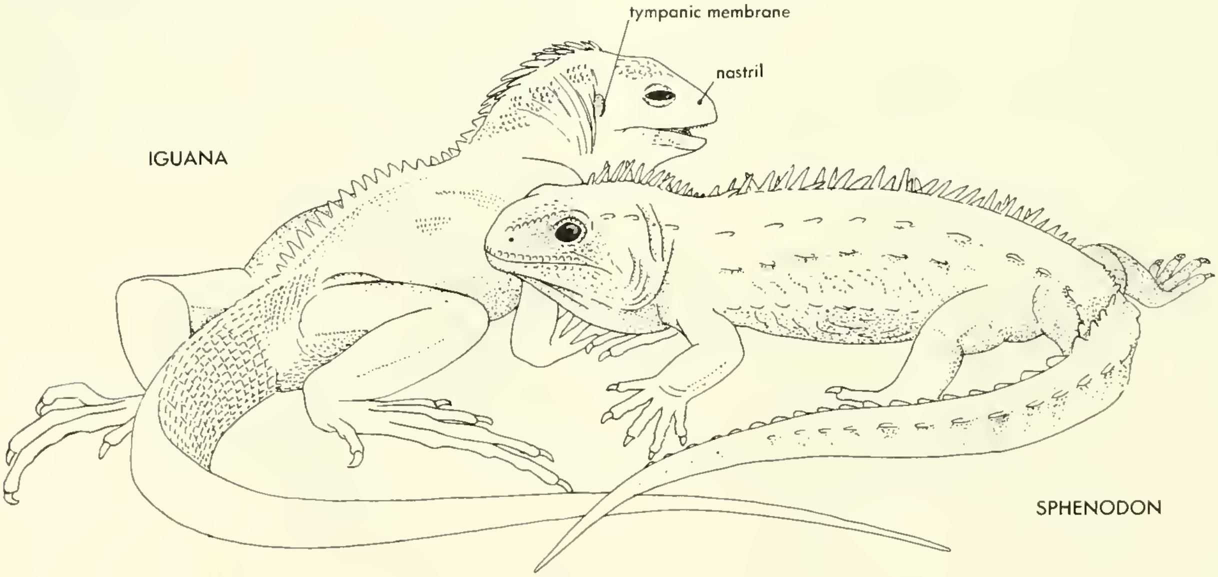


Figure 2-9. The lizard and Tuatara.

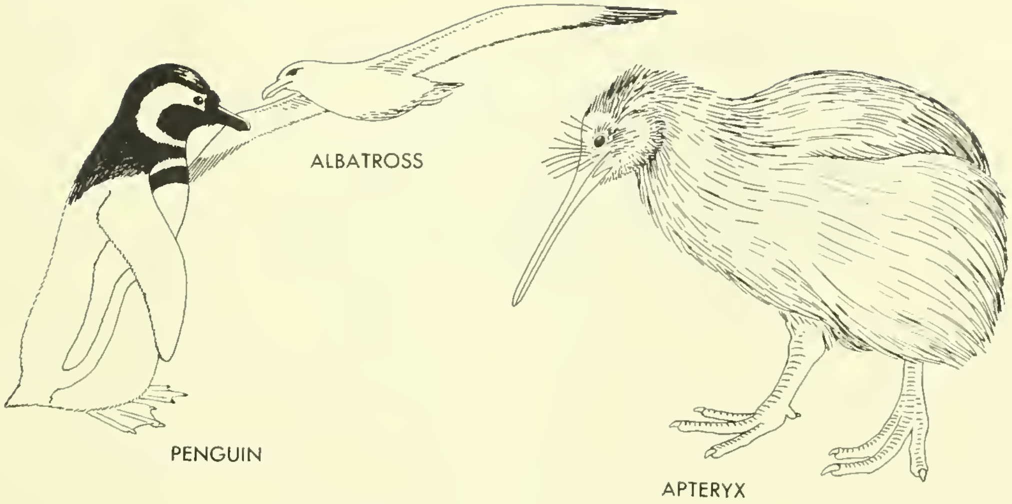


Figure 2-10. Some extremes of the birds.

like feathers are observed. The feathers of the region in front of the eye tend to be hair-like.

The scalation of the leg in the pigeon is modified; scutes are formed by the fusion of several scales. Small feathers may come out of the middle of some of the scutes. In some birds, such as the Barn Owl or the pelican, the leg is covered by small polygonal scales, and, in the case of Barn Owl, small feathers are observed growing out from between the scales or from the posterior margin of the scales.

Mammals

Mammals are defined as having hair and mammary (or milk) glands, which give the group its name.

Monotremes The Spiny Anteater (or Echidna) and the Platypus are unique kinds of mammals (Figure 2-11) which lay eggs much like those of a reptile. The first has the snout elongated and tapered; the second has a duck-like bill covered by hairless, leathery skin. External ears or **auricles** are lacking. The hair has been modified into spines in the case of the Echidna. The tail is short and covered with spines. The limbs are stout with heavy claws for digging. In the case of the Platypus the body is covered with soft hair, the short legs have long, webbed digits, and the tail is flattened for swimming. The female Echidna has a crescentic marsupial fold on the belly; nipples are lacking in both genera. Males of these animals have a **poisonous spur** on the hind legs.

Marsupials The female opossum has a pouch or marsupium in the inguinal region, in which the young undergo

Figure 2-11. Two of the living monotremes.

Figure 2-12. The marsupial and placental mammals.

a part of their early development. The nipples of the mammary glands are in this pouch, which gives the group its name. The eyes are large and prominent and there are large, bare auricles (ears) (Figure 2-12). The body is covered with long hair. The rat-like tail, covered with scales, is prehensile, being used by the animal to hang from branches.

Placental The body of the rat (Figure 2-12) is covered with dense hair, and its long tail is scaled, with some hairs growing out between the scales. The limbs are similar to the opossum's. There is no marsupium; the nipples are arranged in bilateral lines along the belly. The young remain within the mother's body for a longer developmental (gestation) period. They are nourished through a special structure, the **placenta.**

FOSSIL VERTEBRATES

An examination only of living forms results in overlooking many interesting groups represented by fossils. Some of these will be introduced here, whereas others will be referred to in the discussion of specific anatomical areas.

Well-known fossil agnath fishes, related to the cyclostomes, include such genera as *Tremataspis, Cephalaspis,*

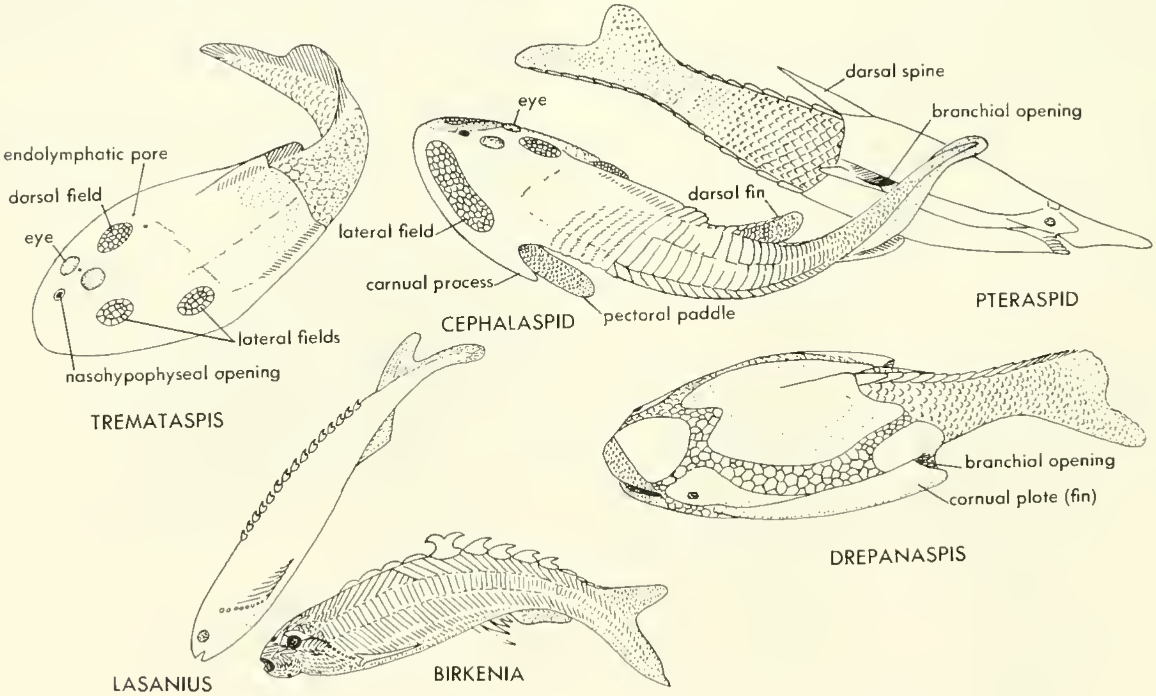


Figure 2-13. Several kinds of fossil agnaths as they are presumed to have looked.

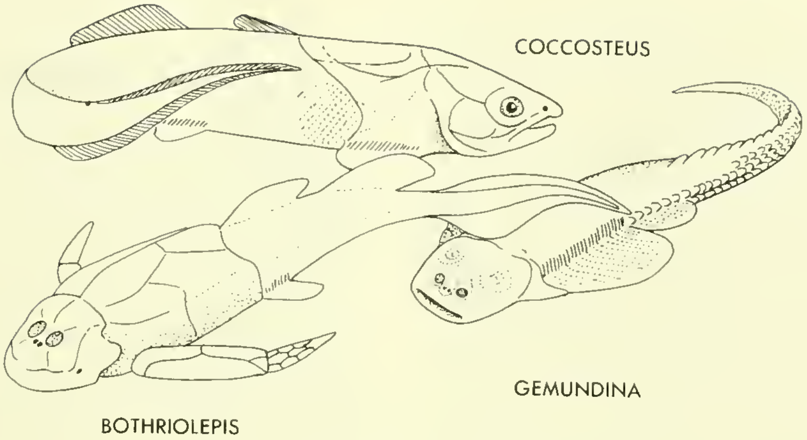


Figure 2-14. Restorations of some fossil placoderms.

Pteraspis, Drepanaspis, and *Birkenia* (Figure 2-13). *Tremataspis* differed from *Cephalaspis* in lacking the horn-like developments of the head margin and in lacking fins. These genera agreed in having the head and trunk largely encased in armor. The tail was covered by scales or plates. The nasohypophyseal duct opened on the top of the head just in front of the eyes, which lay near the midline. Behind the eyes were a dorsal "field" covered by small plates and the openings of the endolymphatic pores.

Drepanaspis and *Pteraspis* (Figure 2-13) differed in having the nasohypophyseal opening at the margin of the mouth or inside the mouth. *Drepanaspis* was a very flattened form apparently of bottom living habit.

Birkenia (Figure 2-13) is an example of the anaspid. It was a laterally compressed fish of small size. It is thought that it foraged along the bottom by more or less standing on its head. This would account for the hypocercal type of tail seen in this group and in *Pteraspis.*

Among the fossil gnathostomes, jawed fishes, the arthrodires are well known, and of these *Coccosteus* and *Dunkelosteus* are the best known. *Dunkelosteus* was large, its head and trunk were covered with bony armor, and the head articulated with the trunk (Figure 2-14). It had paired fins and a long, tapered, isocercal tail.

Bothriolepis (Figure 2-14) is a peculiar looking placoderm related to the arthrodire. Its ventrally located mouth suggests that it was a bottom feeder. Other arthrodires were of many shapes and forms. *Gemündina* (Figure 2-14) was a very flattened, shark-like form, covered with small bony plates.

The shark array had many fossil representatives ranging from the Devonian *Cladoselache* or the carboniferous *Pleuracanthus* (Figure 2-15). The former had a cover of fine scales, and the latter was probably naked.

The acanthodians (Figure 2-15) are sometimes placed with the sharks or with the arthrodires. The fins in this group are of interest in that, with the exception of the caudal, each was formed by a strong spine, behind which was a membrane. The number of lateral fins ranged from two pairs to seven pairs. One or two dorsals were present; the tail was heterocercal. The head and body were covered by

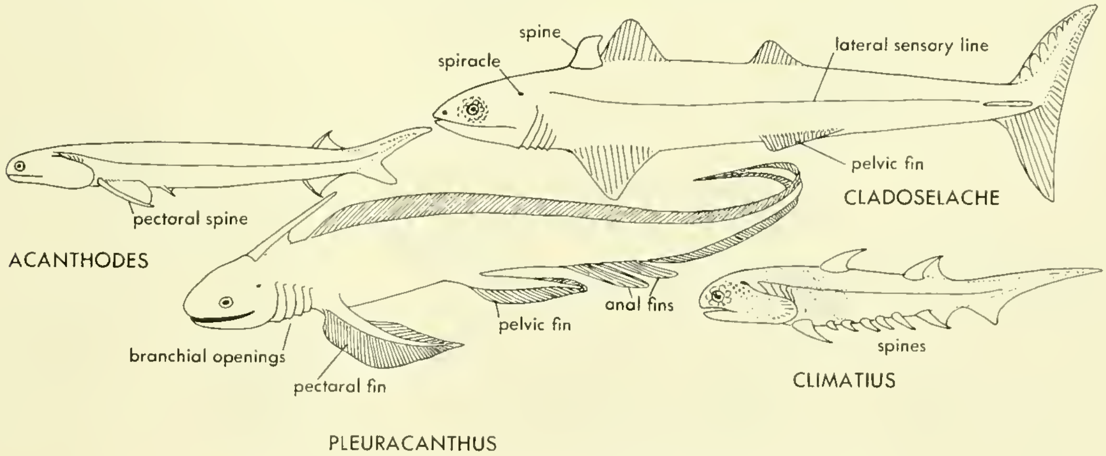


Figure 2-15. External features of some fossil, shark-like creatures as reconstructed.

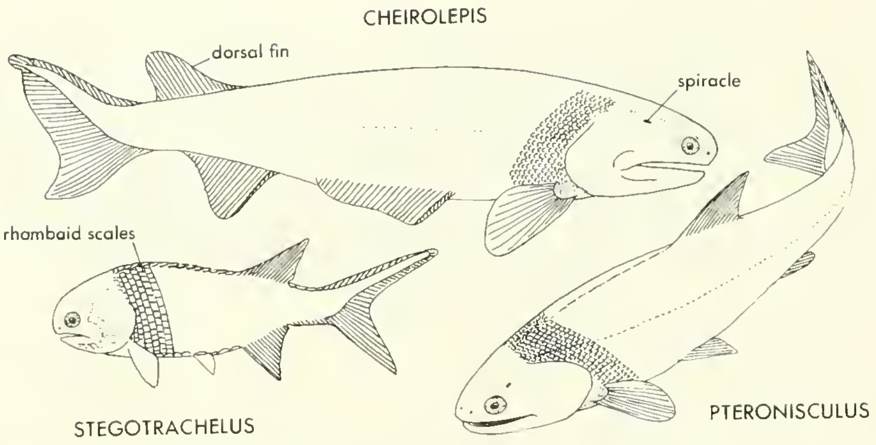


Figure 2-16. Three palaeoniscoid fishes as restored. *Stegotrachelus* and *Cheirolepis* are from the Upper Devonian, and *Pteronisculus* is Triassic.

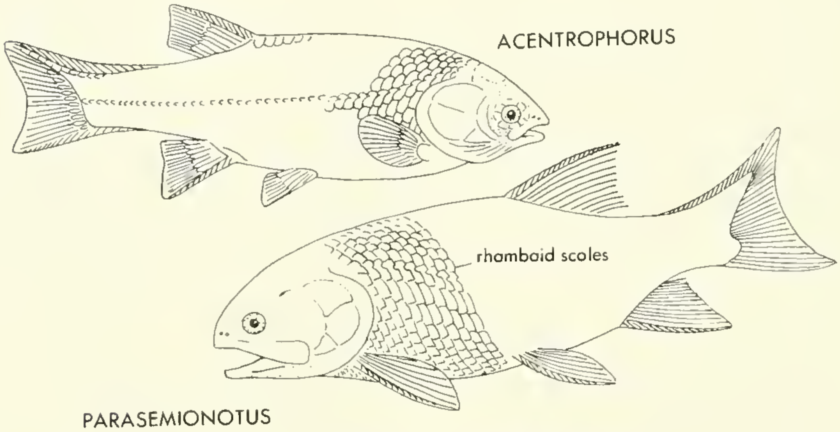


Figure 2-17. Two fossil holosteans. *Acentrophorus*, from the Permian, *Parasemionotus*, Triassic.

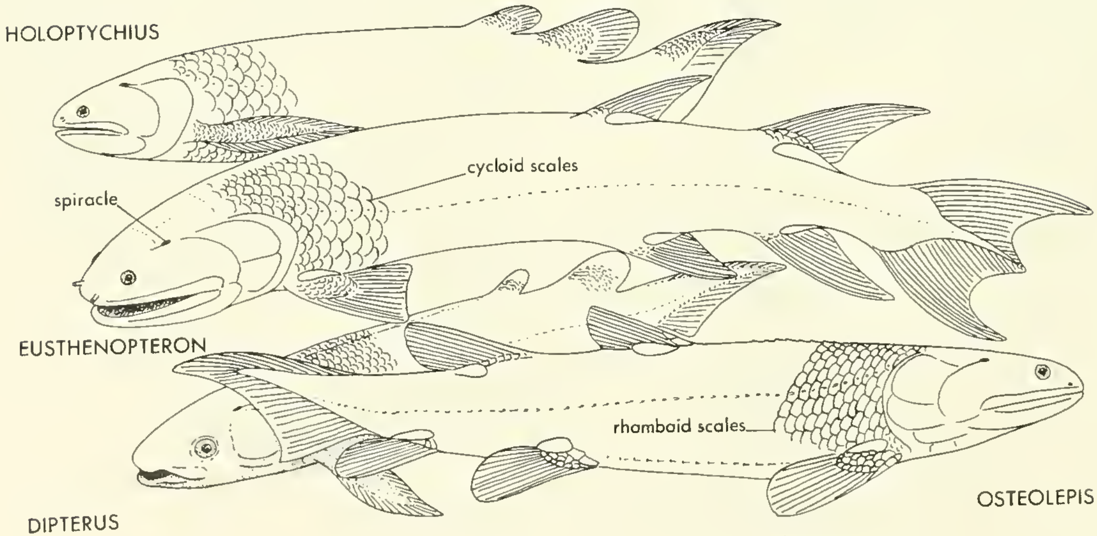


Figure 2-18. Devonian fossil choanate fishes restored.

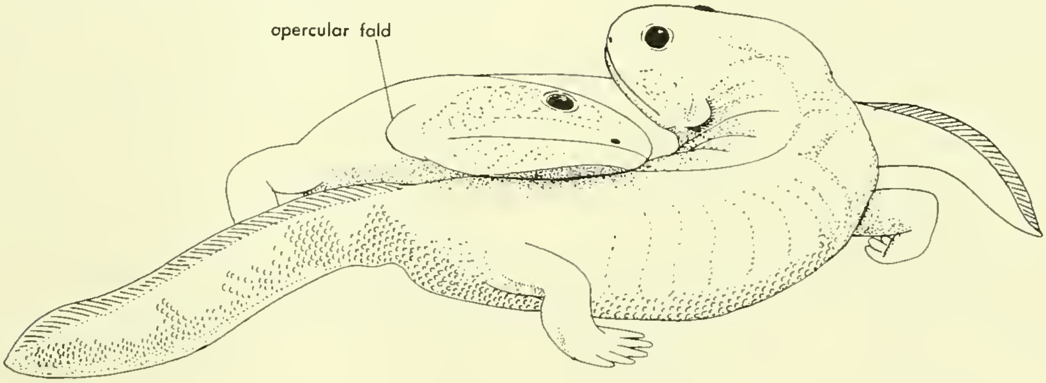
small ganoid scales. The eye was large and far forward on the head. The operculum was large but separate septa extended out from each of the hyoid and branchial arches. The eye was encircled by five plates; the operculum was supported only by branchiostegal rays.

The most primitive ray-finned fishes are represented by such genera as *Cheirolepis* and *Perleidus* (Figure 2-16). These had strongly developed dermal bones covering the head, a rhomboid cover of thick scales with a distinct glassy enamel layer, a single dorsal fin, a heteroceral tail, an anal fin, and two pairs of lateral fins. The membranous part of the fins was supported by jointed fin rays. There was a small fleshy lobe at the base of the fin.

Acentrophorus (Figure 2-17) is the earliest known holostean fish, and in it the holostean features of cheek and jaw were fully developed. In the somewhat later occurring *Watsonulus*, or *Parasemionotus,* there was an interesting combination of features of the holostean and palaeoniscoid.

The crossopterygian fishes (Figure 2-18) are choanate fishes. They are best represented by *Osteolepis* and *Eusthenopteron,* which show many similarities to the assumed ancestor of the Amphibia. These fishes had thick dermal bones covering the head and operculum. The body was covered by rhomboid or cycloid scales of the cosmoid type (based on their histology—*see* Chapter 8). Each had two dorsal fins, a heterocercal or diphycercal (double) tail, an anal fin, and two pairs of lateral fins with fleshy lobes. From these fleshy lobes with their "fringe" of web the term Crossopterygii is derived. In these fishes the fleshy lobes are not nearly as large as those of the dipnoans, nor more extensive than those of *Latimeria. Dipterus* was an early Devonian member of the Dipnoi. The body was covered by cycloid scales of the cosmoid type. There was the same pattern of fins as that seen in the crossopterygian fishes.

The earliest of the amphibians belonged to the ichthyostegid group from the uppermost Devonian of Greenland (Figure 2-19). This kind of animal is imagined as looking much like a salamander. Some of the later labyrinthodonts were very large with proportionally larger heads and shorter tails. They are assumed to be modified in structure as compared with the primitive fish-like form.



ICHTHYOSTEGA

Figure 2-19. The Devonian amphibian Icthyostega as it may have looked.

3

Osteology and the Mammalian Head Skeleton

OSTEOLOGY AND HUMAN ANATOMY

A study of the skeleton of vertebrates must necessarily form the core of a comparative investigation having as one of its goals an understanding of the phylogeny of these animals. This is so because the fossil record is made up almost entirely of skeletal remains. One might argue that the study of fossils is properly paleontology; this, however, would be begging the point. A study of the history of structure is most meaningful in terms of what can be directly observed, and both fossils and living forms can be dissected. Speculation on hypothetical stages leading to the kinds now living, without proper evaluation of the fossil record, leads to the same sort of meaningless esoterism that characterized the *Naturphilosophie* of the early nineteenth century.

Fossils are usually mere fragments of animals and are, therefore, not the most satisfactory sources of information, nor are they easily studied. Many students will wonder what of value can be learned from them. Examination of what is described as a "good" fossil vertebrate, crushed flat and scattered on a slab of rock, does not arouse a feeling of faith in the "scientist's" interpretation and restoration. One might wonder whether the restoration is more real than the idealist's theoretical "ancestral form." A detailed study of skeletal anatomy will reveal to the student that much can be learned from fossils and that this information is quite reliable.

Unlike the paleontologist, the comparative morphologist can limit his discussion to those fossil forms which are known from numerous good specimens. Such selection removes much of the guesswork and supplies a relatively firm footing of morphological detail. Futhermore, this footing is as secure as that involved in a discussion of many living forms, which at present are only poorly known, because accounts of them are lost in a vast and scattered literature or because specimens are unavailable for consultation. Even when the forms are well known, divergence of opinion and the confusion of terminology frequently conceals the salient points.

Of all the parts of the skeleton, the head offers the greatest rewards for study because of the many features capable of independent variation. Despite the vast array of information on the head skeleton, much of it is contradictory and confused. The difficulties center around the concept of homology, which determines the terminology—homologs bear the same name, homoplasts or analogs have differentiating names. It is not our purpose to argue for or against any particular system of terminology or to evaluate the lengthy arguments supporting the divergent opinions—it is enough to recognize where the difficulty lies. To make meaningful comparisons, it is necessary to start from a fixed set of anatomical terms and to work from this to the points of conflict. It is generally agreed that the basis of anatomical terminology should be that applied to the human, the best known chordate.

Consistency in terminology for man is still being sought. The first step in this direction began with the meeting of several German anatomists in Basel in 1895. From this meeting came a list of anatomical terms known as the "Basle Nomina Anatomica," which was quickly adopted by many countries, including the United States. This terminology was refined in a revision of the list published by the Anatomical Society of Great Britain in 1933, and in a German revision, the "Jena Nomina Anatomica," issued the same year. The Fifth International Congress of Anatomists, held at Oxford in 1950, voted to authorize another revision, which was submitted by a committee to the Sixth Congress in Paris, 1955, and was accepted. This "Nomina Anatomica" forms the base for present anatomical studies of man.

In comparative study, use of the "Nomina Anatomica," or N.A., has two serious drawbacks. The first is the necessity of knowing human anatomy sufficiently well to compare the structures of other animals with this base. Certainly the study of human anatomy is a large task in itself and we can only propose to make a start in this direction. The second problem stems from the fact that some structures of man are not really comparable to those of lower forms. Further, the orientation terms of human anatomy are hardly applicable to lower forms, i.e. posterior in the human is dorsal in the tetrapods. As a result, the N.A. needs to be modified, and a compromise Nomina Anatomica Comparate (N.A.C.) is needed. As a beginning in this direction, a group met (Gregory, 1917) to systematize terms for Permian tetrapods. An N.A.C. would depend to a great extent upon agreement as to how similar structures must be to be identified as homologs or how dissimilar they must be to warrant use of different names. These are difficult questions to answer as will be seen from the borderline situations which will be described and discussed.

Summarizing the above, the skeletal system, because it is fossilized, is the only system that gives us a broad overview of the history of structural changes in the vertebrates. The head skeleton is the most informative part of the skeleton since its complexity offers many more opportunities for divergent change. Because description of the head skeleton involves terms and since the basis of anatomical terminology is the "Nomina Anatomica," the human should be considered first. From man the terms can be extrapolated to progressively more distant groups, i.e. reptiles, amphibians, fishes. This procedure can be characterized as going from the known to the unknown, or from the fixed to the controversial. It also, in the final analysis, is going from the simple to the more complex. In this process the limitations of the concept of homology are encountered along with problems of definition, observation, and interpretation.

MAMMALIAN HEAD SKELETON

Introductory concepts

Before beginning a description of the head skeleton, it would be helpful to consider some general ideas concerning it and its origin. These introductory remarks will be repeated and enlarged as the study progresses.

The skull was thought by Goethe, Oken, and Owen to be made up of four to seven modified vertebrae. This view was destroyed by Huxley in his Croonian Lecture of 1858. The vertebra analogy is quite effective in describing the skull but is opposed by its embryological history.

In most descriptions of the head skeleton, the bones are separated into groups based on their origin. Some bones arise in or around cartilaginous precursors and are called **chondral bones;** other bones ossify directly in connective tissue masses and are called **dermal bones.** Chondral bones are of two types: those that arise at the surface of the cartilage, inside of the **perichondrium** (the connective-tissue envelope of the cartilage), and those that arise within the cartilage. The former are **perichondral,** the latter **endochondral.** Growth of a perichondral ossification may result in replacement of the whole cartilage, or the bone may remain as an outer sheath. Endochondral bone may replace the entire mass or retain some of the cartilage on its surface, particularly in regions of contact or articulation with other bones. A chondral bone may also have dermal extensions.

The head skeleton is a functional structure which responds to the needs of the sense organs or the brain and cranial nerves enclosed by it. Its bones also provide passage for arteries and veins serving various parts of the head. The operation of the jaws modify this skeleton, depending on the mode of articulation of the lower jaw, the attachments of muscles, or the types of teeth and proportions. Bones are usually thought of as forcing rigid conformity on other parts, but this is not the case at all. Bone is very plastic, and this plasticity is related in part to its late embryological appearance. Bone or cartilage appear to be functional responses to forces set up in the connective tissue system for support, for mechanical lever action, or for resistance to compression strain. As a continually responding tissue, bone can be laid down or resorbed, and reformed to fit altered needs.

Head skeleton of placental mammals

Human head skeleton The human head skeleton is best observed in the foetus (Figures 3-1, 3-4). It can be subdivided into the divisions and bones given in Table 3-1. The reasons for some of these subdivisions have already been stated or will be understood only after a study of the skulls of other vertebrate groups. Bones found in other mammals besides man are included in this list and set in italics. No description will be given here, for the illustrations (Figures 3-1, 3-4) will help in locating each of the bones. The familiarity gained from locating the bones of the table in the figures will serve in locating these same bones in a laboratory

Table 3-1 ***THE BONES OF THE HEAD SKELETON OF THE MAMMAL ARRANGED ACCORDING TO TYPE AND PLACE OF ORIGIN***

Cranium (brain and sense organ capsule)	Splanchnocranium or Visceral Skeleton (dermal bones with*)
Endocranium (bones of chondral origin) basioccipital exoccipital supraoccipital petrosal basisphenoid orbitosphenoid ethmoid	Mandibular arch—Palatoquadrate and Meckel's cartilage premaxilla* maxilla* palatine* pterygoid* alisphenoid (mixed) incus malleus (mixed) dentary* tympanic*
Dermocranium (bones of membrane origin) postparietal parietal frontal nasal lacrimal squamosal jugal vomer *parasphenoid*	Hyoid arch stapes tympanohyal and stylohyal ceratohyal hypohyal (minor cornua) body or copula
Unclassified (chondral) *entotympanic*	1st branchial arch ceratobranchial I (major cornua)

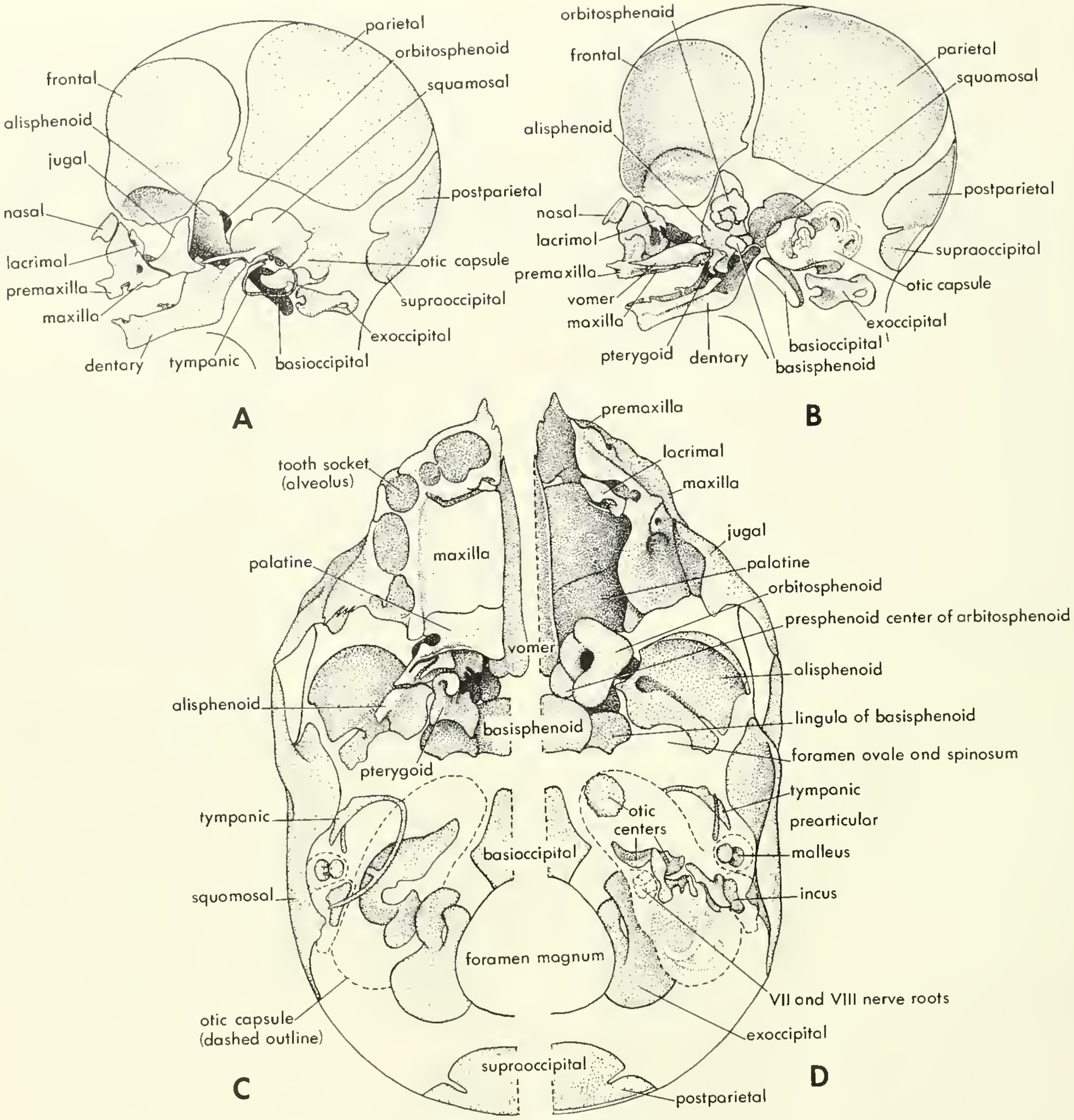


Figure 3-1. Head skeleton of early human faetus (3 months). A, lateral view; B, medial view of right half of skull; C, half the skull as seen from below; D, half as seen from above with roof removed.

specimen of a mammal. A biproduct of this exercise is an introduction to some of the problems of terminology.

To establish terms more usable for comparative study than those of the N.A., the names of several bones in the human skull have been changed. These names are: *os incisivum,* now called premaxilla and separated from the remaining bone which retains the name maxilla; *interparietal,* now called postparietal because it is more descriptive and frees interparietal for use for bones actually lying between the parietals; *zygomaticus,* now called jugal to agree with long-established usage in comparative anatomy and to avoid the descriptive inference of a zygomatic arch; *minor cornua,* now called hypohyal to avoid a descriptive term not applicable to most vertebrates; *major cornua,* now called ceratobranchial I for the same reason.

The retention of such terms as incus, even though it refers to a bone known to be homologous to the quadrate of lower vertebrates, indicates the extent of nomenclature difficulties. The term incus is so well established that it seems neither possible nor useful to supplant it. Use of the term malleus is desirable, for this is sometimes a compound bone and, further, it is established and it designates a new functional unit in the mammal. Several compound bones of the human—the occipital (formed by the basioccipital, exoccipital, supraoccipital, and usually the postparietal), the temporal (formed from the squamosal, petrosal, tympanic, and entotympanic when it occurs), and sphenoid (formed from orbito, ali, and basisphenoids, and pterygoid)—are broken down into their components, whereas the petrosal (formed of prootic and opisthotic) is retained. The use of petrosal is justified because anatomists are unable to associate clearly the several ossification centers with the original opisthotic and prootic bones. The styloid process of the petrosal presents a special problem since it has two centers of ossification, an upper tympanohyal and a ventral stylohyal.

Other terminological problems are related to the following anatomical facts: the alisphenoid, although basically a chondral bone, has a dermal extension; the pterygoid, although basically a dermal bone, has a chondral part, the hamulus; and the entotympanic, when present, arises from an extracranial cartilage, which, like the cartilage for the hamulus, is not present in lower forms. A more detailed review of the mammalian head skeleton will reveal additional problems and contribute to an understanding of the above points.

Head skeleton of other placentals The cat, dog, and rabbit are representatives of the placental mammals. These three animals show the differences that exist between two carnivores, the cat and dog, and between the carnivores and another highly specialized order, the Lagomorpha, the rabbit.

At first glance the skulls of these mammals present several main features (Figures 3-2, 3-3). Posteriorly there is the **cranial capsule** enclosing the brain. From this capsule the **foramen magnum** opens posteriorly, posteroventrally, or ventrally as in the human. Below the cranial capsule are the bilateral **tympanic bullae.** Each of these has a **tympanic fenestra,** or aperture, which in life is spanned by the **tympanic membrane,** or eardrum. Anterior to the swelling of the cranial capsule is the large eye socket on either side, called the **orbit.** Anterior to the orbit is the **snout** or muzzle, projecting forward to the **anterior narial opening.** The **mandible** or lower jaw articulates with the skull lateral to the cranial capsule. The hyoid apparatus, which may or may not be well developed, is suspended from the skull behind the mandibular articulation. The rabbit differs in having the surface of many of the bones fenestrated, particularly the maxilla in front of the orbit.

In adult mammals the four occipital bones are fused usually into a single piece enclosing the foramen magnum, the opening for the passage of the spinal cord from the cranial cavity. The **supraoccipital** is separate in the rabbit. The **postparietal** arises in development as a pair of centers that soon fuse at the midline to form a single triangular piece with an apex pointed anteriorly. Soon after its appearance this midline bone usually fuses with the supraoccipital, sometimes with the parietals. In some cats and dogs it remains free. In the rabbit it is a separate ovoid midline bone.

The **exoccipital** bones largely bear the bilateral occipital condyles which articulate with the vertebral column. Above the foramen magnum the supraoccipital and exoccipitals are drawn out to form the transverse, crescentic, **nuchal (lamboidal) crest**—the postparietal lies anterior to the nuchal crest and forms part of the anteroposteriorly oriented **sagittal crest** in the cat and dog. These crests are related to muscle insertions and origins.

The **basioccipital** is a midline bone bearing a part of each occipital condyle on its posterolateral margins. To either side of it are the large swollen **tympanic bullae,** whose anterior ends lie opposite the ends of the transverse suture separating the basioccipital and **basisphenoid.**

The **tympanic bulla,** housing the middle-ear space, is a compound structure formed from several sources. In man or the rabbit it involves the tympanic bone and an outgrowth from the petrosal. In some insectivores the basisphenoid contributes a margining process, which, together with the tympanic and the petrosal, forms an incomplete bulla. In the cat and dog the petrosal component is replaced by the **entotympanic,** which, along with the tympanic, forms a complete bulla.

The exoccipital has a distinct process extending down behind the bulla. At the posterior inner margin of the bulla there is a large foramen or fossa. This is the posterior lacerate fossa, and the foramen that opens directly through it is the jugular foramen.

Returning to the top of the skull, we find the paired **parietals** lie anterior and lateral to the midline postparietal. The parietal has distinct sutures; it sutures laterally with the squamosal, anteriorly with the frontal, and, between these, with the alisphenoid (not in the rabbit).

The **squamosal** forms the lateral wall of the brain case and from it a large zygomatic process extends outward and forward to contact the jugal. On the under surface at the base of the zygomatic process is the groove of the glenoid articulation. Behind this articular surface is a **postglenoid process** (lacking in the rabbit). Behind the postglenoid process of the dog, in the crevasse above the tympanic fenestra, is a large postglenoid foramen. A minute foramen occurs in this general region in the cat and rabbit, but the exact position is not comparable. The sutures of the squamosal are clear, except in the area around the tympanic fenestra. This bone is fused with the tympanic in the cat or dog, at the upper margin of the tympanic fenestra; posterior to this opening the squamosal is fused with the petrosal. In

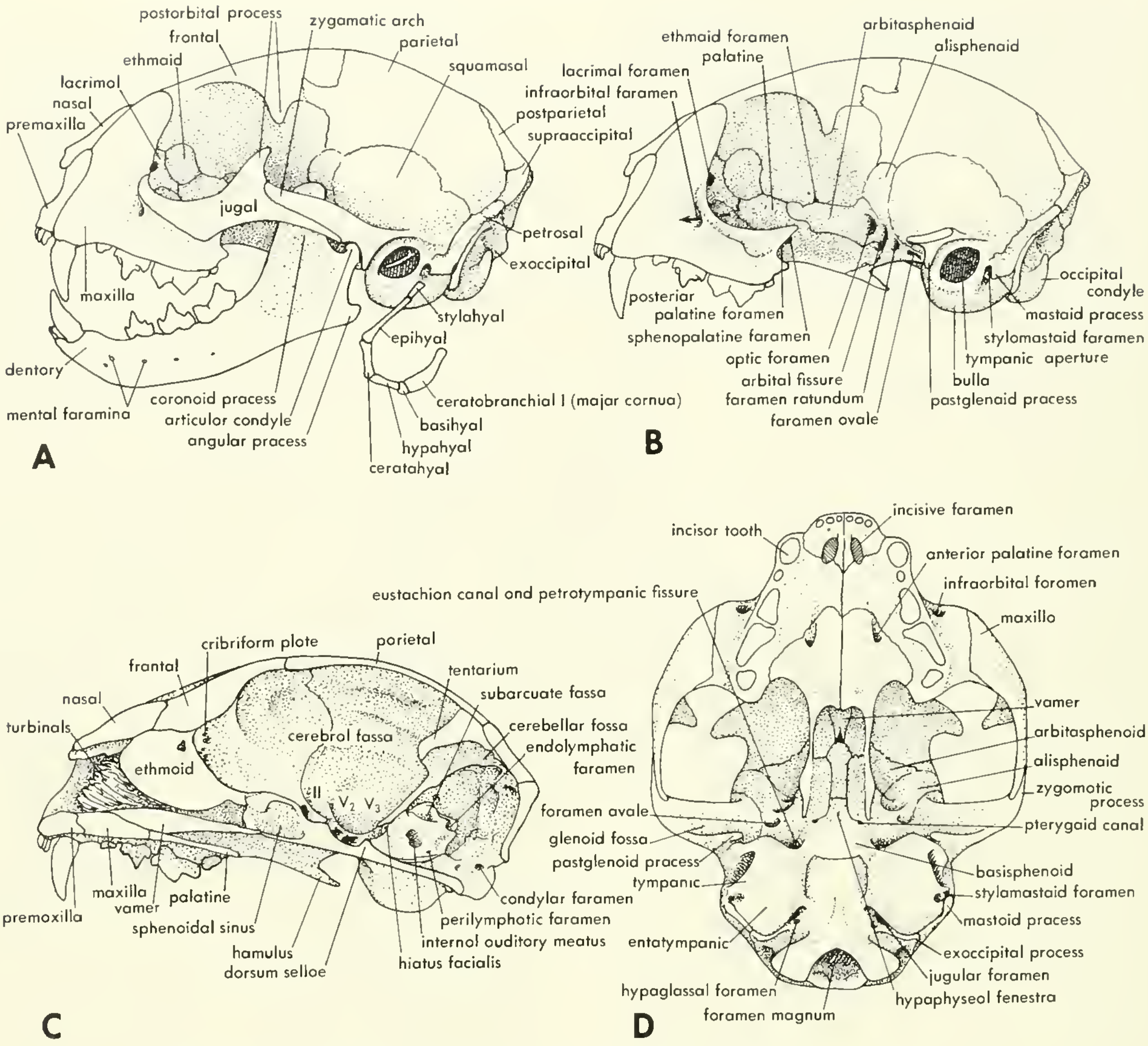


Figure 3-2. Head skeleton of young cat. A, lateral view; B, lateral view of skull with zygomatic arch cut away; C, medial view of right half of skull; D, ventral view of skull.

the rabbit the squamosal has a long, thin post-tympanic process and an irregular ventral suture line.

The **petrosal** is exposed on the outer surface of the cranium in a small area between the squamosal and the exoccipital. In the cat and dog this part of the bone extends down and forward behind the bulla to end as a rounded process, the mastoid process. The stylomastoid foramen (the outer opening of the facial canal) opens just in front of the process—between this process and the tympanic bone.

The **zygomatic process of the squamosal** sutures loosely with the **jugal,** which forms the ventral margin of the orbit. In the cat and less so in the dog the jugal has an upward projecting postorbital process; anteriorly it tapers to a narrow upcurved process ending at the lacrimal canal. Ventrally the jugal sutures broadly with the **zygomatic process of the maxilla.** This suture is lost through fusion in the rabbit.

In front of the parietals are the paired **frontals,** which form the major fore part of the roof of the skull. In the cat and dog each frontal has a postorbital process extending outward and downward behind the orbit. This process in the cat nearly contacts the short upward process from the jugal. The rabbit lacks this process but has an anterior and posterior incisure ("cut out") in the orbit margin. The frontal forms not only the top of the skull between the eyes but also much of the orbit wall. Deep in the orbit it sutures, in the cat and dog, with the alisphenoid (behind), the orbitosphenoid (next anteriorly), the palatine and then the lacrimal (at the anterior margin of the orbit). Frequently in the cat, a small exposure of **ethmoid** forms the orbit wall between the frontal and lacrimal. The alisphenoid is excluded from contact with the frontal by the large orbitosphenoid in the rabbit. Anterior to the orbit the frontal sutures with the maxilla (in front) and nasal (above).

The **nasals** are paired splints of bone lying above the nasal passages. They contact the frontals posteriorly and the maxillae and premaxillae laterally. They form a part of the margin of the external narial opening.

The lateral and ventral margins of the external narial opening are formed by the premaxillae (singular **premaxilla**) bearing the teeth called incisors (three on each side in the cat and dog; two pairs, one in front of the other, in the rabbit). The premaxillae form the anterior part of the palate. The slim **palatal processes** meet along the midline between the large anterior palatine fenestrae. These processes in the rabbit do not contact the maxillae but meet a downward projecting process of the vomers.

Behind the premaxilla is the **maxilla.** Each maxilla bears teeth. In the cat or dog there is a large canine anteriorly. In front of the canine there is a gap in the tooth row called a **diastema** into which the canine of the lower jaw fits. Behind the canine are "shearing teeth," three (premolars) in the cat and four (premolars) in the dog. The most posterior of these teeth in both animals is called a **carnassial** tooth, since its cutting edge matches that of a tooth in the lower jaw in such a way that they function like scissors. The other shearing teeth pass between each other, cutting by means of a sliding action.

The dog has two molars behind the carnassial. The cat has one. The rabbit lacks incisors and has six peg-like teeth in each maxilla; its formula is I $\frac{2}{1}$, C $\frac{0}{0}$, P $\frac{3}{2}$, M $\frac{3}{3}$. The formula indicates the number of incisors (I) in the upper jaw over the number in the lower jaw, the number of canines (C), premolars (P), and molars (M) in a similar fashion.

The paired maxillae meet at the midline of the secondary palate; they suture with the premaxillae anteriorly and the palatines posteriorly. On the lateral aspect the maxilla sutures with the jugal below the orbit margin (by means of a zygomatic process), touches the lacrimal along the anterior margin of the orbit and sutures with the frontal above this, contacts the nasal dorsoanteriorly and the premaxilla anteriorly. Within the orbit the maxilla sutures medially with the palatine and the lacrimal; laterally and anteriorly it contacts the jugal. At the lower anterior margin of the orbit, the maxilla is pierced by the large infraorbital canal.

The posterior part of the secondary palate is formed by the **palatines** lying just behind the maxillae. These bones nearly wrap around either side of the nasal passages and form the secondary palate below those passages. Dorsally the palatines are separated by the vomer. The palatine of either side also extends up into the orbit to suture with the frontal, the lacrimal, and the maxilla. In the orbit of the cat the palatine is pierced by the large sphenopalatine foramen and more laterally by the posterior palatine canal. In the dog the posterior **palatine foramen** lies immediately below the **sphenopalatine foramen.** These foramina are hidden behind the swollen maxilla in the rabbit.

The **lacrimal** is a thin plate of bone in the anteroventral part of the orbit. Its anterior margin forms the margin of the orbit and is pierced by the large downwardly and inwardly directed lacrimal canal. The lacrimal is so loosely attached that sometimes it is lost in prepared skulls of the cat; frequently it is missing in the rabbit.

Behind the palatine and forming the lateral walls of the nasal passages are the pterygoids. The **pterygoid** of either

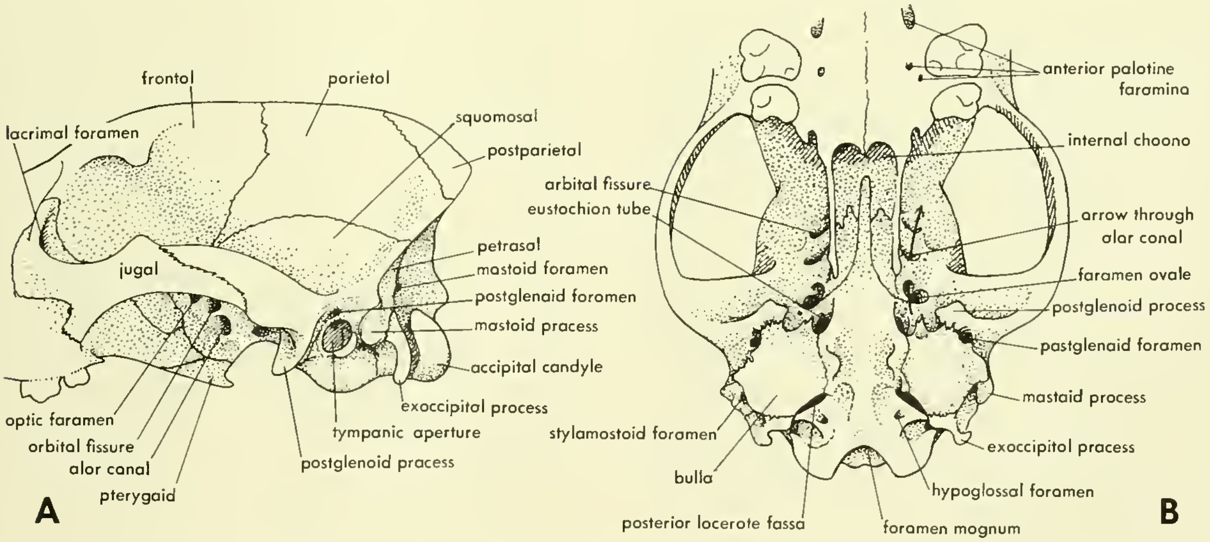


Figure 3-3. Posterior part of skull of dog as seen laterally, A, and ventrally, B.

side extends down and back as a slim process, the **hamulus.** The pterygoids are separated at the midline by the "presphenoid," which upon examination is seen to be but the midline area of fusion of the bilateral orbitosphenoids. The basisphenoid is exposed between the posterior parts of the pterygoid. The suture of the pterygoid with the palatine is not sharp; posterolaterally it is fused with the alisphenoid in the cat or rabbit but not in the dog.

In the roof of the nasal passage, between the pterygoids and palatines, the posterior bifurcated end of the fused **vomers** is seen. In the cat or dog the vomers form a splint of bone which is V-shaped in cross section. The anterior end of this midline splint lies above the posterior tips of the palatal processes of the premaxillae, except in the rabbit. This anterior tip can be seen through the anterior narial opening. The vomerine unit of the rabbit is more exposed and has a deep ventral keel extending down as a process behind the palatal processes of the premaxillae. The more dorsal body of the fused vomers extends well beyond and above the posterior ends of these processes.

The *alisphenoid* forms a part of the cranial wall extending upward and outward from the area of fusion of the pterygoid. The alisphenoid is pierced by the **foramen rotundum** (in front) and the **foramen ovale** (behind). The large **orbital fissure** opens between the alisphenoid and the orbitosphenoid. In the dog the first two foramina are joined by a horizontal channel through the alisphenoid, the **alar canal** (Figure 3-3). In the rabbit a foramen ovale opens under the anterior extension of the bulla, and the fenestra rotundum is confluent (together with) the orbital fissure. The alar canal of the dog, which transmits the internal maxillary artery, is represented in the rabbit by a foramen through the orbital wing of the pterygoid.

Above the orbital fissure the alisphenoid sutures with the orbitosphenoid, above and lateral to this with the frontal and parietal; posterolaterally it contacts the squamosal, the suture passing just inside the glenoid articulation of that bone. In the rabbit the squamosal and orbitosphenoid margin the alisphenoid in the orbit. The posterior limit of the alisphenoid is hidden by the tympanic bulla; medially it is fused with the basisphenoid and pterygoid.

In the orbit, anterior to the alisphenoid and the orbital fissure, is the **orbitosphenoid.** This bone forms a part of the forewall of the cranial capsule. It is margined above by the frontal, in front and below by the palatine, and behind by the alisphenoid. This bone is pierced by the large optic foramen. The orbitosphenoid is largest in the rabbit, where it sends a process out laterally above the alisphenoid. This process reaches the squamosal. There is a small process in the cat that does not contact the squamosal. In the dog the orbitosphenoid is smallest. The bilateral orbitosphenoids fuse at the midline and their palatal exposure is identified as the "presphenoid." Since a presphenoid as a separate identifiable bone is not know to occur in any mammal, or lower form, and since the orbitosphenoid of lower forms may arise from lateral and medial centers of ossification as in the mammal, it is suggested that the term presphenoid be dropped.

The **basisphenoid** is separated by distinct sutures from the orbitosphenoid anteriorly and the basioccipital posteriorly; it is fused laterally with the alisphenoid and sometimes the pterygoid. A small hypophyseal fenestra penetrates this bone at the midline in many cats and in the rabbit.

The tympanic bullae are formed in part from the **tympanic** bone, which encircles, except for a part of the dorsal margin (the **notch of Rivinus**), the **tympanic membrane.** The outer margin of the tympanic is drawn out and upward in the rabbit to form an external auditory meatus. This bone also extends medially to form part of the bulla. In the cat the tympanic forms a septum separating the bullar cavity into an **ossicular cavity** and a **bullar recess.** In the dog this septum is only partly developed. The medial part of the bulla of the cat or dog ossifies in a cartilaginous precursor called the **entotympanic.**

The surface of the bulla medial to the mastoid process is grooved by the connective tissue of the hyoid attachment to the skull. In the rabbit and young cat, this attachment is ossified. This ossification, the **stylohyal,** is not fused to the bulla. In man the stylohyal is fused to the petrosal as the styloid process. It ossifies from two centers, the tympanohyal, next to the petrosal, and the stylohyal.

The tympanic bulla is penetrated near its medial margin by a carotid canal in the rabbit. In the foetal cat such a canal lies between the bulla and the basisphenoid but is vestigial in older stages. In the dog the internal carotid artery enters the **carotid canal** in the **posterior lacerate** fossa. Both the carotid canal and its internal portal (two openings) can be seen when looking at the anterior aspect of the bulla along the palatal surface. From this view, the opening of the eustachian tube and the nearly confluent petrotympanic fissure open lateral to the **internal carotid portal.** In the cat, only the eustachian tube and petrotympanic fissure are seen, whereas in the rabbit the foramen ovale opens above the eustachian tube and petrotympanic fissure.

The cat skull cut sagittally (Figure 3-2 C) reveals many details of structure. The secondary palate extends below the large nasal passage, which is nearly filled with the thin, contorted and rolled sheets of bone making up the **turbinals.** These are identified according to their area of attachment as the maxillary, nasal, and ethmoid turbinals. The **perpendicular plate of the ethmoid** separates the right and left nasal passages and joins the **cribriform plate** separating the nasal passages from the cranial cavity. The turbinals, ethmoid and cribriform plates are secondary ossifications appearing late in development. A section of the frontal and orbitosphenoid bones reveals sinuses connecting with the nasal passages. Such sinuses also are found in the maxilla, and in some mammals more of the bones of the skull are invaded by such air cavities.

The large **cerebral fossa** of the brain case is separated from the posterior **cerebellar fossa** by the **tentorium,** a secondary ossification in the connective tissue between these two parts of the brain. The tentorium is incomplete dorsally in the rabbit, incomplete laterally in the dog. The inner walls of the cranium are irregularly molded, following the surface of the brain and its investing connective tissue and blood vessels. The **sella turcica,** into which the pituitary gland fits, is a shallow depression in front of a transverse raised **dorsum sellae.** The margin of the dorsum sellae is separated by a small gap form the tentorium in the dog, a larger gap in the cat. The dorsolateral margin of the dorsum sellae extends forward as a **posterior clinoid process.** An **anterior clinoid process** is indicated on the orbitosphenoid anterior to the tip of the posterior process.

In the lateral wall of the cerebellar fossa is the main part of the petrosal. The surface of this somewhat triangular mass, whose apex points anteromedially, is marked by two large pits; these are the **internal acoustic meatus** below and the **subarcuate** or **floccular fossa** above.

The **mandible** (Figure 3-2 A) is composed of two rami joined together anteriorly at a symphysis. Each mandibular **ramus** is composed entirely of the **dentary** bone. This is drawn up posteriorly into a tall **coronoid process** extending upward inside the zygomatic process of the skull and filling much of the **temporal fossa.** In the rabbit such a process is lacking; the anterior margin of the **articular process,** which resembles the coronoid process of the cat or dog, is grooved, and its lateral margin may be drawn out as a slight coronoid process.

Behind the coronoid process of the dog or cat is the articular process bearing a transverse articulatory **condyle.** In the rabbit the condyle is small and is found at the anterior margin of the large dorsally extended articular process. Below the articular process is a strong **angular process.**

In their dentition of the lower jaw, the dog and cat are similar, except that the dog has more teeth in its longer ramus; none of these teeth is molariform (shaped like a molar). What is designated as the first molar is also the lower carnassial. The rabbit has only one incisor, no canine, two premolars, and three molars in the lower jaw. The premolars and molars are all similar high-crowned, continuously growing, peg-like teeth with transverse lophs or crests.

Several bones of the reptile lower jaw and visceral skeleton are involved in the mammalian middle-ear structure (see Chapter 4). There are three ossicles for conducting vibrations from the tympanum to the inner ear (Figure 3-4): the **malleus, incus,** and **stapes.** The last of these belongs to the hyoid arch. Its foot plate fits into the fenestra vestibuli of the petrosal. The incus is the homolog of the reptilian quadrate which articulates between the cranium and the lower jaw. The malleus is a compound bone formed by fusion of two lower jaw bones, the prearticular, which forms the anterior process of the malleus, and the articular. In addition to the malleus, the tympanic bone (see above) is of lower jaw origin. It represents the reptilian angular.

The hyoid apparatus of the cat consists of four bony segments extending down from the region of the mastoid process of the petrosal to a transverse **body.** These are, from above downward, the **stylohyal, epihyal, ceratohyal,** and **hypohal.** From the body a large **ceratobranchial 1** (thyrohyal) extends back and upward to the thyroid cartilage. In the dog there are three segments in the hyoid arch; from the body upward these are the hypohyal, ceratohyal, and epihyal. The stylohyoid ligament connects these bones with the bulla. In the rabbit the stylohyal is anchored by connective tissue to the bulla and the exoccipital process. It serves as origin for the styloglossal muscle and for attachment of the stylohyoid ligament which extends down to the small bony hypohyal. The body of the hyoid is large and there is a well-developed ceratobranchial 1 (greater or major cornua). In mammals generally, there is an ossified process for the attachment of the hyoid arch to the cranium. This process is the tympanohyal process. It is concealed within the bulla and thus not readily observable.

Joints of the head skeleton The joints, or articulations, between the bones of the mammalian head skeleton can now be considered in terms of their variations. These joints are for the most part immovable, some are permissive of slight flexion, others articulate freely. The immovable are called **synarthroses** (singular synarthrosis), the others **diarthroses.** Examples of the middle group are considered as synarthroses or **amphiarthroses.** The extreme of the synarthrosis is the **synostosis,** where the two bones are fused together, sometimes indistinguishably. In a synarthrosis the edges of the bones may be separated by little or much connective tissue.

There are several kinds of synarthroses in head skeletons. These include: sutures (true and false), schindyleses, and gomphoses. **True sutures** are joints formed by interlocking finger-like (sutura dentata) or tooth-like (sutura serrata) projections of the bone margins. More complex joints involve both interlocking and overlapping of edges, the sutura limbosa. **False sutures** are those with opposing roughened edges, called the harmonious suture, or with overlapping bones, called the squamose suture. The harmonious suture has the extreme of perfectly plane surfaces appressed together as in the case of the midline suture of the nasals.

In some joints a plate of one bone lies between laminae of another or two other bones; this is a **schindylesis.** An example of this would be the joint between the perpendicular plate of the ethmoid and the vomers.

Gomphosis is the term for the joint between the peg-like roots of the teeth and the walls of the sockets into which they fit.

Many of the skull joints undergo fusion during the developmental process and disappear (by synostosis). In some cases the line of the old joint may remain; in other cases even sections through the bone do not reveal the line of juncture. In the skulls of young animals, bones of the endo-

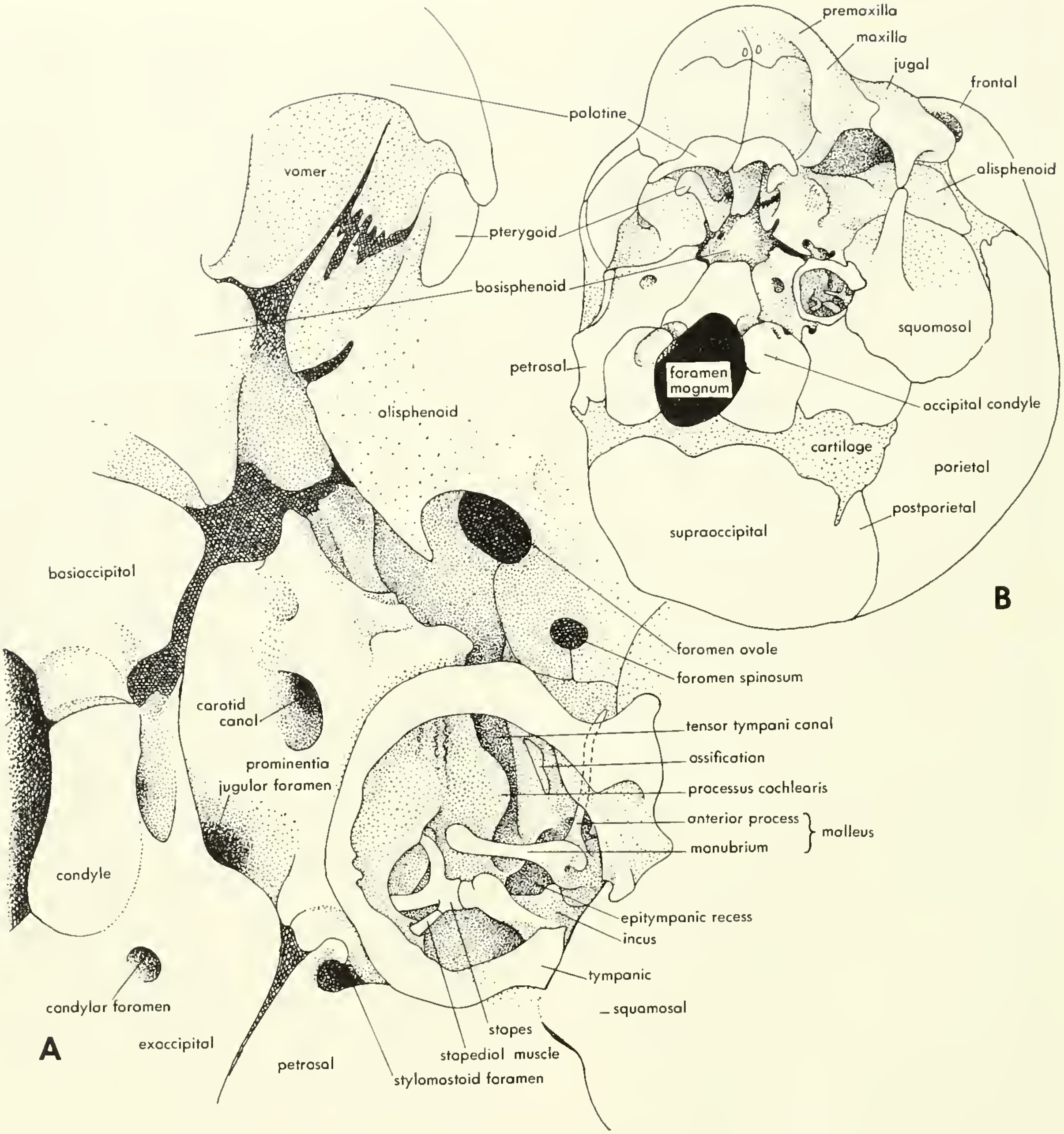


Figure 3-4. Details of tympanic region of human term foetus. B shows outline of skull for orientation of sketch A.

cranium may be joined by cartilaginous areas. This type of union is identified by the term **synchondrosis.** Such a union is usually only a developmental condition; in lower vertebrates it frequently occurs in adults. Also during the developmental period dermal bones may be separated by large connective tissue gaps or **fontanelles.**

One kind of amphiarthrosis is the **symphysis** between the rami of the lower jaw in lower forms. In some mammals this joint has become a true suture, and in others (man) fusion or ankylosis (synostosis) has taken place. Another kind of amphiarthrosis is **syndesmosis;** that is, many bones are joined by ligaments but do not freely articulate.

Movable joints, or diarthroses, are found in the head. One example is the articulation of the mandible with the squamosal. Here are two smooth, cartilage-covered articular surfaces, one a ball and the other socket-like; there is also a fluid-filled synovial sac associated with the functioning of this joint.

General observations The detailed picture of the mammal skull that has been presented indicates that there is a general pattern of bones in spite of many distracting minor variations. A review of the Metatheria (or Marsupialia) and the Prototheria (or Monotremata) as contrasted with the Eutheria (or Placentalia) will serve both to clarify the pattern and to introduce the nonmammalian type.

Head skeleton of the marsupial

The opossum is a readily available example of the marsupials and a good one since it is considered to be one of the least specialized (or altered) members of the group. At first glance the skull resembles that of a carnivore (Figure 3-5). The **premaxilla** has five incisors, and the **maxilla** has a large diastema followed by a large canine, three premolar, and four molar teeth (formula: I $\frac{5}{4}$, C $\frac{1}{1}$, P $\frac{3}{3}$, M $\frac{4}{4}$). The secondary palate has two large fenestrae on either side of the midline and the posterior margin of the palatine has a transverse ridge on it. The **pterygoids** are prominent (usually lost in prepared skulls) and they are not fused to the alisphenoid. In the young animal a small splint of bone lies along the midline spanning the basisphenoid-basioccipital joint. This is the **parasphenoid** (Figure 3-6).

The **alisphenoid** is large and has a lateral process, which contributes to the glenoid articular area (or fossa) for the lower jaw. There is a large **jugal,** whose posterior end also contributes to the glenoid fossa. There is only a small "bulla," formed by the alisphenoid; the bulla does not conceal the petrosal. The tympanic fits into the opening of this bulla but is not fused to any of the surrounding bones. The anterior process of the **malleus** (the prearticular bone) is long and overlaps the tympanic, but it is not fused with that

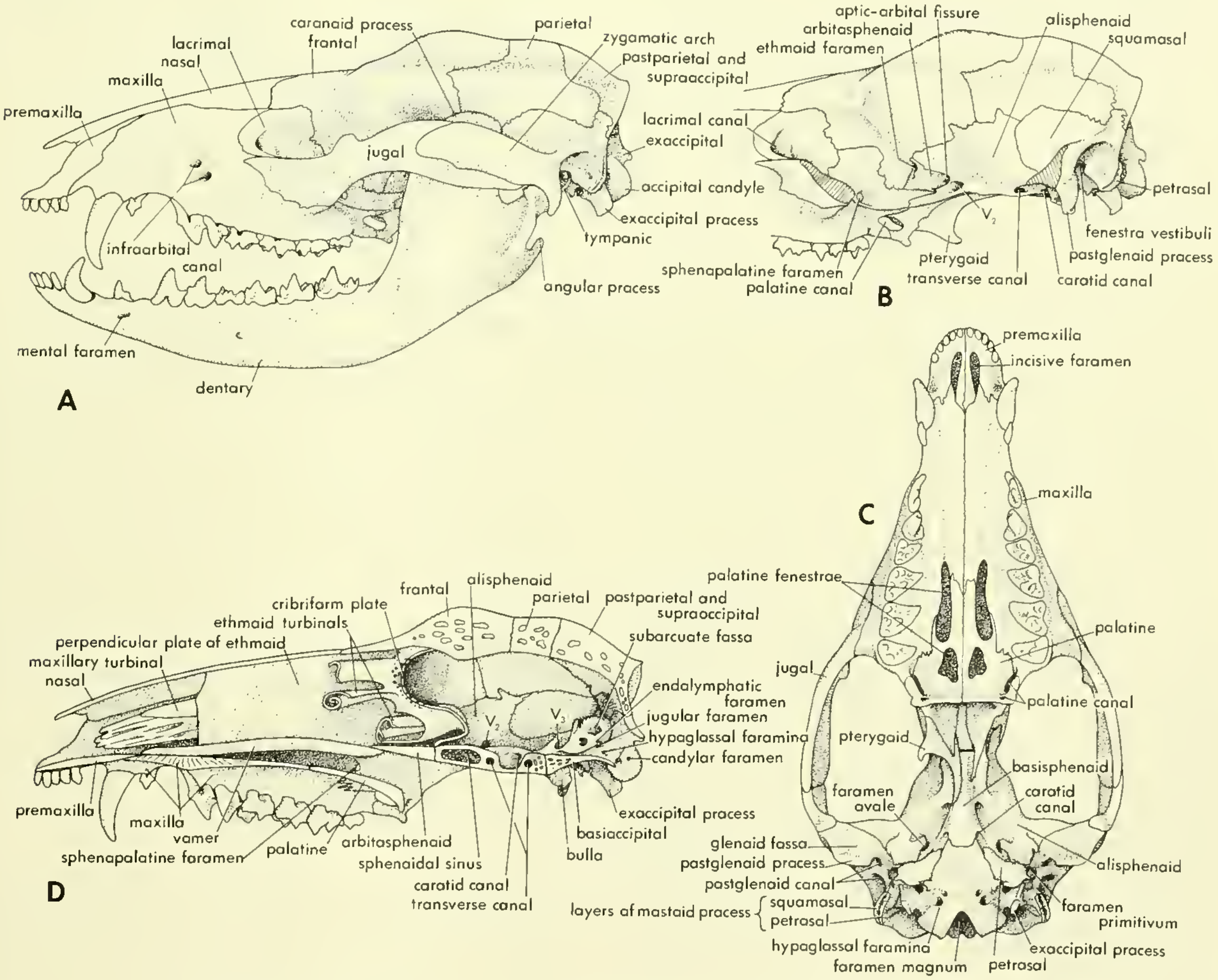


Figure 3-5. Skull and mandible of the opossum. A, lateral view; B, lateral view of cranium with zygomatic arch cut away; C, ventral view of skull; D, medial view of right half of skull.

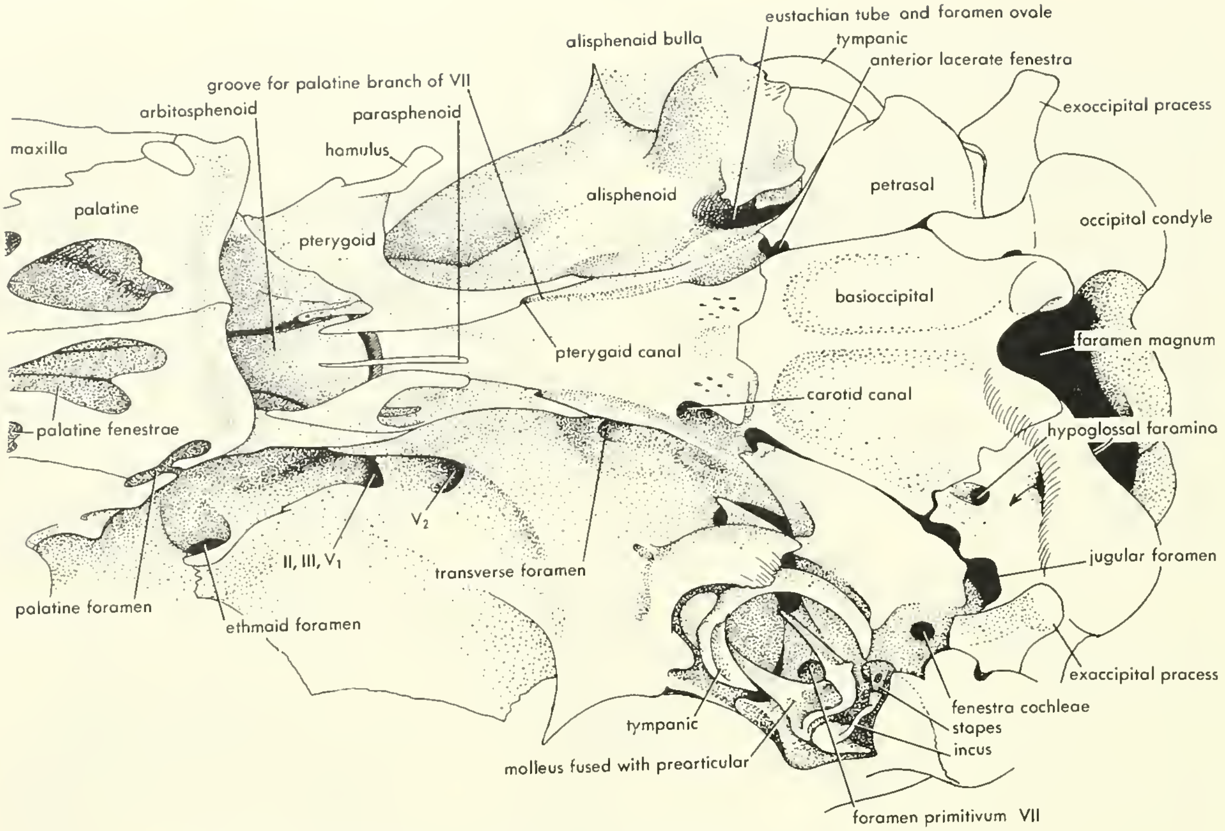


Figure 3-6. Details of base of the skull of a half-grown opossum as seen in a ventrolateral view (ventral aspect up).

bone. The **occipital bones** differ in that the **exoccipitals** meet broadly above the foramen magnum. A **postparietal** is usually lacking in marsupials; in the opossum, however, it is present and is fused with the **supraoccipital.** The cranial capsule is relatively smaller, less rounded, and is roofed by the frontals and parietals, which meet along the midline as a sharp sagittal crest. The **nasals** are narrow anteriorly and much expanded posteriorly.

Internally (Figure 3-5 C,D) the cranial cavity is relatively smaller, lacking a **tentorium** and lacking a plate-like dorsum sellae. The **clinoid processes** connect from front to back on either side of the sellar depression. There is a large **perpendicular plate** of the **ethmoid** fitting into the notch of the **vomers.** As in the placentals, the **turbinals** are ossified, and, the internal foramina of the petrosal are the same. There are no frontal or maxillary sinuses.

The **mandible** is not unusual, except that the **angular process** is medially rather than posteriorly directed. The **hyoid** (Figure 3-11 A) is much like that of the rabbit. There is a pair of small plate-like hypohyals, each tapering laterally to a point at the attachment of the stylohyoid ligament. The hypohyals articulate with a thick body, or copula, which in turn articulates posterolaterally with a large ceratobranchial 1.

The head skeleton of the opossum differs markedly from those placentals we have examined, but when compared with others, especially the insectivores, it is found to represent only an extreme. The marsupial head skeleton is best characterized as having an unequal number of incisors above as compared with below, as having the jugal contributing to the articular area of the mandible, and as having a basically alisphenoid bulla (a posterior chamber from the petrosal may be added). The fenestrated palate, a confluent optic-orbital fissure, and the lack of a postparietal (the opossum is exceptional in having this bone) are typical but not absolutely distinctive. The appearance of a parasphenoid rudiment in the young is matched in several placentals (camel, flying lemur).

Head skeleton of the monotreme

The monotreme head skeleton can rarely be studied from actual specimens but is worth describing and illustrating. Of the three living genera found in Australia and New Guinea, two can be compared as representatives of the group: the Duck-billed Platypus, *Ornithorhynchus*, and the Spiny Anteater (or Echidna), *Tachyglossus.* The exact details of the structure and development of the head skeletons of these two egg-laying mammals are not clearly understood, but a provisional account can be given. From their general form and from the fusion of the bones throughout their skulls, it can be assumed that these head skeletons will reflect many specializations. Because of the fusion of parts, their anatomy must be studied from pouch or nest young.

***Ornithorhynchus*, the Platypus** The bill is made up of nasals, **maxilla**, and **premaxilla** (Figure 3-7). The latter is

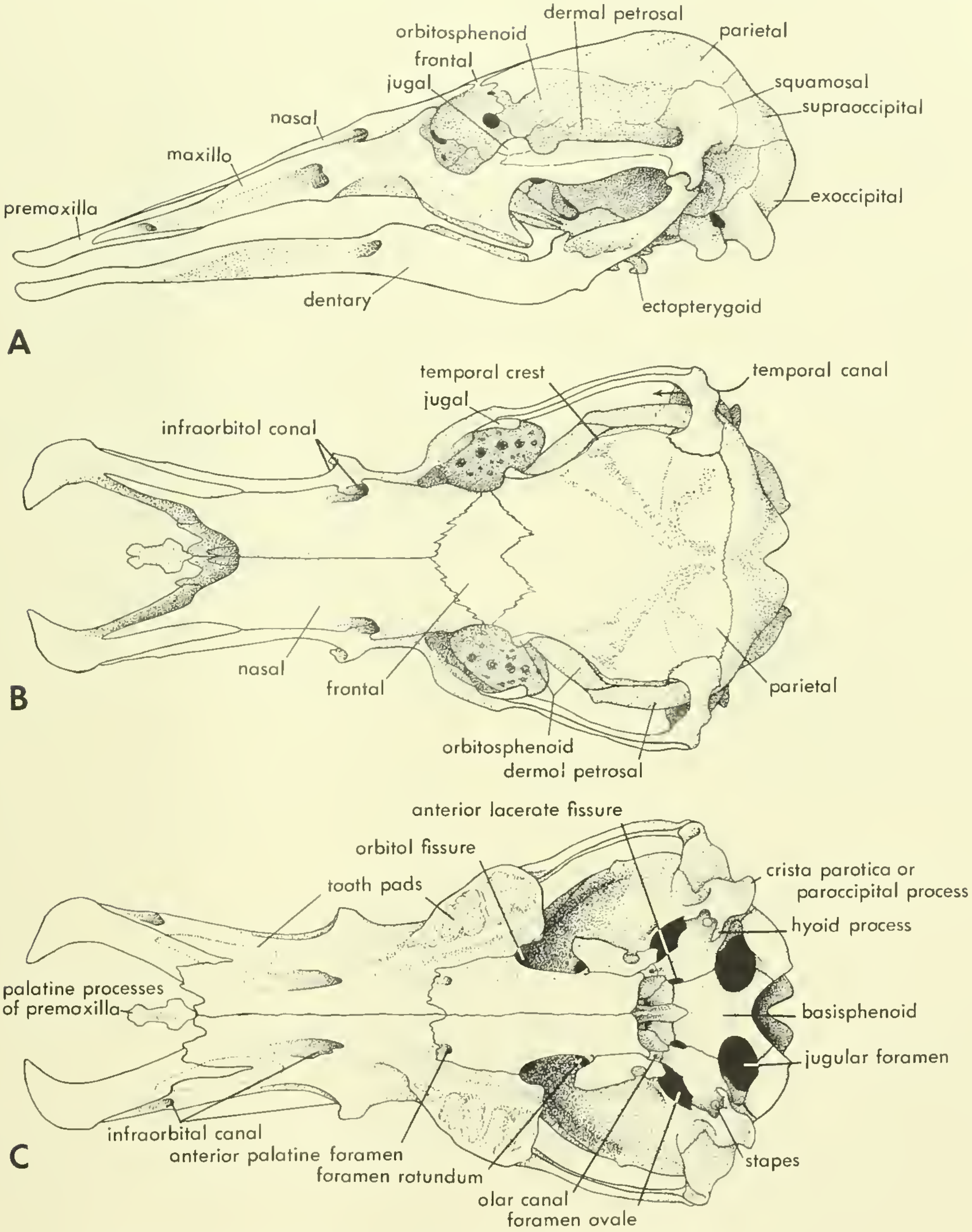


Figure 3-7. Skull and mandible of the Platypus (*Ornithorhynchus*). A, lateral view of skull and mandible; B, dorsal view of skull; C, ventral view of skull.

subdivided into dorsal, ventral, and palatine process parts. In the young there are teeth on the maxilla and premaxilla, but in the adult only horny tooth pads mark the positions of these teeth. Of interest is the fact that the **prenasal processes** of the premaxillae, which meet at the midline between the external nares, bear an **egg tooth** for cutting the shell at the time of hatching. Tooth and processes then disappear.

The secondary palate involves the maxilla and **palatine** and extends far back into the mouth. The maxilla has a strong **zygomatic process,** which overlaps for a considerable part of its length the process of the **squamosal.** The **jugal** is reduced to a small bit of bone, which forms the postorbital process of the zygomatic arch of the adult when fusion obliterates the sutures. The **frontals** are very small and extend well down into the **orbit.** There is no **lacrimal;** the **lacrimal canal** opens between the frontal and the maxilla. The palatine extends up into the orbit to meet the frontal. Behind the frontal there is a large parietal forming the roof of most of the cranial cavity. The posterior aspect of the cranium is covered by the four occipitals.

The lateral aspect of the capsule is covered in part by the squamosal, which has a dorsal and a ventral wing between which passes the temporal canal. This canal opens posteriorly as the posttemporal fossa and anteriorly into the temporal fossa. The ventral wing of the squamosal forms the **glenoid articular area** for the mandible. The squamosal has a strong **zygomatic process.**

Medial to the squamosal and forming much of the wall of the brain capsule is a **dermal plate,** fused with (and in development appearing to grow out from) the **petrosal.** The petrosal has a posterior mastoid part, with a strong ventral **mastoid process,** and a ventral vestibular part. The latter contacts the **basioccipital** medially and the **basisphenoid** anteromedially. On either side of the nasal passage, the basisphenoid has a strong downgrowth, which sutures ventrally with the palatine portion of the secondary palate. This **basipterygoid** extension is usually described as the "alisphenoid," but such an identification seems to be based more on the feeling that it is necessary to have this characteristic mammalian bone in the monotreme than upon its form or embryological development. This case brings up the question of how far homologies can be carried. It seems best to abandon use of alisphenoid, whose dermal component has already been described as forming a part of the petrosal.

The **pterygoid** lies inside of the ventral extension, the **basipterygoid process,** of the basisphenoid. It is exposed in the orbit, above the palatine and anterior to this process, where it forms the lateral wall of the choanal passage. On the midline and separating the right and left nasal passages is the nearly vertical plate of the ventrally fused **vomers.** The vomers are exposed posteriorly, where they extend back to slightly overlap the basioccipital.

At the posterior end of the secondary palate and extending out horizontally to either side is a plate of bone that remains free in the adult skull and is usually lost in preparation. The exact nature of this plate is not clear, but it is here identified as **ectopterygoid.**

Between the pterygoids, and anterior to the basisphenoid, is the midline fused mass of the **orbitosphenoids.** It extends upward and backward on either side as a large cranial-wall wing.

The **tympanic bone** is a semi-ring lying horizontally in the floor of the tympanic cavity. It is fused to the anterior process of the **malleus,** and this is fused or tightly bound to the **incus.** The **stapes** is **columelliform** (not penetrated by a stapedial foramen) with a round foot plate fitted into the **fenestra vestibuli.**

An internal view of a half skull cut on the median sagittal plane (Figure 3-8 D) is comparable to what we have seen in the placental, but the turbinals are quite small. There is a small perpendicular plate of the ethmoid fused to the anterodorsal end of the orbitosphenoid. The transverse ethmoid ossification is perforated to either side by an olfactory foramen but is not cribriform.

The dorsum sellae has strong posterior clinoid processes extending forward on either side of the sella. There is no tentorium but there is a midline sagittal ossification in the **falx cerebrae,** the connective tissue sheet extending down from the cranial roof between the cerebral lobes of the brain. There is a large subarcuate fossa.

The mandible is highly specialized and has large posterior fossae on the outer and inner surfaces behind external and internal processes. The latter can be compared with the angular process. There is a large mandibular foramen on the inner aspect and a large foramen on the outer surface at the vertical of the anterior margin of the horny tooth plates. The anterior end is flattened dorsoventrally with a large foramen and distal groove on its upper surface and a somewhat more distal but corresponding foramen and groove on the lower surface. The two rami of the mandible are joined well back from their spatulate tips.

The hyoid appartus (Figure 3-11 B,C) is like that of the dog or cat, differing in that the hyoid arch has two ossified segments, the hypohyal and ceratohyal. The body is a transverse piece to which a fairly large ceratobranchial I is attached. This ceratobranchial is closely bound to the margin of the thyroid cartilage. Behind the ceratobranchial I is a pair of ossicles associated with the thyroid cartilage which represent the ceratobranchials II, and behind these another pair more closely joined to the thyroid cartilage, the ceratobranchials III.

Tachyglossus, the Echidna *Tachyglossus* has a long, toothless snout, and the **secondary palate** extends far back, the palatines ending at medial but well-separated points (Figure 3-9). These features are related to its ant-eating habit. The **palatines** bear the quite large **ectopterygoids** on their posterolateral margins.

The **pterygoids** lie along the dorsolateral wall of the

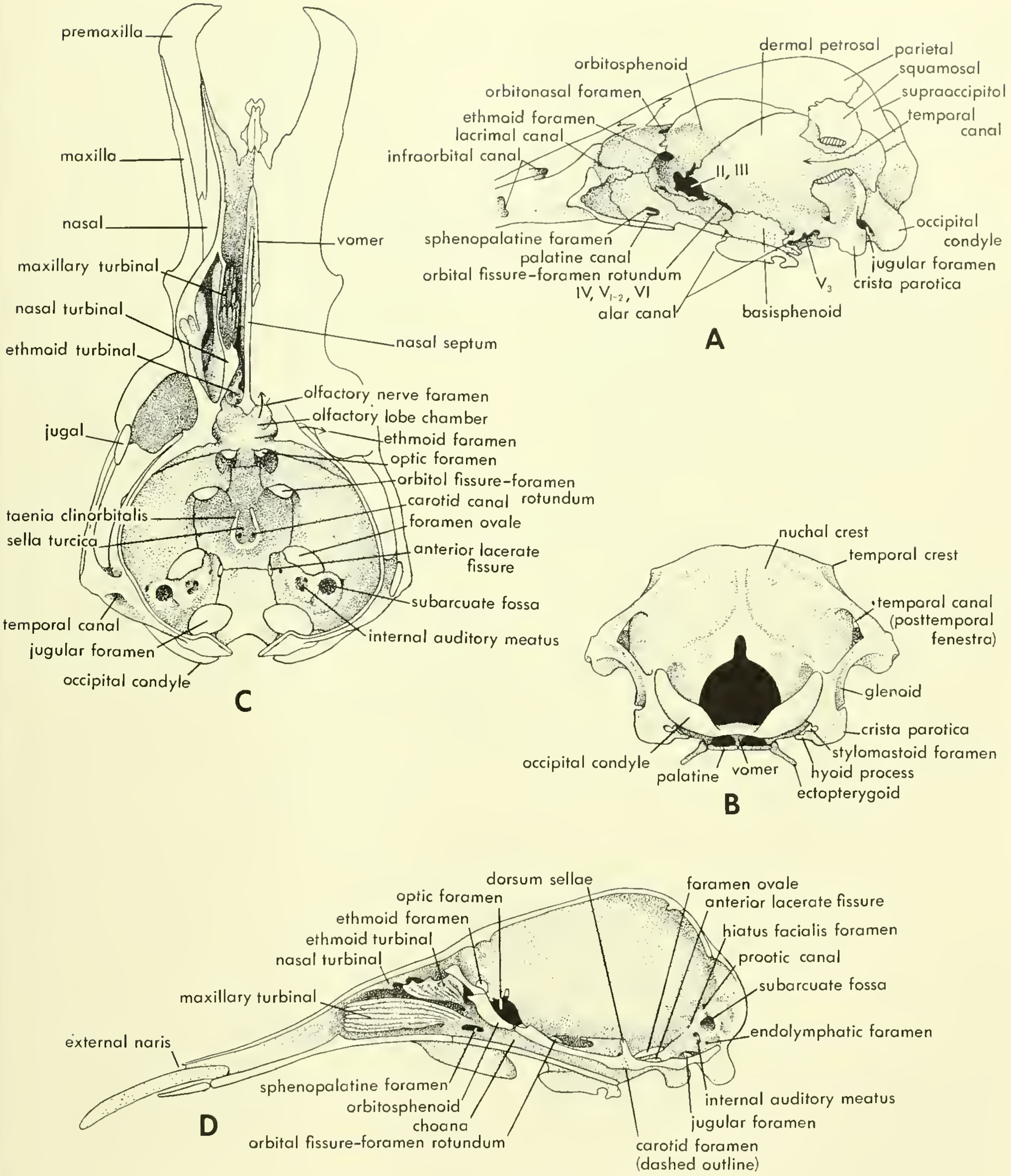


Figure 3-8. Skull and mandible of the Platypus (*Ornithorhynchus*). A, lateral view of cranium with zygomatic arch cut away; B, posterior view of cranium; C, dorsal view of skull with cranial roof removed; D, medial view of right half of skull.

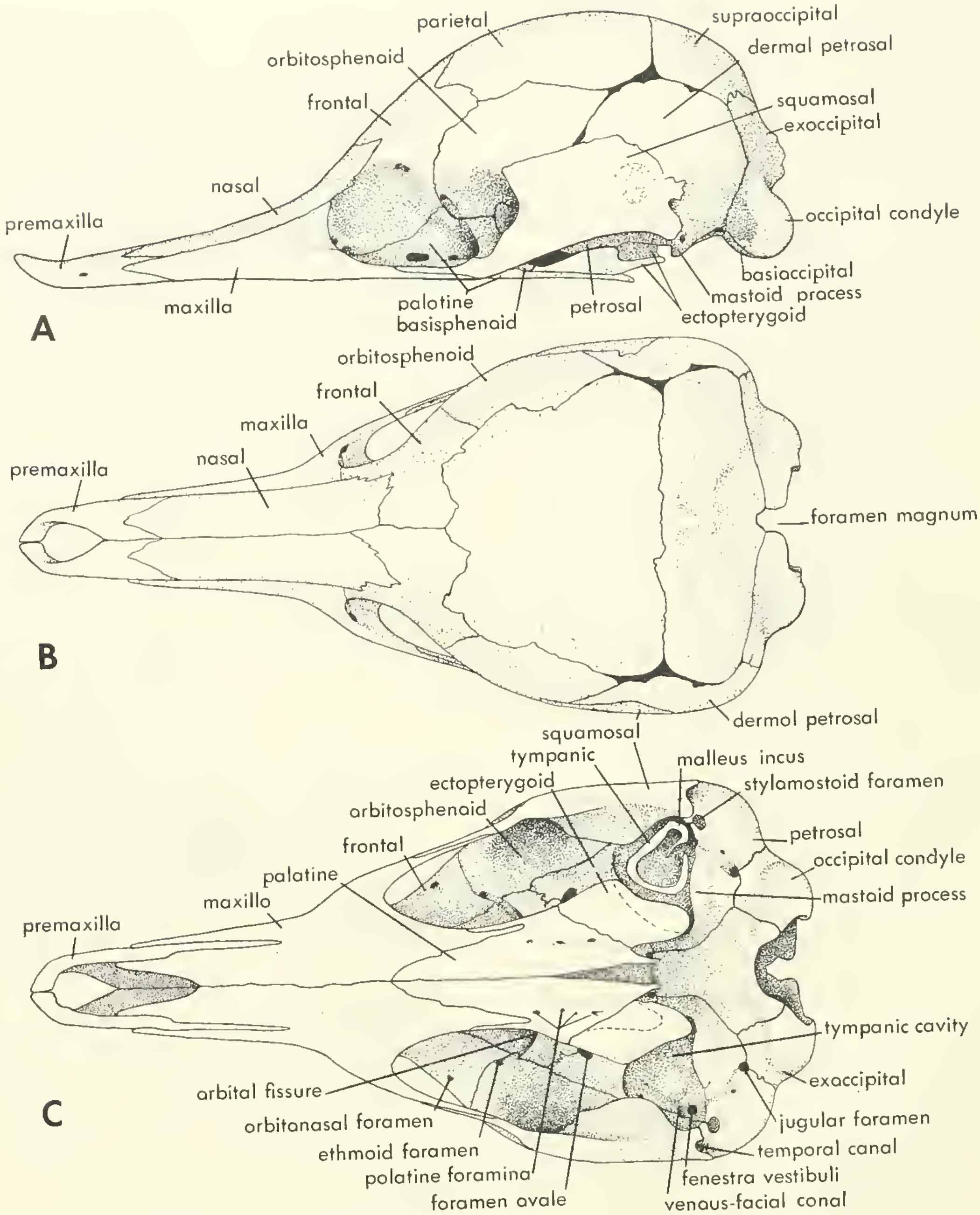


Figure 3-9. Skull of Echidna (*Tachyglossus*). A, lateral view; B, dorsal view; C, ventral view.

choanal passage from just above the sphenopalatine foramen to midway back on the ectopterygoid. Midway in their length they are fused to the **basipterygoid processes** of the **basisphenoid** and pierced by the **pterygoid** canal for the palatine (Vidian) nerve.

Separating the second quarter of the length of the nasal passages (from front to rear) are the **vomers.** The two plates are fused ventrally and diverge dorsally to enclose the ventral margin of the bony **nasal septum** (vertical plate of **ethmoid**). The vomer extends from the anterior end of the pterygoid to a point just behind the anterior end of the **palatine processes of the maxillae,** where these meet at the midline.

The palatine extends up into the orbit to meet the frontal and orbitosphenoid. This orbital extension is peculiar in that it extends backward, overlapping the **orbitosphenoid,** so that it encircles the confluent opening of the optic foramen, orbital fissure, and foramen rotundum (the **optic-orbital-round fissure**). The palatine is penetrated by a large **sphenopalatine foramen,** which acts also as the orbital portal of the **palatine canal.** This canal has several palatal openings posterior to the vertical of the orbital opening. Posterior to the sphenopalatine opening, the orbital wing is pierced by the **pterygoid canal.**

The **frontal** is small and forms much of the medial wall of the orbit. It is pierced at the upper orbit margin by an **orbitonasal foramen.** The **parietals** are large and form much of the roof of the cranium. Below the parietal is the large cranial-wall wing of the **orbitosphenoid** extending forward and down to meet and fuse with its opposite along the midline from below the **ethmoid foramen** ventroposteriorly to between the optic-orbital-round fissures.

Behind the orbitosphenoid is the large **dermal plate of the petrosal.** Between the ventroanterior margin of the petrosal, the posterior margin of the palatine, and above the anterior end of the ectopterygoid, there is a small exposure of the **basisphenoid**—again usually identified as the alisphenoid. This **basipterygoid process** extends outward and slightly downward and is not pierced by a canal. Behind this process, between the petrosal and the ectopterygoid, is a large foramen for the mandibular branch of the trigeminal nerve. This is an analog of the foramen ovale. Its position behind the basisphenoid wing is used to support the contention that the wing is a vestigial alisphenoid. It seems best to consider this process a part of the basisphenoid, identifiable as the basipterygoid process.

A long narrow **temporal canal** passes between the **temporal fossa,** inside the cover of the **squamosal,** and the small **posttemporal fossa,** which is no more than a foramen at the posterior margin of the squamosal. The squamosal lacks a distinct articular area for the mandible.

The squamosal and maxilla have long zygomatic processes, which form the zygomatic arch. There is no jugal bone. The carotid canal passes up and forward from the posterolateral angle of the basisphenoid to its foramen in the lateral wall of the sella.

The petrosal bones, at either side of the **basioccipital,** lie above a distinctly triangular **tympanic fossa.** Below the fossa lies the tympanic bone, to which is fused the anterior process of the malleus. The incus is fused to the malleus. The fossa is margined behind by a transverse **mastoid process,** laterally by the squamosal, and anteromedially by a ridge of the dermal part of the petrosal that extends to the outer margin of the ectopterygoid and then above that bone, along with a corresponding elevation of the ectopterygoid. The posterior end of the ectopterygoid is separated from the petrosal by a gap. This gap is said to transmit blood vessels; the eustachian tube passes lateral to the tip of the ectopterygoid.

The tympanic fossa opens posterolaterally through a **primitive stylomastoid foramen** between the lateral, but very small, **tympanohyal process** and the medial **mastoid process.** At the anterior end of the fossa there is an **anterior lacerate fissure** between the vestibular portion and the dermal wing of the petrosal. This fissure passes forward and upward into the cranial cavity. In the posterolateral corner of the fossa is the round **fenestra vestibuli,** into which fits the columelliform stapes. Above, lateral and anterior to this, is the common opening of the facial canal and the vena capitis lateralis canal.

The internal view of the skull (Figure 3-10 A,D) shows a cribriform plate complete with nasal septum and turbinals. The sella has well-developed lateral margins formed by the clinoid processes and a low dorsum sellae. The carotid canal opens through the lateral wall of the sella near its posterior end. The anterior lacerate fissure has its internal opening just lateral to the dorsum sellae. There is no subarcuate fossa but otherwise the foramina of the petrosal are typical. A perilymphatic foramen has not been identified but is probably present in the margin of the petrosal adjacent to the internal portal of the jugular foramen.

The mandible is highly modified; there are weak internal and external processes posteriorly. The foramina are like those of the placental.

The adult hyoid (Figure 3-11 D) appears to be like that of the platypus except that only the hypohyal is ossified in the hyoid arch.

The monotreme head skeleton is unique, as compared with those of the other mammal groups, in several features: lack of an identifiable alisphenoid and replacement of this bone by a dermal wing of the petrosal, presence of both a pterygoid and ectopterygoid which do not lie in contact, the position of the pterygoid in the dorsolateral wall of the nasal passage, the presence of a temporal canal passing between the cranial wall and the squamosal, the squamosal not forming part of the cranial wall, the absence of a jugal, and the presence of ceratobranchials II and III.

In addition to these characteristics there are other minor features, such as lack of defined incisive foramina (or palatal processes of the premaxillae), and the presence of external and internal processes on the mandible.

On the whole the features of this type of head skeleton, along with its lack of teeth, the modification of the snout, and extension of the secondary palate far back, suggest specialization more than retention of primitive features. The lack of a bulla and the passage of the vena capitis lateralis through the tympanic fossa are primitive.

DEVELOPMENT OF THE HEAD SKELETON

Chondrocranium

The chondrocranium can be defined as the cartilaginous forerunner of the adult endocranium (enclosing the brain, inner ear, and nasal passages and forming the socket for the eye) and of the visceral skeleton. It varies in form as it changes its function at different ages of the animal. In the

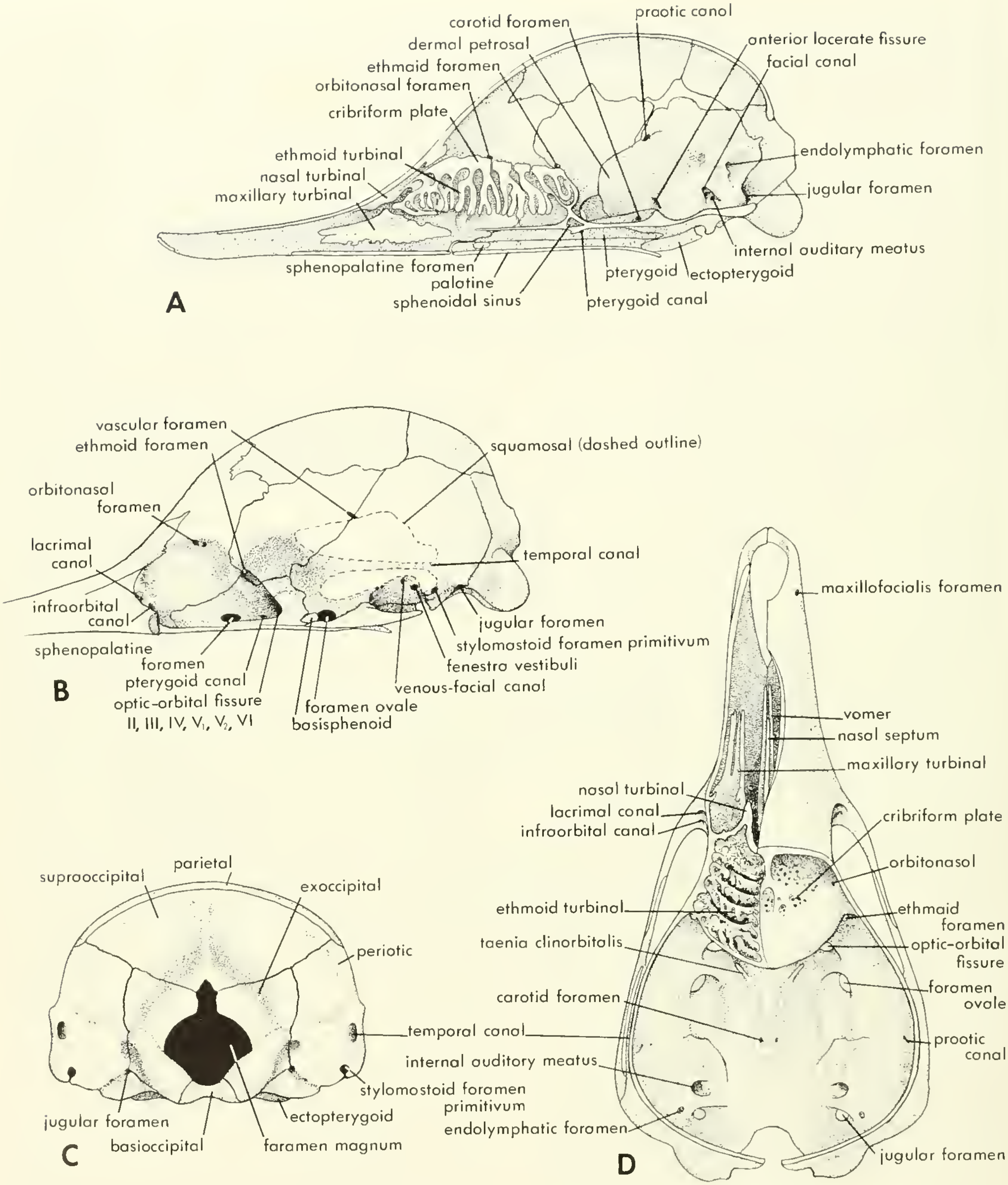


Figure 3-10. Skull of Echidna (*Tachyglossus*). A, medial view of right half of skull; B, lateral view of cranium with the zygomatic arch cut away; C, rear view of skull; D, dorsal view with roof of cranium and roof of nasal passage on left side removed.

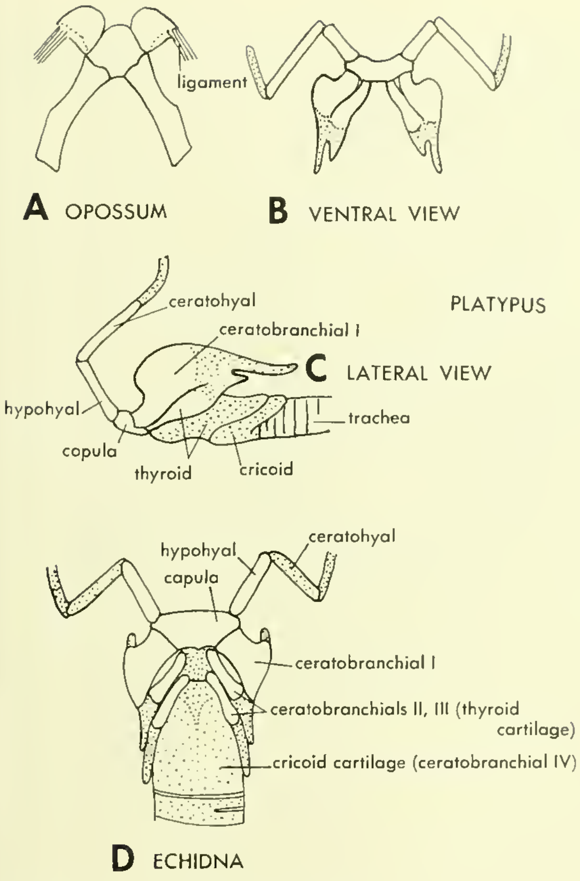


Figure 3-11. Hyoid apparatus of a marsupial and the monotremes. A, opossum; B and C, Platypus; D, Echidna.

adult it is largely replaced by endochondral bone, and in the embryo it may be represented by several separate chondrification (cartilage forming) centers. First, the fully formed chondrocranium, at the time of the beginning of ossification of the chondral bones, will be described, then its origin and development.

The chondrocranial skeleton of man, cat, and the rabbit, as representative placentals, will be described. The terminology is extremely complex but can be simplified.

Placental mammals The fully formed chondrocranium of man (Figure 3-12) underlies the brain and encloses the nasal passages and the inner ear. The **otic capsules,** enclosing the inner ear, are perhaps the most apparent structures. These lie to either side above and forward to the large **foramen magnum.** There is a large **internal auditory meatus,** a deep **subarcuate fossa,** and a small **endolymphatic foramen,** as already described for the bony ear capsule. Below the posterior part of the internal meatus, on the ventral inner aspect of the capsule, is a small **perilymphatic fenestra.** The otic capsule consists of a large **cochlear portion** anteroventrally, an intermediate **vestibular part,** and a dorsoposterior **canalicular region.**

The otic capsules are connected by the **basal plate** in front of (below) the foramen magnum and behind (or above) by the **occipital arch** and **tectum posterior.** Above and behind the capsules are the **parietal plates.** Behind the otic capsules are a line of foramina. In the occipital arch, next to the foramen magnum, is the **hypoglossal** foramen, through which the two roots of that nerve pass. Lateral to the hypoglossal foramen is the **jugular foramen,** marking the ventroanterior margin of the **metotic fissure,** which in less developed chondrocrania separates the occipital arch from the otic capsule. Above and behind these foramina is the **occipitocapsular fissure** and above this a **mastoid foramen,** a remnant of the **parietocapsular fissure.**

Laterally the otic capsule projects around the dorsal and posterior margins of the **tympanic fossa** as a **paroccipital process.** An anterior extension from this paroccipital process of the capsule is called the tegmen tympani ("roof of the ear cavity"). The outer opening of the facial canal lies medial to the tegmen tympani, which in the course of further development extends forward and medially to form the lateral prefacial commissure dividing this outer opening into an upper hiatus facialis and a lower foramen primitivum. The tegmen forms the outer wall of the facial sulcus of the ossified petrosal mass. The prefacial commissure is the area of cartilage lying dorsal to the facial canal between the inner portal of that canal and the **hiatus facialis.**

Below the tegmen tympani lies the **fenestra vestibuli** (fenestra ovale); into it fit the cartilaginous stapes, and below this, at an early stage, is the **fenestra perilymphaticus.** During the course of development, the fenestra perilymphaticus becomes subdivided by a process (**processus recessus**) into an outer **fenestra cochleae** (fenestra rotunda) and an inner **foramen perilymphaticus.**

The hyoid arch is represented by a long strand, **Reichert's cartilage,** attached to the posterior margin of the tympanic fossa just anterolateral to the notch of the **primitive stylomastoid foramen** of the facial nerve canal.

The basal plate, lying between the otic capsules, continues forward, bearing on its dorsal aspect a cartilaginous **dorsum sella** and in front of this a hollow for the pituitary gland, the **sella turcica.** To either side of the sella area is a ventrolateral projection, the **basitrabecular process,** or the **processus alaris;** to the tip of this is fused (or closely bound) the laterally projecting **ala temporalis,** penetrated by the **fenestra rotundum.** A posteriorly directed process from the processus alaris, the **alicochlear commissure,** extends back to fuse with the cochlear mass and thus encloses the internal carotid foramen and separates it from the rest of the **alisphenocapsular fissure,** which also gives rise to the **anterior lacerate fissure** of the bony skull. The **pterygoid cartilage** is suspended from the **lamina pterygoideus** of the ala temporalis by a mesenchyme strand. The pterygoid cartilage gives rise to the hamular part of the pterygoid bone.

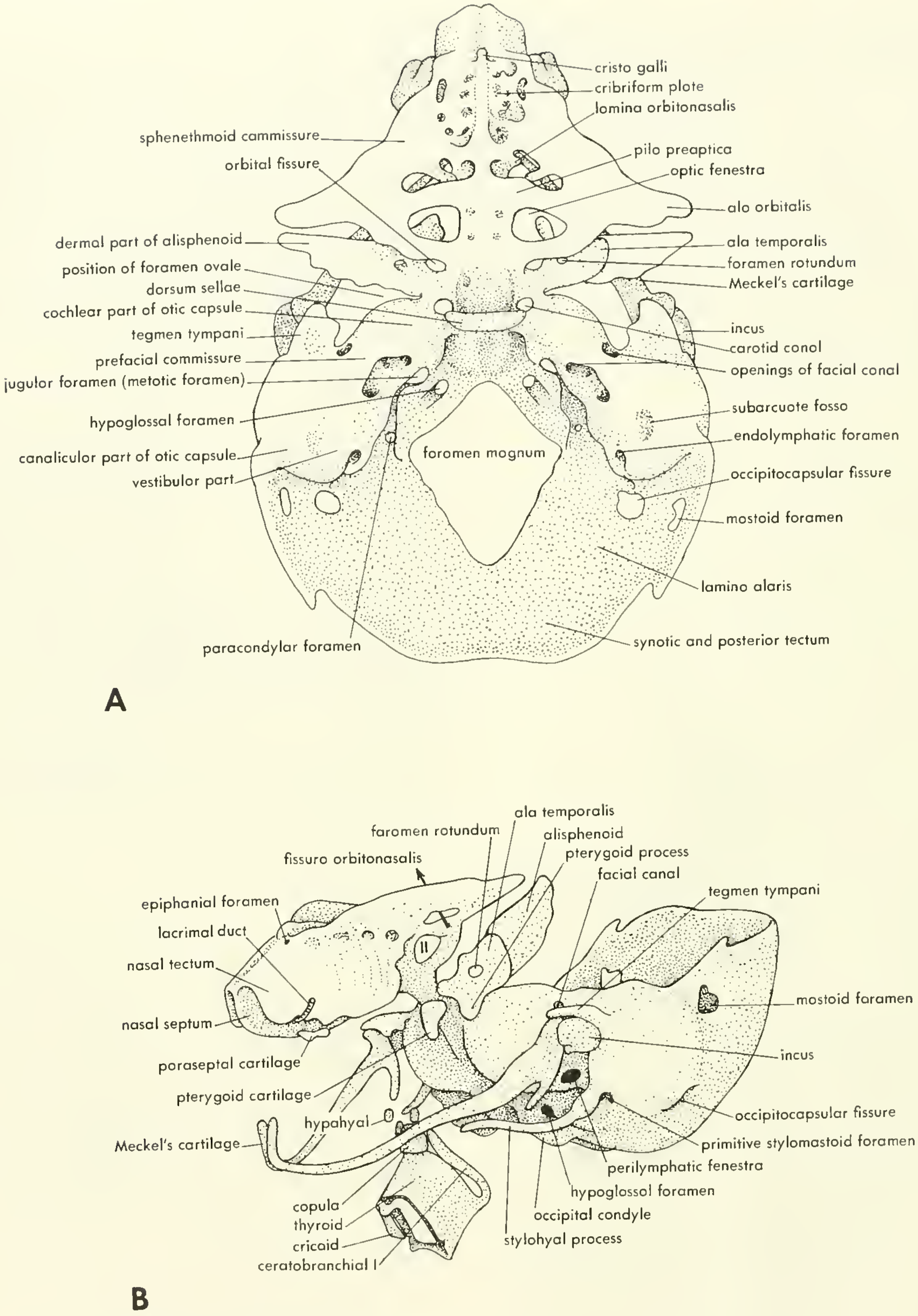


Figure 3-12. Chondrocranium of an 8-cm human foetus. A, dorsal view; B, anterolateral view. (After Hertwig, 1898)

Anterodorsal to the basitrabecular process is the **pila metoptica** ("pillar behind the optic nerve") of either side. The gap between these is the **orbital fissure.** The pila metoptica lies behind the **optic foramen** and the **pila preoptica** forms the anterior margin of that opening. Both pilae join the **ala orbitalis** or orbital wing laterally. Separating the pila preoptica from the nasal capsule is the **orbitonasal fissure;** the orbital wing is connected lateral to this fissure to the nasal capsule by the **sphenethmoid commissure.** The sphenethmoid commissure and orbital wing lie in the upper and medial walls of the orbit of the eye.

Extending upward from the **basis cranii** (cranial base), in front of the optic foramina, is a midline vertical plate of cartilage identified as the **interorbital septum.** This septum continues anteriorly as the **nasal septum.**

The nasal capsules are formed by lateral cup-like masses (**paranasal cartilages**), fused above with the dorsal margin of the nasal septum; posteriorly they contact the nasal septum but do not fuse with it. The dorsoposterior gap between these cups and the nasal septum are closed by a fenestrated, cartilaginous, **cribriform plate.** Above this rises the dorsal margin of the nasal septum, the **crista galli.** Lateral to the cribriform area is the attachment of the sphenethmoid commissure. Anterior to the end of this commissure is the **foramen epiphaniale.**

Posteroventrally there is a small connection, the **lamina transversalis posterior,** between the cup and the nasal septum. Anterior to this connection there is no contact; the **fenestra narina** is continuous with the **fenestra choanae.** The internal walls of the nasal capsules have three medially projecting shelves giving rise to the **turbinals.** Near the anterior end of the nasal septum there is a small lateral projection from the ventral margin, the **anterior transverse lamina** (lamina transversalis anterior). From the tip of it rises a backward projecting spur, the **paraseptal cartilage,** associated with the Jacobson's organ. The anterior transverse lamina does not reach the lateral wall of the capsule to complete a **zona annularis** (Figure 3-15).

The visceral skeleton is represented by several cartilaginous structures. The ala temporalis has already been described. The **quadrate cartilage** is transformed into the incus. The lower jaw is represented by **Meckel's cartilage,** which posteriorly is much expanded with a ventromedially projecting manubrial process. This posterior part gives rise to much of the malleus.

The hyoid arch consists of the cartilaginous stapes and Reichert's cartilage from the posterior margin of the paroccipital process margining the tympanic fossa, and also a body and a small nodule of ceratohyal.

The first branchial arch is represented by a large **ceratobranchial I** connected with the **thyroid cartilage.** The thyroid cartilage represents a fusion product of the **ceratobranchials II** and **III.**

The earlier stages of development of the chondrocranium reveal the origins of the various parts in terms of centers of chondrification (Figure 3-13). Cartilage is formed in a mesenchymatous blastema (condensation) and is preceded by a procartilaginous stage. Later as the cartilage grows and expands into new areas, a more direct conversion of mesenchyme cells, from the inner aspect of the enclosing perichondrium, takes place.

The first cartilages to appear are the paired **parachordals** lying at either side of the anterior end of the notochord. These develop a connection at their anterior ends, above the notochord, called the **crista transversa.** Posteriorly the parachordals are continuous with two pairs of **occipital arches,** between which pass the hypoglossal roots. The more anterior pair of these arches seems to be related to the parietal plates appearing above the otic capsules. The two arches of a side fuse for most of their distal length, isolating the hypoglossal foramen between their bases and next to the parachordal.

Lateral to the parachordals are the free **otic capsules,** and well anterior to the ends of the parachordals there is a midline **trabecula communis** (formed by fusion of paired trabeculae).

Following this stage, the otic capsules fuse with the **parietal plate,** then with the **basal plate** formed by anterior-to-posterior fusion of the parachordals above and below the notochord. Above the position of the original crista transversa an **acrochordal** chondrification appears which forms the dorsum sellae and soon fuses to the crista transversa. Anterior to the dorsum sellae, at either side of the hypophyseal

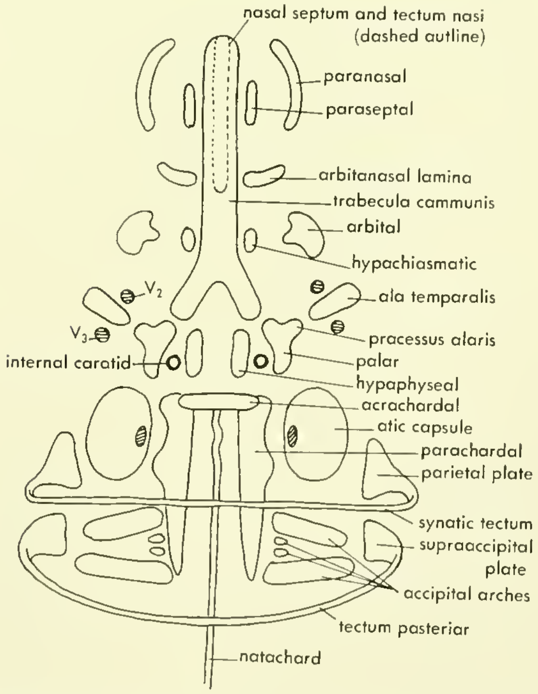


Figure 3-13. Diagram showing relative positions of the various chondrification centers.

duct (Rathke's pouch from the stomodaeum) and medial to the internal carotid arteries, are the paired, **hypophyseal cartilages** connecting with the trabecula communis anteriorly. Anterior and lateral to the internal carotid arteries are paired, **polar cartilages,** each laterally giving rise to a processus alaris. This process extends posteriorly, lateral to the internal carotid artery, to form the **alicochlear commissure** with the capsule. This commissure later breaks down. The polar cartilages fuse with the trabecula anteriorly and with the hypophyseal cartilages medially. The latter fuse medially, forming the **hypophyseal plate** and obliterating the hypophyseal foramen, and posteriorly with the basal plate. The **ala temporalis** appears lateral to the processus alaris and almost immediately attaches to its tip. This chondrification comes to enclose the maxillary branch of the trigeminal nerve, thus forming the foramen rotundum.

Further forward, lateral to the trabecula communis, an **orbital cartilage** appears dorsolateral to the optic nerve. Then a center appears ventral to the nerve, the **ala hypochiasmatica.** The orbital cartilage extends medially below the nerve to connect with the trabecula and to the ala hypochiasmatica, which also fuses medially with the trabecula. The dorsal end of the orbital cartilage extends medially and down to connect with the ala hypochiasmatica and the trabeculae completing encirclement of the optic foramen. The first (posterior) of these connections is the **pila metoptica,** the latter the **pila preoptica.**

To this point, the trabecula communis has extended forward and upward as the **interorbital** and **nasal septum.** The **paranasal cartilages** have appeared covering the lateral and posterior aspects of the nasal passages. Anteriorly the paranasal cartilages fuse with the dorsal margin of the nasal septum. The paraseptal cartilages have appeared and established contact with the nasal septum through the anterior transverse laminae. The final steps include formation of the cribriform plate by medially directed strands from the nasal capsule margin and the tips of the occipital arches meeting behind or above the spinal cord to form the **tectum posterior** enclosing the foramen magnum.

The chondrocranium of the cat is much like that of man, differing only in details. Bilateral supraoccipital plates arise, separated from the rest of the occipital arch, and join the arch to the otic capsules. The tectum posterior is a connecting growth between the supraoccipital plates. Above the otic capsule a separate parietal plate arises and extends forward as the orbitoparietal commissure connecting with the orbital cartilage. The ala temporalis arises well before the appearance of the processus alaris and does not fuse with that structure when they come in contact. The hypophyseal cartilages appear as a single crescentic mass behind the hypophyseal duct. The polar cartilages are indistinct, arising in contact with the hypophyseal cartilage and primarily forming the alicochlear commissures. The dorsal margin of the nasal septum is extended laterally as the tectum nasi; its margin is indicated by the epiphaniale foramen. The orbitonasal lamina of the nasal capsule arises separately, later fusing with the paranasal cartilage and with the midline septum just posterior to the cribriform area. The crista galli is inconspicuous.

The definitive chondrocranium of the cat shows certain differences which can be summarized as follows: (1) A posterior **basicochlear fissure** is present between the otic capsule and the basis cranii, anterior to the jugular foramen. (2) There is a large parietocapsular fissure in place of the small mastoid foramen. (3) There are large parietal plates connected with the otic capsules in front of the parietocapsular fissure (or fissures), the supraoccipital cartilage behind and the orbital cartilage in front. (4) The lamina orbitonasalis is fused with the interorbital septum and connected by a commissure with the pila preoptica. (5) Two pairs of epiphaniale foramina are present. (6) Anterior and posterior transverse laminae connectives join the nasal septum and the lateral capsular wall in front of and behind the fenestra choanae. (7) The paraseptal cartilages are connected to the posterior transverse laminae rather than to the anterior one.

The rabbit differs (Figure 3-14) from the cat in that it lacks a zona annularis; the anterior transverse lamina does not extend across from the paraseptal cartilage to the nasal septum; the paraseptal cartilages are joined anteriorly and posteriorly to the incomplete transverse laminae. In the cat the paraseptal cartilages are joined to the medially incomplete posterior transverse lamina and are free anteriorly. The cat has a posterior basicochlear fissure rather than an anterior basicochlear fissure characteristic of the rabbit, which has an occipitocapsular fissure, lacking in the cat. The cat has a single hypoglossal foramen through which pass three roots, whereas the rabbit has two pairs of foramina. The rabbit has a larger tegmen tympani, which fuses sooner with the cochlear part of the capsule to separate the foramen primitivum from the hiatus facialis. The ala temporalis of the cat has a foramen rotundum; that of the rabbit lies between the maxillaris and mandibular roots and is penetrated by an alar canal. Meckel's cartilage of the cat is fused at the tip.

Marsupial The chondrocranium of the opossum is much like that of some of the placentals, but it differs in having a wider orbitoparietal commissure; two hypoglossal foramina; a dorsal nasal tegmen, which grows out from the dorsal margin of the nasal septem and forms an anterior cupola; a wide zona annularis, formed by the anterior transverse lamina; and a paraseptal cartilage with a parallel lateral process. It also differs in lacking a parietocapsular fissure, a tegmen tympani subdividing the outer opening of the facial canal, an ala temporalis, a pila metoptica, and a lamina transversus posterior to the nasal capsule; and in having the Meckel's cartilages fused anteriorly.

The opossum differs from other marsupials in that: A small parietocapsular foramen may be present. A cartilaginous ala temporalis is usually present which may or may not

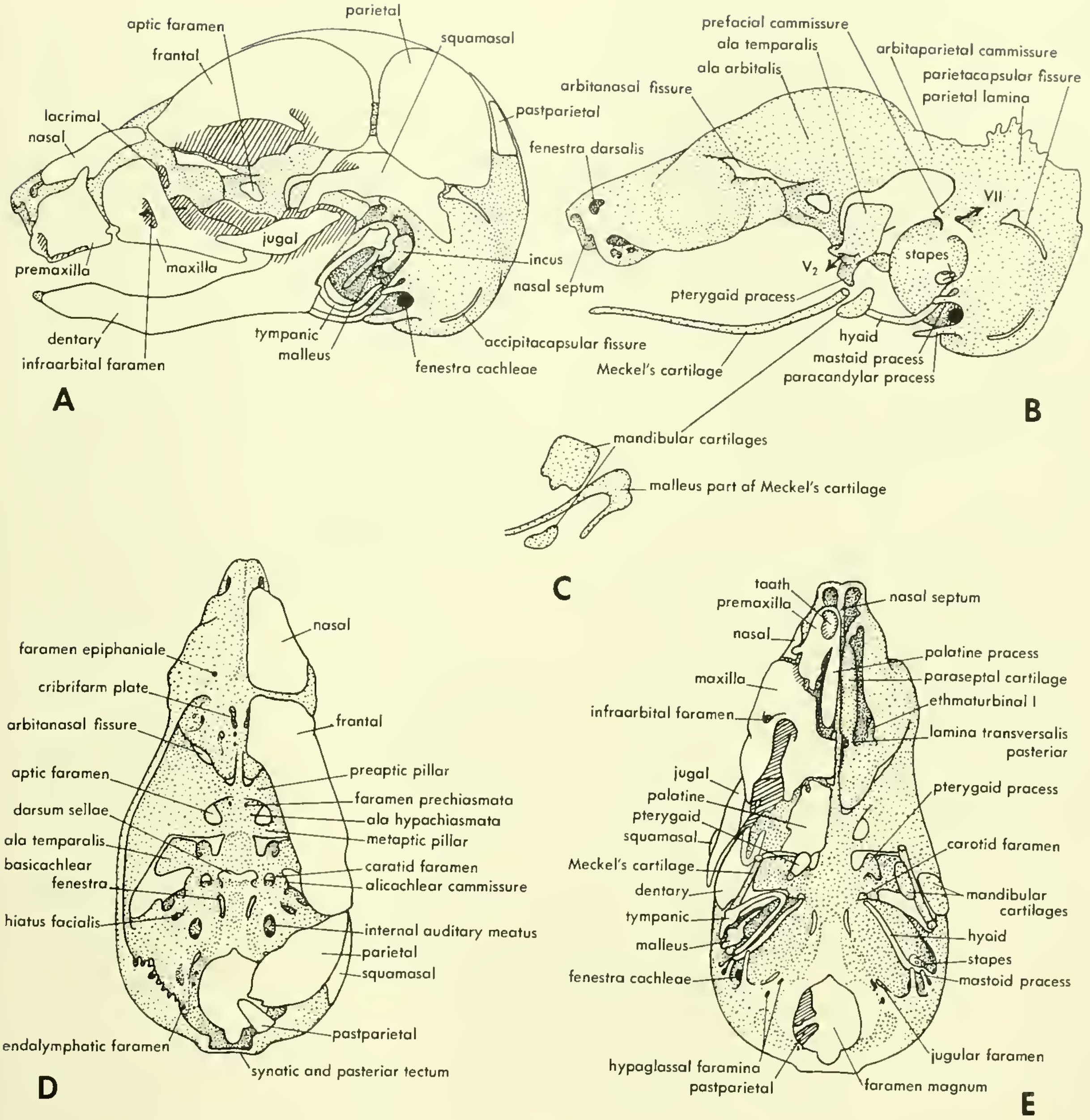


Figure 3-14. Chondrocranium and early ossifications in the hare, *Lepus cuniculus*. (After Voit, 1909)

be perforated by the maxillary branch of the trigeminal nerve (i.e. in the latter instance lying between the maxillary and mandibular branches). The posterior basicochlear fissure may be confluent with the jugular foramen as it is in some placentals. There may be three separate pairs of hypoglossal foramina. The preoptic pillar may attach to the lamina orbitonasalis through its ala minima rather than with the trabecula. The lamina transversus posterior of the nasal capsule may be present, along with the anterior lamina, and is connected with the paraseptal cartilage.

The marsupial hyoid and branchial cartilages are like those of the placental; the second and third ceratobranchial form the thyroid cartilage.

Monotreme The fully formed chondrocranium of *Ornithorhynchus* (Figure 3-15) has well-developed side walls and a broad tectum posterior, which includes a connection between the parietal plates called the synotic tectum. The occipital condyles are large and the otic capsules are completely connected with the side walls. There is no hypoglossal foramen

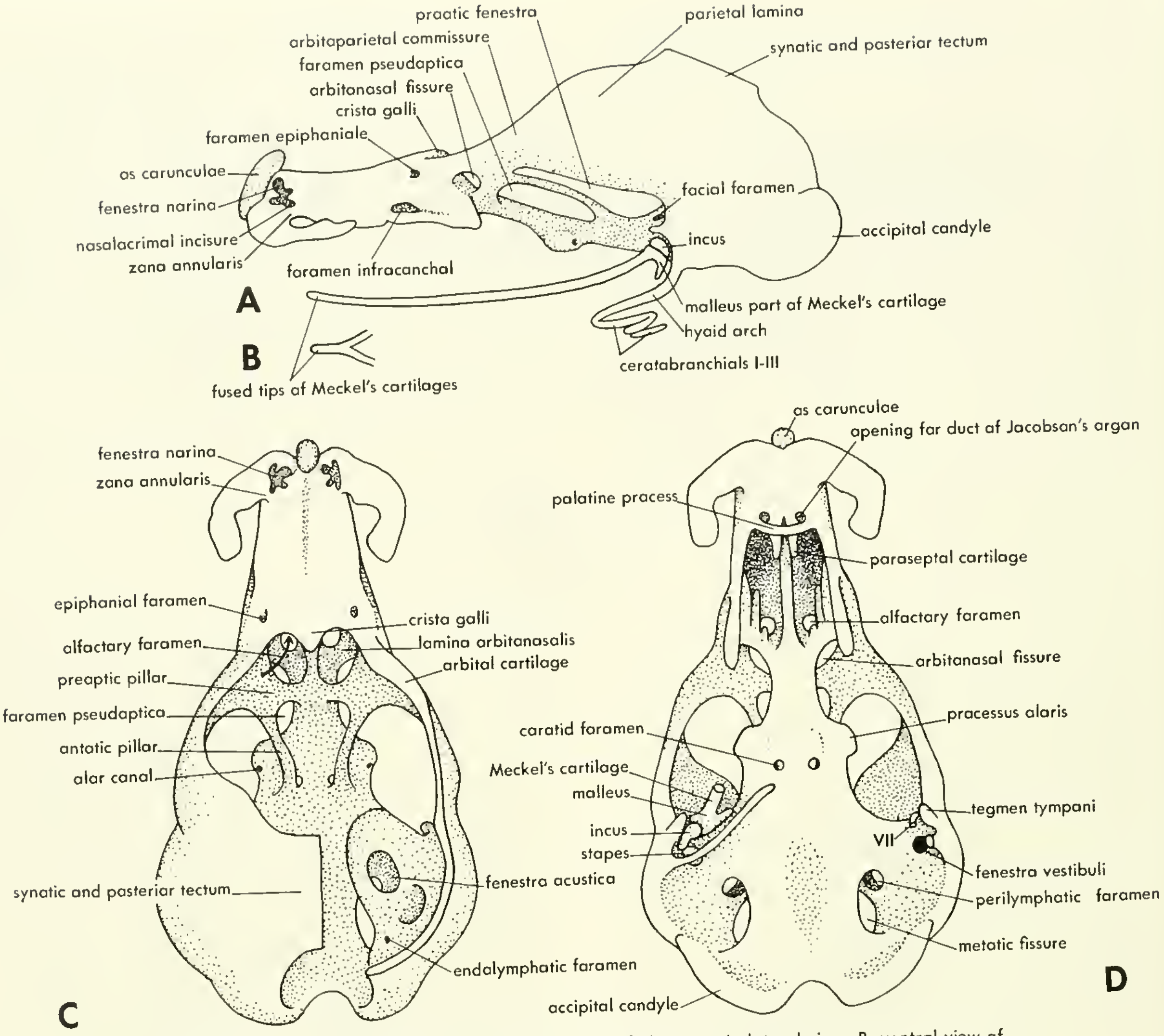


Figure 3-15. Chondrocranium of 122-mm embryo of Platypus. A, lateral view; B, ventral view of tip of Meckel's cartilage; C, dorsal view with part of cranial roof removed; D, ventral view with most of Meckel's cartilage removed. (Modified from DeBeer, 1937)

in the occipital arch; instead this foramen is confluent with the jugular foramen, into which also opens the fenestra perilymphaticus.

The paroccipital process has a small tegmen tympani and forms a lateral margin to the tympanic fossa. The hyoid attaches to this margin lateral to the fenestra vestibuli.

There is a broad orbitoparietal commissure, and from the orbital plate there is a posteroventral antotic pillar and a ventral preoptic pillar. The pila antotica attaches at the sides of the dorsum sellae. The broad preoptic pillar attaches to the trabecular stem behind a slight interorbital septum leading up and forward to a knob-like crista galli. To either side below the crista galli is a large, round olfactory foramen; a cribriform plate is not formed. The nasal capsule is solid above and laterally, except for a small foramen epiphaniale at the end of the sphenethmoid commissure of the orbital plate, and a nasolacrimal foramen on the same vertical but near the ventral margin of the lateral wall of the capsule. The hind wall of the capsule, the lamina orbitonasalis, is fused with the midline plate and lacks any flooring. Anteriorly there are paired fenestrae narinae separated by a thin and fenestrated septum. The margins of these fenestrae show dorsal and ventral processes that join and more nearly enclose the fleshy external naris. There is a broad zona annularis formed by the lamina transversus anterior between the marginal processes. The paraseptal cartilages attach to this transverse connective and extend posteriorly as vertical plates curving outward above and below the Jacobson's organ and its Stenson's duct. Anteriorly the duct is enclosed by the paraseptal cartilage opening ventrally at its anterior end. Below the paraseptal cartilages is a strap-like connective presumed to be formed from the ectochoanal processes seen in other mammals.

In its development this chondrocranium differs from those of other mammals in that there is but one pair of occipital arches involved, the most posterior one. The orbital cartilage arises as a separate center, which becomes connected with the basis cranii through the pila antotica and only later through the pila preoptica.

The polar cartilages are in fact only the posterior ends of the trabeculae, which gradually extend forward and fuse at the midline to form the trabecula communis. The processus alaris has a condensation of procartilage at its tip; this later becomes incorporated into it and the line of fusion is indicated by the alar canal. This transitory element is assumed to represent the ala temporalis, but the fact that it is never a distinct element denies this.

The anterior transverse laminae extend out from the ventral margin of the nasal septum to give rise to the marginal process. The lateral wall of the capsule then contacts the anterior transverse lamina to form the broad zona annularis. The lateral wall is penetrated by a foramen, the incisure infraconchae. This foramen is formed by ventral closure of a notch in the side wall by forward growth of the processus maxillaris anterior.

The chondrocranium of *Tachyglossus* is quite similar. In its development, the trabeculae show their bilateral origin more clearly but still fuse to form an anterior trabecula communis. The polar portions lie lateral to the internal carotids. A tectum transversum appears, temporarily joining the anterior parts of the parietal plates across the midline. Such a tectum also appears on occasion in man.

There is no evidence of an ala temporalis, and even the procartilage condensation observed in the platypus is lacking. The nasal septum arises from an independent center above the trabecula communis. Throughout the nasal region there are many separate chondrification centers. The dorsum sellae is only slightly developed.

Meckel's cartilages are the same as in the placentals; they are partially fused at the symphysis. The hyoid arch and branchial skeleton are similar to the placental's, but ceratobrachials I and II remain more distinct and are not lost in the thyroid cartilage.

In summary, the monotreme chondrocranium is well marked from that of the other mammals by the presence of a common jugulohypoglossal foramen, a pila antotica, a large olfactory fenestra, palatal processes extending posteromedially from the anterior transverse lamina, and marginal processes extending laterally; also, the lack of a pila metoptica, a recognizable ala temporalis, and a posterior transverse lamina for the nasal capsule.

Development of the bony head skeleton

Placental The first appearance of bone in the head region is followed by the progressive appearance and development of centers until the adult form is achieved. In the course of development, additional bones may appear between the typical bones. Such bones are more frequently observed along the dorsal midline, particularly in the anterior or bregmatic fontanelle between the paired frontals and parietals. Another variation is the subdivision of typical bones into two or more parts. For example, the parietals of some Australian aborigines are divided into lateral and medial parts.

The first bones to appear are the dermal bones of the jaws, then the anterior side wall of the brain case and palate, and finally the posterior brain case (Figure 3-16). The endochondral bones appear about midway in the dermal sequence, beginning with the occipitals, and ending with those of the otic and nasal capsules. The sequence of appearance shows some variation; irregular centers or subdivisions of centers can occur. Dermal bones appear first as reticula (networks) of fibers and chondral bones appear as granular masses. In section the chondral bones are observed to involve perichondral laminae and a network of endochondral fibers.

In the various placentals examined, there are some variations that should be noted. The postparietal fuses with the supraoccipital, or the parietals; it may remain distinct from both (Figures 3-1, 3-16). Two centers of origin are involved in the parietal of man, one above the other, whereas in the cat, rabbit, or rat only one center occurs. A similar situation is observed in the pig, where the exoccipital arises from two main pairs of centers. In man the supraoccipital may arise from two pairs of centers; the more lateral one has sometimes been identified as the tabular bone. The extreme of variation is observed in the petrosal mass, which shows many (three to thirteen) and sometimes irregularly positioned centers.

Two bones that present difficult situations for evaluation are the alisphenoid and the orbitosphenoid, not only because of variation in dermal ossification centers but also endochondral centers. The alisphenoid by definition arises through ossification of the ala temporalis, usually from one center, although two are observed in the cat. Associated with the chondral bone is a dermal plate derived by outgrowth from the chondral center into the mesenchyme. Extension of a chondral bone into adjacent mesenchyme occurs with other bones as well—for example, the supraoccipital of some insectivores extends beyond the cartilaginous precursor as does also the orbitosphenoid. The alisphenoid may be attached very early in its ossification to the basisphenoid (rabbit) or it may remain separate for some time (man, cat).

The orbitosphenoid is even more variable in form and origin. In the rat (Figure 3-17) there are the typical lateral (orbital wing or outer part of pila metoptica) and medial (in the trabecula or ala hypochiasmatica) centers and, in addition, a small pila preoptica center. The trabecular center appears first and fuses at the midline to form a distinct "presphenoid." Then the lateral center appears, followed

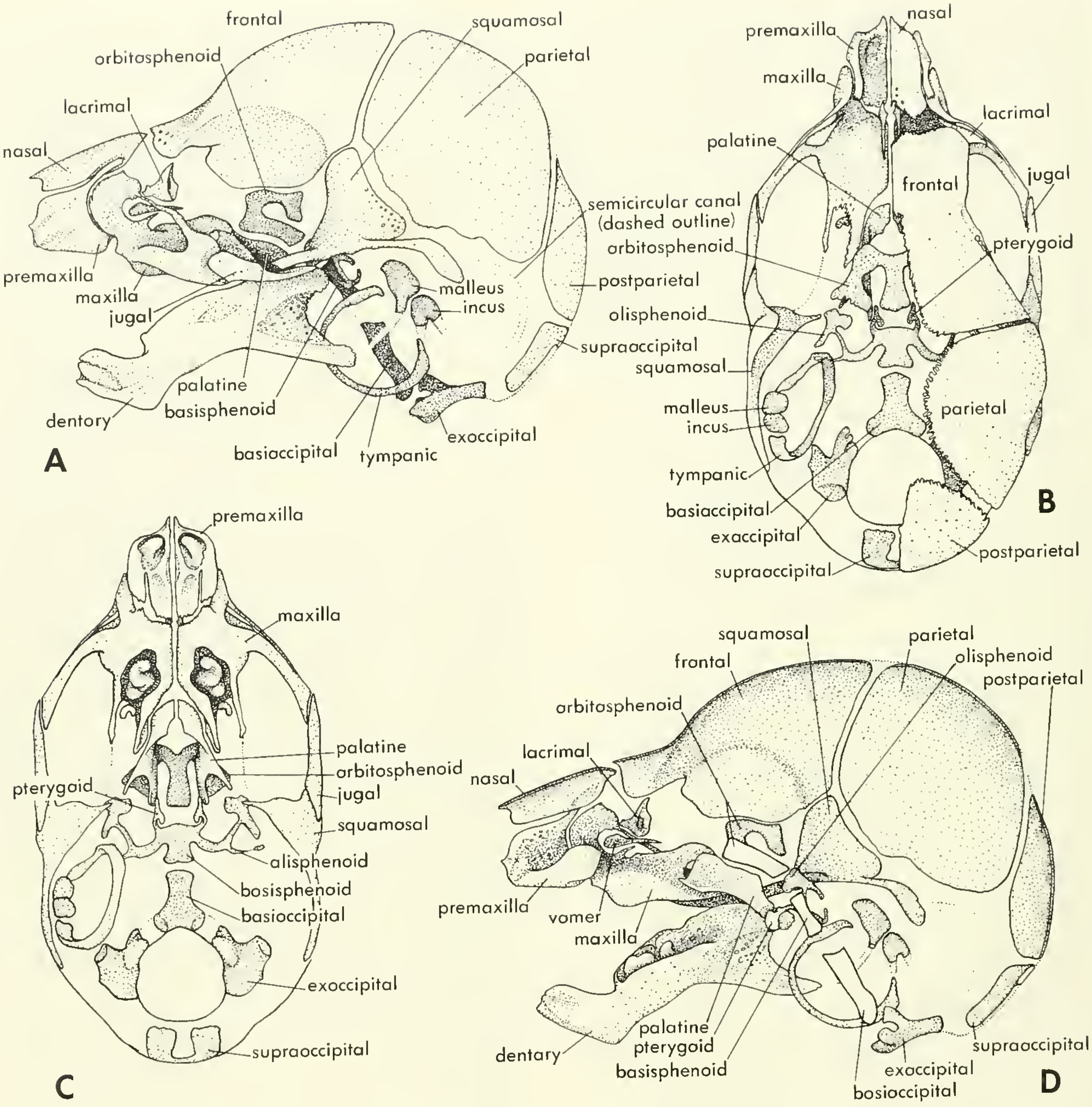


Figure 3-16. Head skeleton of 50-mm foetal rabbit. A, lateral view; B, dorsal view with roof of left side removed; C, ventral view of skull, the lower jaw removed; D, medial view of right half of head.

by the anteromedial center. A similar pattern appears to be followed by the rabbit (Figure 3-16). In man there are two or three pairs of centers enclosing the optic nerve foramen and extending medially to fuse at the midline. The third pair of centers, when present, is that in the pila preoptica. The most medial pair is identified with the term presphenoid; however, since there is never a separate bone here in even young mammals (after weening), the term is superfluous. The "presphenoid" centers are best developed in the rat (Figure 3-17). In some insectivores there is apparently only one pair of centers for this bone, and this center appears in the preoptic pillar. These centers may remain separated by the anterior part of the basisphenoid or join across the midline. There is some dermal extension of these centers in forming the definitive bone.

The alisphenoids, orbitosphenoids, and pterygoids fuse with the basisphenoid in man to form the os sphenoidale.

The basipterygoid is usually represented by paired centers but sometimes there is only a single median center (many insectivores) or two pairs of centers (man). The more lateral pair of centers in man, the lingulae, appear in the alicochlear commissures.

The pterygoid is also thought to be a compound bone in its origin, having two centers, one above the other. One center encloses the pterygoid cartilage, the hamulus, and the other forms the plate connecting this process to the base of the cranium. Two pterygoid appear to be two parted in the rat and in some other mammals (flying lemur, etc.), but usually only a single ossification center is known to occur. In man or the cat, ossification begins in the dermal base of the pterygoid and spreads to the hamular process.

Ossification of the chondral parts of the ethmoid region, the interorbital septum, orbitonasal lamina, cribriform plate and crista galli, and nasal capsule is late and irregular. Separate centers appear in each of these subdivisions and eventually fuse to form a bony continuum.

The visceral skeleton presents points of interest—the ala temporalis has already been discussed as a part of the alisphenoid. The mandible is made up of the dentary only. The tympanic appears early as a semicircle of bone, and above its anterolateral free end a small dermal prearticular (or supraangular) appears which later fuses with the endochondral ossification of the posterior end of Meckel's cartilage, the malleus. In man (Figure 3-4), this anterior process is caught between the petrosal and tympanic, and the entrapped part becomes ligamentous, attaching the malleus to the tympanic wall. The incus begins to ossify after the malleus and the stapes ossifies late in development. Except for the basihyal, ossification in the hyoid is late, and there is much variation in the extent of ossification.

Marsupial Comparisons of the opossum with the placental indicates close agreement. The opossum differs in lacking an ala temporalis; the alisphenoid is entirely dermal in origin but extends outward from the tip of the processus alaris much as it would if the ala were present. This dermal anlage encloses the foramen rotundum instead of lying between that foramen and the foramen ovale. Lack of an ala temporalis is not typical of marsupials, most of which agree with the placental in having this structure. The pterygoid stems from a single center and has only a small cartilaginous, or a procartilaginous, precursor for the hamulus. The presphenoid centers of the orbitosphenoid appear first and fuse at the midline. To this, the splint-like preoptic pillar center attaches when it appears. There is no posterolateral or lateral center of ossification; the main one of most placentals, as a result the optic foramen and orbital fissure, are confluent. The nature of the pterygoid and orbitosphenoid can be matched also in placentals. A small midline spur of bone, the parasphenoid, becomes attached to the ventral aspect of the basisphenoid near its anterior margin. The usual absence of

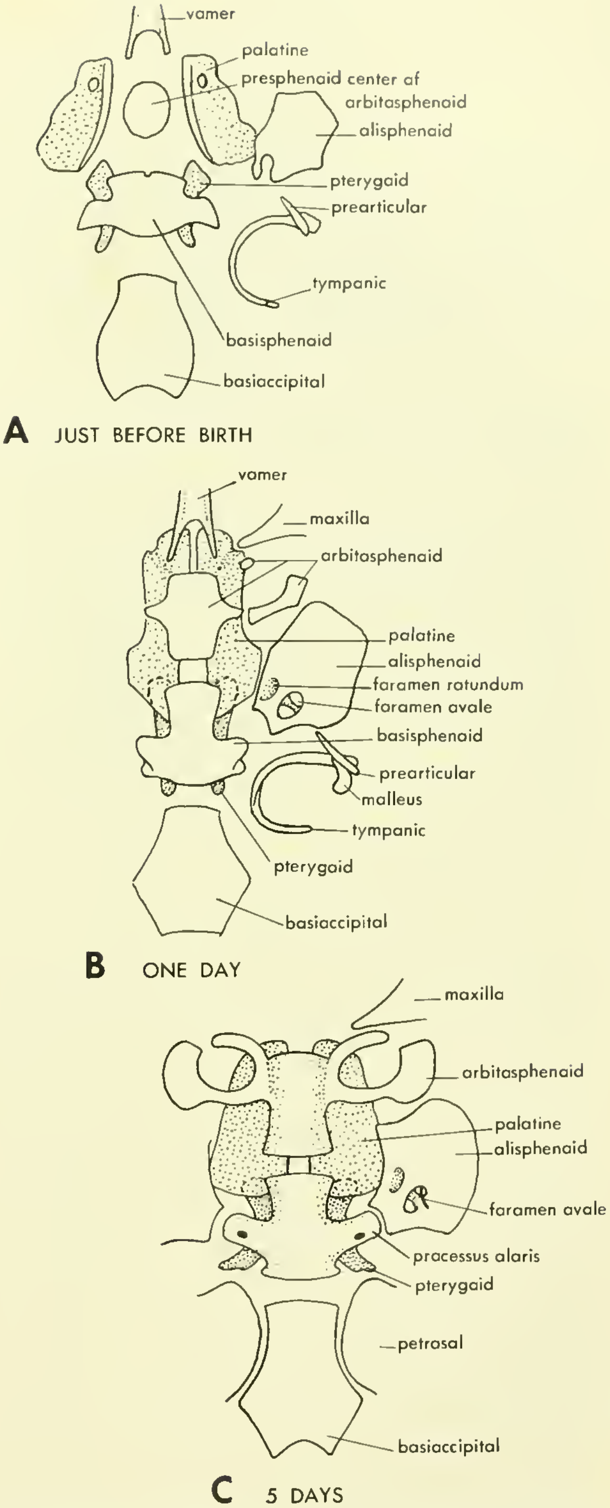


Figure 3-17. Ossifications in the basis cranii of the rat at three stages of growth as seen from above. A, just before birth; B, one day old; C, five days old.

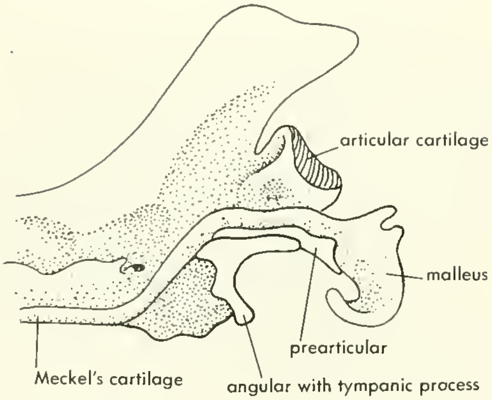


Figure 3-18. A stage in the development of the tympanic bone of the opossum. (After Taeplitz, 1920)

a postparietal and parasphenoid in marsupials suggests a modified skull rather than a primitive one.

In its visceral skeleton the opossum is of interest only in the origin of the tympanic (Figure 3-18). Here there is an anterior process extending along Meckel's cartilage, indicating the origin of this bone from one of the bones of the lower jaw, generally identified as the angular of the reptile.

Monotreme Details of the development of the montreme skull reveal that there is no postparietal or lacrimal, but there is a dermal extension from the petrosal occupying the area of the alisphenoid, which is lacking. There are two "pterygoid" bones in the palate, which arise separately and remain separated by the palatine—except perhaps at their extreme posterior ends. The bone on the lateral wall of the nasal passage appears to be the pterygoid, but it lacks the hamular process with its characteristic muscle associations. The outer bone, which we have called the ectopterygoid, has been compared with the hamular portion. From this comparison stems the concept that the mammalian pterygoid is two parted. The solution to this problem will come only through studies of the critical developmental stages of those placental species described as having a two-parted pterygoid. As a last point, the ear capsule of the monotreme is said to arise from two centers of ossification comparable to those of lower vertebrates.

General observations From this examination of the cartilaginous embryonic head skeleton and the development of the bony head skeleton, we arrive at conclusions parallel to those reached from study of the adult. Although there is a great deal of variation among mammals, a basic general plan is discernible. From this the marsupials show some divergence and the monotremes show marked differences. The origin of many parts of the mammalian skull will take on more meaning after a review of the reptile skeleton and its development.

4

The Head Skeleton of other Tetrapods and the Choanate Fishes

OTHER TETRAPODS

The tetrapods are the "four-footed" animals and include the mammals, reptiles, birds, and amphibians. The head skeletons of living examples of these several kinds of tetrapods must be reviewed in order to establish a basic pattern for all and also to indicate some of the variations that characterize each of these end products of the evolutionary process. These several evolutionary lines can then be traced back through their fossil representatives so as to arrive at some notion of the head skeleton of their common ancestor.

Reptiles

The reptiles are generally presumed to have evolved from the amphibians and to have given rise to the mammals and birds. The first known reptiles are from the Upper Pennsylvanian (see Table 4-1), but it is not until the Permian that enough details are revealed to compare them with living representatives. By the Upper Pennsylvanian the reptiles had already radiated into many diverse types, and during the Mesozoic there were further radiations of types giving rise to birds and mammals.

There are three main lines of reptiles: turtles (Chelonia), Lepidosauria, and Archosauria. The snakes, lizards, and Sphenodon are lepidosaurs, whereas the dinosaurs and crocodilians are archosaurs. The birds are viewed as a derivative of the archosaurs. Of the living reptiles, the snakes and lizards are the most widespread, and the lizard retains a close resemblance to what might be imagined as the ancestral reptile, at least in terms of the larger number of bones in the head skeleton. On this basis it can be considered as less modified than the alligator or turtle.

The lizard will be considered first. A check-list of the bones to be observed is given in Table 4-2.

Lizard Species of *Tupinambis* and *Iguana* are readily available as representatives of this type (Figure 4-1). The skull is diapsid (Figure 4-26), that is, it has two temporal fenestrae, but the inferior fenestra lacks a ventral, labial bar. Both fenestrae are large and the skull roof is reduced and separated from the endocranium. This separation is effected by the confluence of the orbit cavity with the temporal and posttemporal fossae and the inward extension of the roofing bones around the edges of the muscle masses as this separation occurred. The lizard thus has parts of two cranial walls, one lying outside the temporal musculature and one inside. The mammal fully developed the inside wall but lost the outer.

In sharp contrast to the mammal, there is a joint between the fused otic capsule-occipital segment of the skull and the overlying roof (Figure 4-2). This joint permits some movement between these parts. The quadrate can be rocked back and forth and the snout raised and lowered. Shifting of parts within the skull is identified as **kineticism.**

The roof lacks a postparietal bone, a case of loss. In *Iguana* there is a **parietal foramen,** a case of retention of a primitive feature. **Prefrontal, postfrontal,** and **postorbital** bones are present. The **squamosal** is much reduced and there is a **supratemporal.** The cranial cavity is open anteriorly. The anterior margin of the **oticoccipital segment** of the endocranium is notched by the foramen of the fifth nerve, and ventrolaterally it bears a flange under which the facial nerve exits. Below this flange, the splint-like stapes extends out parallel to the strong **paroccipital process** of the opisthotic bone. The paroccipital processes of either side along with the **supraoccipital** articulate with the roof.

There is a single rounded **occipital condyle** rather than the two separate articular processes (condyles) of the mammal. The **exoccipital** and **basioccipital** contribute to this condyle. The basioccipital has strong, bilateral ventral processes. A flange of the **opisthotic bone** connects this ventral process with the cranium and forms the posterior margin of the tympanic fossa. This rim divides the **metotic fissure** into a posterior **jugular foramen** for the tenth and eleventh nerves and a **recessus tympanicus** for the ninth nerve and **perilymphatic fenestra.** The exoccipital is perforated just behind the jugular foramen by the hypoglossal roots.

TABLE 4-1 GEOLOGIC TIMETABLE*

Era	Period	Epoch	Duration in Millions of Years	Time from Beginning of Period to Present (Millions of Years)	Geologic Conditions	Plant Life	Animal Life
Cenozoic (Age of Mammals)	Quaternary	Recent	0.025	0.025	End of last ice age; climate warmer	Decline of woody plants; rise of herbaceous ones	Age of man
		Pleistocene	1	1	Repeated glaciation; 4 ice ages	Great extinction of species	Extinction of great mammals; first human social life
	Tertiary	Pliocene	11	12	Continued rise of mountains of western North America; volcanic activity	Decline of forests spread of grasslands; flowering plants, monocotyledons developed	Man evolving; elephants, horses, camels almost like modern species
		Miocene	16	28	Sierra and Cascade mountains formed; volcanic activity in northwest U.S.; climate cooler		Mammals at height of evolution; first manlike apes
		Oligocene	11	39	Lands lower; climate warmer	Maximum spread of forests; rise of monocotyledons, flowering plants	Archaic mammals extinct; rise of anthropoids; forerunners of most living genera of mammals
		Eocene	19	58	Mountains eroded; no continental seas; climate warmer		Placental mammals diversified and specialized; hoofed mammals and carnivores established
		Paleocene	17	75			Spread of archaic mammal
	Rocky Mountain Revolution (Little Destruction of Fossils)						
Mesozoic (Age of Reptiles)	Cretaceous		60	135	Andes, Alps, Himalayas, Rockies formed late; earlier, inland seas and swamps; chalk, shale deposited	First monocotyledons; first oak and maple forests; gymnosperms declined	Dinosaurs reached peak, became extinct; toothed birds became extinct; first modern birds; archaic mammals common
	Jurassic		30	165	Continents fairly high; shallow seas over some of Europe and western U.S.	Increase of dicotyledons; cycads and conifers common	First toothed birds; dinosaurs larger and specialized; insectivorous marsupials
	Triassic		40	205	Continents exposed; widespread desert conditions; many land deposits	Gymnosperms dominant, declining toward end; extinction of seed ferns	First dinosaurs, pterosaurs and egg-laying mammals; extinction of primitive amphibians

	Appalachian Revolution (Some Loss of Fossils)					
Paleozoic (Age of Ancient Life)	Permian	25	230	Continents rose; Appalachians formed; increasing glaciation and aridity	Decline of lycopods and horsetails	Many ancient animals died out; mammal-like reptiles, modern insects arose
	Pennsylvanian (Carboniferous)	25	255	Lands at first low; great coal swamps	Great forests of seed ferns and gymnosperms	First reptiles; insects common; spread of ancient amphibians
	Mississippian (Carboniferous)	25	280	Climate warm and humid at first, cooler later as land rose	Lycopods and horsetails dominant; gymnosperms increasingly widespread	Sea lilies at height; spread of ancient sharks
	Devonian	45	325	Smaller inland seas; land higher, more arid; glaciation	First forests; land plants well established; first gymnosperms	First amphibians; lungfishes, sharks abundant
	Silurian	35	360	Extensive continental seas; lowlands increasingly arid as land rose	First definite evidence of land plants; algae dominant	Marine arachnids dominant; first (wingless) insects; rise of fishes
	Ordovician	65	425	Great submergence of land; warm climates even in Arctic	Land plants probably first appeared; marine algae abundant	First fishes, probably freshwater; corals, trilobites abundant; diversified molluscs
	Cambrian	80	505	Lands low, climate mild; earliest rocks with abundant fossils	Marine algae	Trilobites, brachiopods dominant; most modern phyla established
	Second Great Revolution (Considerable Loss of Fossils)					
Proterozoic		1500	2000	Great sedimentation; volcanic activity later; extensive erosion, repeated glaciations	Primitive aquatic plants—algae, fungi	Various marine protozoa; toward end, molluscs, worms, other marine invertebrates
	First Great Revolution (Considerable Loss of Fossils)					
Archeozoic		???	???	Great volcanic activity; some sedimentary deposition; extensive erosion	No recognizable fossils; indirect evidence of living things from deposits of organic material in rock	

* From Dodson, "Evolution: Process and Product," Revised Edition, Reinhold Publishing Corp., 1960. After Villee, "Biology," W. B. Saunders Co., 1957.

TABLE 4-2 THE BONES OF THE HEAD SKELETON OF THE REPTILE ARRANGED ACCORDING TO TYPE AND PLACE OF ORIGIN

Cranium (brain and sense organ capsule)	Splanchnocranium or Visceral Skeleton (dermal bones with*)
Endocranium (bones of chondral origin)	Mandibular arch—Palatoquadrate and Meckel's cartilage
basioccipital	premaxilla*
exoccipital	maxilla*
supraoccipital	quadratojugal*
opisthotic	palatine*
prootic	pterygoid*
basisphenoid	epipterygoid
orbitosphenoid	quadrate
Eye	
sclerotic plates	articular
	mental
Dermocranium (bones of membrane origin)	angular*
	supraangular*
parietal	dentary*
frontal	prearticular*
nasal	coronoid*
septomaxilla	splenial*
lacrimal	
prefrontal	Hyoid arch
postfrontal	stapes
postorbital	extracolumella (cartilage)
supratemporal	ceratohyal
squamosal	hypohyal
jugal	body or copula
vomer	
parasphenoid	
	Branchial arches
	ceratobranchials I, II

The floor of the skull is covered by an elongated **parasphenoid** which is fused with the **basisphenoid.** The basisphenoid has strong **basipterygoid processes** articulating with the **pterygoids. Parabasal canals** pass between the basisphenoid and parasphenoid on either side. This canal gives passage to the internal carotid artery and the palatine branch of the seventh nerve.

In the membranous anterolateral wall of the cranium is a small y-shaped bone, the **orbitosphenoid.** The bones of either side do not fuse ventrally in a "presphenoid union." There are small **septomaxillaries** visible in the opening of the external naris. These bones overlie the Jacobson's organs opening through the **incisive foramina** of the palatal surface, and they are of both dermal and endochondral origin. The eye is surrounded by a ring of about fourteen **sclerotic plates.**

The upper jaw consists of separate **premaxilla** and **maxilla.** These bear conical teeth. The palatoquadrate complex differs in having large **palatal** and **interpterygoid fenestrae,** confluent incisive fenestrae, and internal narial openings, and also differs in its component bones. The **palatine** sutures anteriorly with a large vomer; behind the palatine are **pterygoid, ectopterygoid,** and **quadrate.** From the dorsal side of the pterygoid, an **epipterygoid** extends upward to contact the side of the cranium. The V_1 branch of the trigeminal nerve passes medial to this bone, whereas the V_2 and V_3 branches pass outward behind it (Figure 4-2 C). The pterygoid bears a row of teeth in *Iguana.*

The lower jaw (Figure 4-2 D,E) is composed of seven bones rather than of the dentary alone. The **dentary** bears conical teeth similar to those of the upper jaw. The teeth show some variation from front to rear and some of them have three cusps. A small **mental bone** may occur in **Meckel's cartilage** at the anterior symphysis, or joint.

The hyoid arch consists of the **stapes** above and a part of the **hyoid apparatus** below. The stapes is a long slender bone with an ovoid foot plate fitted into the **fenestra vestibuli** of the otic capsule. Distally it attaches through the **extracolumella** to the paroccipital process above, the tympanic membrane laterally, and the quadrate anteroventrally (Figure 4-3). The stapes plus the extracolumella forms the columella.

The hyoid apparatus consists of a **copula** ("joining piece") with a long **lingual** (or entoglossal) **process.** This process is detached in the case of *Tupinambis* (Figure 4-3). Parts of three pairs of arches attach to the copula. The only ossification in the hyoid apparatus is that of the **ceratobranchials I,** although other areas may be well calcified.

EMBRYOLOGICAL DEVELOPMENT Of the lizards, the development of *Lacerta agilis* is best known (Figures 4-4 to 4-6). The first structures to appear include **Meckel's cartilage,** the widely separated **trabeculae,** a **parachordal plate** formed by connection of the parachordals below the notochord, and, fused to this, an **occipital arch** on either side. In the **otic capsule** a center of chondrification appears laterally and gradually spreads out. The three hypoglossal roots become enclosed from behind forward by the appearance of **preoccipital arches.** The trabeculae join anteriorly as a trabecula communis but remain separated posteriorly from each other and from the parachordals. The **palatoquadrate** is represented by a **quadrate** rudiment and a separate crescentic-shaped piece formed of the **pterygoid** and **ascending processes.** The hyoid apparatus consists of basihyals, forming a **lingual process** and body (**copula**) and **hypohyal, ceratohyal, ceratobranchial I** and **ceratobranchial II** arch centers—the latter appear as bilateral processes from the rear of the copula.

The definitive chondrocranium is quite different in appearance from that of the mammal but contains many of the same elements (Figures 4-5, 4-6).

The development of the head bones is known from several other lizards but not for *Lacerta.* In contrast to the mammal, the otic capsule is ossified from two centers and postparietal centers are never present. The nature of the epipterygoid and the orbitosphenoid as palatoquadrate and cranial wall elements respectively is clearly revealed.

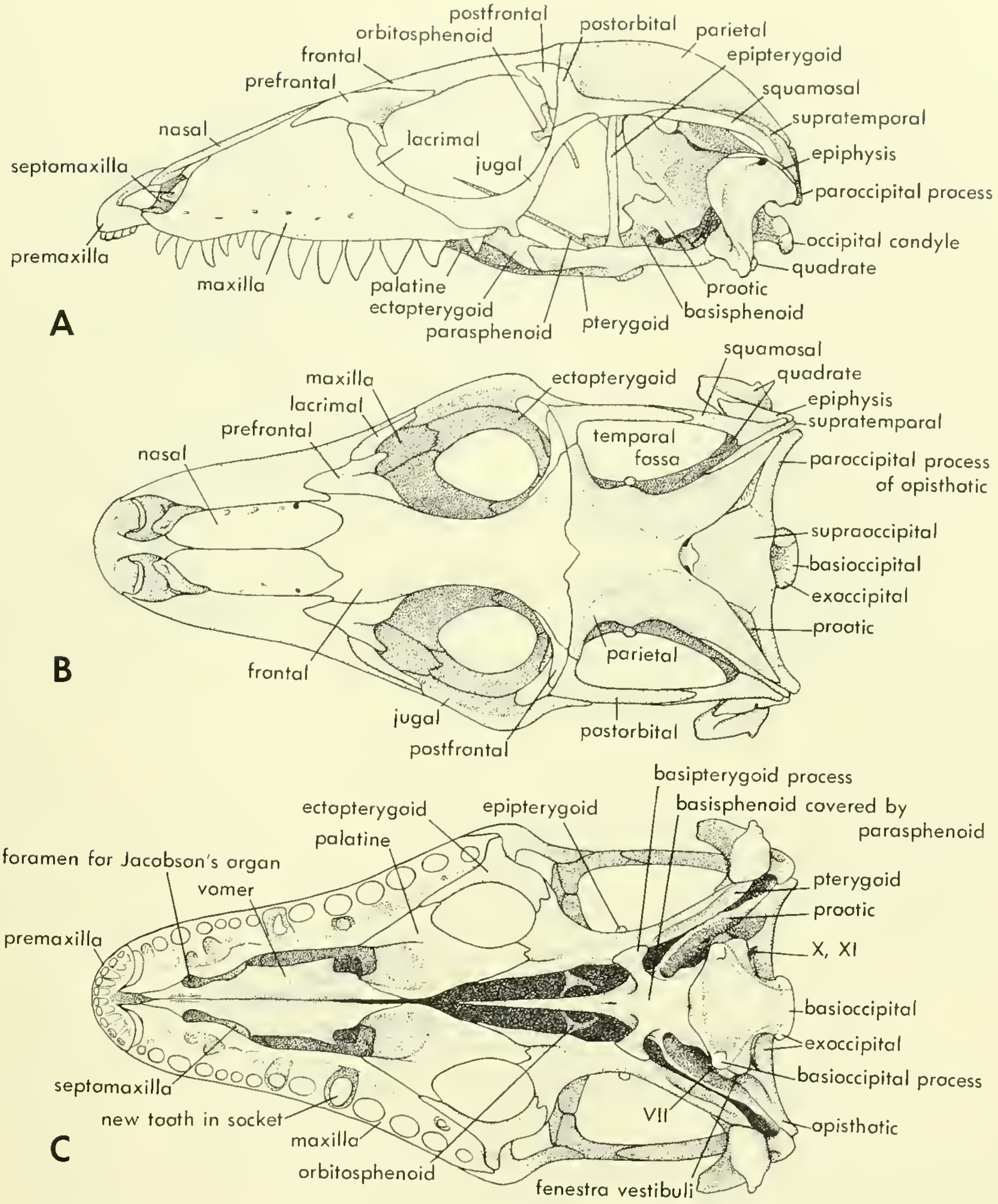


Figure 4-1. Skull of the Tegu lizard, *Tupinambis nigropunctatus.* A, lateral view; B, dorsal view; C, ventral view.

Sphenodon, the Tuatara The Tuatara head skeleton looks like that of the lizard (Figures 4-7, 4-8). The arches of this diapsid reptile are even better developed than the lizard's, and the inferior temporal fenestra is margined below by a labial arch, formed in part by a **quadratojugal.** The roof is similar, and a **parietal foramen** is present. A supratemporal and lacrimal are lacking. The palate differs in having the **pterygoid** contacting the **vomer** medial to the **palatine.** The joint between the roof and the **oticoccipital segment** is not capable of movement. Since the **palatoquadrate complex** is strongly attached at all points, this skull is nonkinetic. There is no orbitosphenoid. The teeth are fused to the jaw margin in the acrodont style of attachment. The lower jaw lacks a splenial. The **hyoid apparatus** is like

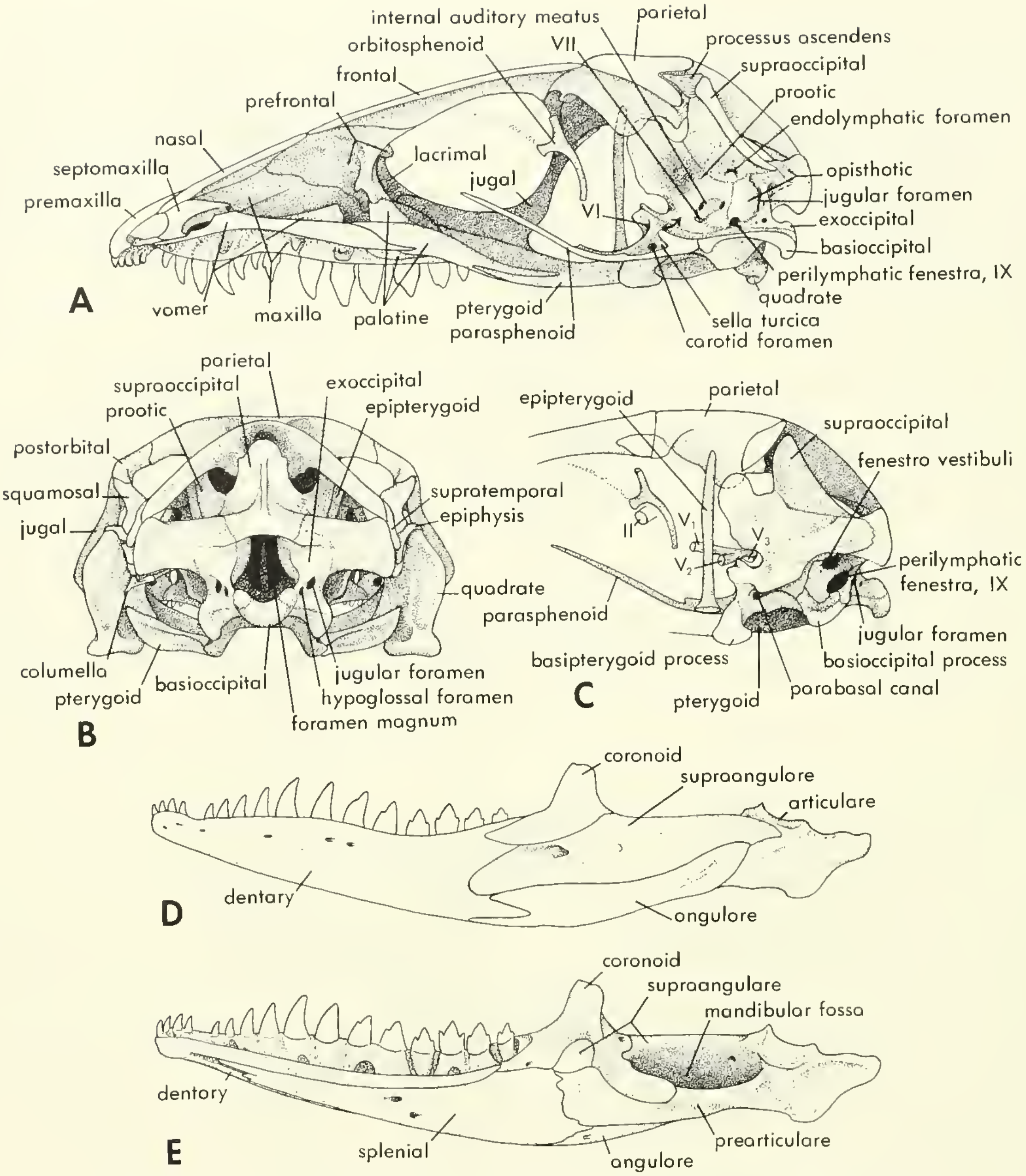


Figure 4-2. Skull and mandible of the Tegu lizard, *Tupinambis nigropunctatus.* A, medial view of right half of skull; B, rear view of skull; C, lateral view of cranium with temporal arch removed; D, lateral view of mandible; E, medial view of mandible.

the lizard's but attaches dorsally through the epihyal to the **extracolumella.** The development of the head skeleton follows the pattern of the lizard.

The similarity between the Tuatara and the agamid lizard *Uromastix* in terms of vomer-pterygoid relationship, acrodont dentition, and over-all appearance indicates either close common ancestry with parallel evolution of structure or a case of convergent evolution from quite dissimilar ancestors. The former view is now generally accepted. In terms of retaining the supratemporal and in its usual pleurodont style of tooth anchorage, the lizard is just as primitive as the Tuatara.

Turtle In strong contrast to the diapsid is the anapsid, in which there are no temporal fenestrae and the skull is nonkinetic. The only living anapsids are the turtles. The following description (the "type" turtle) is based on the variations observed in *Caretta caretta,* the Loggerhead Turtle; *Macro-*

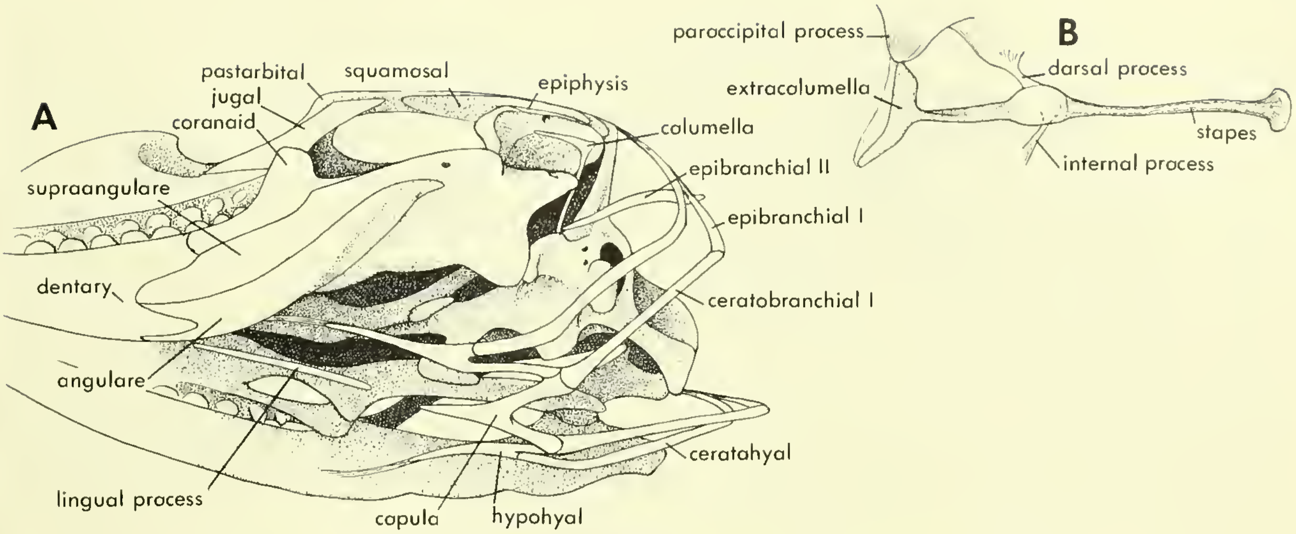


Figure 4-3. Ventrolateral view of skull; A, with hyoid apparatus in position and detail of columella; B, as seen in ventroposterior view.

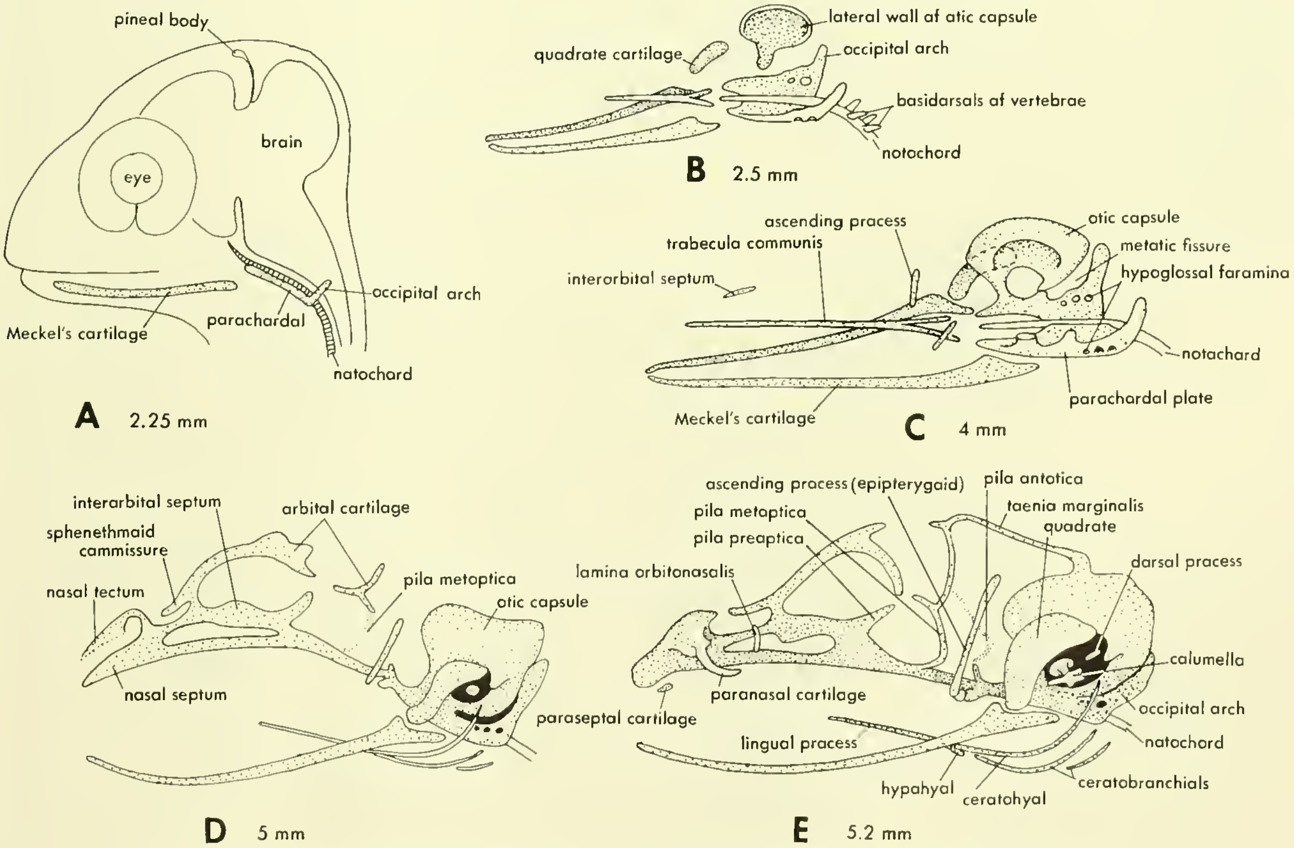


Figure 4-4. Several stages in the development of the chondrocranium of the lizard, *Lacerta*. A, lateral view of head, 2.5 mm in length, with first skeletal condensations; B, rudiments of head cartilages at 2.5-mm head length as seen in dorsolateral and slightly anterior view, otic capsule of left side removed; C, head length of 4 mm as seen in B; D, skeleton at head length of 5 mm. as seen in lateral view; E, slightly larger than D as seen in lateral view. (After DeBeer, 1937)

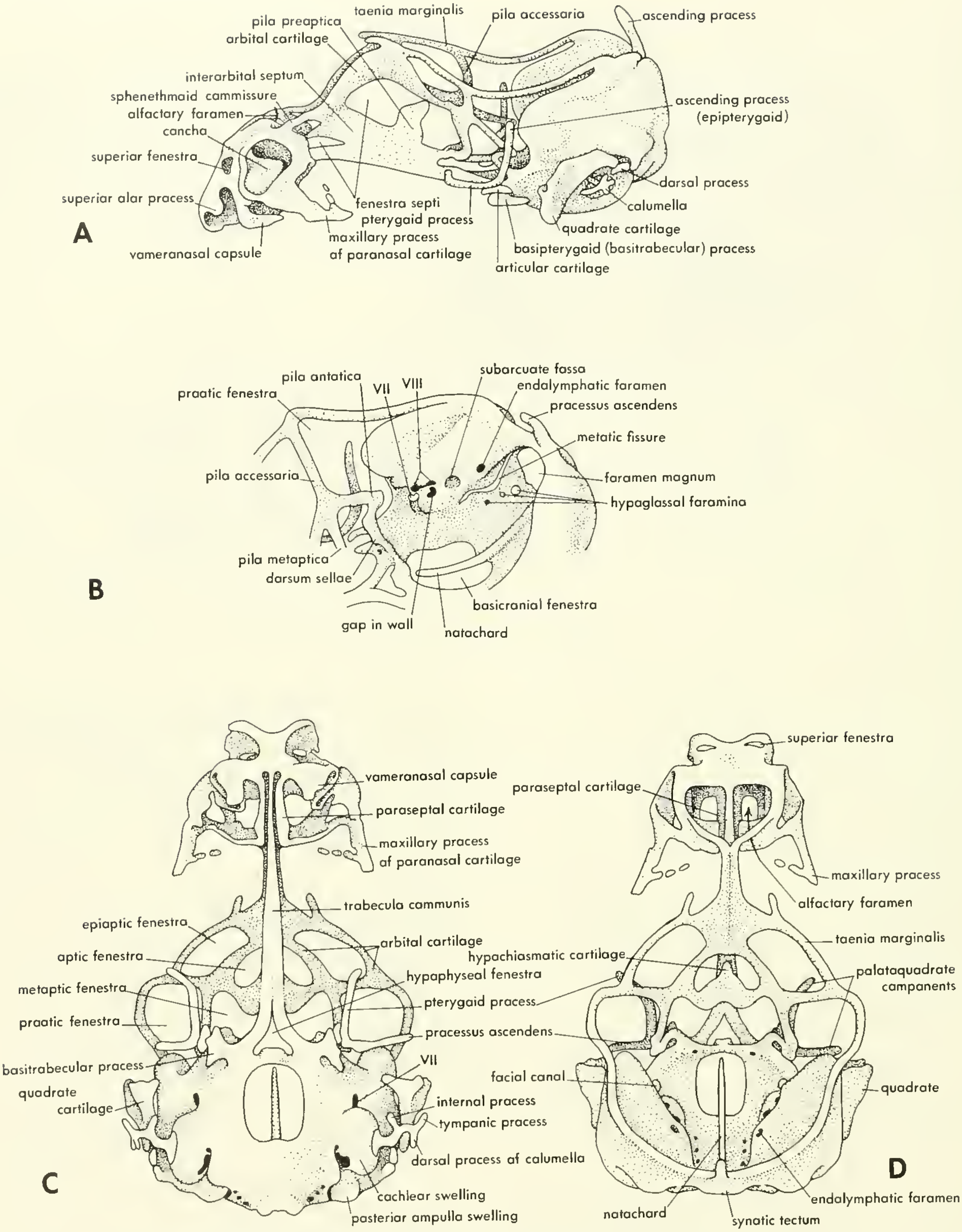


Figure 4-5. The fully developed chondrocranium of *Lacerta*. A, dorsolateral view; B, nearly dorsal view of right otic capsule region; C, ventral view; D, dorsal view. (From Gaupp, 1900)

clemys temmincki, the Alligator Snapping Turtle; *Chelydra serpentina,* the Snapping Turtle; and *Terrapene carolina,* the Box Turtle.

The solid roof may be emarginated posteriorly (Figure 4-9). In *Terrapene* it is largely missing, except for a lateral squamosal-postorbital arch. The **parietal** forms a part of the endocranial wall, extending down in front of the trigeminal nerve to contact the palatoquadrate (pterygoid)—the V_1 branch passes medial to this process, which lies in the position of the lizard epipterygoid. There has been extensive loss of bones in this type of skull: the lacrimal, postfrontal, supratemporal, postparietal, septomaxilla, and splenial are lacking. The nasal, ectopterygoid, and epipterygoid are usually lacking; the epipterygoid is at best rudimentary and the ectopterygoid may never be present. The parasphenoid is lacking or much reduced.

Other peculiarities are as follows: the **vomers** fuse medially and suture with the **pterygoids;** the posterior margin of the **quadrate** is deeply incised or encloses the shaft of the stapes; and the jaw margins are toothless and covered by a horny sheath. The **hyoid apparatus** consists of a plate-like **copula** to which are attached **hyoid cornua** (horns) and **ceratobranchial I** and **II** processes.

The development of this type of head skeleton shows a few modifications. No bones other than those observed in the adult are evident during developmental stages. The **vomer** develops from bilateral centers but these soon fuse. Two **parasphenoid** centers appear in the sea turtle, *Lepidochelys,* but disappear as the **pterygoids** meet below the basisphenoid, obliterating the basipterygoid processes and closely investing most of the basisphenoid. An anterior process of the supraoccipital is present.

The head skeleton of the turtle appears to be modified in almost every respect. Further evidence of the simplification (or inherent simplicity) of this type is the lack of a pouched Jacobson's organ and the lack of conchae, folds

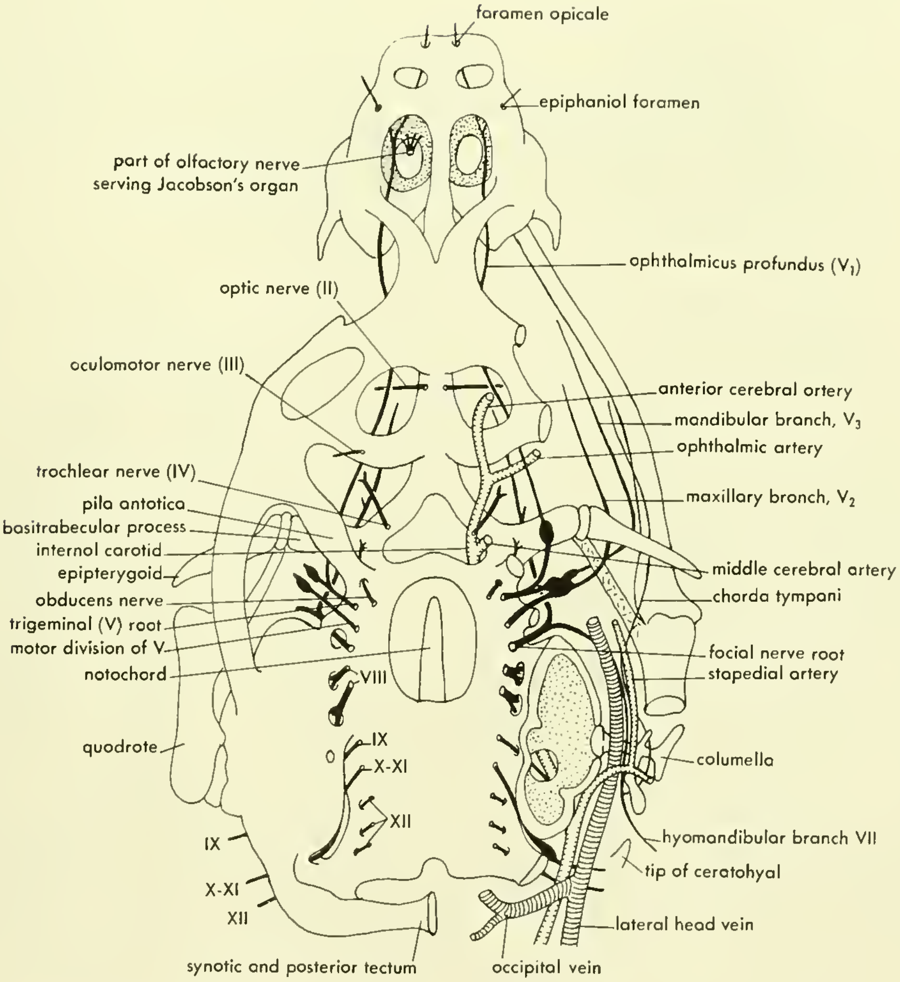


Figure 4-6. Relationships of nerves and blood vessels to the definitive chondrocranium as seen in dorsal view. (After Goodrich, 1930)

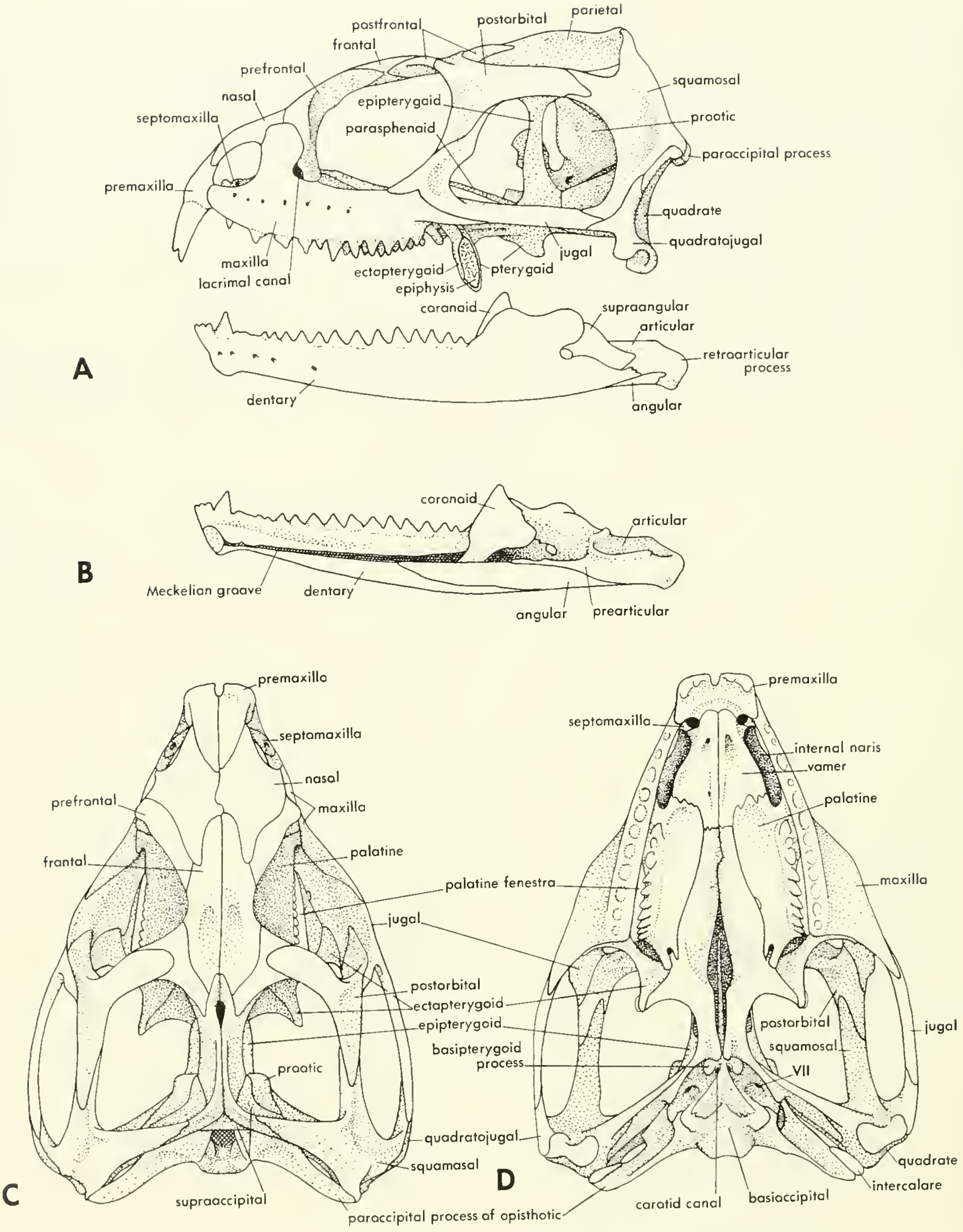


Figure 4-7. Skull and mandible of Sphenodon. A, lateral view; B, medial view of mandible; C, dorsal view of skull; D, ventral view of skull.

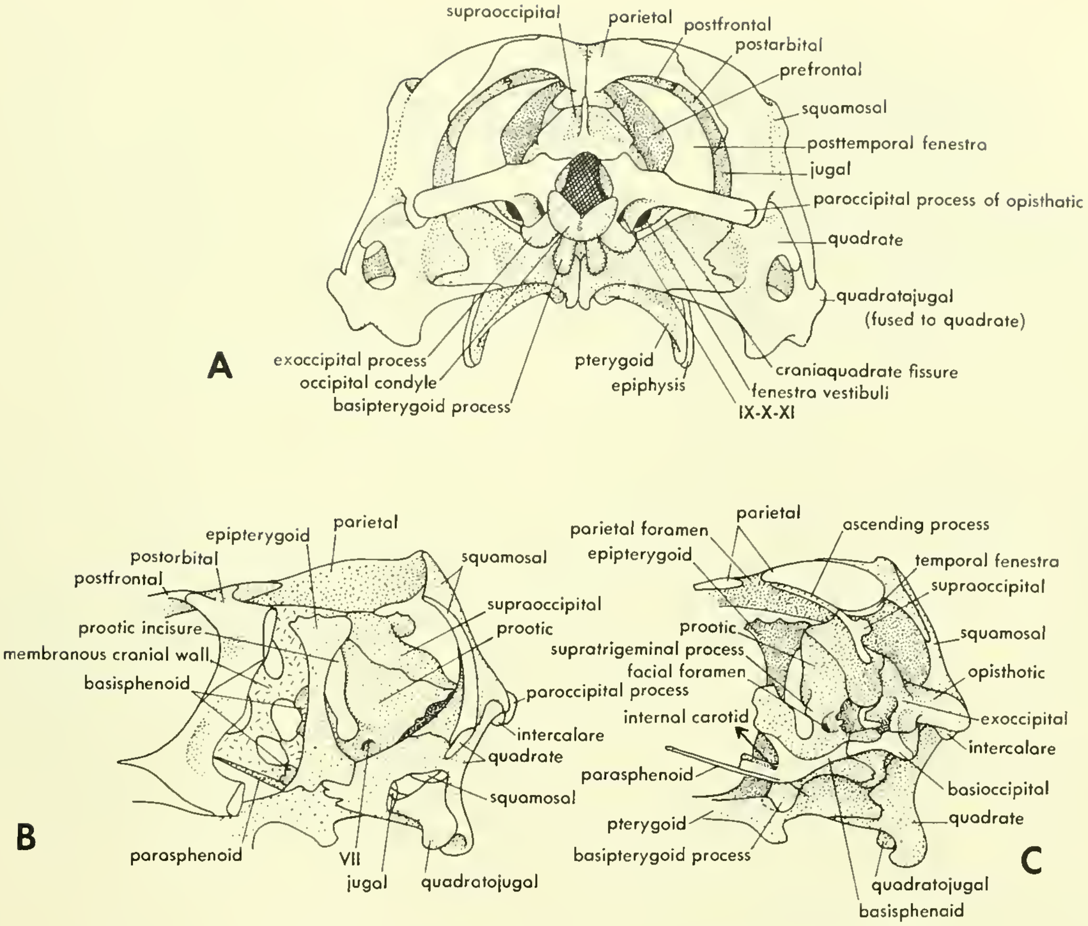


Figure 4-8. Skull of Sphenodon. A, rear view; B, lateral view of cranium with temporal and labial arches removed; C, medial view of right half of cranium.

from the lateral nasal wall into the nasal passage. The basic peculiarities of this type of skull suggest a relationship to the diadectomorphs. The peculiarities of this type, and the diadectomorphs described below, led Olson (1947) to divide the reptiles into two subclasses, the Parareptilia and the Eureptilia.

Alligator The crocodilians are the sole remaining archosaur. They are a close-knit group and are quite similar in most details. The American alligator and crocodile differ in the width of the snout, in the contact of the nasal process of the premaxilla with the nasal between the external nares in the alligator, and in the disposition of the teeth.

The alligator skull has a diapsid roof (Figure 4-10). The superior temporal opening is small, and the posttemporal fossa is reduced to a chink. A septomaxilla and epipterygoid are lacking. The **vomers** do not contact or even approach the **premaxillae,** a state related to the forward outgrowth of the snout which left the vomers far behind (Figure 4-11). There is a secondary palate, a parallelism to that of the mammal, which extends the nasal passages back to the area of the glottis. Extensions of the maxilla, palatine, and pterygoid are involved in this secondary palate. Along with these palatal changes, the pterygoids are moved backward and medially, eliminating the basipterygoid processes and suturing with the **basis cranii.** As a result of this contact, the internal carotid artery and the palatine nerve become enclosed in a "pterygobasipterygoid" canal. Bony **eustachian tubes** are also formed. The parasphenoid has three centers in the embryo but is largely obliterated by the palatal changes.

The **orbitosphenoid** ossifies in the antotic pillar, then spreads into the metotic pillar and the region of the **epipterygoid,** where it achieves contact with the pterygoid. Ossification follows the same pattern as chondrification. In the lizard this bone arises in the **metoptic pillar,** and the **antotic pillar** sometimes never forms.

A sclerotic ring of bony plates is lacking. The conical teeth are thecodont, that is, set in sockets like those of the mammal, and are replaced by new teeth developing in the base of the socket (see Figure 8-64). These teeth do not form a

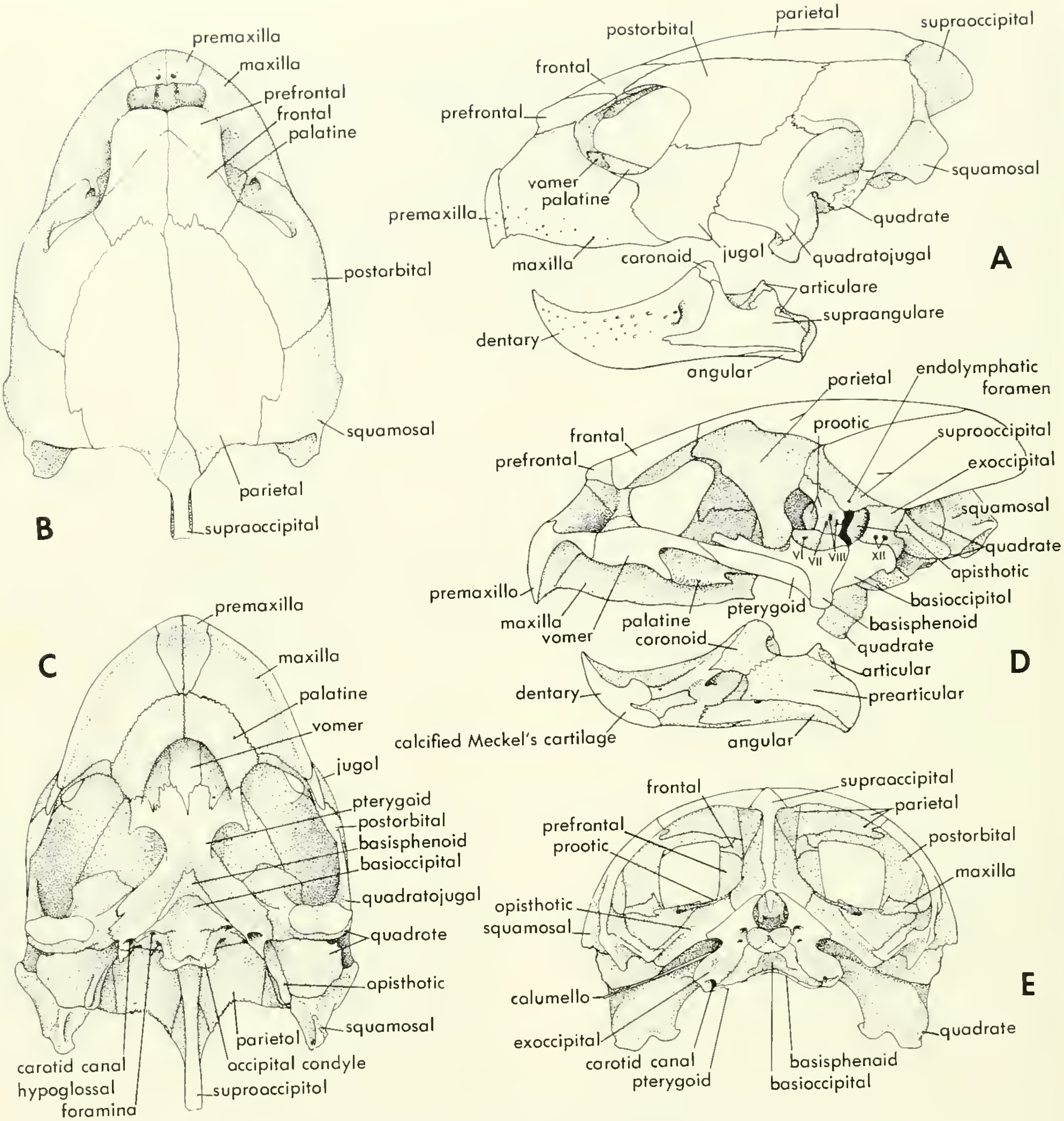


Figure 4-9. Skull and mandible of the Turtle based on *Lepidochelys* and *Caretta*. A, lateral view of skull and mandible; B, dorsal view of skull; C, ventral view of skull; D, medial view of right half of skull and mandible; E, rear view of skull.

root as in the mammal. The skull is nonkinetic. It is peculiar in being pneumatic; that is, there are sac-like outgrowths from the middle-ear cavity which lie between or within the surrounding bones.

The lower jaw (Figure 4-11 D,E) lacks a prearticular, which is largely replaced by the angular. A small prearticular fragment is said to appear in the embryo but later fuses with the articular. The hyoid apparatus consists of a broad plate, the copula, to which is attached the first ceratobranchial.

In its development, the head skeleton of the crocodilian (Figure 4-12) is quite different from that of the lizard or the turtle. Some of the special features will be mentioned in comparisons with the bird.

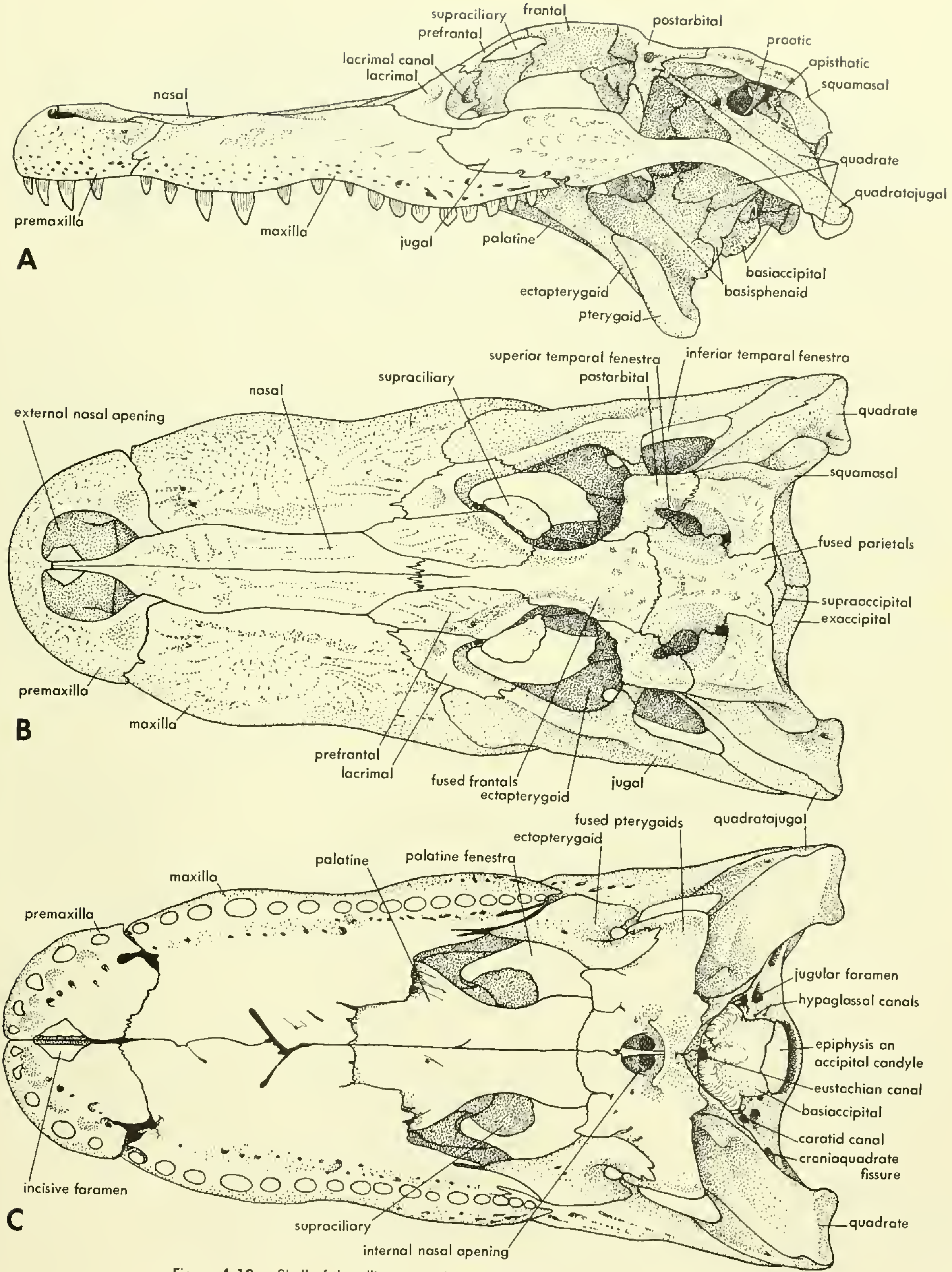


Figure 4-10. Skull of the alligator. A, lateral view; B, dorsal view; C, ventral view.

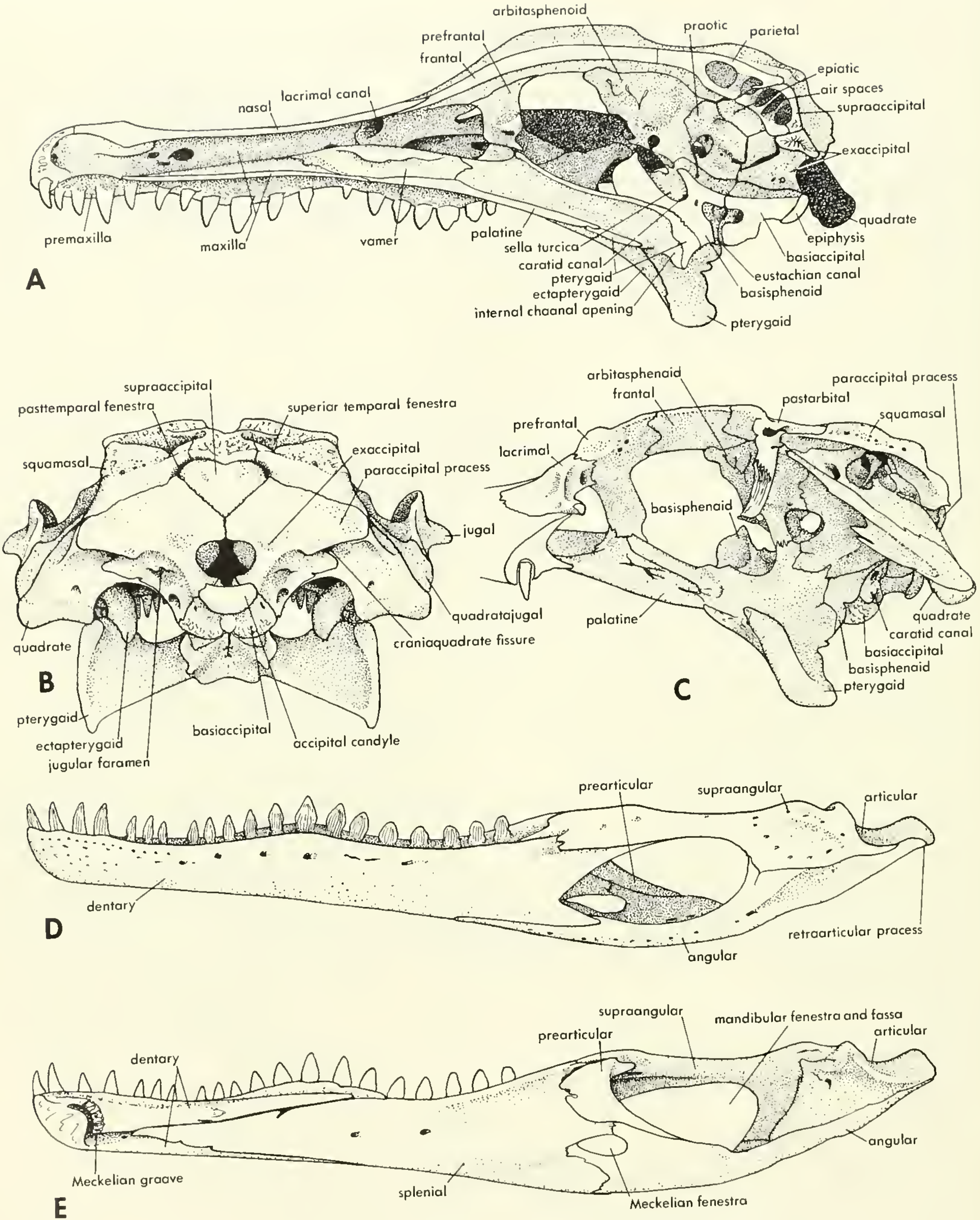


Figure 4-11. Skull and mandible of alligator. A, medial view of right half of skull; B, rear view of skull; C, lateral view of cranium with labial arch and quadratojugal removed; D, lateral view of mandible; E, medial view of mandible.

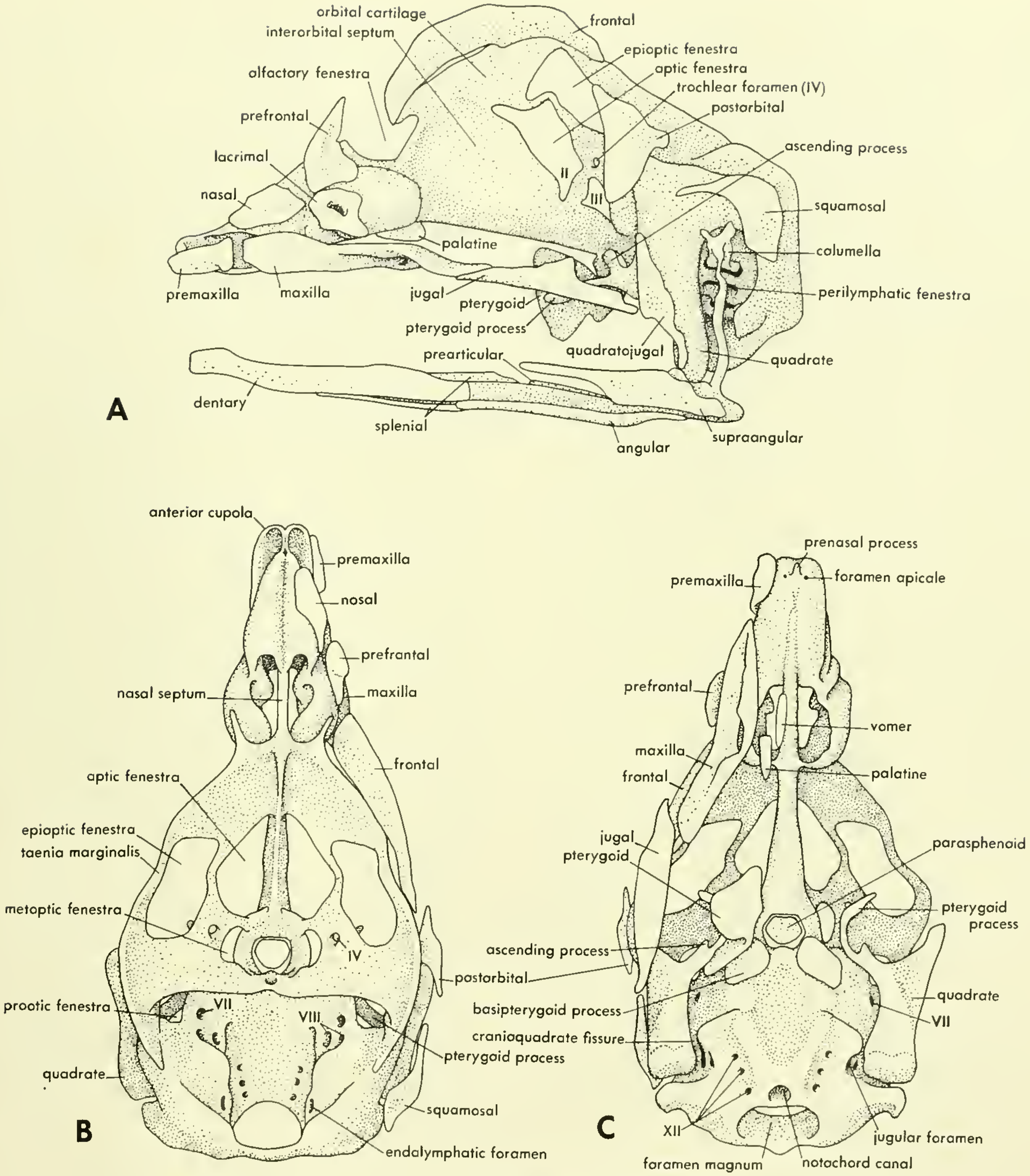


Figure 4-12. Chondrocranium and some of the dermal bone rudiments observed in the head of an embryo (13-mm head length) of *Crocodilus biporcatus.* (After Shiino, 1914)

Bird

The head skeleton of the chicken, as an example of the bird, contributes several useful points to the discussion of the nature and evolution of the osseous system. The type of flight practiced by the bird demands a high level of development of the eye and brain for the coordination and direction of action. Both of these features are reflected in the head in terms of the large size of the orbit and brain case. Restriction of weight is also suggested by the relatively thin or very spongy bones. The bones have dense surface lamellae joined by strands or trabeculae of bone. Fusion of the component bones adds to the strength of the brain case. Reduction of the jaws to a horn-sheathed beak may be related to both weight restriction and to the style of feeding.

Because of the fusion of parts in the cranium, the head skeleton of the adult chicken is not appropriate for study. Chicks taken during the first month of development can be cleared and stained. Such preparations clearly indicate all of the bones as well as something of their origin (Figures 4-13, 4-14).

Although of diapsid origin, the bird possesses only a **labial arch,** a part of which is the **quadratojugal.** The posttemporal fossa has been obliterated by expansion of the brain case out to the skin. The **parietal, frontal,** and **squamosal** make important contributions to the endocranial wall.

There has been some loss of bones in the skull of the bird; a lacrimal (the prefrontal is usually identified as the lacrimal), postfrontal, postorbital, supratemporal, ectopterygoid, and epipterygoid are lacking. The **pterygoid** is peculiar in that the anterior part fuses to the palatine and articulates with the posterior part. In the primitive bird, the pterygoid was a single element suturing with the **vomer** anteriorly. The **quadrate** is streptostylic, that is, capable of rocking; the kinetic skull is described as **prokinetic,** with flexion occurring at a hinge between the nasals and the frontals. Air sacs from the middle ear enter the bones of the cranium; a eustachian tube passes through the cranial base to reach the pharynx. The mandible has been modified by loss of the coronoid.

The head skeletons of the alligator and the bird have some distinctive common features. These include the pneumatization of bones and several details of the chondrocranium, such as the extensive flooring of the nasal cavity by the anterior cupola (Figure 4-12 B), the fusion of the posterior cupola of the nasal capsule with the interorbital septum, the loss of the organ of Jacobson early in development, the position of the orbitosphenoid in the pila antotica, the loss of the hyoid arch component of the hyoid apparatus, and the lack of an ascending process of the synotic tectum.

The most marked differences involve the relationships of the palate to the endocranium, a feature in which the alligator is undoubtedly atypical, and the outlines of the skulls, which reflect the functional differences between these forms.

Origin of birds and mammals

The origin of the bird from the reptiles, at least in terms of the skull, is revealed by the remarkable fossils identified as *Archaeopteryx* (and *Archaeornis*). Although this fossil type is not known in detail, it links the bird and the archosaur (Figure 4-15). There is some question as to whether *Archaeopteryx* has achieved the status of a bird or is still a reptile. In terms of the skull, the latter view seems more reasonable. In spite of the reptilian nature of *Archaeopteryx,* the exact source of the birds from the archosaurs is not known.

The origin of the mammal is better documented than that of the bird. It is now generally assumed that the mammals are polyphyletic; that is, they stemmed from several lines of mammal-like reptiles identified as **therapsids** and not from an ancestral mammal. They can also be viewed as monophyletic on the grounds that all stem from therapsids.

The head skeletons of mammal-like reptiles range from highly unlike to quite similar to the mammal. The cynodonts are usually referred to in contrasting these two groups because of the similarity of their skulls.

The brain case of the cynodont is very small, rising to a sagittal crest formed by the parietals. A **parietal foramen** is present. The **squamosal, jugal,** and **postorbital** enclose the single, large temporal fossa (**synapsid type**) and outline the **suborbital fenestra.** A **prefrontal** and **septomaxilla** are present. On the broad occipital surface there are large **tabular bones** as well as a **posttemporal canal** opening into the confluent orbital and temporal spaces. The **opisthotic** forms a distinct **paroccipital process.** A **secondary palate** is present which includes a palatine contribution. **Ectopterygoids** as well as **pterygoids** are present, and the latter suture with the basis cranii. An **epipterygoid** (alisphenoid) is present and is sutured into the cranial wall, contacting the parietal above and the prootic behind. The **quadrate** is no longer connected with the palatal complex (it is in some of the cynodonts) but is sutured to the **squamosal** and much reduced in size. The **stapes** articulates distally with the quadrate. The lower jaw is basically **dentary** but a small **coronoid, splenial, prearticular,** and **angular** are present. The angular, with its reflected lamina, is usually thought to have given rise to the **tympanic ring,** but, at least in one species of cynodont, this ring is a part of the prearticular.

The intermediate nature of the cynodont is quite apparent. The approach to the mammal is carried even further in an ictidosaur, *Diarthrognathus,* in which the posterior process of the dentary articulates with the squamosal lateral to the much reduced quadrate (Figure 4-16). Establishment of the dentary-squamosal articulation frees the articular and quadrate; the quadrate is already in contact with the stapes, for conversion into middle-ear bones. With this complex conversion, identified as **Reichert's theory,** the full mammal type is reached.

The morphological sequence between primitive reptile and mammal is in the process of undergoing an almost final delineation. Huxley has commented that mammals, like birds, are only extremes of the reptile plan (a grade), not a monophyletic new functional type derived from reptiles (a clade). Many taxonomists are beginning to ask, what is a mammal? An arbitrary line must be drawn across a continuous and overlapping series of species separating mammal

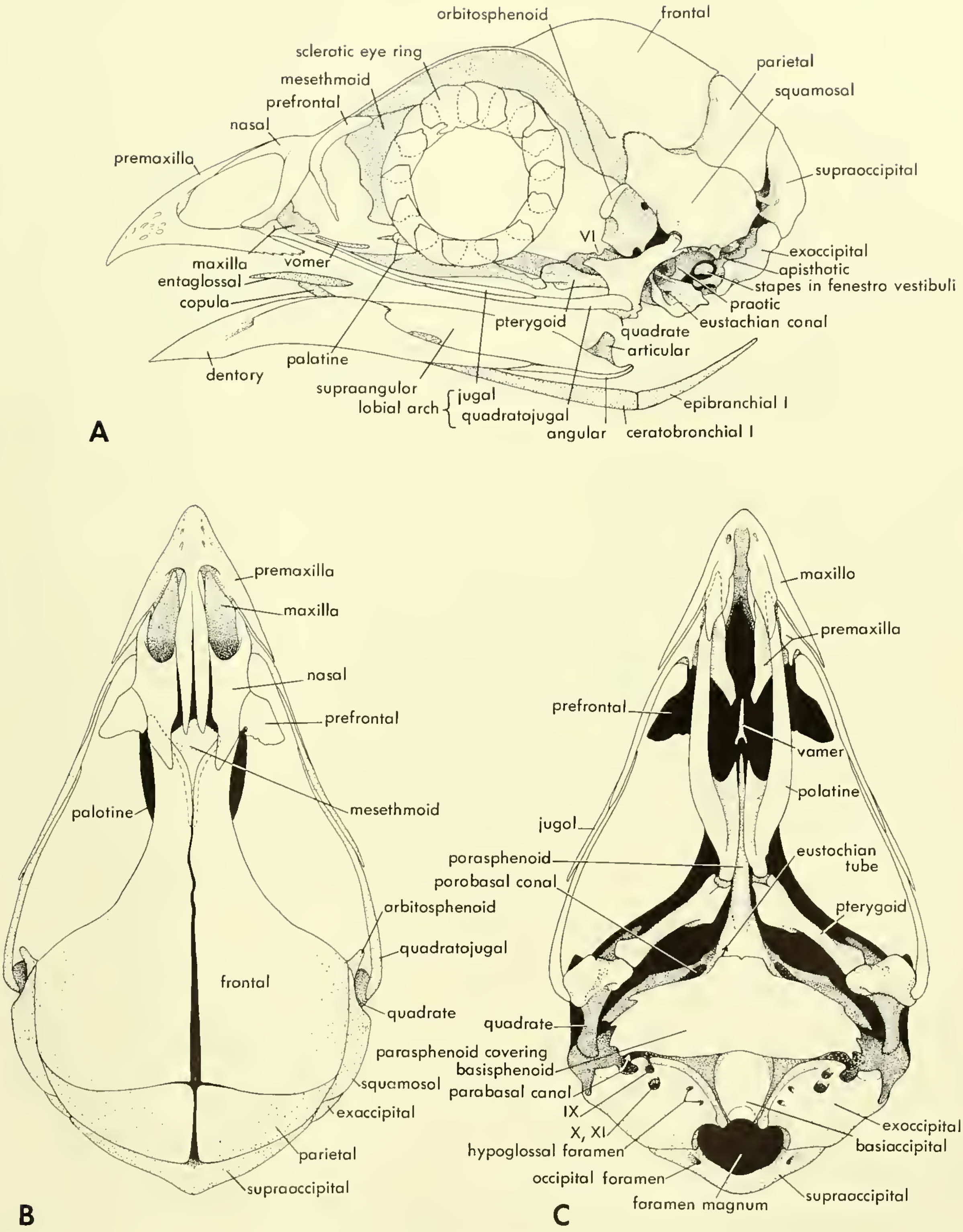


Figure 4-13. Head skeleton of the chick (shortly after hatching). A, lateral view; B, dorsal view; C, ventral view.

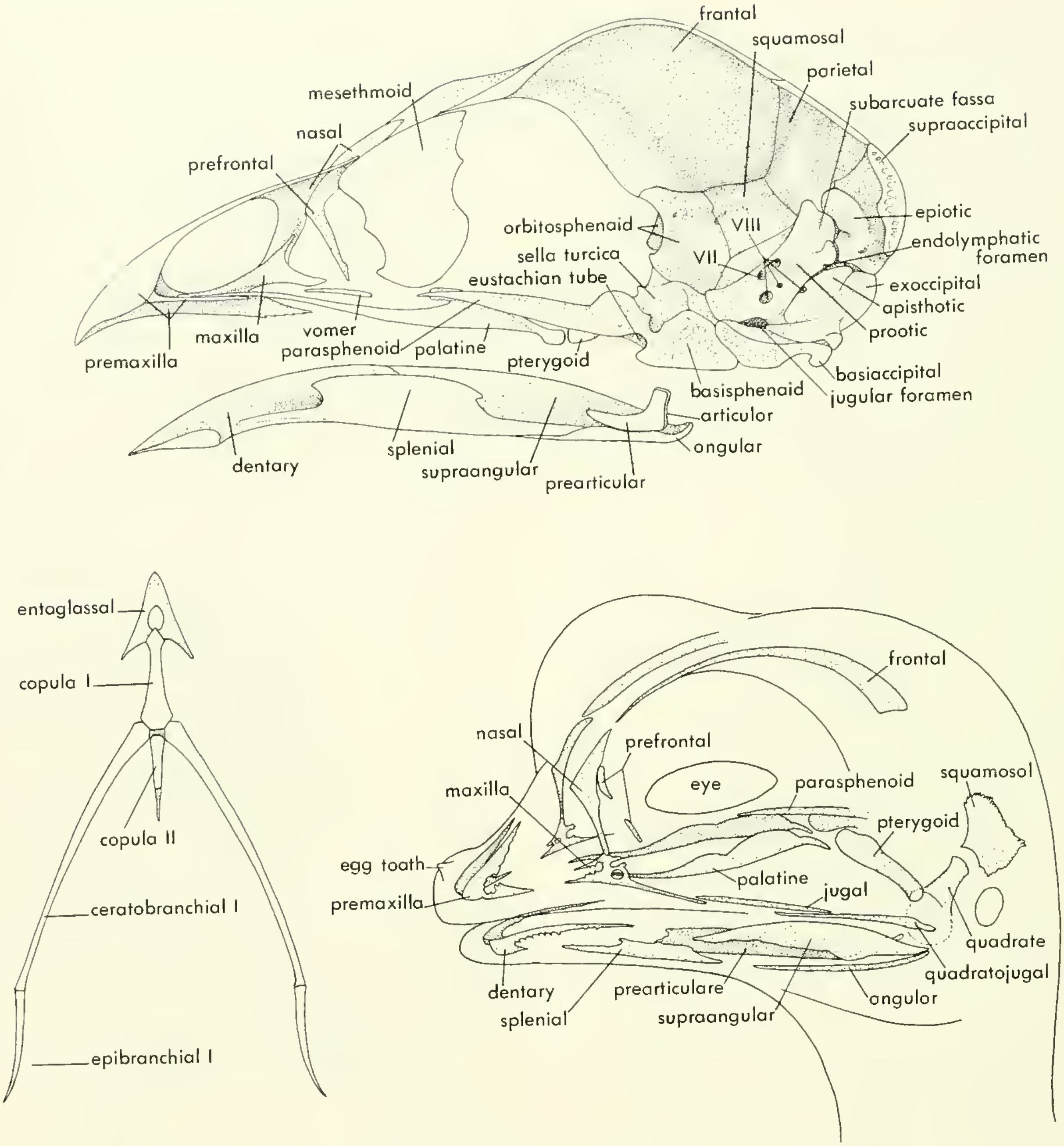


Figure 4-14. Head skeleton of the chick. A, medial view of right half of skull and mandible; B, ossifications of embryo of 11-days incubation; C, hyoid apparatus as viewed from below.

from reptile. There is some divergence of thought as to whether the position of this line should be based on morphology or function.

A review of the origin of the reptiles, and the therapsid line which gave rise to the mammals, should follow a consideration of the diversity and evolution of the Amphibia.

Living amphibians

The ancestral amphibian is assumed to have evolved from some fish-like form; therefore, it must have been quite different from the living representatives, which lack gills and have limbs rather than fins.

Among the living tetrapods, amphibians are best defined as lacking the amniote type of egg (see Chapter 7) and having a larval form that metamorphoses into the adult. The question here is whether or not there are also identifying cranial features.

Living amphibians belong to three groups: the frogs and toads, the salamanders, and the Apoda or Gymnophiona. Only the first two groups will be described; the last contains little-known, worm-like, burrowing forms, the coecilians. A check-list of the bones of the amphibian head skeleton is given in Table 4-3.

Salamander or urodele Two American salamanders, *Cryptobranchus allegheniensis* (Figure 4-17) and *Necturus maculatus*, illustrate much of the range of variation seen in urodeles. In shape, the skulls of these two genera are quite unlike. Neither has retained an apparent outer roof, but the **parietal** bones form the top of the endocranium. Postparietals and supratemporals are lacking in this group as is the parietal foramen. The **nasal** and **maxilla** are lacking in *Necturus* but not in *Cryptobranchus*. Neither has a labial arch and the **quadratojugal** if present is fused to the **quadrate.** The

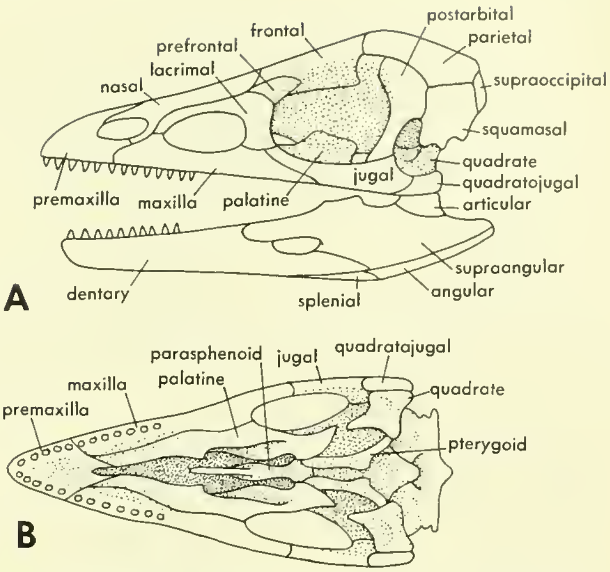


Figure 4-15. Skull and mandible of *Archaeopteryx*. (After Heilmann, 1927, and Kleinschmidt, 1951)

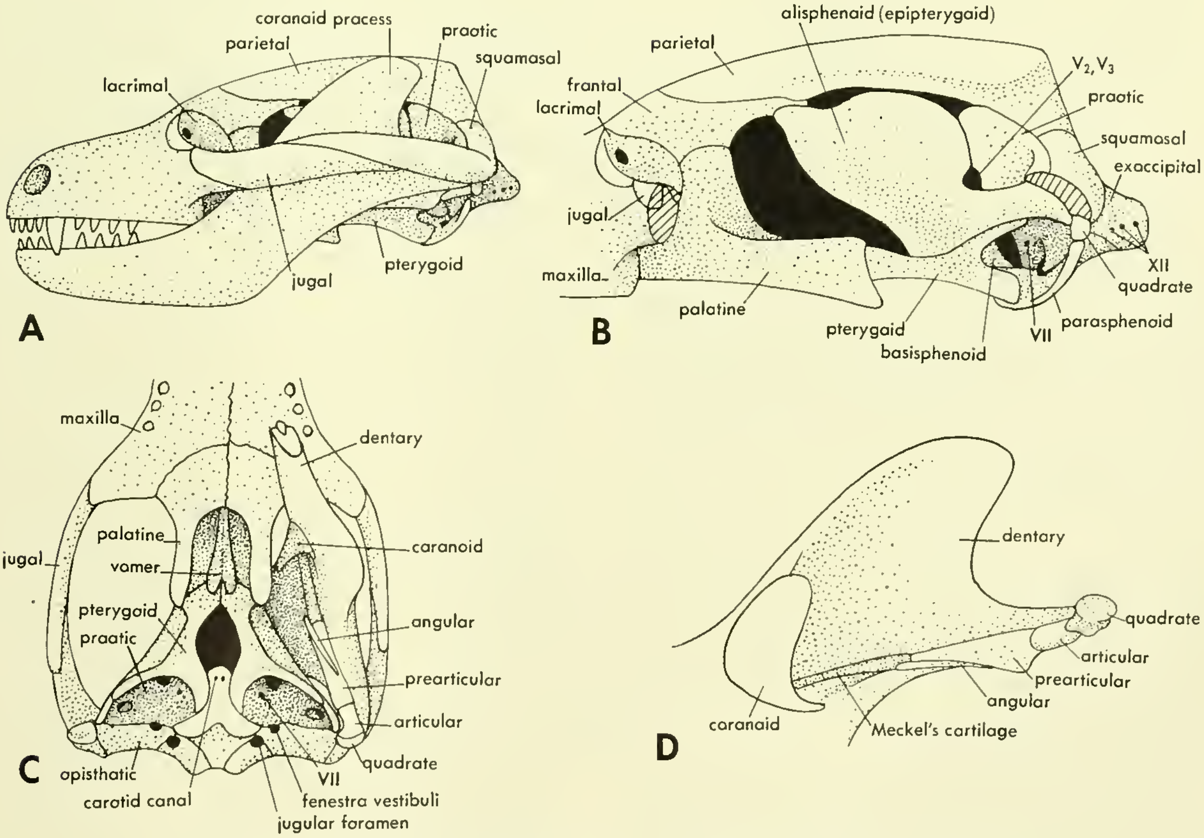


Figure 4-16. Skull and mandible of *Diarthrognathus*. A, lateral view; B, lateral view of cranium with zygomatic arch; C, palatal view; D, inner view of posterior end of mandible. (After Crompton, 1958)

TABLE 4-3 THE BONES OF THE HEAD SKELETON OF THE LIVING AMPHIBIA ARRANGED ACCORDING TO TYPE AND PLACE OF ORIGIN

Cranium (brain and sense organ capsule)	Splanchnocranium or Visceral Skeleton (dermal bones with*)
Endocranium (bones of chondral origin) exoccipital opisthotic prootic orbitosphenoid Eye sclerotic cartilage or plates Dermocranium (bones of membrane origin) parietal frontal nasal septomaxilla prefrontal squamosal jugal vomer parasphenoid	Mandibular arch—Palatoquadrate and Meckel's cartilage premaxilla* maxilla* quadratojugal* palatine* pterygoid* quadrate articular mental angular* supraangular* in *Cryptobranchus* dentary* prearticular* coronoid* Hyoid arch stapes ceratohyal hypohyal basihyal Branchial arches ceratobranchials I, II, III hypobranchials I, II copulae I, II

vomers are broad separate plates bearing teeth. A palatine is lacking. The **pterygoid** forms much of the palatoquadrate complex; the quadrate is little more than the articular area for the lower jaw—the **squamosal** supports the palatoquadrate and attaches it to the cranium through its suture with the otic capsule and parietal. The pterygoid sutures with the broad **parasphenoid** covering the ventral aspect of the cranium. This is a nonkinetic skull.

In this group the number of endocranial ossifications is reduced; supraoccipital, basioccipital, basisphenoid, and ethmoid bones are lacking. *Cryptobranchus* lacks an **opisthotic**, as do most amphibians, but this element is present in *Necturus*. An **orbitosphenoid** is lacking in *Necturus;* its place is taken by a process of the **frontal**. The bilateral occipital condyles are processes of the exoccipitals. The eye is encircled by a **sclerotic cartilage**.

The lower jaw is formed of the usual complement of dermal bones, lacking only the splenial. A **coronoid** is present (and bears teeth) in *Necturus* but not *Cryptobranchus*. The latter is unique in that it appears to have a **supraangular**. There are **articular** and **mental** ossifications in Meckel's cartilage.

The hyoid apparatus, or visceral skeleton, is formed from parts of several arches (Figure 4-18). There is a region of ossification in the **ceratohyal**, the **first** and **second hypobranchials**, and the **second** and **third ceratobranchials** of *Cryptobranchus*. Of the two genera, the branchial skeleton of *Cryptobranchus* is the better developed; yet it is *Necturus* which has two pairs of branchial openings, between ceratobranchials I and II, and II and III, and a large external gill on each of the three ceratobranchials. *Cryptobranchus* has a single pair of external openings between ceratobranchials III and IV and no external gills.

The **stapes** of both has a short stylus and a large footplate set in the fenestra vestibuli of the otic capsule. There are extensive cartilaginous areas above and below the **footplate**. The **stylus** is curved toward and sutures with a process from the **squamosal** in *Necturus;* there is a ligamentous attachment to the same area in *Cryptobranchus*. This association of stapes and quadrate (through squamosal) is assumed to function in transmission of vibrations (sound) into the inner ear.

EMBRYOLOGICAL DEVELOPMENT The details of development are not known for either of the genera described but can be inferred from accounts of other salamanders. Chondrification begins in the visceral skeleton with the appearance of the posterior part of the **palatoquadrate**, **Meckel's cartilage**, the **ceratohyal**, and four **ceratobranchials** with their **copulae**. In the endocranium the **trabeculae** shortly appear, well separated—a condition described by the term **platytrabic**. Each trabecula is continuous with the **orbital cartilage** of its side through the **preoptic**, **metoptic**, and **antotic pillars**. The posterior end of the trabecula attaches to the **parachordal**. The developmental process is partly indicated in Figure 4-19.

The **stapes** appears in association with the fissure-like **fenestra vestibuli** and, as a part of the hyoid arch, is joined to the **ceratohyal** by a strand of mesenchyme cells which later become attached to the palatoquadrate.

The dermal bones develop as in higher forms; those which are lacking in the adult are not indicated at anytime in the embryo. On the outside of the quadrate there is a small quadratojugal center which fuses with that bone. The endocranial bones arise as perichondral ossifications, and the exoccipital of *Cryptobranchus* spreads into the area ordinarily occupied by the opisthotic. The orbitosphenoid arises in the orbital cartilage. The pila antotica does not ossify nor does the ascending process of the palatoquadrate.

GENERAL OBSERVATIONS The salamanders described do not include all of the variations observed in urodeles. A **septomaxilla**, **lacrimal**, and **basioccipital** are present in some. The palatoquadrate complex may pivot on the prootic; that is, the skull may be kinetic. **Sclerotic bones** occur in at least one salamander, while others lack even the cartilaginous ring. In development the larva may have a horny upper jaw, and an **intermandibular cartilage** occurs in some.

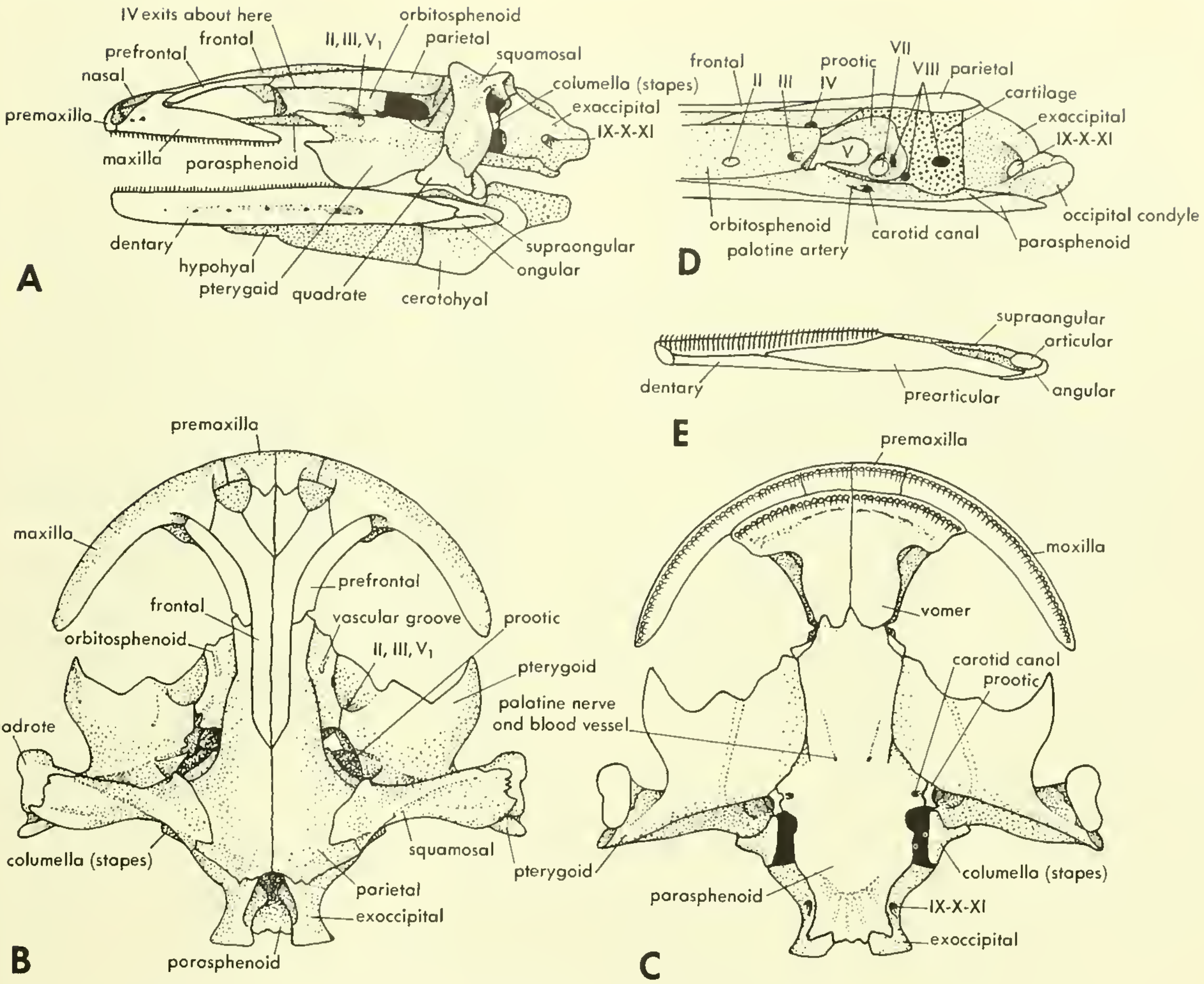


Figure 4-17. Skull and mandible of *Cryptabranchus*. A, lateral view of head skeleton; B, dorsal view of skull; C, ventral view of skull; D, medial view of right half of cranium; E, medial view of mandible.

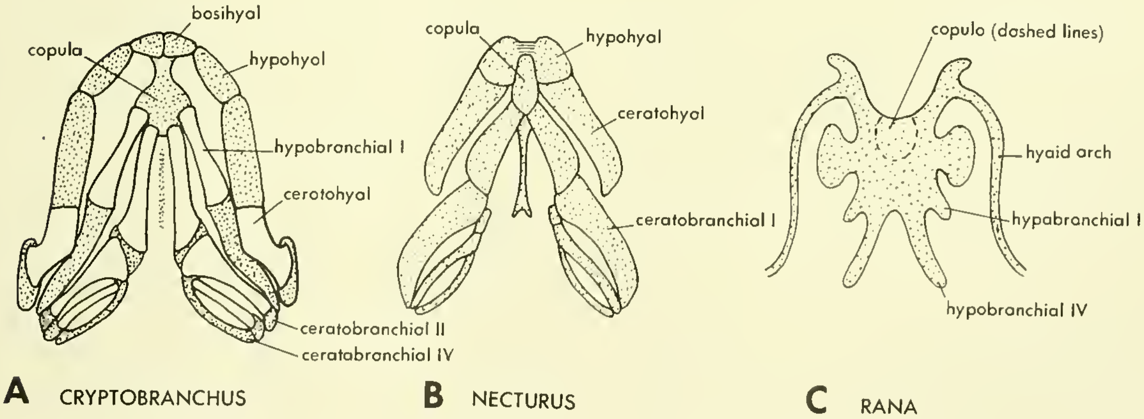


Figure 4-18. Hyoid apparatuses of *Cryptobranchus*, *Necturus*, and *Rana* as seen from below.

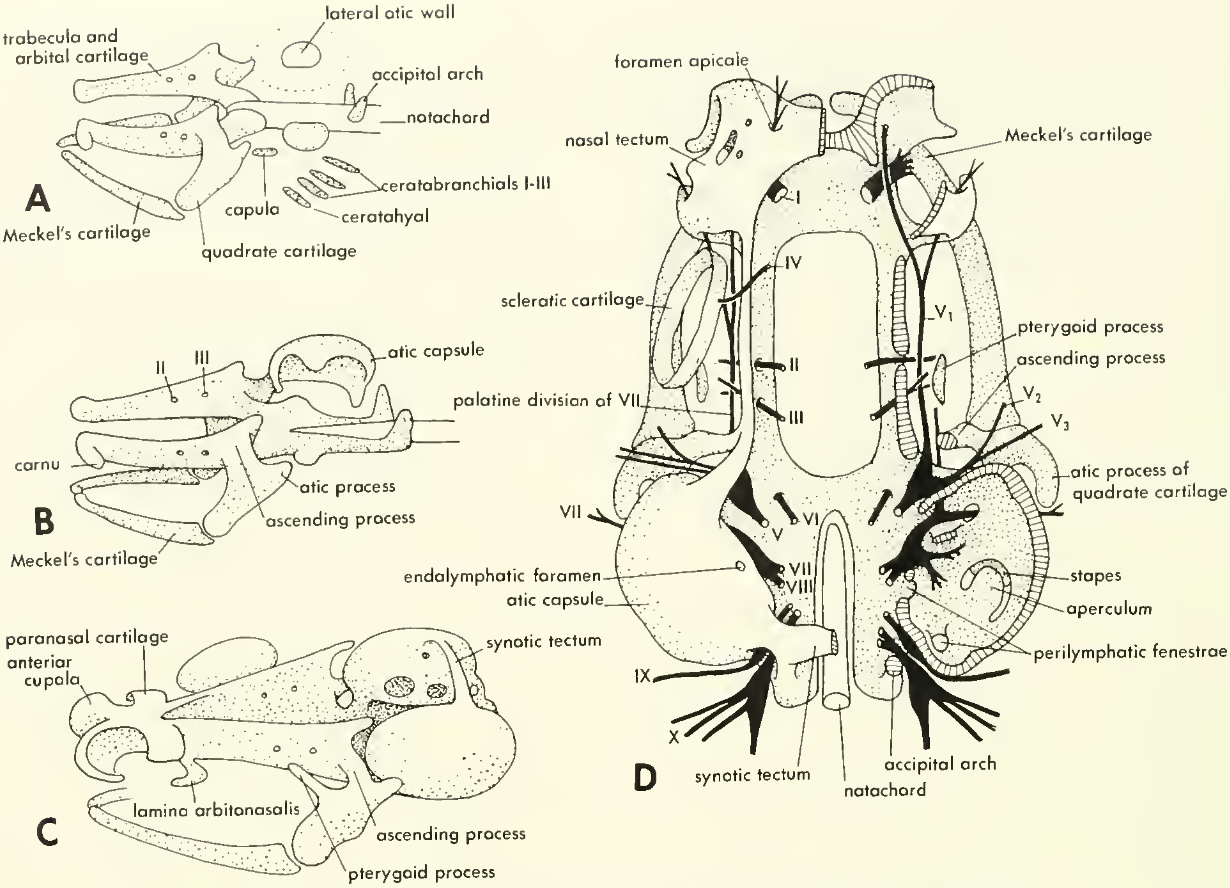


Figure 4-19. Development of chondrocranium in *Ambystoma*, a salamander, and *Salamandra.* A, head skeleton 9-mm larva of *Ambystoma* as seen in dorsolateral view; B, 11-mm *Ambystoma;* C, 23-mm *Ambystoma;* D, 23-mm *Salamandra* in dorsal view with one half of the roof removed. (A, B, C after DeBeer, 1937; D after Goodrich, 1930)

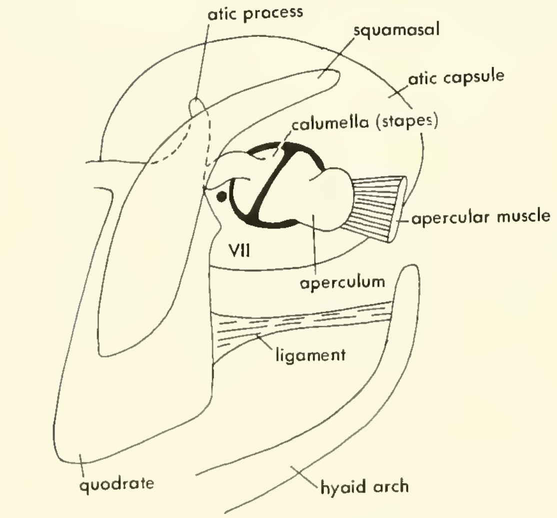


Figure 4-20. Otic capsule region of salamander (*Salamandra*) showing operculum. (After Kingsbury and Reed, 1909)

Description of the salamander would be incomplete without reference to the **operculum** (Figures 4-19, 4-20). Whereas the stapes is a part of the hyoid arch, the operculum is a piece of the otic capsule wall, which becomes almost completely separated from that wall by a membranous gap. This bit of wall never ossifies and serves for the insertion of an opercular muscle that has its origin on the suprascapulum of the pectoral girdle. This muscle (or ligament) functions in transmitting sound vibrations from the pectoral girdle to the inner ear.

Frog or anuran The frog is a fine example of a highly modified animal (Figure 4-21). The roof of the skull is much reduced; the **squamosal** forms an incomplete temporal arch and the fused **frontal** and **parietal** (**frontoparietal**) of either side form the roof of the endocranium. There is no apparent parietal foramen (see Figure 13-6). What is usually identified as the nasal is probably the **prefrontal. Palatines** are present, and the **pterygoid** articulates with the otic capsule behind the palatal division of the seventh cranial nerve.

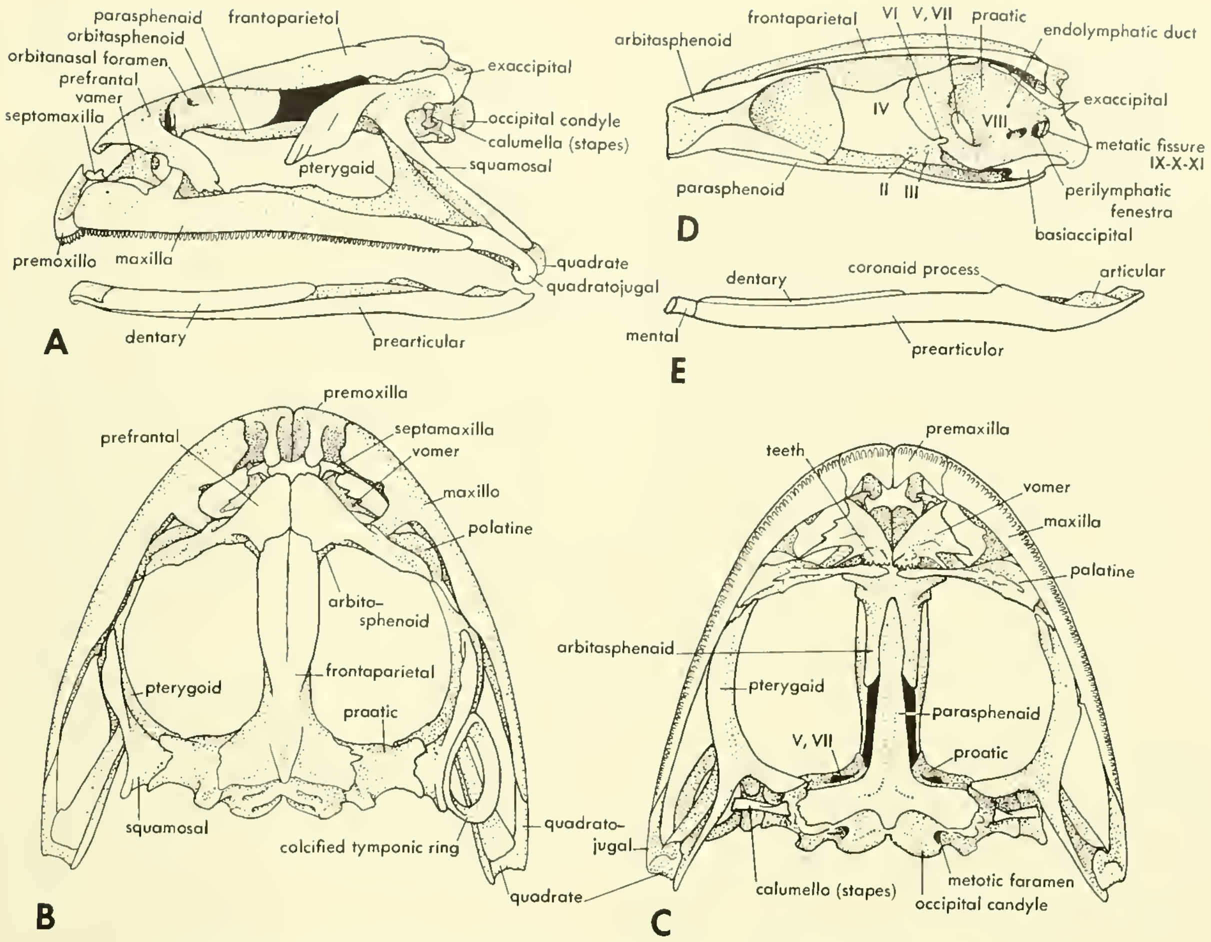


Figure 4-21. Skull and mandible of the Bullfrog. A, lateral view of skull and mandible; B, dorsal view of skull; C, ventral view of skull; D, medial view of right half of endocranium; E, medial view of right half of mandible.

The pterygoid sutures along much of the length of the quadrate process of the squamosal. The **quadrate** is much reduced and limited to the articulation area. The small **quadratojugal** is fused to the quadrate. A broad **parasphenoid** covers the ventral aspect of the cranium and extends forward between the orbits.

The endocranium has **exoccipital, prootic,** and **orbitosphenoid** ossifications only. The exoccipital invades the area of the opisthotic, but in the Bullfrog there is evidence of a separate ossification center for this **opisthotic** portion. The orbitosphenoid ossification lies anterior to the optic nerve and as such might be viewed as an ethmoid. In the primitive amphibian this bone extended both in front of and behind the optic nerve. There is a calcified operculum behind the **stapes** in the lateral wall of the otic capsule. The operculum is an irregular mass as closely attached to the stapes as to the capsule wall.

The **premaxilla** and **maxilla** bear slim pointed teeth, which are like those of the salamander in that the point is easily broken off, along an **abscission line,** from the base. The teeth are attached in the **pleurodont** fashion to the jaw. The mandible is without teeth. It is formed of a small **dentary,** a large **prearticular** that makes up most of the ramus and is fused to the small calcified **articular,** and a small **mental** ossification on either side of the symphysis.

The hyoid and branchial arches give rise to a **columella** and the **hyoid apparatus.** The latter is a completely cartilaginous structure formed of a broad **copular plate** attached to the cranium through the hyoid arch. The **epihyal** is attached to the cranium behind the area of contact of the basicranial process of the pterygoid and below the **fenestra vestibuli** and the columella.

EMBRYOLOGICAL DEVELOPMENT The development of the frog head skeleton is of interest because of the early appearance of larval jaws lying anterior to the definitive jaws (Figure 4-22). These larval jaws suggest a way that the jaws of the gnathostomes might have arisen in phylogeny. This

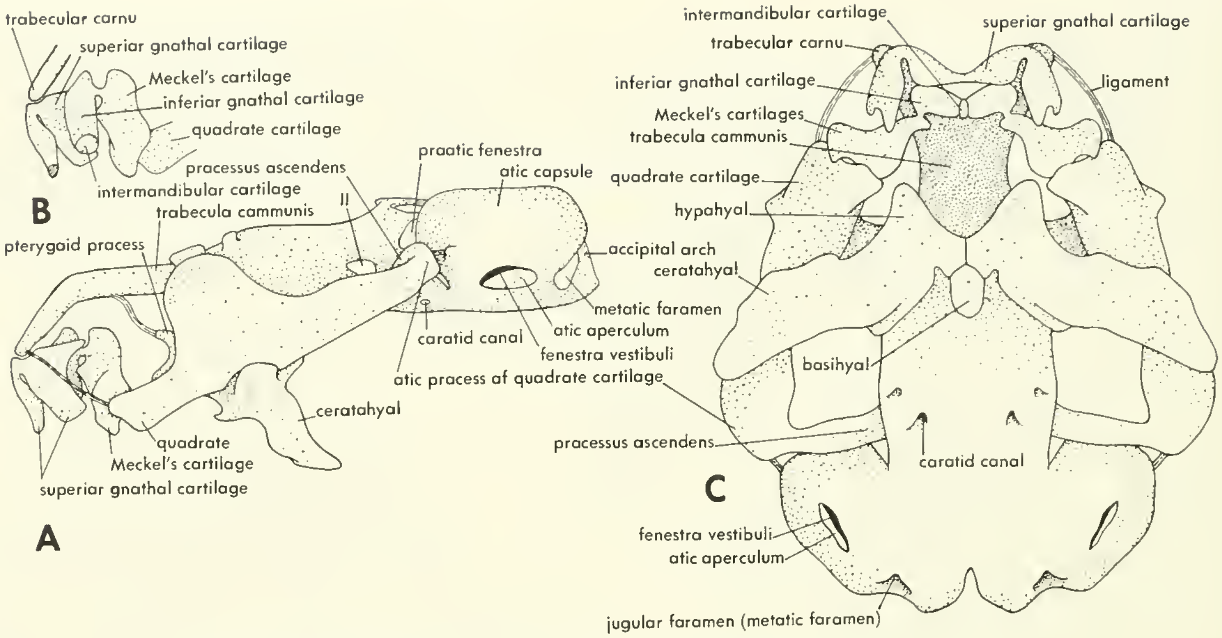


Figure 4-22. Cartilaginous jaws and chondrocranium of tadpole. A, lateral view of entire chondrocranium; B, medial view of right half of jaws; C, ventral view of chondrocranium.

type of chondrocranium also is peculiar in that the anterior parts appear before the posterior region.

Metamorphosis is a rather lengthy process—from an alga-feeding existence to a carnivorous one, from small premandibular jaws armed with horny teeth to large mandibular jaws armed with bony teeth. The **superior gnathal cartilage**, the upper jaw of the larva, gradually disappears and is replaced by the premaxilla. The **inferior gnathal cartilage**, which supports the horny teeth of the larval lower jaw, becomes attached to the anterior end of **Meckel's cartilage**, and the dentary arises lateral to it. Ossification converts the inferior gnathal to the mental bone.

As these changes occur, the gap of the mouth moves back and the articulation between Meckel's cartilage and the quadrate moves back with it. At first the palatoquadrate has its mandibular articulation anterior to the vertical of the eye. With the posterior shift of this articulation, the palatoquadrate undergoes drastic shortening and rotates backward to form the definitive suspensorium. In this rotation, the otic process of the otic capsule becomes shortened and flexed and gradually disappears. At no time in its development does the frog have a basitrabecular (basipterygoid) process or a basal attachment of the palatoquadrate in the region of such a process.

The development of bones begins during metamorphosis. The bones of the jaws appear early, the teeth later. Several bones present problems as to their homology. The palatine and pterygoid appear to be properly named but the prefrontal, frontoparietal, and squamosal are in doubt. These problems cannot be solved until transitional fossil forms, linking the anurans with the basic skull pattern, are found. However, speculations on the probable homology of these parts are in order.

The prefrontal is usually identified as the nasal, perhaps because of its arising above the orbitonasal lamina. This position is more typical of the prefrontal. A true nasal lies over the nasal capsule and forms a part of the margin of the external naris—this is not true of the bone of the frog. The lack of contact between this bone and the nasal processes of the premaxilla and the presence of a strong orbital process extending down medial to the lacrimal duct support its identification as the prefrontal.

The frontoparietal presents a more easily solved problem. According to Gaupp's (1906) account, there are two pairs of centers for this bone. Recent observations suggest that these bones arise from both single and double pairs of centers. The general pattern among tetrapods, where large orbits are involved, has been elongation of the frontals and reduction in the size of the parietals. It is likely that reduction of ossification in the anuran line has involved suppression of the parietal and its replacement by or fusion with the frontal.

The squamosal of the anuran is a double structure in its embryological development. One part is associated with the muscular process of the palatoquadrate; the other arises over the otic capsule above the paroccipital or parotic process. The latter ossification center has been equated with the postfrontal (or the supratemporal), but its lack of contact with the frontal and its association with the otic capsule is against the assumption that is belongs to the circumorbital series. The two centers observed in the toad appear to belong to a single bone, the squamosal. Separation can be attributed to the shortening and rotation of the palatoquadrate during metamorphosis.

What has been called the angular of the lower jaw is described here as the prearticular in spite of the lack of a foramen for the medial mandibular (chorda tympani) division of the hyomandibular nerve.

General observations on living amphibians The frog head skeleton differs from that of the salamander in several features. The frog has a prootic foramen for the trigeminal and facial nerves anterior to the otic capsule and the prootic ossification. The palatine branch of the facial nerve passes over the area of contact between pterygoid and otic capsule rather than behind and under it. The orbitosphenoid of the frog lies anterior to the optic nerve and invades the orbitonasal lamina and nasal septum. That of the salamander lies behind the nasal capsule and encloses the optic foramen. The frontal and parietal of the frog are fused, the quadratojugal is distinct and continues the labial arch back to the quadrate—with which it is fused in both types. The frog has a tympanum, ringed with cartilage or calcified cartilage, and the stapes extends out to this membrane suspended in the cavity of the middle ear. The parasphenoid of the frog has a narrow rostral part, a processus cultriformis, whereas that of the salamander is broad. The inner aspect of the otic capsule of the frog is ossified, isolating the various openings in bone.

The two groups agree in that the orbital series of bones is undeveloped: both lack the postfrontal, the postorbital, the jugal, and usually the lacrimal (some salamanders have the latter). Both lack the tabular and postparietal; of the temporal series, the supratemporal is questionably retained in the anurans. Both have a large interpterygoid fontanelle, the opening between the pterygoid and the parasphenoid rostrum, and a reduced or absent palatine. There is no ectopterygoid or epipterygoid. The teeth of the jaws are numerous and pleurodont and agree in having a tooth denticle fused to a hollow bony base which in turn is fused along its outer aspect to the jaw margin. In both, the otic capsule is usually formed by the prootic and exoccipital; usually a basioccipital is lacking. A supraoccipital is always lacking. The stapes is usually associated with an operculum in the frog and some salamanders. In both the upper jaw is fixed in position, the palatoquadrate connecting through cartilage with the neurocranium.

Fossil Amphibians

Early Amphibians In terms of the head skeleton the frogs and salamanders show much agreement, even though this has been judged by some as indicative of parallel changes rather than direct common ancestry. The frogs perhaps extend back in time to *Protobatrachus* from the early Triassic of Madagascar. The salamanders trace back to the lower Cretaceous and are then lost. Salamander-like organisms are known from the Upper Pennsylvanian; these are the branchiosaurs.

The branchiosaurs are small in size. In their life history, which is known in some detail, they went through a period with internal and external gills followed by a period with only external gills. As adults they were lung breathers. These small animals have been viewed as the larvae of larger forms, but, if not adults themselves, they approximate the adult form of the ancestral amphibian better than the larger forms. At least some of the genera of this group agree with the living forms in having four digits on the forelimb; these are *Amphibamus* and *Branchiosaurus* (Figure 4-23).

The dermal skulls of *Amphibamus* and *Branchiosaurus* agree in most details. The roof consists of paired **postparietals,** paired parietals between the anterior ends of which is a **parietal foramen,** then paired **frontals** and **nasals.** Lateral to the postparietals is a small **tabular** in *Branchiosaurus* but not in *Amphibamus.* Lateral to the parietal is a large **supratemporal** in both, but neither has an intertemporal.

The circumorbital ring of bones consists of **prefrontal, postfrontal, postorbital, jugal,** and **lacrimal** in both. The lacrimal and jugal do not meet below the eye in *Amphibamus.* The lacrimal in at least one species of *Branchiosaurus* contains a canal for the **lacrimal duct** extending from the orbit margin, where it has two openings, to below the ventral margin of the external narial opening. There is no septomaxilla at the posterior margin of the external narial opening. The **squamosal** is a large plate forming much of the anterior and ventral margins of the **tympanic notch.**

The upper jaw consists of **premaxilla, maxilla,** and **quadratojugal** and the **palatoquadrate complex** of **pterygoid, epipterygoid,** and **quadrate.** There is a broad **vomer plate** to either side of the midline. The **parasphenoid** has a broad **basiotic expansion** and a long, narrow, **cultriform process.**

The **endocranium** was largely cartilaginous but **exoccipital** ossifications have been observed as well as a center in the otic capsule (opisthotic?). The delicate stapes had a foot plate expansion and a shaft perforated by a foramen. There was a **sclerotic ring** of more than twenty overlapping, bony plates. The lower jaw is not well known but had **dentary, angular, supraangular, prearticular, coronoid,** and **articular** ossifications. The cartilaginous branchial skeleton is not known.

Even more primitive than the branchiosaur, in terms of having a larger number of bones in the cranial roof, and in having grooves for sensory canals, is *Eugyrinus wildi* from the Lower Pennsylvanian. In general size, shape, and flattening of the head skeleton, this is a branchiosaur. In addition to the bones described above there was an **intertemporal** and a **septomaxilla.** The **parasphenoid** is grooved and perforated by the internal carotid and there are slight **basipterygoid processes.** In the palate there is a large pair of **vomers** and, to the sides behind the **internal nares,** a

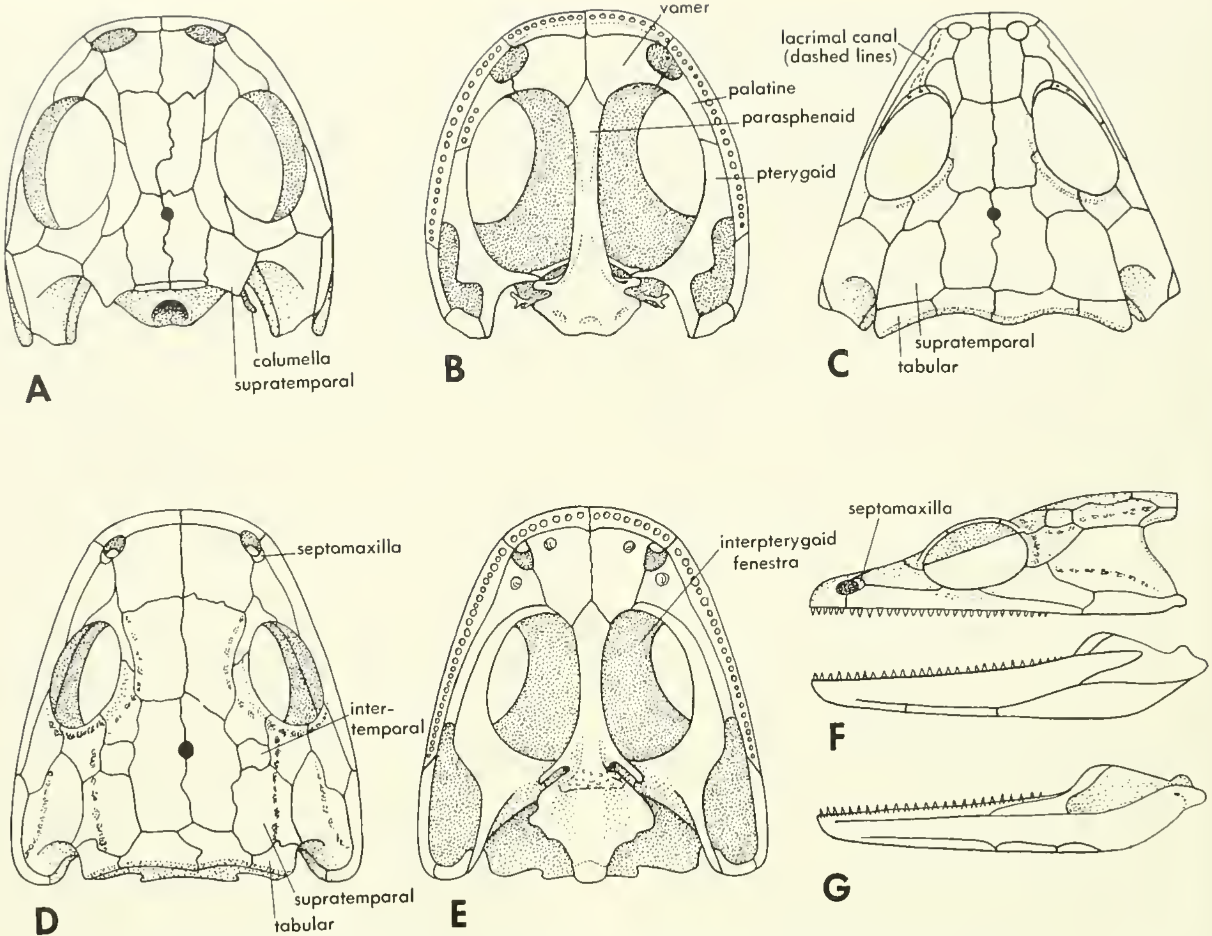


Figure 4-23. Fossil amphibians, branchiosaurs, and *Eugyrinus*. A, B, dorsal and ventral views of *Amphibamus*, a branchiosaur; C, dorsal view of *Branchiosaurus*; D, E, dorsal and ventral views of *Eugyrinus*; F, lateral view of skull and mandible or *Eugyrinus*; G, medial view of mandible of *Eugyrinus*. (After Gregory, 1950, and Watson, 1940)

pair of **palatines.** The vomer and **palatine** each had a large tooth or **tusk** affixed to them. The posterior part of the palatine was probably separated as the **ectopterygoid.** The pterygoids were triradiate (three-pronged) and there were large **interpterygoid fontanelles.** A small **epipterygoid** extended up from the palatoquadrate, near its attachment to the basipterygoid process, and passed between the V_1 and V_2 branches of the trigeminal nerve.

The endocranium had slight **exoccipital** and **basioccipital** perichondral ossifications. These bones contributed to the single **occipital condyle.** The exoccipital was perforated by a hypoglossal foramen and formed the posterior margin of the vagus foramen. There was no supraoccipital; the postparietal and tabular had slight flanges extending down over the occipital surface. The otic capsule was ossified, probably from prootic and opisthotic centers.

The mandible was quite primitive in its cover of dermal bones. It was like that of the branchiosaur but had two small **splenials** along the ventral inner margin. The articular region appears to have been ossified from the **supra-angular.** There was a foramen for the internal mandibular branch of the facial nerve (**chordi tympani**) just below the articular area. The branchial skeleton is not known.

Along with the Seymouriamorpha, *Eugyrinus* is classed as an anthracosaur. The anthracosaurs, or coal lizards, are presumed to be on the direct line of evolution to the reptile.

The anthracosaur usually described is *Palaeogyrinus* (Figure 4-24). Only the skull of this Pennsylvanian form is known, but in some detail. The roof was like that of *Eugyrinus* in composition but not in shape. *Palaeogyrinus* was also considerably larger in size; its skull was about six inches long as compared with three-quarters of an inch for that of *Eugyrinus*. The dermal bones showed a canal pattern somewhat more elaborate than that of *Eugyrinus*; a distinct groove arched over the quadratojugal and up toward the preopercular canal groove. The palate differed in having a small interpterygoid fontanelle, which is presumed to be more like a crossopterygian fish and therefore primitive. There was a toothed ectopterygoid and a small epipterygoid in the palatoquadrate complex. The vomers were broad plates and the parasphenoid had a long, slim rostral process. There were distinct basipterygoid processes.

The endocranium was well ossified from behind the olfactory capsules to the occiput. There were distinct exoccipitals and a basioccipital that contributed to the single occipital condyle. The exoccipital was perforated by the hypoglossal foramen and extended forward to the metotic foramen that served nerves IX, X, and XI. A "supraoccipital" lay above

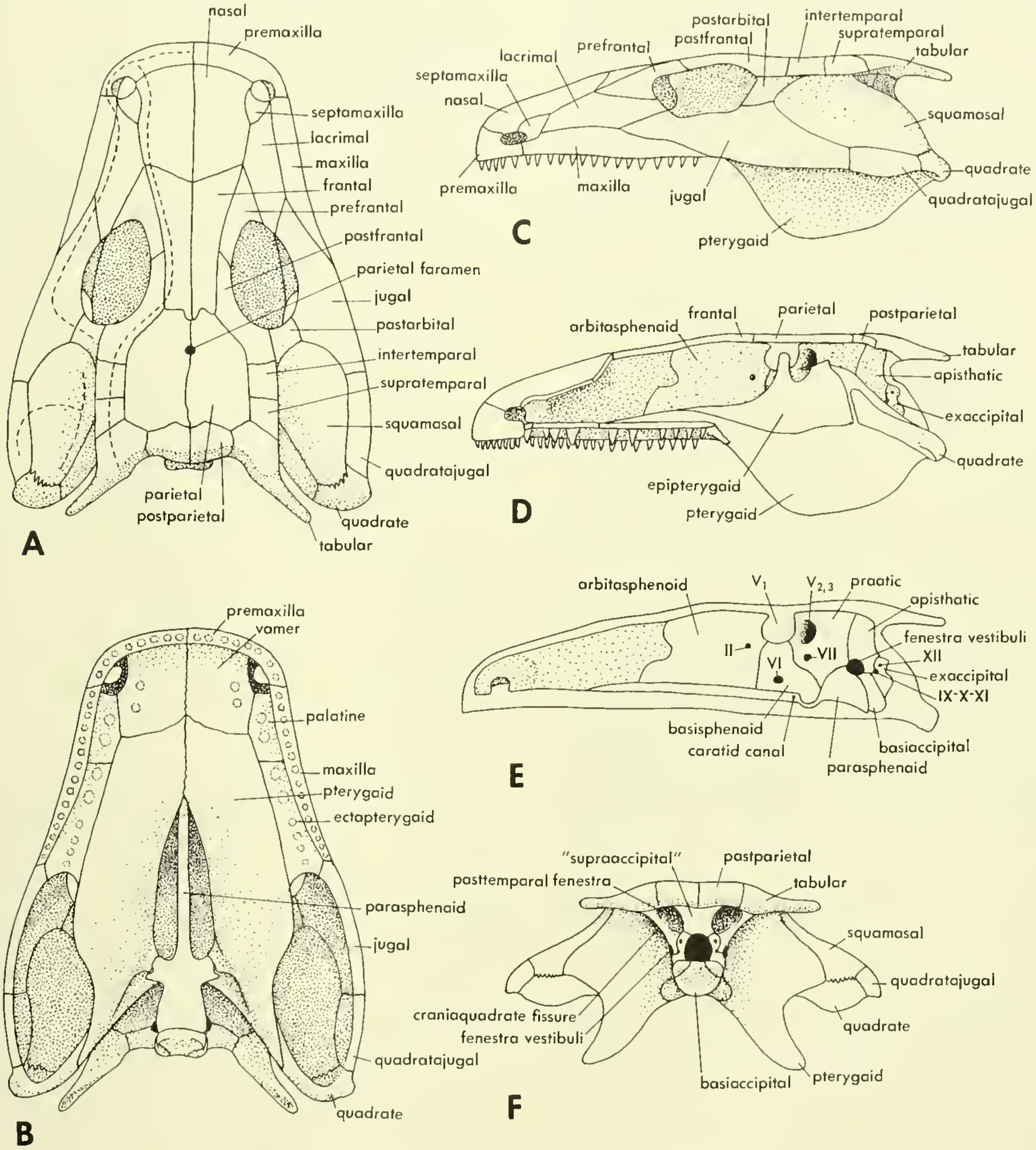


Figure 4-24. Skull of *Palaeogyrinus*, an early Pennsylvanian amphibian from Scotland. A, dorsal view with sensory-line system indicated on right half by dashed lines; B, palatal view; C, lateral view; D, lateral view with bones of cheek removed; E, lateral view with palatoquadrate complex removed; F, rear view. (After Romer)

the foramen magnum. Since this is the only occurrence of such a bone in amphibians, it is suggested that it is a secondary ossification or calcification of the cartilaginous area observed here in other fossil forms.

The parasphenoid extended high up on the sides of the otic region nearly reaching the fenestra vestibuli, which marks the line of union of prootic and opisthotic—these two bones are indistinguishably fused and therefore only presumed to be present. The anterior margin of the prootic forms the posterior wall of a large prootic foramen. This foramen has been described as a notch between oticoccipital and ethmosphenoid division of the endocranium (as in the crossopterygian fish); however, ventrally there was no indication of such divisions—the basisphenoid region was fused with the parasphenoid and the otic capsule. The basisphenoid area had lateral basipterygoid processes and extended forward as the interorbital septum below and the lateral and ventral walls of the anterior part of the cranium above, that is, as the orbitosphenoid. Marking the limit between the basisphenoid and orbitosphenoid was a large orbital fenestra. This endocranium was solidly roofed except for a parietal foramen.

The endocrania of *Edops craigi* (Pennsylvanian) and *Eryops megalocephalus* (Lower Permian) are better known but of a somewhat different plan. Both of these are large species, the first with a head length of about two feet, and the second, one and a half feet. In these the otic region is continuous with the ethmosphenoid region. The details of structure suggest some specialization but contribute little to the problem at hand.

The oldest amphibians known are from the uppermost Devonian or the Lower Mississippian. These are the ichthyostegids and acanthostegids from Greenland, and several fragmentary types known as *Elpistostege*, *Otocratia*, and *Loxomma*.

The icthyostegids are well known in terms of the dermal head skeleton but the endocranium is not yet fully described. *Ichthyostega* (Figure 4-25) is of moderate size with a head length of about eight inches. It lacks the intertemporal bone but has a small preopercle and subopercle. The sensory canals are embedded in the bone or lie so superficially that even grooves are not formed. The external naris is peculiar in its marginal position. The palate has minimal interpterygoid fontanelles and the parasphenoid is limited to the rostral portion. The lower jaw was encased in dermal bones; there were three coronoids and an ossified Meckel's cartilage. The hyoid arch is not known nor is the state of the branchial skeleton—presumably they were cartilaginous. The endocranium has been described as having ethmosphenoid and oticoccipital divisions like that of a crossopterygian.

If this endocranium is two parted then the ichthyostegid must be viewed as distinct from other early amphibians. In terms of their dermal shield, there is some support for this view but not enough to lead to the necessary conclusion that an amphibian type of structure was developed at least twice. Such a polyphyletic origin is not warranted in terms of the facts at hand.

Seymouriamorphs and origin of reptiles The seymouriamorphs are Upper Pennsylvanian and Permian fossil forms considered reptiles by some and amphibians by others. Since well-differentiated reptiles were already present at the time these animals occurred, they can be viewed as relicts, if indeed their line was ancestral to the reptiles.

The head skeleton of *Seymouria*, an early Permian form, has been described in detail (Figure 4-26). This head skeleton is quite similar to those already described, and thus it would be difficult to ascribe to it any definitely reptilian features. The lacrimal canal, the transverse posterior flange of the pterygoid, and the form of the sella turcica and dorsum sellae suggest the reptile. Basically, this is an amphibian skull; evidence of reptilian affinity is better marked in other parts of the skeletal system.

Earliest reptiles

The first reptiles in the fossil record show a bewildering amount of variation in the few details known. It is generally believed that there are two basic lines of Lower Permian forms: the diadectomorphs and the captorhinomorphs.

These lines differ in such features as the loss or great reduction of the otic notch and loose connection of the roof and cheek in the captorhinomorphs. The palate of the diadectomorph generally lacked interpterygoid fenestrae and the pterygoid was sutured to the basis cranii rather than articulated with a large basipterygoid process. The diadectomorph had a well-ossified endocranium with a trigeminal foramen, whereas the captorhinomorph had the anterolateral cranial wall, anterior to and above the trigeminal, widely open.

The two lines agreed in having the posterior part of the roof reduced in size with the result that the postparietals which were fused at the midline were moved, more or less, onto the occipital surface. Modification of the roof was accompanied by loss of the intertemporal and sometimes loss of the supratemporal or tabular. These changes were less marked in the diadectomorphs. Both groups also agreed in the reduction in the number of the coronoids and splenials to one of each, and in the presence of a small Meckelian fenestra.

The earliest known reptiles are hard to place in either of these groups (Figure 4-27). *Cephalerpeton*, from the Upper Pennsylvanian of Mazon Creek, Illinois, is possibly a captorhinomorph but so little of its skull is known that this must be largely conjectural. *Petrolacosaurus* is also of Upper Pennsylvanian age but is extraordinarily lizard-like in its greatly reduced premaxilla and in the form of the palate and its articulation with basipterygoid process. It could be considered a captorhinomorph but has also been compared with the Eosuchia.

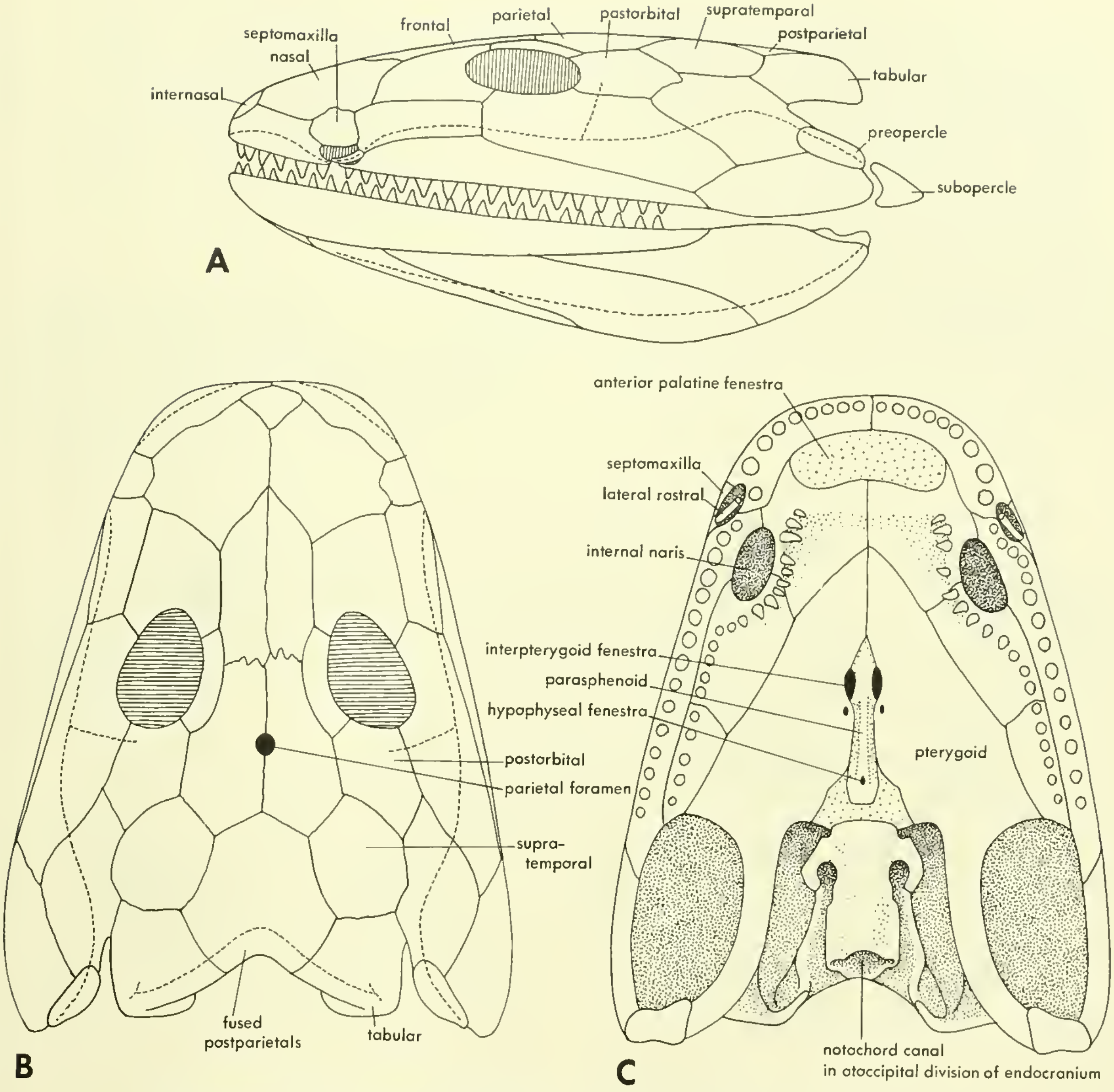


Figure 4-25. Skull and mandible of *Ichthyostega.* A, lateral view; B, dorsal view of skull; C, palatal view of skull. (After Jarvik, 1952, Säve-Söderbergh, 1932)

The eosuchians are known from the Upper Permian. The most primitive members belong to the Family Millerettidae, which has been raised to a separate order by some. In the millerettids the shield was basically anapsid, postparietals were still paired but lay on the occipital aspect, the intertemporal was lacking but the supratemporal and tabular were present. The posterolateral margin of the skull was slightly notched, as for a tympanic membrane (an amphibian feature). In some species the cheek had a small chink in it between jugal and squamosal (a synapsid opening). The palate was captorhinomorph-like, but the parasphenoid rostrum was toothed and the ectopterygoids were small. *Petrolacosaurus* agreed in all known details with this description.

Synapsid reptiles, the pelycosaurs, were common in the early Permian and are known also from the uppermost Pennsylvanian. Since the group is quite well defined and frequently highly specialized in form when first encountered, it is probable that its ancestors were contemporaries of *Petrolacosaurus* or occurred even earlier in time. It is quite probable that, since the pelycosaurs retain both supratemporal and tabular bones in the cranial roof along with

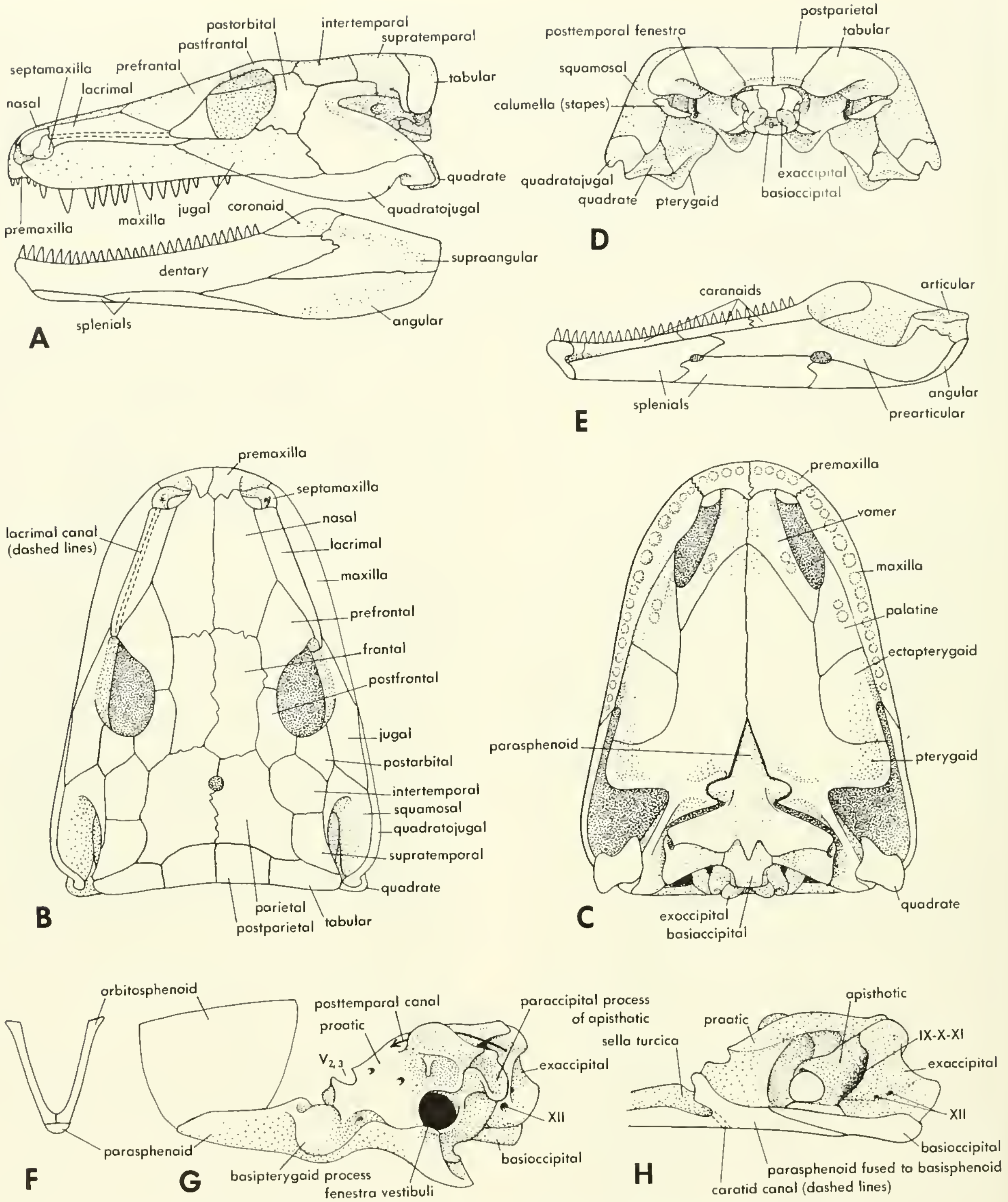


Figure 4-26. Skull and mandible of *Seymouria*. A, lateral view of skull and mandible; B, dorsal view; C, palatal view; D, rear view of skull; E, medial view of mandible; F, cross section of orbitosphenoids and parasphenoid; G, lateral view of endocranium; H, medial view of posterior part of right half of the endocranium. (After White, 1939, and Romer, 1955)

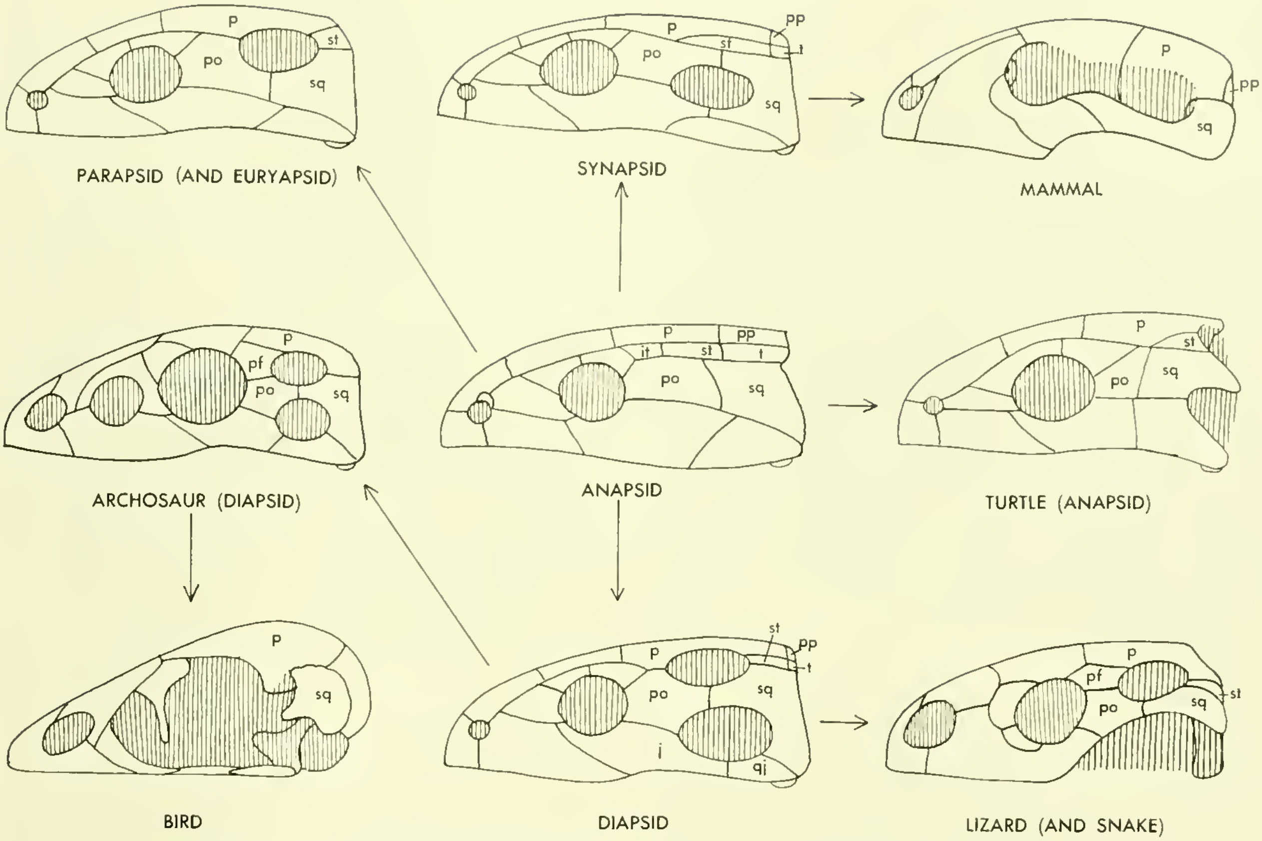


Figure 4-27. Evolution of the reptilian skull roof in terms of the temporal fenestrae or the loss of the cranial roof. Outlines of skulls are semidiagrammatic.

fused postparietals, this type represents an early and primary branch of the reptiles.

Goodrich (1916) cast some doubt on the idea of the reptiles being monophyletic, that is, all known reptiles stemming from a single primitive reptilian or prereptilian line. He proposed that the reptilian line giving rise to the mammals (this line as known now begins with the pelycosaurs) was distinct from that to which the other reptiles and birds belong, and that their basic difference in aortic arch plan must be traced back to separate amphibian lines. Watson has agreed with Goodrich and has suggested that the structure of the ear region also identifies these two lines.

It has also been proposed that the captorhinomorphs gave rise to the synapsids, whereas the diadectomorphs gave rise to the turtles and the other reptiles. Since the palatal structure of lizards or birds denies a diadectomorph origin, it must be assumed that the earliest members of this line had a basipterygoid articulated palate. It is simpler to assume at this stage in our knowledge that there were several primitive reptilian types, not just two. For example, the eosuchians (or Millerosauria) are no more modified than the others and could with equal verity be selected as an ancestral type. Why should the captorhinomorphs be selected as ancestors of the pelecosaurs when these groups, as now known, are contemporary?

General observations on the tetrapods

The head skeleton of the tetrapod can now be considered in more general terms. There can be little doubt that there was a common ancestral pattern of bones from which the head skeletons of the various living lines have evolved. In each of the three evolutionary lines—mammal, reptile, and amphibian (the bird is only a modified reptile)—there has been a reduction in the number of bones. For example, in each line the postparietals have been reduced in size and fused to each other and to other elements, or lost. Reduction in the number of bones is related to the loss of the outer cranial roof; this loss is associated in part with the freeing of the muscles of mastication. Reduction has also been a biproduct of the reorganization of the head skeleton in response to shortening of the jaws, the development of different kinds of kinesis, and the development of a neck. Reduction has been most marked in the living amphibians;

these are usually thought to be the most primitive and therefore should retain more of the original skeletal plan rather than less.

The living amphibians and reptiles agree in such improbable details as having a septomaxilla in the wall of the nasal passage; however, this may not be the same structure in the two groups nor the homolog of the similarly named bone of the early amphibian. The reptile and amphibian also agree in retaining all or most of the bones of the lower jaw and the primitive articulation. The mammal line differs in retaining the postparietals right down to the present and in its reorganization of the jaw apparatus which features an articulation of the dentary with the squamosal and conversion of the posterior jaw elements and quadrate into two middle-ear bones and the tympanic ring. Another part of the palatoquadrate complex, the epipterygoid, has become an integral part of the brain capsule in the mammal.

The convergence of these three lines as one goes back in time suggests a common ancestor not unlike some of the early amphibians. The problem now is to trace the tetrapod pattern into the fishes to see if it arose there or is a common inheritance of all vertebrates.

CHOANATE FISHES

The choanate fishes are of special interest because they are the assumed ancestors of the tetrapods. A study by Erik Jarvik contended that the choanate group, as usually defined—including crossopterygians and dipnoans—is not a natural one. The argument was based on the idea that the dipnoans lacked a true internal naris. The opening into the mouth, which has been called the internal naris, actually corresponds to the posterior external nasal opening of the crossopterygian, in the opinion of Jarvik. To avoid the consequences of this lack of agreement in choanae, these same fishes have been re-identified as the Sarcopterygii or the "fleshy-finned fishes" (see Chapter 6).

As suggested by the lack of agreement in nasal capsule development, there are several well-marked groups of choanate fishes, and each of them should be examined in attacking the problem of the origin of the tetrapod from a fish ancestor.

Crossopterygians

Osteolepiform The osteolepiform is usually described as the representative, or type, of the crossopterygian fish. Its selection is based on its presumed similarity to the amphibian. There are two well-known genera, *Osteolepis* and *Eusthenopteron* (Figure 4-28). These genera represent two different families, the Osteolepidae and Rhizodontidae.

The head skeleton in this group is made up of the bones listed in Table 4-4. The osteolepiform skull shows many variations; bones appear to be fragmented in some individuals and occasionally extra bones, anamestics or Wormian bones, appear between those regularly observed. The snout, the lower jaw, and to a lesser extent the cheek do not show suture lines because of the continuous cosmine and enamel layers over them. Sutures can be distinguished in these area when the outer layers of bone are removed or when viewed from the inside.

Although the osteolepiform skull and the amphibian skull have always been compared, opinions differ as to the nature of the comparisons. The difficulty stems in part from the addition of the extrascapular series to the roof (Figure 4-29) and the lack of paired nasal and frontal plates. These are repre-

TABLE 4-4 THE BONES OF THE HEAD SKELETON OF THE CROSSOPTERYGIAN FISHES ARRANGED ACCORDING TO TYPE AND PLACE OF ORIGIN

Cranium (brain and sense organ capsule)	Splanchnocranium or Visceral Skeleton (dermal bones with*)
Endocranium (bones of chondral origin)	Mandibular arch—Palatoquadrate and Meckel's cartilage
ossified in two pieces	
anterior: sphenethmoid	premaxilla*
posterior: oticoccipital	maxilla*
	quadratojugal*
Eye	suprapterygoid(s)*
	pterygoid*
sclerotic plates	ectopterygoid*
	palatine*
Dermocranium (bones of membrane origin)	palatoquadrate
	articular
Roof, snout, and floor	mental
extrascapulars (median and lateral)	angular*
	supraangular*
postparietal	posterior splenial*
parietal	anterior splenial*
tabular	dentary*
supratemporal	prearticular*
intertemporal	coronoids*
posterior spiracular	
tectal	Hyoid arch
nasal	opercle*
internasal (s)	subopercle*
vomer	marginal gulars*
parasphenoid (rostral and basitemporal parts)	lateral gulars*
	anterior medial gular*
	hyomandibula
	ceratohyal
Circumorbital and sensory line of snout	hypohyal
	basihyal
prefrontal	urohyal
postfrontal	
postorbital	Branchial arches
jugal	pharyngosuprabranchials I to IV
lacrimal	
lateral rostral(s)	epibranchials I to IV
medial rostral(s)	ceratobranchials I to V
	hypobranchials I to IV
Cheek	basibranchials (copulae I, II)
preopercle	
squamosal	

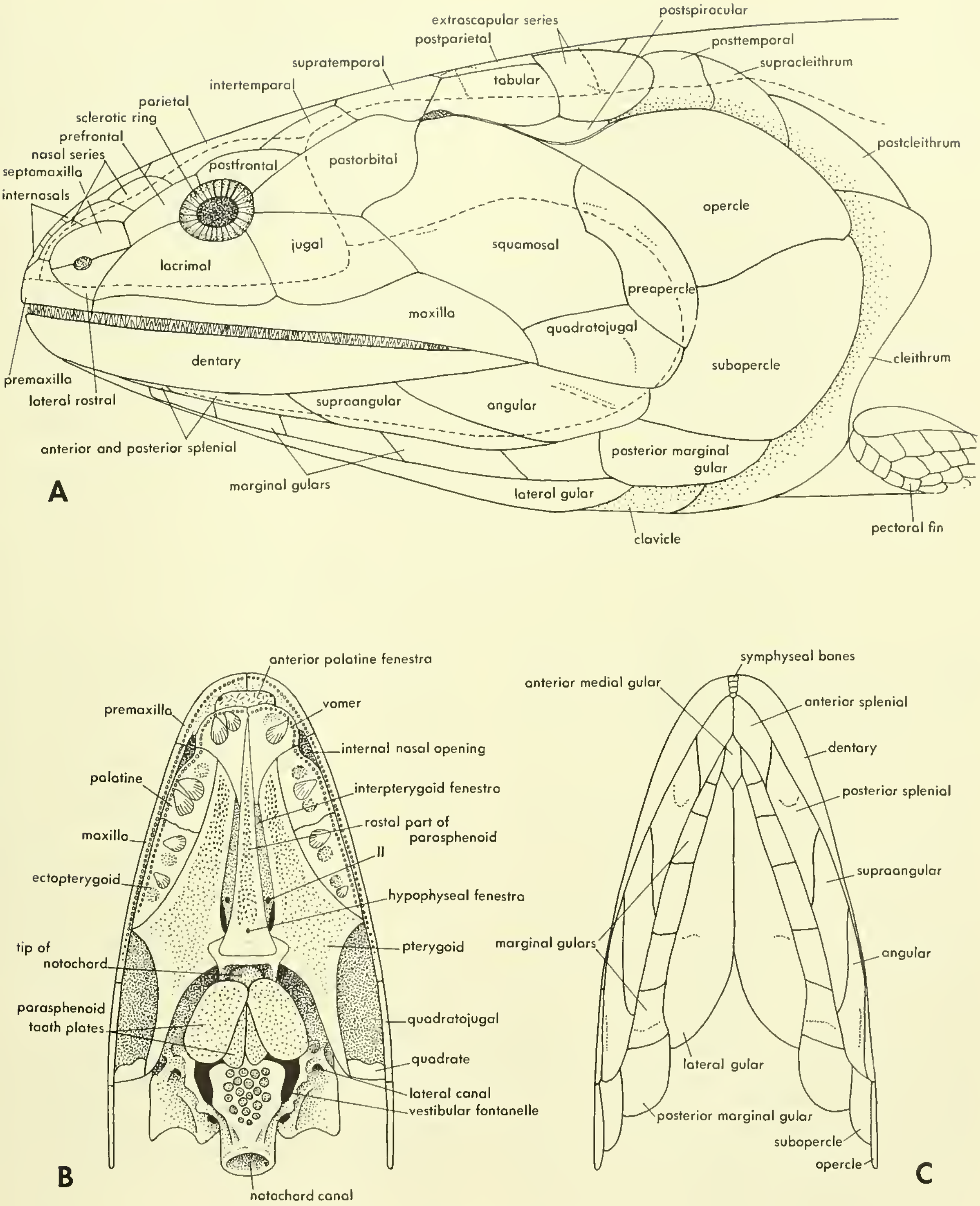
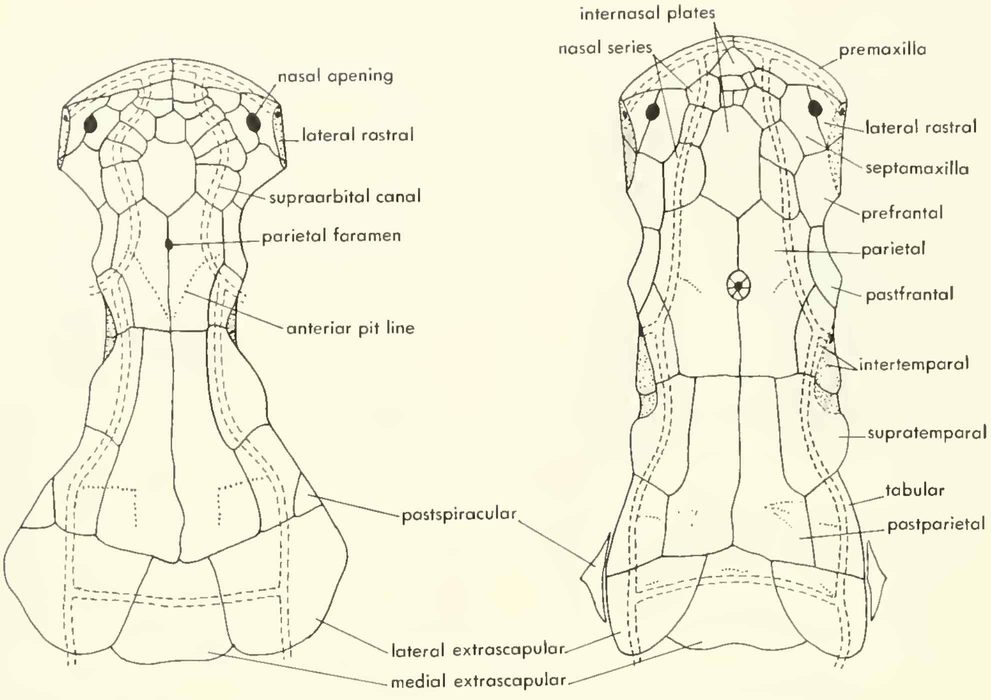


Figure 4-28. Dermal head skeleton of *Eusthenopteron*. A, lateral view of head and pectoral girdle; B, palatal view of skull; C, ventral view of head showing gular area. (After Jarvik, 1944)



OSTEOLEPIS EUSTHENOPTERON

Figure 4-29. Skull roofs of an osteolepid (*Osteolepis*) and a rhizodontid *Eusthenopteron;* representatives of the two families of Osteolepiform fishes. (After Jarvik, 1948)

sented in the crossopterygian by a series of "nasal" plates along the sensory canal and an irregular group of internasals (Figure 4-29). Primarily on the basis of the position of the parietal foramen, Westoll (1941) suggested the homologies of the bones in these two groups which are used in this discussion.

The roof of the skull appears to be hinged between the **parietals** and **postparietals.** The cheek is separated from the roof by a **spiracular cleft;** a **postspiracular** bone is wedged between the **supratemporal** and **tabular.**

The osteolepiform had a large **operculum** covering the gill openings (Figure 4-28). The operculum was supported by an **opercle** and **subopercle.** The **interramal** area of the throat was covered by **gular plates.** The dermal bones of skull and jaw contained sensory canals from which short tubes, sometimes numerous and branching, extended to the surface of the bone.

The endocranium (as described for *Eusthenopteron*, Figure 4-30) was divided into two parts along a line passing through the foramen of the profundus division of the trigeminal nerve and below the parietal-postparietal suture of the dermal roof. Since this joint is not movable, identification of it as a hinge is misleading. The anterior part of the endocranium is the **ethmosphenoid,** the posterior division the **oticoccipital.** The posterior division is subdivided by a fissure, actually a synchondrosis which may be bridged ventrally by thin ossifications, into an otic and an occipital segment. The occipital segment enclosed the foramen magnum above and the **notochord canal** below. It extended forward between the otic capsules from which it was partly separated by an ovoid **vestibular fontanelle.** The jugular foramen opened between this segment and the otic capsule

The otic capsules were joined by a synotic tectum in which was a small posterior fenestra. Just above the otic capsule were hollows in this roof; these are the **fossae Bridgei.** Each fossa was margined laterally by a **pterotic wing.** On the lateral aspect of the otic segment was a large **lateral commissure** with grooves anterior and posterior to it. This commissure formed the outer wall of a chamber into which opened the facial foramen. The lateral head vein also passed through this chamber The posterior portal was used by the hyomandibular division of the facial nerve. Above and below this portal were articular areas for the **hyomandibula.**

The ethmosphenoid division of the endocranium contained the anterior part of the brain cavity and the olfactory nerve canals. Posteriorly it consisted of the orbitosphenoid ossifications fused across the midline above and below. There was a wide parietal canal opening in the roof and a midline cerebral fenestra, filled by cartilage, posteriorly. The posterior orbital margin was somewhat raised and culminated above in a **basipterygoid process,** which lay behind the **pituitary vein foramen.**

The hyomandibula (Figure 4-31) had two articular facets proximally, an anteroventral one and a posterodorsal one.

Midway along its length it angled downward and was perforated by the **hyomandibular foramen.** Just below the angle, along the posterior outer margin, was the articular area for the opercle. There was no opercular process. Distal to the hyomandibula and lying between the outer and inner condyles of the quadrate area was a rectangular **symplectic,** which took part in the articulation of the lower jaw. Attached to the medial aspect of the symplectic, at its synchondrosis with the hyomandibular, was the **ceratohyal posterior.**

The ceratohyal segment of the hyoid arch was long, slim, and curved and it subdivided about midway into anterior and posterior ossifications. The anterior end of the ceratohyal segment articulated with a medially directed **hypohyal,**

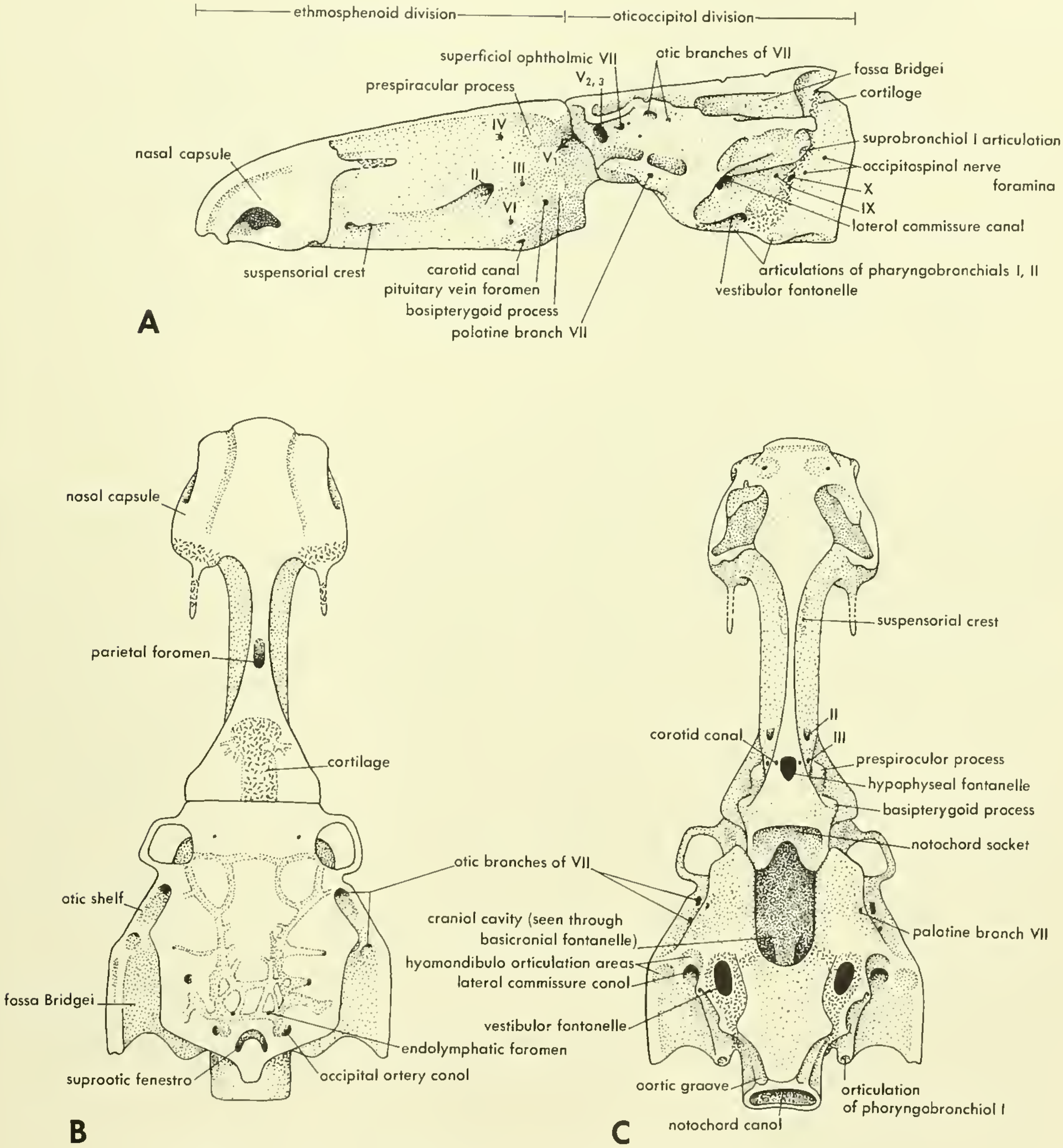


Figure 4-30. Endocranium of *Eusthenopteron*. A, lateral view; B, dorsal view; C, ventral view. (After Jarvik, 1954)

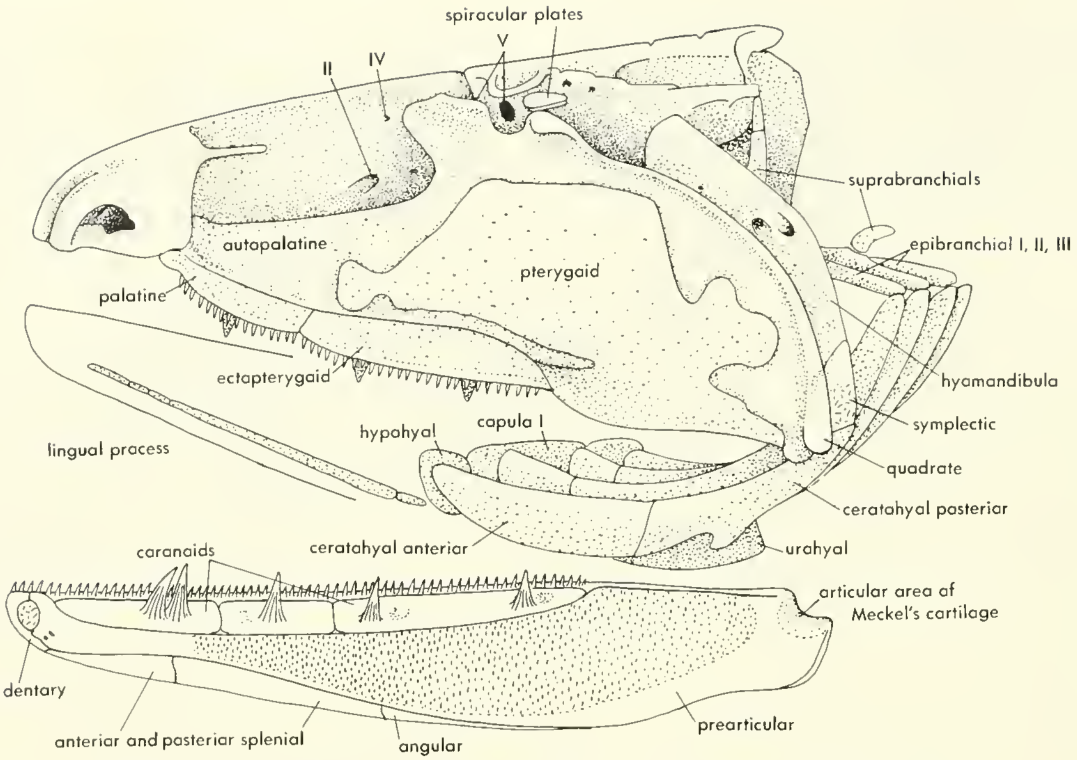


Figure 4-31. Visceral skeleton, mandible, and endocranium of *Eusthenopteron*. (After Jarvik, 1954)

which in turn articulated with the anterior aspect of an anterior **copula.** No basihyal is known but there was a long **sublingual rod** lying below the position of a basihyal. Below the anterior copula was a midline, deeply keeled, **urohyal.**

The branchial arches probably numbered five. The first arch had **hypobranchial, ceratobranchial, epibranchial,** and fused **pharyngo-** and **suprabranchial segments.** The pharyngobranchial articulated with the basis cranii medial to the vestibular fontanelle and the suprabranchial with a process medial to the tip of the pterotic wing. The second arch was similar, except that the suprabranchial was smaller and attached to a slight dorsal process on the anterior end of the epibranchial. This suprabranchial attached to the base of the otic section just above, and anterior to the aortic groove. The third and fourth arches lacked suprabranchials and articulated below with a posterior copula. Fifth ceratobranchials were probably present.

Porolepiform crossopterygian The porolepiform skull is fairly well known only for *Holoptychius fleming* (Figure 4-32). Only fragments of *Porolepis* have been found, but these constitute the earliest remains of crossopterygians. Within this group there is variation in the openings of the nasal capsule. Species of *Porolepis* had two outer openings and an internal choana. *Holoptychius* had only a single outer opening in the position of the posterior opening of *Porolepis*. In terms of the snout both genera agreed in having the nasal capsules widely separated by bilateral **internasal cavities,** between which was a median septum. These cavities opened ventrally between the widely separated vomers.

The **skull table** or roof differed in that the temporal canal passed through what appears to be the postparietal. On the basis of the canal, this was probably the **supratemporal** which had extended medially to exclude the postparietal, just as it does in *Polypterus*. Anterior to the hinge line was a parietal. The pineal or parietal organ has pitted the underside of a small ossicle in the skull roof of *Holoptychius* anterior to the **parietals.** The large **intertemporal** is not included in the anterior part of the roof; it bears a canal or outlet tube to the surface in *Holoptychius* but not in *Glyptolepis* or *Porolepis*.

The cheek differs in that there are three canal-bearing units between the jugal and the lower jaw. The distal one is usually identified as the preopercle, the other two, and some irregular bones below them, as the squamosals. It is more probable that the so-called preopercular unit, which extends down behind the quadratojugal, overlaps the lower jaw somewhat, and extends back over the operculum slightly, is missing in the osteolepiform. The preopercular bone of the osteolepiform lies above the quadratojugal in the position of the second squamosal of *Holoptychius* or *Glyptolepis*. The cheek of the porolepiform is thus better described as having a single **squamosal,** and two **preoperculars,** the more distal of which is lost in osteolepiforms. The

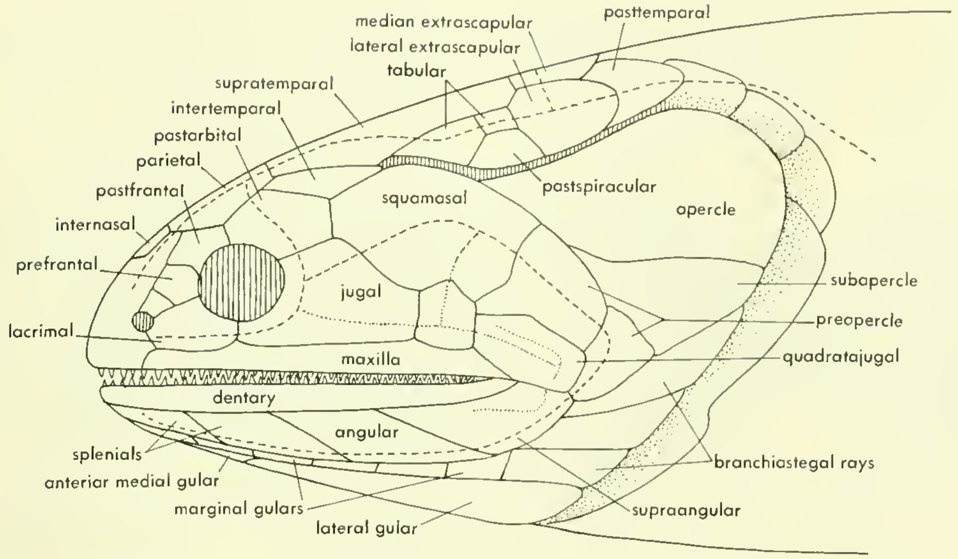


Figure 4-32. The head and pectoral girdle of *Holoptychius flemingi.* (After Jarvik, 1960, 1948)

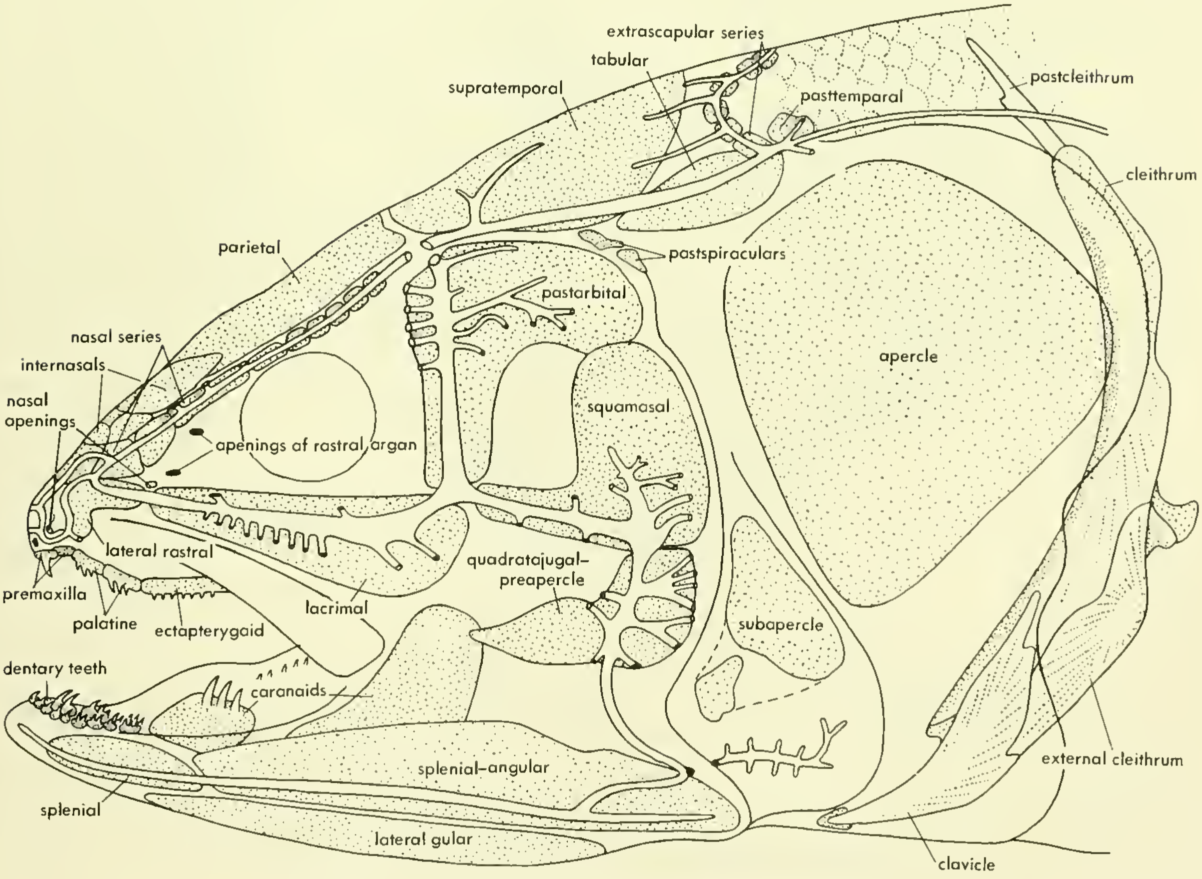


Figure 4-33. The head of *Latimeria.* (After Millot and Anthony, 1958)

irregular bones are anemestics. The operculum differs in having three posterior **marginal gulars** rather than a single unit. Much of the endocranium is as yet unknown but was probably divided into two divisions.

Coelacanth or actinistian crossopterygian The coelacanths are the best known of the crossopterygians because of the living species, *Latimeria chalumnae* (Figures 4-33, 4-34). The earliest fossil coelacanth, which is at least partly known, is

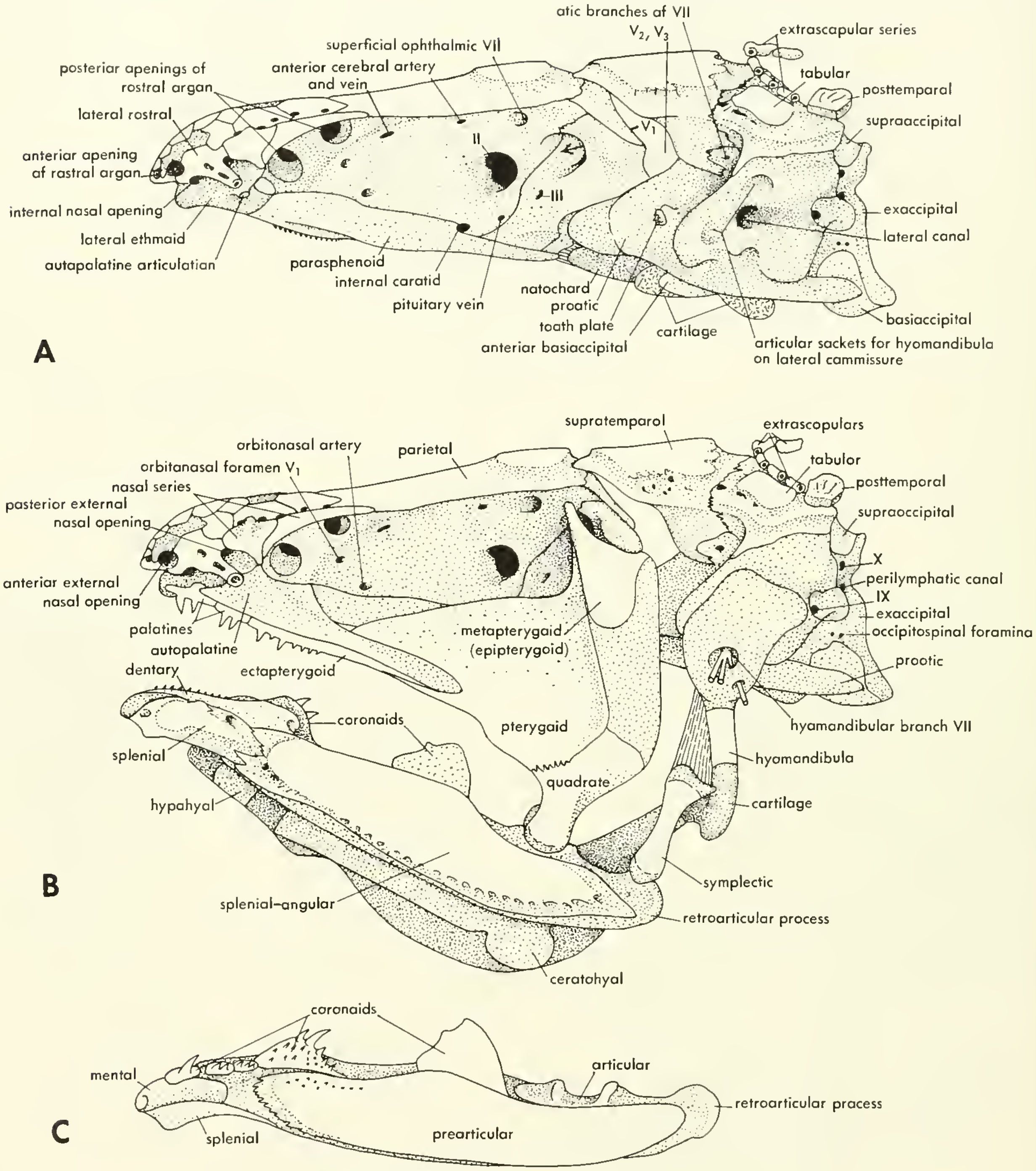


Figure 4-34. The endocranium and jaws of *Latimeria*. A, lateral view of endocranium; B, lateral view of head skeleton (without branchial arches); C, medial view of mandible. (After Millot and Anthony, 1958)

Diplocercides kayseri from the Upper Devonian. The species of this group share several distinctive features and are easily identified. Except for apparent reduction in ossification and fragmentation of some bones, *Latimeria* is typical of this group, which differs in many ways from the other crossopterygians. These differences, such as the rostral organ—a sac-like structure which has three openings to either side on the snout, the reduction of the bones of the jaw margins, and the cranial roof and cheek pattern, suggest specialization. The peculiar ossifications of the endocranium suggest an independent history of fragmentation of the solid structure of the ancestral form. The peculiar hyomandibula is also noteworthy. Only in the single-pieced ceratohyal is there a greater resemblance to the amphibian than that shown by other crossopterygians.

Dipnoan

This last group of the choanates contains the lungfishes. Their fossil history began in the Lower Devonian with *Dipnorhynchus* but it was not until the Middle Devonian *Dipterus platycephalus* that much detail was preserved.

Dipnorhynchus is represented by two good cranial roofs, showing the supraorbital sensory canal completely separate from the temporal canal; there is also a parietal foramen (Figure 4-35). In *Dipterus* (Figure 4-36) these canals joined and there was a distinct anterior pit line and canal; the parietal foramen was lacking. In both genera the snout was covered by an unbroken cosmine layer, which concealed the underlying plates, if present. The external nostril lay on the margin of the jaw and there was no evidence of premaxilla or maxilla. The cheek was much shortened but it had three canal units in about the position of those of the porolepiform; this suggests homology. The last of these units partly overlay the posterior end of the mandible and connected directly with the mandibular canal series. The quadratojugal was present and bore a pit line.

There was a temporal series of bones comparable to that of the rhipidistian, but here the similarity ends. There were many individual roof plates, which appear to be quite variable in shape, interrelationships, and even occurrence. In the history of this group, there appears to have been a competition for space among the individual plates, with the living species retaining only a small number.

The endocranium, known from the Devonian genus *Chirodipterus,* was well ossified and formed a single unit to which the palatoquadrate was fused (**autostylic** type of jaw suspension) (Figure 4-37). Covering the ventral aspect of the cranium was a large parasphenoid with a hypophyseal foramen near its anterior end. The notochord was unconstricted. The visceral skeleton is unknown for the early forms.

Of the living forms, *Neoceratodus* (Figure 4-38) appears to be least modified (more like the fossil forms in appearance). The cranial roof is much altered in this group, and the various plates can only arbitrarily be assigned names. Among living fishes the lungfishes are peculiar in having midline plates in the cranial roof. The endocranium is cartilaginous, except for the exoccipitals, which in *Protopterus* (Figure 6-59) meet above the foramen magnum. The visceral skeleton of *Neoceratodus* is especially of interest since it appears to be intermediate between the crossopterygian and amphibian types.

The hyomandibula is small and cartilaginous in *Neoceratodus;* it is lacking in *Protopterus* and *Lepidosiren.* A second part of the hyoid arch lies below the head vein and the hyomandibular nerve; it is fused with the otic capsule below and behind the posterior entrance of the cranioquadrate fissure. This cartilaginous process connects by a ligament with the cartilaginous process connects by a ligament with the palatoquadrate and with the suspensory ligament of the ceratohyal.

The ceratohyal is a single ossification with cartilaginous ends; it articulates with the hypohyal in front. The hypohyals are joined across the midline by connective tissue and articulate in front with a short cartilaginous basihyal. In the position of a urohyal there is a cartilaginous rod. There are five branchial arches. The first four consist of epibranchials, which are only nodules, and cartilaginous ceratobranchials. The fifth arch has only the ceratobranchials; it has no hypobranchials, basibranchials, or copula.

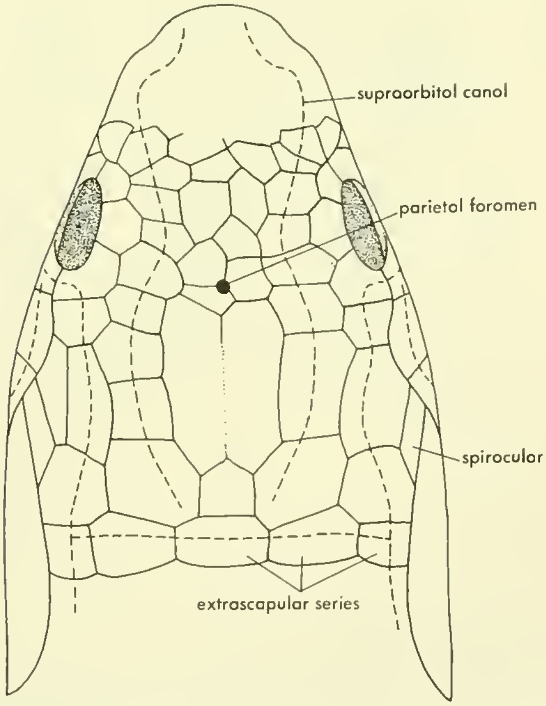


Figure 4-35. Cranial roof of *Dipnorhynchus sussmilchi.* (After Westoll, 1949)

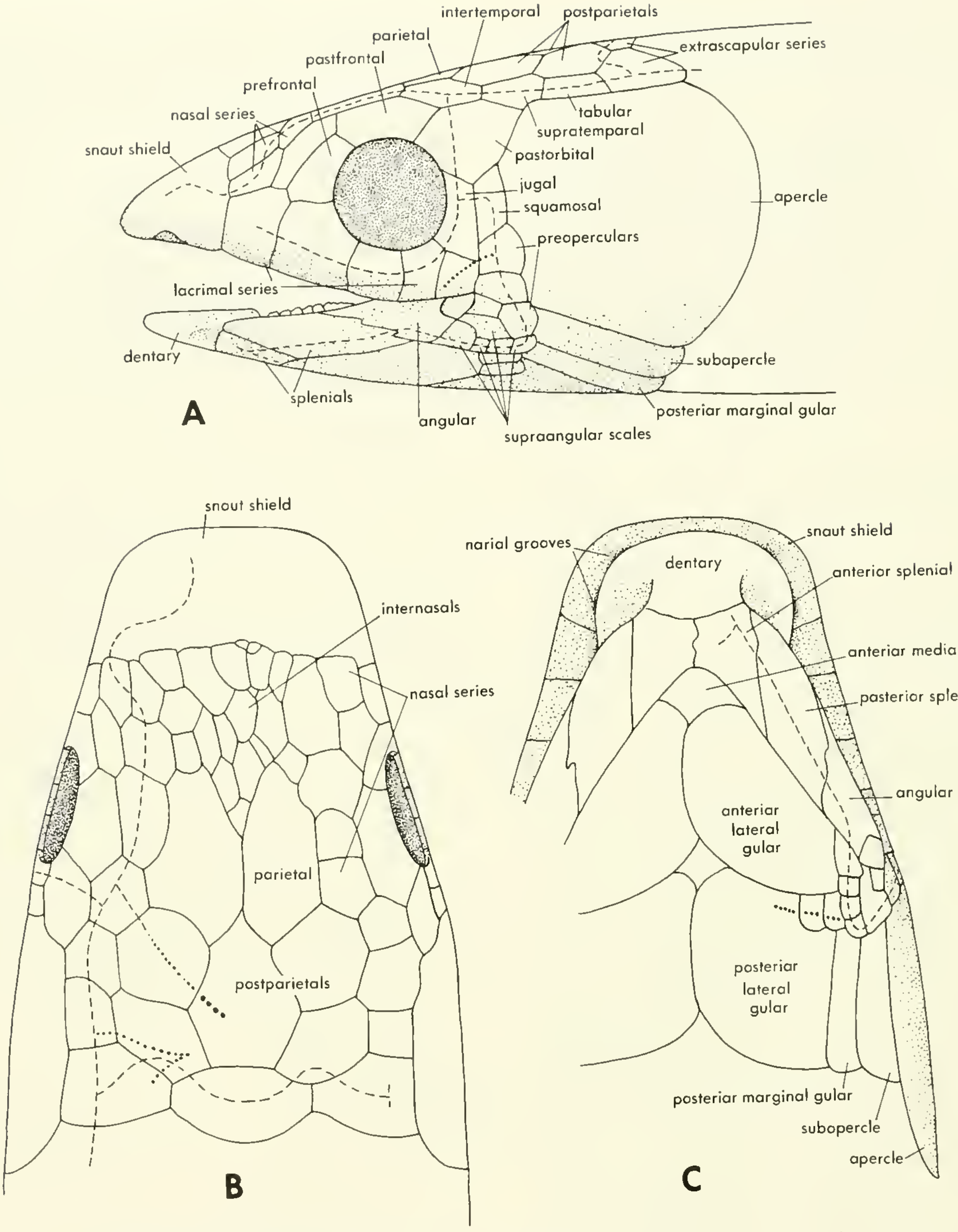


Figure 4-36. Dermal head skeleton of *Dipterus platycephalus*. A, lateral view; B, dorsal view; C, ventral view. (After Westall, 1949)

Embryological development The development of the crossopterygian head skeleton is not known but that of the dipnoan is summarized in Figure 4-39. The similarity to the amphibian (Figure 4-19) is marked and could be interpreted as relationship or parallelism. Of particular interest are the autostylic suspension of the palatoquadrate and the fragmentation of the hyoid arch.

The palatoquadrate develops an ascending process which passes lateral to the profundus (V_1) branch of the trigeminal and fuses to the orbital cartilage. An otic process attaches

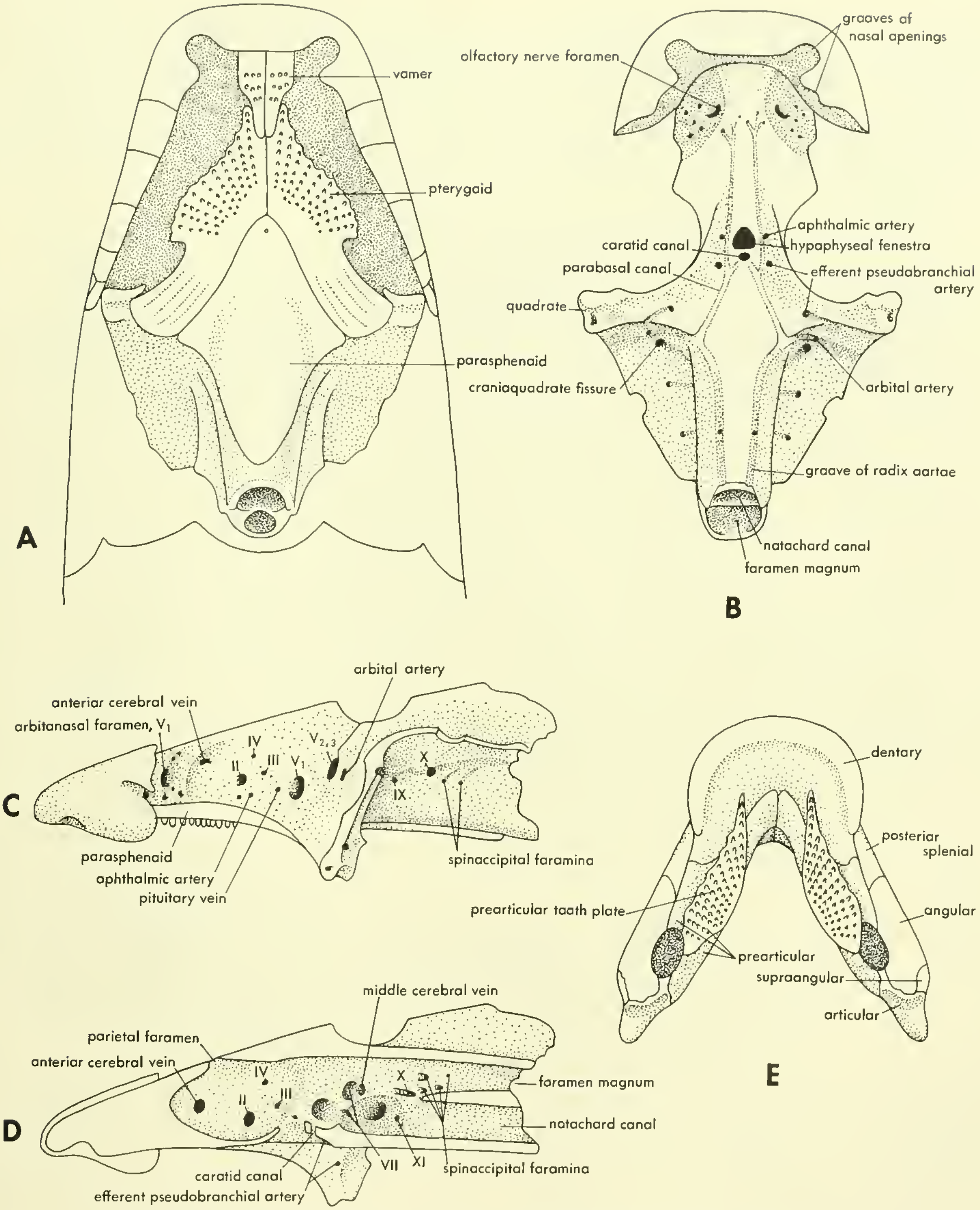


Figure 4-37. Endocranium and jaws of *Dipterus*. Endocranium reconstructed from that of *Chirodipterus* (described by Säve-Söderbergh, 1952). A, palatal view of skull; B, ventral view of endocranium; C, lateral view of endocranium; D, medial view of right half of endocranium; E, dorsal view of lower jaw.

the quadrate to the ear capsule. A blastema of the pterygoid process extends forward from the quadrate region to the tip of the orbitonasal process but later disappears.

The origin of the hyomandibula of *Neoceratodus* has been fully described. There are several centers of chondrification involved in the upper region of the hyoid arch. The first to chondrify is the symplectic. This is followed by the pharyngosuprahyal, the epihyal, and the **laterohyal,** which is a new development in the dermal tissue. The pharyngosuprahyal at first is continuous with the blastema of the remainder of the arch. It then joins the basal plate of the cranium medioventral to the lateral head vein. Following this, connection is lost laterally—specifically it detaches from the epihyal condensation. The lateral end of the pharyngo-

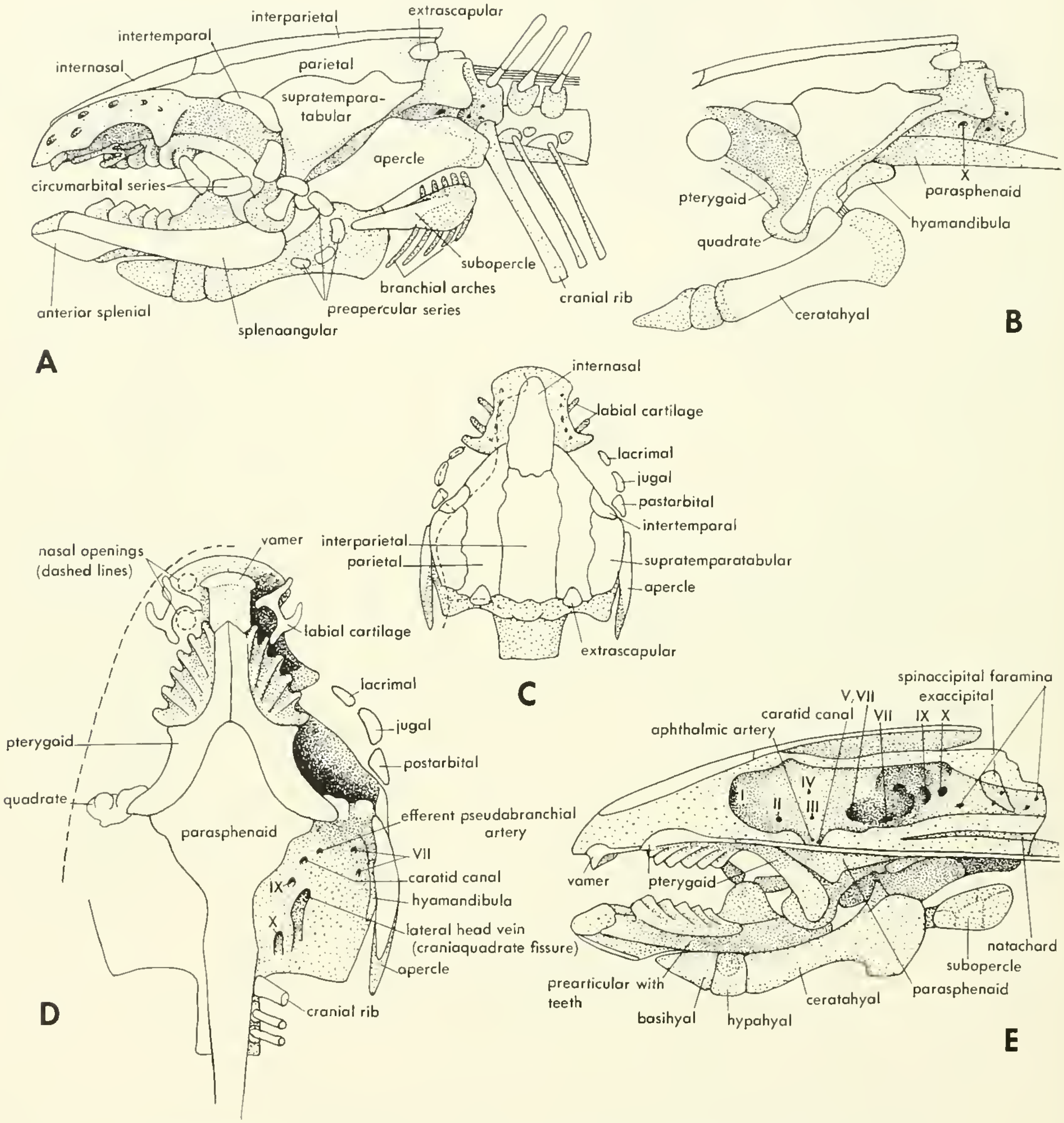


Figure 4-38. Head skeleton of *Neoceratodus.* A, lateral view of head skeleton; B, lateral view of cranium with opercular and cheek bones removed; C, dorsal view of skull; D, palatal view of skull; E, medial view of right half of head. (In part after Holmgren and Pehrson, 1936)

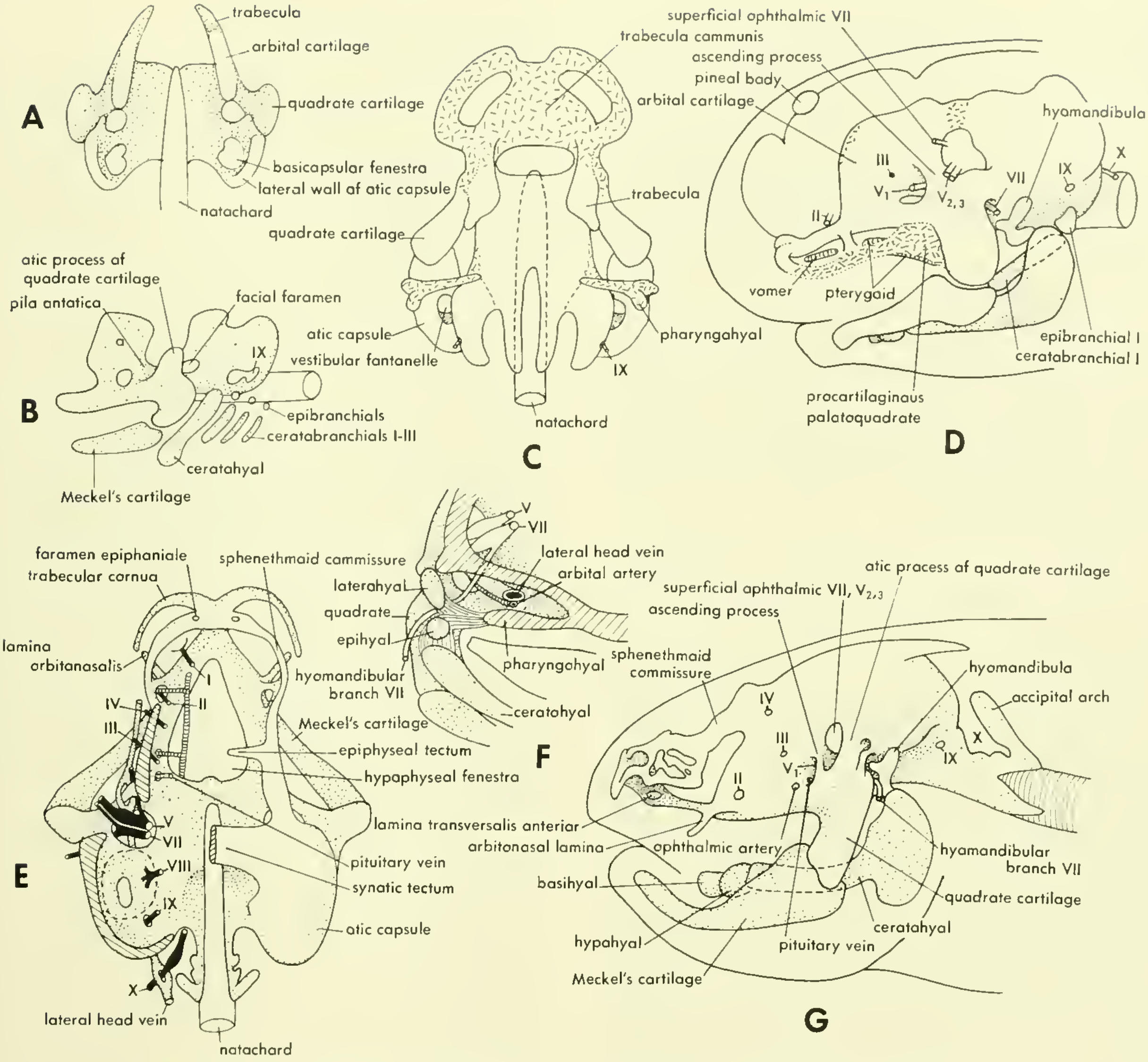


Figure 4-39. Development of chondrocranium of *Neoceratodus*. A, B, dorsal and lateral views of head skeleton of 12-mm larva (After DeBeer, 1937); C, ventral view of head skeleton of 11.5-mm larva (after Bertmar, 1959); D, lateral view of head skeleton of 12.6-mm larva (after Bertmar); E, dorsal view of head skeleton of 20-mm larva with part of left side cut away (after DeBeer); F, lateral view of head skeleton of 27-mm larva (after Holmgren and Stensiö, 1936); G, sectional view of head skeleton, looking forward, showing relationships of parts of hyoid arch to other structures (after Bertmar, 1959, and Goodrich, 1930)

suprahyal lies between the palatine and hyomandibular branches of the facial nerve and its suprahyal process extends upward to contact and fuse with the otic capsule lateral to the head vein. Thus the lateral commissure is formed from the pharyngosuprahyal.

Meanwhile an epihyal chondrification has appeared above the symplectic, and this center is joined above by a laterohyal center of subepidermal mesenchyme. The latter element expands, chondrifies, and fuses with the epihyal to form the hyomandibula of the adult, which lies behind the hyomandibular branch of the facial nerve. The symplectic may fuse with the quadrate, lie in the ligament joining the quadrate and ceratohyal, or disappear.

The hyomandibula is better developed in the crossopterygian, where it articulates with the lateral commissure by two heads, above and below the level of the head vein. This is the same situation as in the actinopterygian.

Although the stapes of the tetrapod has been compared with the hyomandibula, it agrees better with the pharyngosuprahyal, which contacts the otic capsule below the lateral head vein and in front of the hyomandibular nerve. The palatine and hyomandibular branches in the tetrapods usually emerge separately, suggesting the involvement of a "lateral commissure." No such commissure is indicated in development and indeed could not be present if its substance is involved in the formation of the stapes.

The dermal bones of the skull appear early in the course of development, the tooth-bearing bones of the mouth first, followed by those of the cranium. Canal bones are found along the infraorbital canal, starting with the postorbital and continuing through an infraorbital (jugal), and lacrimal. Two small extrascapular canal bones lie along the posterior margin of the roof. The bones of the roof arise deep in the dermis and are never related to canal units. In *Protopterus* and *Lepidosiren* the posterior cranial roof lies below the vertebral muscles; in *Neoceratodus* the muscle lies between this roof and the endocranium.

General observations on the choanate fishes

Whereas the crossopterygian agrees in many details with the tetrapod pattern, the dipnoan does not. Because the living lungfish is less like the crossopterygian in its bone pattern than its early fossil predecessors (*Dipterus*) were, it can be assumed that a process of change had already begun before the lungfish were first encountered in the fossil record. The lack of the jaw margins and the specialized tooth plates of the fossil forms supports such a proposition.

The Dipnoi are peculiar among the groups so far examined in that they appear to lack some of the common skeletal inheritance of the choanates and appear to have lost much of what they had acquired during their evolution. It has been suggested that this is not a case of loss but, to the contrary, that in this group the full pattern was never present. Such a view must be based on the assumption that the tetrapod pattern actually arose among the choanate fishes and that one branch of this ancestral group, the Dipnoi, diverged from the stem before the development of that pattern. Any conclusion regarding this possibility must await a consideration of the skeletons of other fishes.

ORIGIN OF THE AMPHIBIAN OR TETRAPOD

Of the two groups, crossopterygian or dipnoan, which is closer to the amphibian? Säve-Söderbergh has pointed out the unlikelihood of the origin of amphibians directly from crossopterygians. This view can be based on the lack of agreement in the dermal bones of the snout, specifically the presence of a frontal and nasal as opposed to a series of nasals, and also on the autostylic palatoquadrate of the amphibian and the possible loss of the hyomandibula.

Holmgren has assumed a dipnoan origin for the urodeles in spite of the obvious specializations of the Dipnoi when first encountered in the fossil record. Even though Jarvik's analysis of the nasal openings of dipnoans is discounted, the loss of maxilla and premaxilla and the form of the pterygoid and prearticular dental plates remain as salient features. Offering some support to the dipnoan origin are the autostylic jaw suspension, reduction of the hyomandibula, and connection of the pharyngosuprahyal to the otic capsule. Also lending credence to this view is Westoll's use of the cranial pattern of the early dipnoan as suggestive of the ancestral type for the choanates.

To complicate the discussion of the origin of amphibians, Säve-Söderbergh, Holmgren, and Jarvik have asserted that the Amphibia arose from two choanate-fish sources. Säve-Söderbergh and Holmgren derive the Urodela from a source near the Dipnoi and the other amphibians indirectly from the osteolepid crossopterygians. Jarvik derives the urodeles from a porolepiform and the anurans and other tetrapods from an osteolepiform source. The arguments supporting these viewpoints are long and detailed. Neither assumption is particularly supported by the foregoing accounts.

The origin of the amphibian is much more difficult to document than that of the reptile, because, we have been moving back further in the time scale with each of the groups considered and are now near the beginning of the fossil record. Although there is little doubt that a relationship exists between the early "choanate fishes" and the "choanate" amphibians, assessing this relationship is impossible because of the lack of fossil material. The Amphibia, when first encountered in the fossil record, had already undergone a great deal of radiation and were perhaps contemporaneous with reptiles.

5 The Head Skeleton of Fishes

The observed similarities in the general pattern of bones in the heads of osteolepiform and actinopterygian fishes was a part of the evidence on which the Class Osteichthyes, or bony fishes, was founded. The validity of this class and the possible origin of the choanates, and therefore the tetrapods, from an actinopterygian-like fish should now be investigated.

GNATHOSTOME FISHES

Most fish have bony jaws (i.e. with premaxilla, maxilla, and dentary) like those of the choanates and tetrapods. These fish are placed in the gnathostome division. Jawless fish are called agnaths and are discussed later in this chapter.

Actinopterygian or ray-finned fishes

Most of the living actinopterygians are identified as teleosts, or true bony fishes, but there are a few species of chondrostean and holostean fishes that, beneath their specializations, are presumed to retain some of the primitive features of the group. Primitive features are identified in this case as those observed in the early fossil representatives of this group, the palaeoniscoids.

Only a few kinds of actinopterygians will be described for the purpose of indicating something of their range of variation and thus the potential of the group as ancestors to the higher forms.

The head skeleton of the actinopterygian is made up of the components listed in Table 5-1. This list is nearly a duplicate of that for the choanate (Table 4-4, p. 92; the differences are critical to the discussion of the nature of the interrelationship. It should be pointed out here that in most descriptions of the fish skull the parietals are called "frontals." This use of frontal is defended on the grounds that it is established and that the bones of the fish cranial roof have not been demonstrated convincingly as homologs of the tetrapod bones. It is a premise of this account that there is virtue in retaining the terminology pattern established in the previous descriptions. This view is based on the contention that the student's task is made easier with such a pattern, and that, since there is already a rich synonymy, which must be mastered for full understanding of the literature, there is no addition to the ultimate load. It may also be the decision of the reader that this usage is justified, in the final analysis, on grounds of some sort of homology.

As a starting point for an analysis of the actinopterygian, the structure of the teleost head skeleton will be examined.

Teleost To give some flexibility to the description, three species will be considered: the salmon (Figures 5-1, 5-2), the cod (Figure 5-3), and the perch. Of these the salmon is best known both in terms of its adult anatomy and its development.

The roof differs in several ways from what has already been observed. The **extrascapular series** is made up of tubular (sensory canal) bones varying in number from two pairs in the cod to five pairs in the salmon. Since these are closely bound to the skin, they are easily lost in preparing skeletons. A single plate lies in the region of the supratemporal and tabular of either side; this is called the **supratemporotabular.** The **intertemporal** lies outside the roof and is more easily described as a part of the circumorbital series. There is no parietal foramen.

Anterior to the **parietals** are paired nasals, and midline **internasal** and **mesethmoid.** The latter is a chondral bone and is lacking in the salmon. The nasals may be well developed or vestigial in the form of canal tubes. The **circumorbital series** consists of the intertemporal, two **postorbitals,** a **jugal,** an **"infraorbital,"** and a **lacrimal.** Identification of these units is completely arbitrary since the total number of bones in this series varies. *Elops* (Figure 5-4) has three **lateral rostral** units, continuing forward from the lacrimal, and a **median rostral,** apparently fused with the internasal. *Elops* also has two **supraorbitals,** the salmon one. The ventral aspect of the cranium is covered by a midline toothed **vomer** in front and the **parasphenoid** behind. The vomer is partly embedded in the cartilage of the rostrum. The parasphenoid has a slim rostral part and spreads over the basis cranii posteriorly.

TABLE 5-1 THE BONES OF THE HEAD SKELETON OF THE ACTINOPTERYGIAN FISHES ARRANGED ACCORDING TO TYPE AND PLACE OF ORIGIN

Cranium (brain and sense organ capsule)	Splanchnocranium or Visceral Skeleton (dermal bones with*)
Endocranium (bones of chondral origin except where marked with an *) basioccipital exoccipital supraoccipital intercalare* epiotic prootic sphenotic basisphenoid orbitosphenoid (anterior and posterior parts) mesethmoid lateral ethmoid kinethmoid preethmoid Eye sclerotic plates Dermocranium (bones of membrane origin) Roof, snout, and floor extrascapulars postparietal parietal supratemporotabular intertemporal nasal internasal vomer parasphenoid Circumorbital and sensory line of snout supraorbital postorbital(s) jugal, infraorbital lacrimal(s) lateral rostral(s) medial rostral Cheek preopercle suprapreopercle	Mandibular arch—Palatoquadrate and Meckel's cartilage premaxilla* maxilla* quadratojugal* quadrate metapterygoid or epipterygoid autopalatine pterygoid* ectopterygoid* palatine* articular retroarticular Meckelian ossicle mental angular* supraangular* dentosplenial* or dentary coronoids Hyoid arch opercle* subopercle* interopercle* branchiostegal rays* lateral gulars* anterior medial gular* hyomandibula symplectic interhyal ceratohyal (anterior and posterior parts) hypohyal basihyal urohyal Unclassified entoglossal Branchial arches pharyngosuprabranchials I to IV epibranchials I to IV ceratobranchials I to V hypobranchials I to IV basibranchials I to IV

The cheek is covered, between the circumorbital series and the preopercle, by scales like those of the body—not by squamosoids (imbricated plates). The **preopercle** is a canal bone, but its anterior margin extends inward and contributes to the area of origin (attachment) of the jaw muscles. In the salmon a small **suprapreopercle** lies above the preopercle. The preopercular canal enters the temporal canal or emerges on the surface near that canal.

The bones of the upper jaw are arranged in two functional styles. The **premaxilla** forms the toothed margin of the upper jaw in the cod or perch and is movable in the protrusion and opening of the mouth; in the salmon it is more fixed and the **maxilla** forms much of the toothed margin. In both styles the maxilla is tied to the mandible by a strong ligament, so that as the mouth opens it is pulled down.

The palatoquadrate complex (Figure 5-3 B,D) consists of a **palatine** fused to the **autopalatine,** an **ectopterygoid,** and a broad **pterygoid** plate. The **quadrate** and **metapterygoid** are endochondral ossification of the palatoquadrate cartilage, as is the autopalatine. The lower jaw consists of a **dentosplenial** (assumed to be compound), an **angular, articular,** and **retroarticular.** There is a small ossification on Meckel's cartilage at the insertion of the adductor muscles of the jaw, the **Meckelian ossicle;** anteriorly there is a small **mental** bone. The palatoquadrate plus the **hyomandibula** and **symplectic** form the suspensorium for the lower jaw. The hyomandibula is bound to the metapterygoid and to the symplectic, and also articulates above with the cranium.

The operculum is supported by a large **opercle,** a **subopercle,** and an **interopercle.** A series of **branchiostegal rays** continue the opercular flap into the gular area. An **anterior medial gular** occurs in some teleosts (*Elops*).

The **endocranium** is difficult to understand because of the overlapping and interdigitating of bones. In the salmon (Figure 5-2) the bones are partly endochondral, joined by synchondroses, whereas in the cod or perch they are largely perichondral with overlapping sutures, synchondroses, or combinations of these. There is usually a more or less continuous chondrocranium within and between these bones.

The **occipital series** is like that of the higher forms. There is a large **prootic** ossification in the otic capsule and variable smaller centers idenified as the **epiotic** and **opisthotic.** In the region of the opisthotic there is a dermal bone, the **intercalare,** which serves for the ligamentous attachment of the pectoral girdle. The intertemporal and supratemporotabular have perichondral extensions on the otic capsule, the **sphenotic** and **pterotic.** The sphenotic bears a hyomandibular facet. A small strut of bone dividing the anterior opening of the myodome in some fishes is called the **basisphenoid.** The **orbitosphenoid** is a single or a two-parted ossification in the orbit wall. Anteriorly there are **mesethmoid** and **lateral ethmoid** ossifications. Two **sclerotic plates** are present in the eye of the salmon.

There is a **lateral commissure** forming the posterior margin of the orbit and buttressing the sphenotic. Inside this commissure lies the **lateral canal** or trigeminal-facial canal or chamber, into which open separate trigeminal and facial foramina. The geniculate ganglion of the seventh and the Gasserian ganglion of the fifth nerve fill much of this chamber. The cod lacks a lateral commissure.

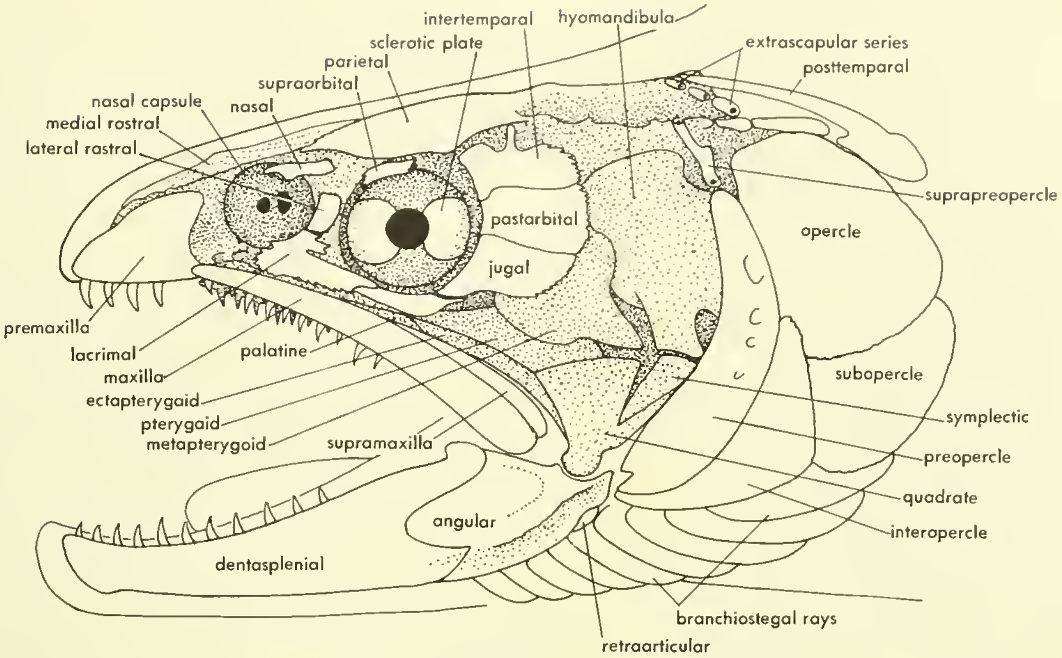


Figure 5-1. Lateral view of the head skeleton of the salmon.

The **myodome** is a cavity between the base of the cranium and the parasphenoid. The prootics meet above this space, and form part of its lateral wall. This cavity contains the posterior parts and the areas of origin of the external, internal, and inferior rectus muscles of the eye. The myodome is small in the cod and does not extend below the level of the basis cranii. The salmon is peculiar in also having an **anterior myodome,** a midline chamber extending forward nearly to the tip of the rostrum (Figure 5-5).

The **hyomandibula** articulates with the sphenotic and pterotic parts of the otic capsule wall. It has an opercular process extending posteriorly, as well as a process extending out to the preopercle. The body of the bone is perforated by the hyomandibular branch of the seventh cranial nerve. The distal end articulates anteriorly with the **symplectic** and posteriorly with the **interhyal;** both of these joints are synchondroses. The interhyal is a small bony rod between the hyomandibula and the posterior end of the triangular **ceratohyal posterior.**

The ceratohyal is divided into anterior and posterior parts; in the cod or perch (Figure 5-3 D), these are joined internally by straps of bone, which meet along a deeply interdigitating suture line. The **hypohyal** is made up of dorsal and ventral parts, synchondrally joined. The hypohyals join at the midline where the dorsal portion is attached to the midline **basihyal.** A **urohyal** extends ventroposteriorly as a thin midline plate. In the salmon there is an anteriorly projecting, tooth-bearing, **entoglossal** attached to the basihyal.

Behind the hyoid arch are four branchial arches. With the exception of the first, each of these has four segments; from below upward these are **hypobranchial, ceratobranchial, epibranchial,** and **pharyngobranchial.** In the salmon the first arch lacks a pharyngobranchial but has a large **suprabranchial,** which attaches to the prootic just above the internal cartotid foramen. Each of the four epibranchials has a dorsal process on its upper end. A fifth pair of ceratobranchials is present.

EMBRYOLOGICAL DEVELOPMENT In the teleost, cartilage first appears at either side of the notochord, forming the **parachordal rods** (Figure 5-6). Anteriorly these rods turn outward; posteriorly they are flattened and extended dorsolaterally by the rudiments of the **occipital arch. Meckel's cartilage,** the **ceratohyal,** and **hyomandibula** are present. Well anterior to the tips of the parachordals a pair of **trabeculae** chondrify. **Polar cartilages** appear between the ends of the trabeculae and parachordals. Distal to the **hyomandibula,** but joined with it by a procartilaginous connective, is the **sympletic.** The **first** and **second ceratobranchials** are present and also an **intermandibular cartilage** between the tips of Meckel's cartilages.

The trabecula and parachordal are joined by the polar cartilage. **Anterior** and **posterior centers** appear in the **otic capsule;** these are connected by **anterior basicapsular** and **basivestibular commissures,** respectively, with the parachordal. A posterior capsular commissure soon forms behind the glossopharyngeal nerve.

An occipital arch develops and the anterior ends of the trabeculae become joined by a plate. The **lateral commis-**

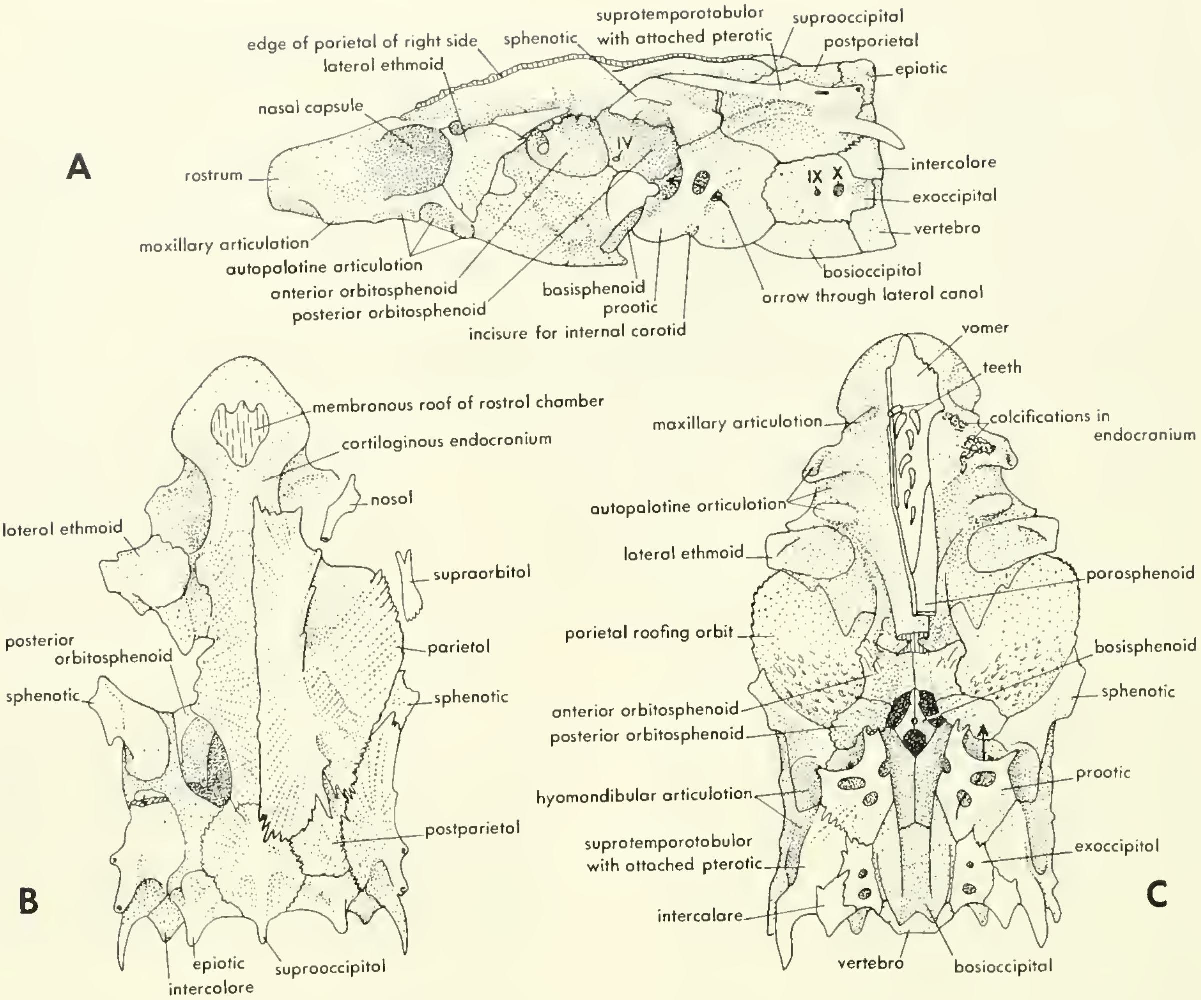


Figure 5-2. Endocranium of the salmon. A, lateral view; B, dorsal view; C, ventral view.

sure is formed by a **prootic process** growing down from the anterior margin of the otic capsule to meet a **basal process** from the parachordal. The occipital arch fuses with the rear wall of the otic capsule above the vagus or jugular foramen, and a long, thin **orbital cartilage** extends from the otic capsule to the region of the **nasal capsule.** The trabeculae have moved relatively closer together and are joined across the midline for much of their length as a **trabecula communis.** From the lateral margins of the anterior plate of the trabeculae, an **orbitonasal lamina** extends upward on either side, and medially a nasal septum forms. The anterior end of the orbital cartilage forks. One part extends medially to join the nasal septum, the other grows out laterally to the orbitonasal lamina; thus the roof of the nasal capsule is initiated and the orbitonasal foramen isolated.

A transverse **acrochordal connective** develops between the parachordals. The tip of the notochord projects into this "dorsum sellae." The otic capsules are now completed laterally but are open medially. A slender **epiphyseal tectum** has developed between the orbital cartilages. The **palatoquadrate cartilage** is complete and its anterior end is in contact at two points with the nasal capsule and trabecular plate. A small **basitrabecular process** grows out in front of the palatine branch of the facial nerve and fuses with the lateral commissure, thus forming a foramen for that nerve. Posteriorly a **synotic tectum** joins the otic capsules. With the gradual closure of the **epiphyseal fenestra,** a **taenia medialis** appears extending from the posterior margin of the epiphyseal commissure nearly to the synotic tectum. It soon joins the synotic tectum to isolate bilateral **cerebral fenestrae.** A small **interorbital septum** is formed from the **preoptic pillars** of the orbital cartilages; it is perforated by the olfactory nerves leaving the cranial cavity. The trabecula communis now disappears in the region below the middle of the orbit.

Conversion of this chondrocranium to that of the adult requires some drastic alterations. The interorbital septum reaches the trabecula communis. The olfactory nerve emerges from a foramen into the orbit and passes forward next to the membranous septum. Anteriorly it passes laterally between the inferior and superior oblique muscles to reach the olfactory foramen in the olfactory capsule. The olfactory capsules become separated by the midline rostral chamber opening into the orbits at either side of the interorbital septum—this chamber is the anterior myodome.

The **posterior myodome** (Figure 5-7) is formed by the rectus eye muscles "pushing" their area of origin (attachment) down through the **hypophyseal fenestra** and then back below the level of the trabeculae on to the basis cranii. The posterior parts of the trabeculae degenerate, and a new **pseudohypophyseal fenestra, the sellar fenestra,** is formed by ossification in the connective tissue septum

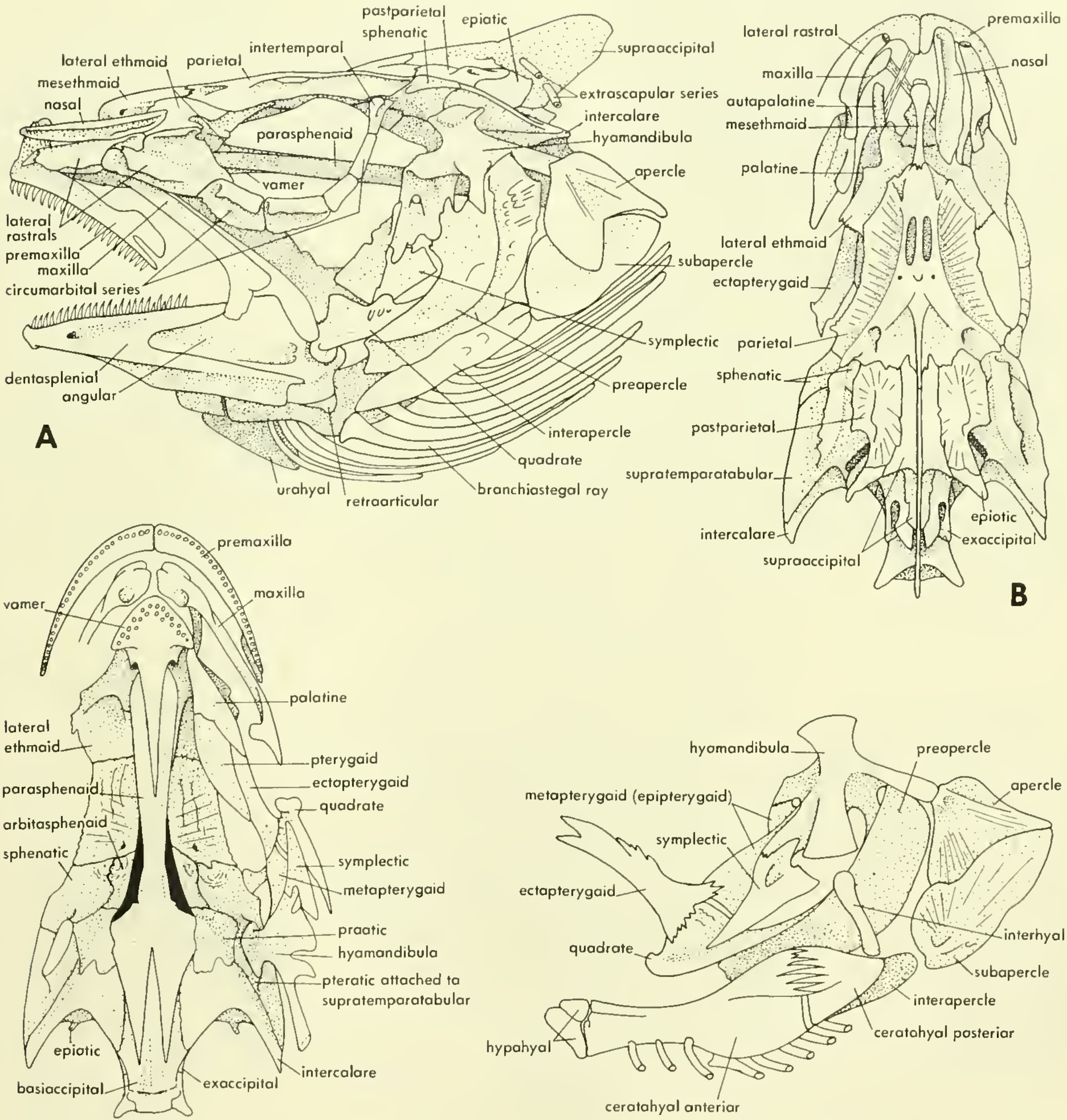


Figure 5-3. Head skeleton of the cod. A, lateral view; B, dorsal view of the skull with nasal and circumorbitals of left side removed; C, ventral view of skull with palatoquadrate complex and hyomandibula of right side (to left) removed; D, medial view of suspensorium of right side.

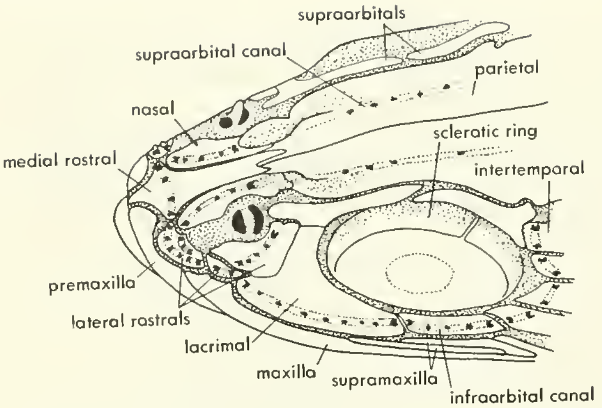


Figure 5-4. Anterolateral and somewhat dorsal view of snout skeleton of *Elops saurus* showing "supraorbitals" and "rastrals." (After Nybelin, 1957)

which separates the myodome into bilateral chambers, and by the attachment of this medial bone to the diverging anterior ends of the prootic. A **prefacial commissure** forms between the facial and trigeminal foramina, which in turn is separated from the optic fenestra by an antotic pillar. The notochord is obliterated by constriction.

The development of the bony cranium begins very early, less than 10 mm in length. Teeth appear first and then the jaw and palate bones to which they attach. Many of the bones of the head skeleton arise either in association with the organs of the sensory canals or with teeth, and it has been assumed that the stimulus for bone formation resided in those structures (Figure 5-8). Observations indicate that some bones arise in relation to canal organs and become tubes enclosing the canals. Other bones arise in a like manner but deeper basal plates develop and spread out away from the

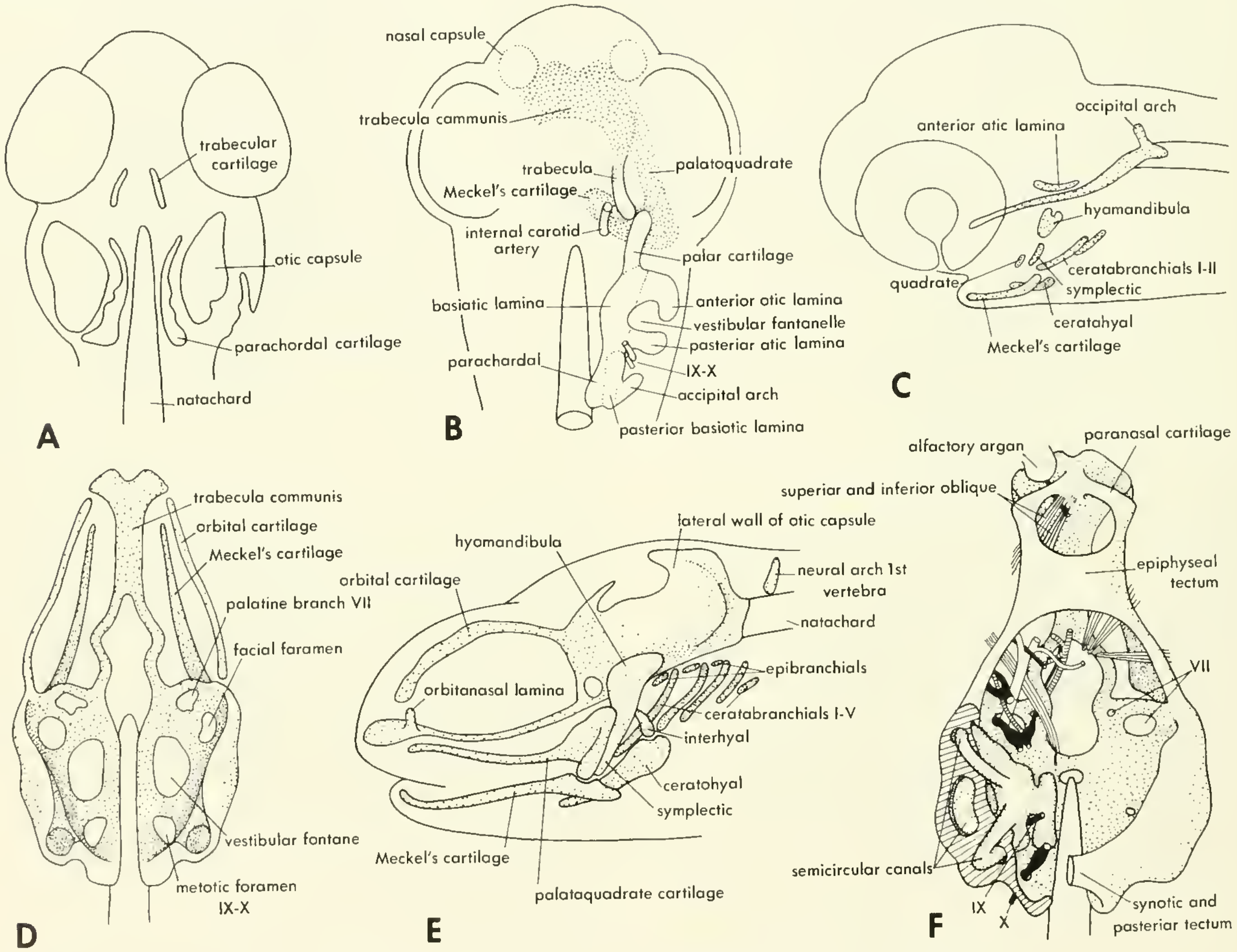


Figure 5-5. Early development of the cartilaginous head skeleton of the salmon. A, dorsal view of 9.3-mm larva; B, dorsal view of early larva in which cartilaginous and blastemic parts are indicated; C, lateral view of 10.5-mm larva; D, dorsal view of 14.2-mm larva; E, lateral view of 15.5-mm larva; F, dorsal view of chondrocranium of larva about 20 mm long with part of left side cut away. (A, C, D, E after DeBeer, 1937; B after Bertmar, 1959)

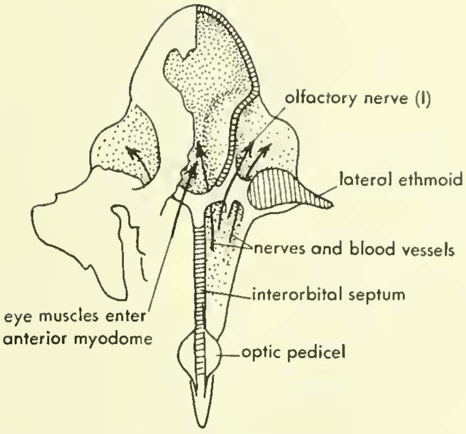


Figure 5-6. Snout part of the adult endocranium showing the anterior myodome; the roof of the right half has been cut away (cross hatching indicates surfaces).

canal. In still other bones, the basal plate appears at much the same time as the canal organ center.

In contradiction to the concept of sensory organ of tooth origin of bones is the fact that not all bones of the fish arise in relation to one of these sources; further, there is experimental evidence that bones will develop, somewhat later perhaps, after the surgical removal of the sensory organs. Also, in many animals sensory organs are never developed but bones arise much as the basal plate of the fish canal bone. It has long been assumed that the sensory organ, as a more differentiated structure lying in a canal and enclosed by a concentration of connective tissue, presents an area with a higher metabolic rate and substrate conditions that might serve as a first condensation point. There is little question that in fishes the sensory organ centers are characteristic and useful in determining homologies.

The origin of the **maxilla** and **dentosplenial** is of special interest. A strand of mesenchyme extends out and back from the anterior end of the palatoquadrate (Figure 5-9). This strand posteriorly is associated with Meckel's cartilage and its end grows down and forward with that structure. The strand now lies in both upper and lower lip margins and appears to give rise to the maxilla above and the dentosplenial below. Anterior to the tip of the maxillary blastema, a **premaxillary** blastema condenses from the mesenchyme underlying the snout. Behind this, pairs of **vomer** and **palatine** anlages appear. Behind the dentary, an **angular** blastema forms. All of these blastemas are similar and represent bone origins that cannot be directly associated either with teeth or sensory structures. A small **quadratojugal** appears and fuses to the **quadrate.**

The **internasal** and vomer have chondral relationships; the former may be fused to the **mesethmoid.** The **basisphenoid** arises membranously in *Salmo* and has three centers: a ventral midline and bilateral dorsolateral centers. In some teleosts the basisphenoid has a cartilaginous precursor. This cartilage must be viewed as secondary. The **intercalare** is basically an ossification in a ligament, not a primary component of the endocranium. The chondral bones all arise perichondrally.

The **hyomandibula** arises in a way comparable to that

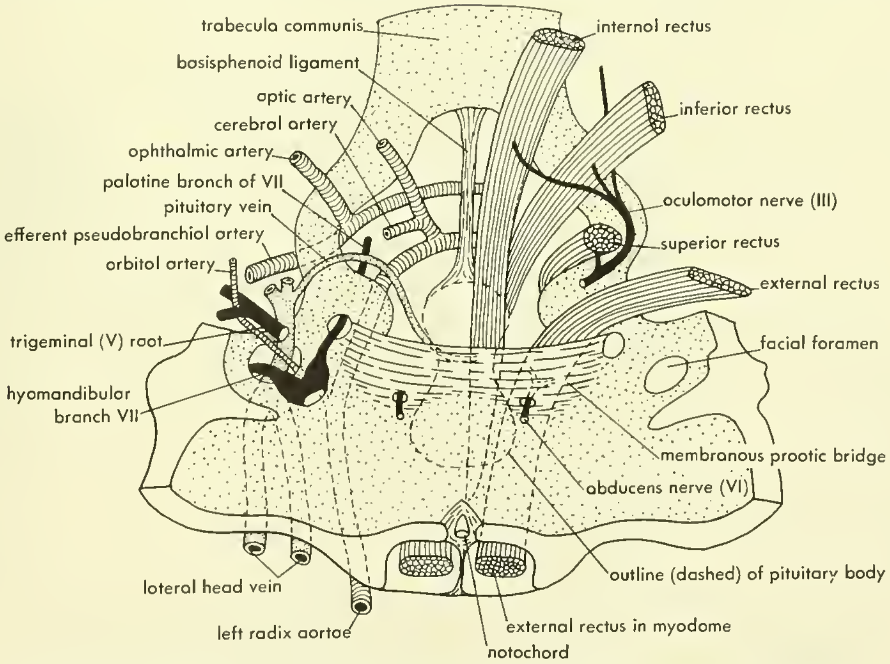


Figure 5-7. Migration of eye muscle origins through the hypophyseal fenestra and the beginning of the myodome in a 22-mm larval salmon. (After Goodrich, 1930)

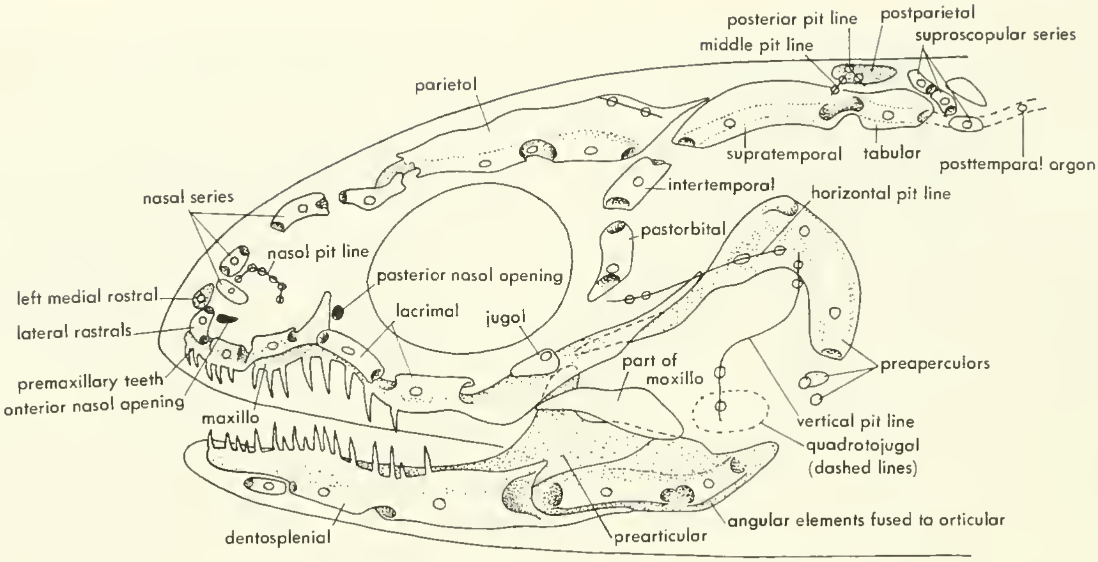


Figure 5-8. Dermal bones forming in relationship to the lateral-line sensory organs in a 24-mm larva of *Polypterus*. (After Pehrson, 1947)

observed in *Neoceratodus* (Figure 5-10). The **epihyal** is fused with a **laterhyal** in the course of development. The laterohyal extends the epihyal upward, outside the head vein and nerves, to an articulation with the **lateral commissure** and **otic capsule.** The lateral commissure probably is derived from the **pharyngosuprahyal,** although it never has any contact with the hyoid arch and develops as dorsal and ventral processes from the chondrocranium.

Palaeoniscoid The earliest representatives of the actinopterygians are called palaeoniscoids. These are, from their first appearance, a diverse assemblage, for the large part only poorly known. The earliest known forms, from the Middle and Upper Devonian, are *Cheirolepis, Stegotrachelus, Moythomasia,* and *Stereolepidella.* That the palaeoniscoids were abundant in the Devonian is indicated by scales and bone fragments.

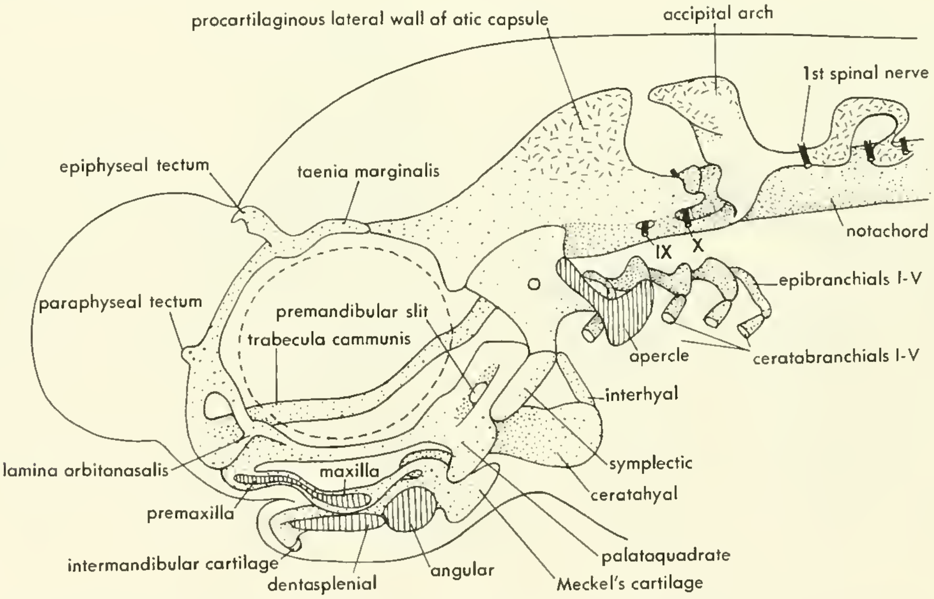


Figure 5-9. Lateral view of head skeleton (cartilage and blastema) of 8-mm larva of *Hepsetus odoë* showing blastemic beginning of dermal jaw bones. (After Bertmar, 1959)

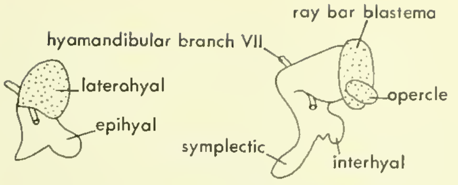


Figure 5-10. Development of the hyamandibula of the salmon from epihyal and laterahyal blastemas.

Although the palaeoniscoids had declined in numbers by the beginning of the Triassic, several genera are well known. These compare well with the earlier genera in superficial detail. As a type for the palaeoniscoids, the species of the Triassic genus *Pteronisculus* will be used (Figures 5-11, 5-12).

In summary, the palaeoniscoid type had a complement of dermal bones similar to that already described for the teleost or osteolepid crossopterygian. The primary differ-

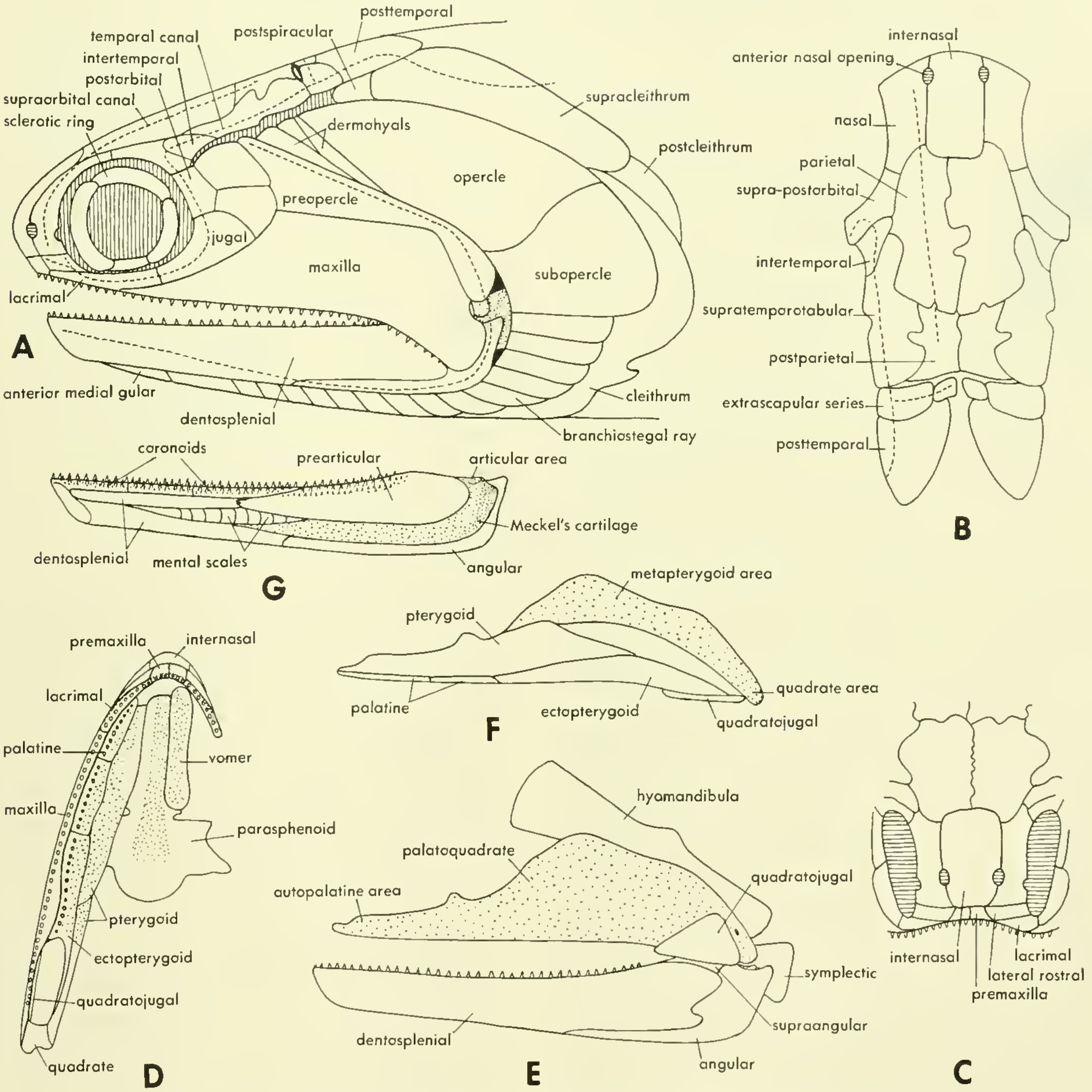


Figure 5-11. Head skeleton of *Pteronisculus*. A, lateral view of head and pectoral girdle; B, cranial roof; C, anterior view of snout; D, palatal view with palatoquadrate of left side (to right) removed; E, lateral view of suspensorium, palatoquadrate, and lower jaw; F, medial view of right palatoquadrate complex; G, medial view of mandible. (After Nielsen, 1942)

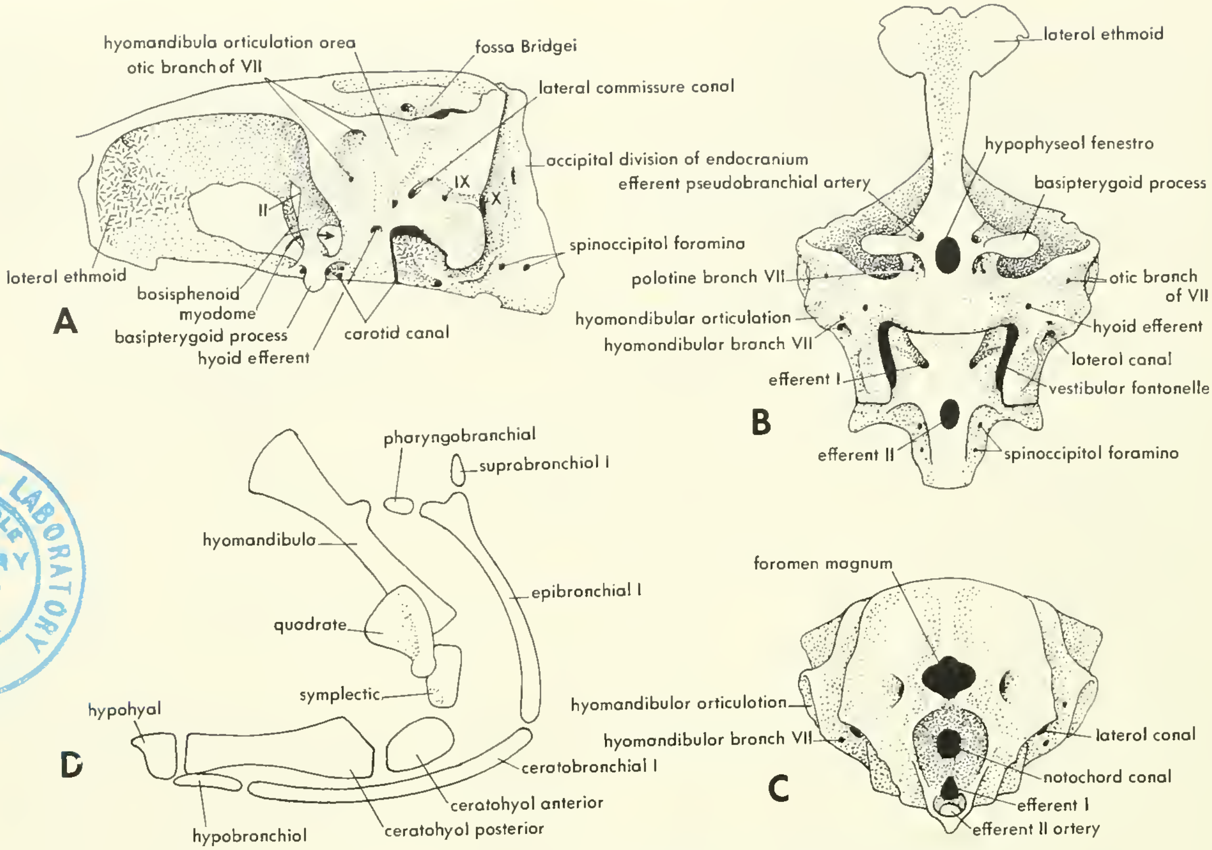


Figure 5-12. Endocranium and visceral skeleton (except jaws) of *Pteronisculus*. A, lateral view of endocranium; B, ventral view; C, posterior view; D, lateral view of hyoid and first branchial arches (quadrate shown in relation to hyomandibula and sympletic). (After Nielsen, 1942)

ences might be attributed to the jaw apparatus. The **suspensorium,** as represented by the hyomandibula, was directed posteroventrally, with the articulation process of the quadrate well behind the vertical of the eye. The cheek was solidly covered. There was a well-developed **dermohyal** between the operculum and preopercle, and sometimes there were additional plates behind or below this. The bony **operculum** was relatively narrow, in an anteroposterior direction, and continued onto the throat as a ray-supported membrane; there was never an interopercle, although a large plate of branchiostegal origin sometimes lay below the subopercle. The **intertemporal** was included in the roof. In at least one genus (*Moythomasia*), there was a **parietal foramen.** The snout had a large **internasal,** large lateral **nasals,** which margined the eye (except in *Cheirolepis*), and generally lacked separate **medial rostrals**—these were usually fused with the **premaxilla,** though both were sometimes lacking. The eye was proportionally large, with four **sclerotic plates,** and the snout short.

Among what have been called palaeoniscoids, there was marked divergence from this picture. The suspensorium, as an extreme, was vertical and the cheek was free of bony plates (*Dorypterus*). Reduction of many bones in size, or even their loss, is observed in several forms. In others there has been a reduction in the number of bones but a retention of a heavy dermal armor; the branchiostegals have been replaced literally or functionally by **gular plates** in *Haplolepis.*

The **endocranium** (Figure 5-12) was well ossified but had some areas of cartilage. It was composed of **occipital** and **ethmosphenotic divisions** separated by a fissure. The basioccipital region enclosed the restricted notochord canal as well as the aortic canal. There was a large **vestibular fontanelle** between the **otic capsule** and the **basioccipital.**

Relationships among actinopterygians The actinopterygian fishes appear to be characterized by the myodome. In the salmon there are three stages of its development: (1) without a myodome, (2) with a myodome for the external rectus, and (3) with a double myodome, having an additional space, which contains the origins of the other recti, above and behind that for the external rectus. The second stage is possibly the ancestral form since it occurred in many palaeoniscoids. Loss of the myodome in some kinds of ray-finned fishes suggests neoteny, the retention of an embryonic stage into the adult. The advanced nature of the teleosts as a group is supported by the presence of a double myodome (stage 3).

The compound (epi- and laterohyal) **hyomandibula** of the teleost is like that of the palaeoniscoid or crossopterygian and is associated with a **symplectic** and an **interhyal** (or **stylohyal**). In its development the symplectic is the distal part of the epihyal. The interhyal appears to be a part of the epihyal or to have an independent origin between epihyal and ceratohyal. It involves two tissues in its origin, a medial part, which is continuous with the hyoid arch blastema, and a lateral part, which may represent the bases of hyoid rays.

The palaeoniscoid lacks the interhyal, but *Acipenser* appears to have it. *Polypterus* has a single element in the position of an interhyal but lacks the symplectic, suggesting an "either-or" situation in primitive fishes and an evolutionary trend toward elements to support both lower jaw and hyoid. *Lepisosteus* and *Amia* agree in having cartilaginous interhyals, whereas the teleost represents the acme with an ossified interhyal.

Although quite different, the palaeoniscoid and teleost types are generally thought of as extremes; that is, the teleost is a product of an evolutionary sequence having the holostean as an intermediate stage.

The nature of the holostean type can be considered in terms of the fossil record. This type is first observed in the Upper Permian genus *Acentrophorus* (Figure 5-13). The small species of this genus are like those of the later Family Semionotidae. The endocranium of *Acentrophorus* is not know but the suspensorium is quite holostean. An internasal is present but occurs in other holosteans as well. The premaxilla was probably fused to the rostrals. This genus already showed modification away from the ancestral pattern in that the parietals were fused at the midline.

Following *Acentrophorus*, holosteans are lacking in the fossil record until the Middle Triassic. In the Upper Triassic they appear in numbers. Their sudden blossoming in a variety of forms has been interpreted as indicating that several lines of palaeoniscoids, through functional changes in the jaw apparatus, suddenly assumed the guise of the holostean.

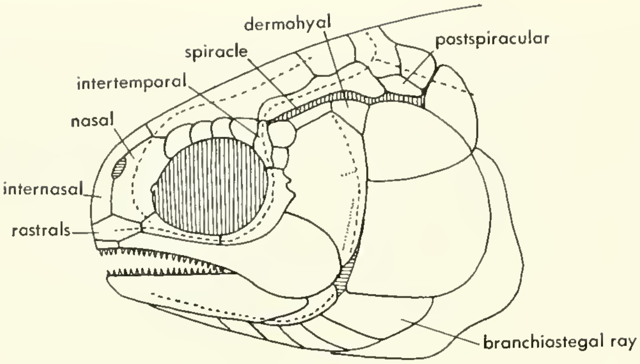
In the early Triassic, the palaeoniscoids are represented mainly by the subholosteans. This group is defined as having the body and fins essentially holostean, while the skull remains palaeoniscoid. The name itself implies that there were several lines of fishes undergoing parallel modification leading to the holostean stage. Of the subholosteans, two families are particularly suggestive of the holostean in that the nasals meet at the midline and in the general pattern of the cranial roof: these are the Perleididae and the Ospiidae. The former is quite palaeoniscoid but transitional in scale structure; the latter is transitional in the form of the lower jaw, the freeing of the maxilla, and the presence of a large dorsal branchiostegal ray in the position of an interopercle. An enlarged branchiostegal ray is also observed in the perleidids.

More like the holostean are the species of the subholostean Family Parasemionotidae. These resemble the holostean semionotids in some features but retain the massively ossified endocranium of the palaeoniscoid. Contemporary with the parasemionotids and included with them are forms having the preopercle reduced to a canal bone and the cheek covered by several irregularly shaped squamosoids. It is possible that their endocrania were subdivided into the several separate bones of the holostean.

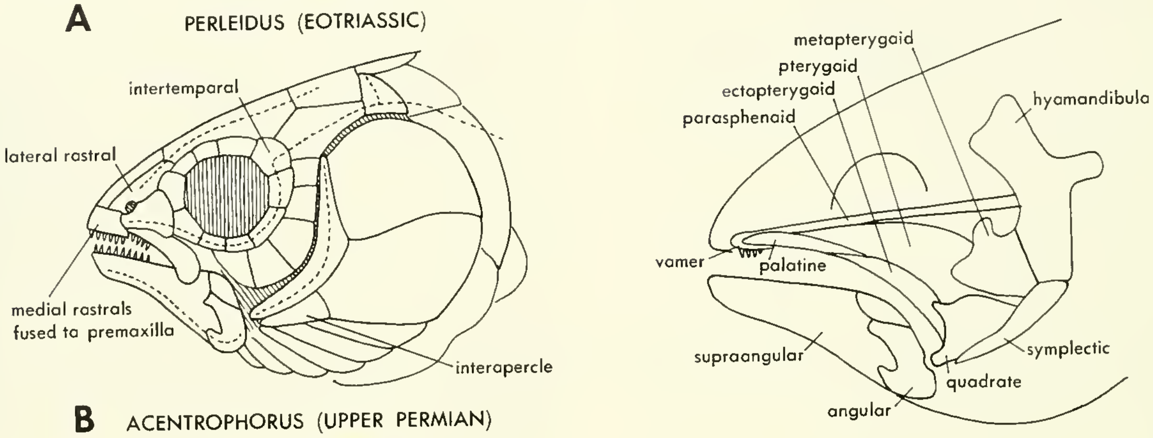
The critical feature of this subholostean-holostean transition was the acquisition of an interopercle—an interopercle of constant form and relationships. It seems unlikely, even assuming that it was a response to a mechanical need, that the interopercle was arrived at by the conversion of a branchiostegal ray—and in several lines of fishes independently. Its origin in development and its overlapping of the subopercle in the adult suggest that the interopercle is a fragmentation product of the subopercle produced by the mechanical changes in the jaws. These can be summed up as the forward movement of the point of articulation of the mandible, to a position in which the axis of the suspensorium is vertical or even directed ventroanteriorly, accompanied by a jaw angle that moves laterally as well as forward when the mouth is opened. The first of these has involved the acquisition of the J-shaped preopercle, which necessitated attenuation of the ventral part of the subopercle; whereas the second, the lateral movement of this area, would be aided by an oblique (posteriorly and down) joint across the subopercle.

Lepisosteus (Figures 5-14, 5-15) has acquired a J-shaped preopercle with the forward shift of the suspensorium, but the cheek is not flexible and no interopercle is present nor is it likely that one was present in the ancestry of this type. It is probable that several details were interrelated in the formation of the interopercle and that only some of the lines of subholosteans acquired the interopercle. It is just as possible that the interopercle was acquired by a single line that produced *Acentrophorus* and the much later Triassic parasemionotids. Comparison of the living "holosteans," *Lepisosteus* and *Amia* (Figures 5-14, 5-15), suggests that two quite distinct types of fishes are involved. Differences exist that go much deeper than the obvious specializations of the jaws. Differences such as the presence of the dermohyal in *Lepisosteus,* a cheek covered by squamosoids, and a large quadratojugal suggest that this fish, like the sturgeon, is a palaeoniscoid, or subholostean. *Amia* on the other hand is a typical holostean in every feature.

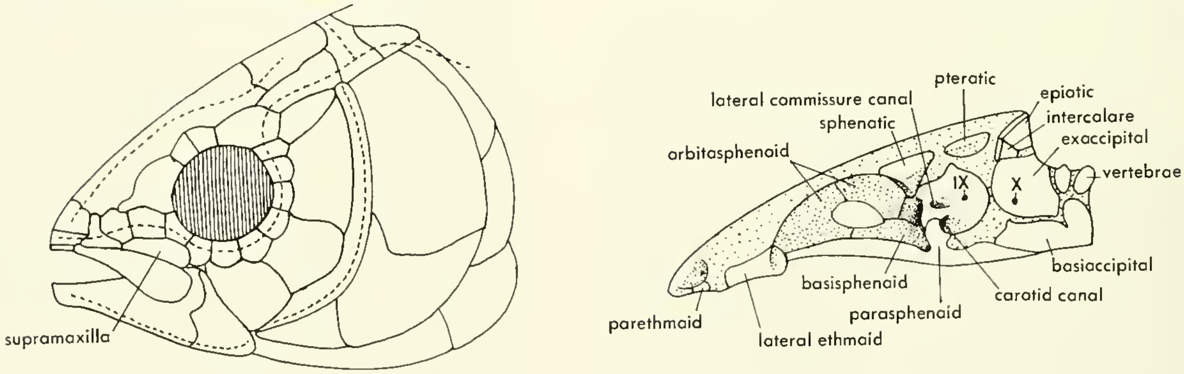
The systematic position of *Polypterus* is an undecided question. This type differs in its lack of a dermohyal, myodome, posterior ceratohyal, symplectic, and fifth branchial arch. The cheek region is sufficient in itself to cause doubt as to the place of the brachiopterygian; the presence of a spiracle suggests a very primitive type. It is quite probable that this line of fishes radiated from the ancestral stem at about the same time as the several known palaeoniscoid lines. To include it as a palaeoniscoid does violence to the definition of



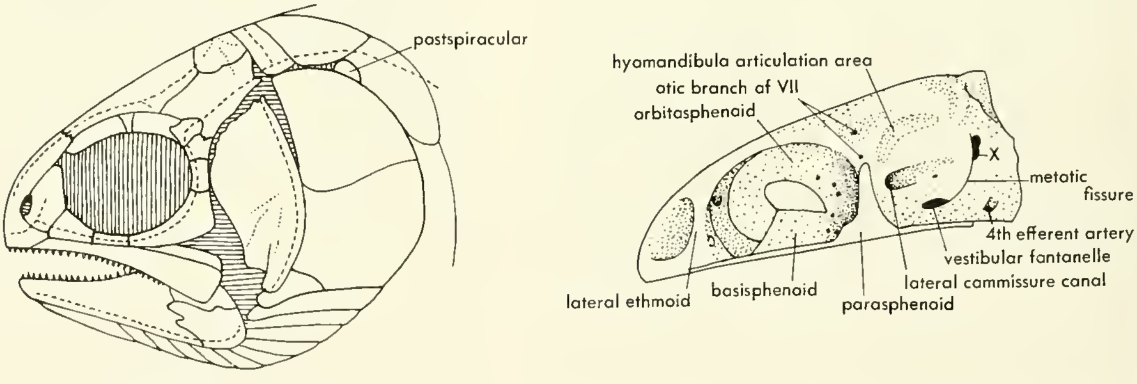
A PERLEIDUS (EOTRIASSIC)



B ACENTROPHORUS (UPPER PERMIAN)



C LEPIDOTUS (UPPER LIAS-JURASSIC)



D WATSONULUS (EOTRIASSIC)

Figure 5-13. Comparison of the dermal bones of the head, as seen in lateral view, and the endocrania of two subholosteans, A and D, and two holosteans, B and C.

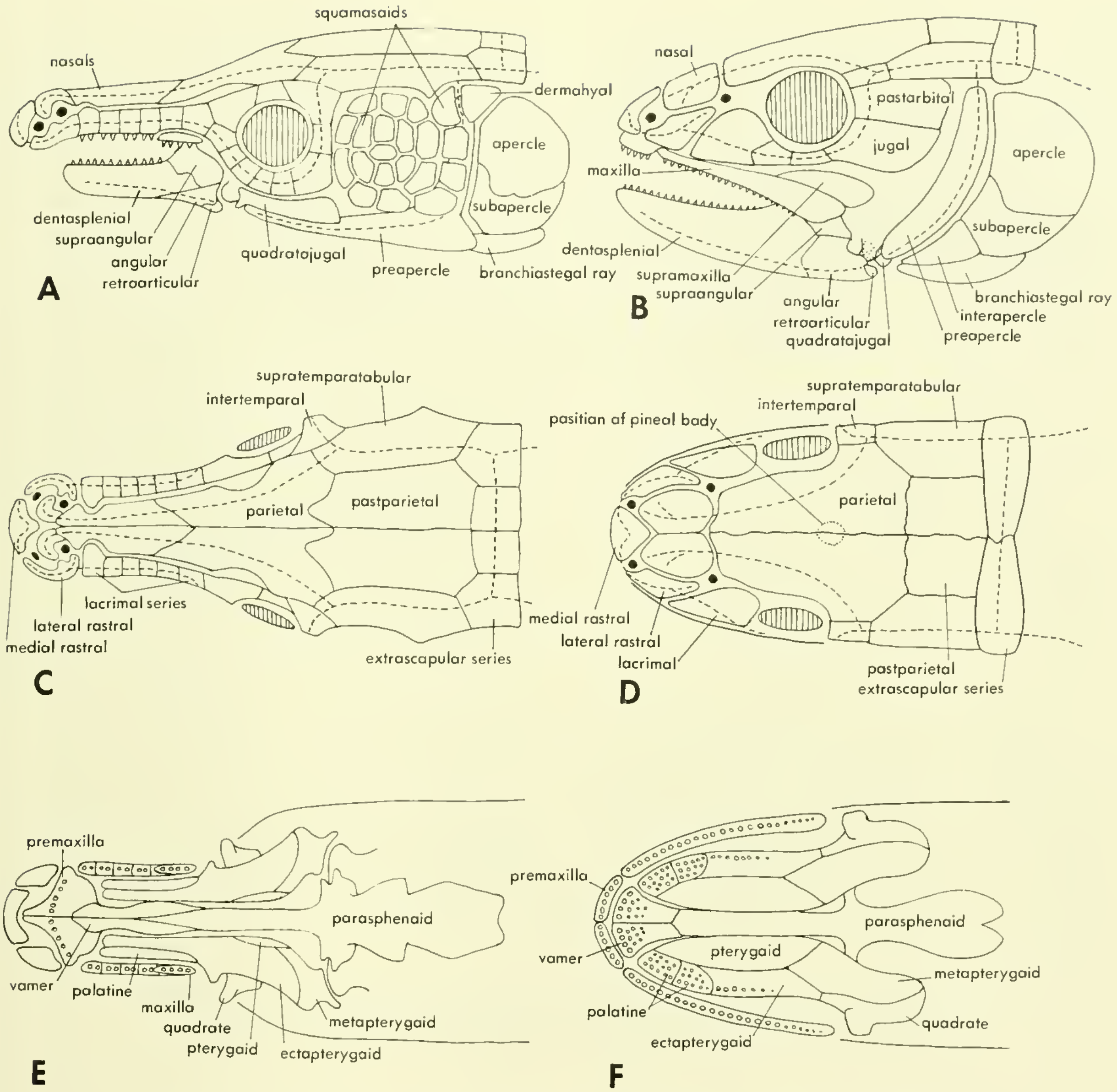


Figure 5-14. Semidiagrammatic sketches comparing the head skeletons of *Lepisosteus*, to the left, and Amia, on right. A and B, lateral views of heads; C and D, dorsal views of heads; E and F, palatal views.

that group; not including it fails to recognize the great variation known to occur in that group.

Relationship with the choanates A relationship between the actinopterygians and the choanates can be based on the similarities of the head skeletons. Until quite recently, such comparisons were used to demonstrate the common pattern of bones in the Osteichthyes. Goodrich remarked that the similarity of roof patterns was one of the strongest pieces of evidence of common ancestry. Westoll pointed out that the parietal fenestra, and several other landmarks of the cranium, had fixed relationships and that what had been called the frontal in the crossopterygian fish was the homolog of the amphibian parietal. Westoll rearranged the names of the bones of the crossopterygian to agree with those of the amphibian but assumed that the bones of the actinopterygian, which had been homologized with those of the crossopterygian, were so different as not to be comparable.

The problem of the origin of the roof pattern is one on which there has been much discussion but little agreement.

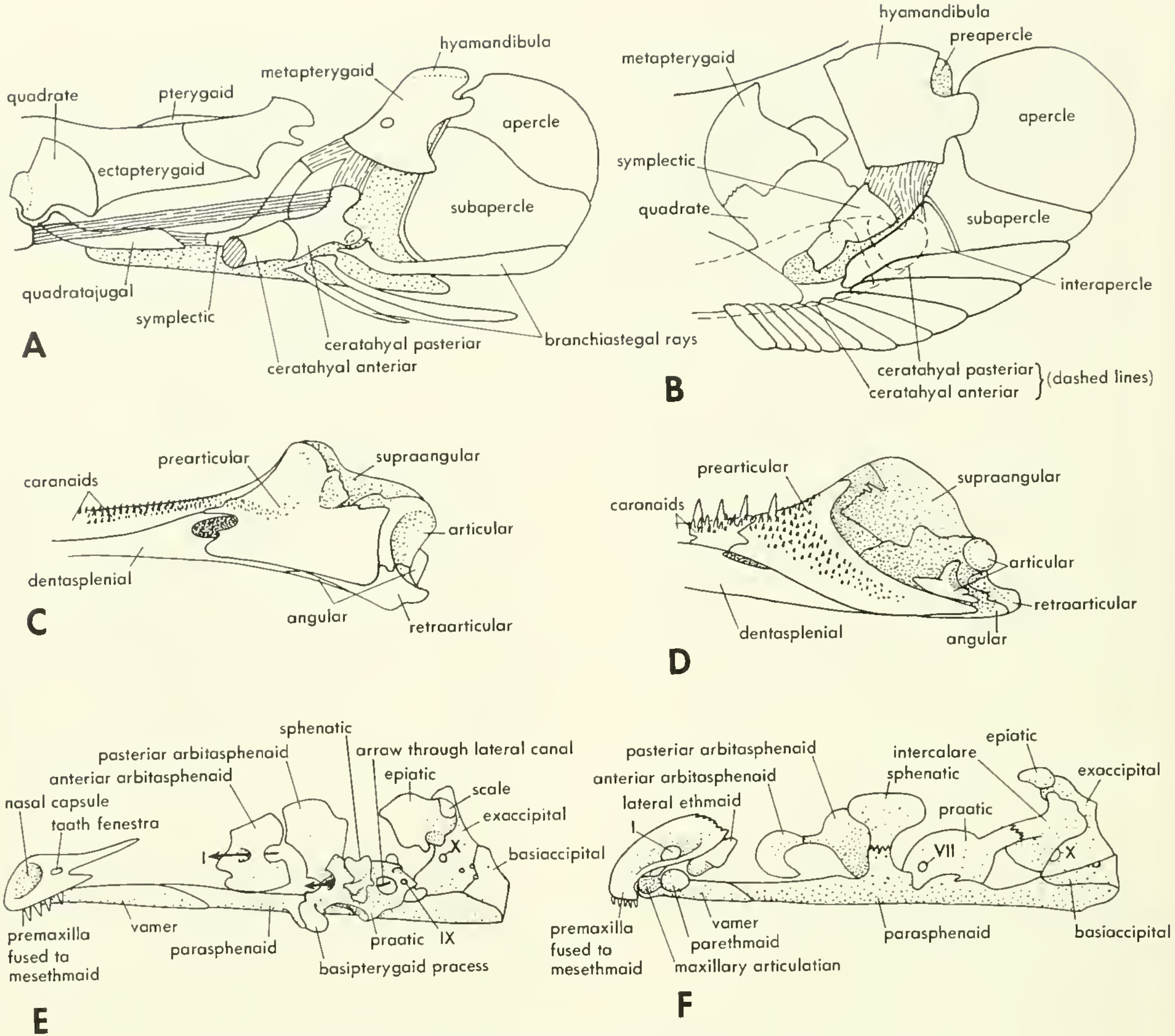


Figure 5-15. Semidiagrammatic sketches comparing the head skeletons of *Lepisosteus*, to the left, and *Amia*, to the right. A and B, medial views of suspensorium and operculum; C and D, medial views of posterior ends of mandibles; E and F, lateral views of endocrania.

The general opinion is that the ancestral gnathostome had a dermal cover of many small individual scales or plates and that, through fusion of these, each of the several lines of gnathostomes (amphibian, choanate, and actinopterygian) evolved its own head cover of plates. The process also involved reduction in the number of ossification centers, each plate tending to have only a single center. The differences in pattern between these lines can then be ascribed to the independent processes of plate formation, while the similarities must be due to parallel solutions to the problems of forming a head shield of plates, problems involving similar head shapes and makeup in the several groups, as well as similar functional needs. This parallelism suggests that the basic pattern observed in these groups is functionally controlled. The idea that the roof pattern is functionally controlled is shaken by the observed loss of this pattern in the dipnoans and in some of the actinopterygians. The alternative view, and the one most strongly suggested by the evidence, is inheritance of a common pattern, or partial pattern, by the several lines.

In comparing the three basic types—tetrapod with choanate fishes with actinopterygian, the question becomes one of whether there is more inheritance involved in one case than the other. Surely, as choanates, the crossopterygian should be closer to the amphibian but its cranial pattern does not indicate this. The snout of the crossopterygian is essentially an unbroken shield or a mosaic of small irregular plates as compared with the relatively uniform pattern of paired bones in the amphibian; therefore, in terms of the dermal bones, only the roof and the sheath of the lower jaw can be common inheritance. The question whether the roof and cheek of the actinopterygian were already largely defined at the time of origin of this line must remain unanswered, although comparisons suggest that the roof was and the cheek was not. The fact that among crossopterygians and dipnoans there are several cheek patterns supports this view. In most respects, the general pattern of actinopterygian and crossopterygian are the same, particularly in terms of the visceral skeleton. The greatest area of disagreement is in the dermal cover of the mandible. To be sure, some actinopterygians also deviate from the basic roof pattern, just as the dipnoan and actinistian or some individuals within any species, deviate.

The number of ossifications in the otic region of the actinopterygian endocranium is larger than in the choanate or amphibian. The appearance of a supraoccipital in the teleost suggests a parallelism to that of the higher tetrapods. The metapterygoid ossification of the palatoquadrate appears to be the homolog of the choanate epipterygoid.

In summary, one can say that the actinopterygian and choanate are much alike; from this it follows that the common ancestor was not far removed from either or from the amphibian. The Osteichthyes as a natural group appears to be legitimate but might include the tetrapods. The problem now becomes one of looking for features distinguishing bony fishes from the other kinds of jawed fishes, or to search for the roots of the Osteichthyes among the other gnathostomes.

Chondrichthyes

The chondrichthians, acanthodians, and arthrodires are sometimes associated together on the basis of the similarity of their chondrocrania. This association of forms, which at first glance seem to be so diverse, tests the criteria used in the preceding discussions, both in terms of how these are used and their intrinsic value.

As presently conceived, the cartilaginous fishes (Chondrichthyes) are subdivided into two subclasses: the Elasmobranchii, and the Holocephali. The first of these is a large array of species which can be separated into the sharks, rays, and torpedos. Of these only the shark will be considered.

Sharks The head skeleton of the shark is cartilaginous throughout with some calcification in the basis cranii. This condition is typical of the group, which extends back to the Upper Devonian. Teeth, which may be those of sharks, come from earlier rock strata.

The Dogfish Shark, *Squalus acanthias,* is most commonly dissected. It will be compared with other sharks such as *Heptanchus, Chlamydoselachus,* and *Hexanchus.*

The endocranium of *Squalus* (Figure 5-16) is much like that of some osteichthians. It differs in the flaring **orbital margins,** the presence of an **optic pedicel,** the weak development of the olfactory capsules, the large **precerebral fossa,** and the **capsular canal** passing from the brain cavity below the nasal capsule. The basis cranii shows perichondral calcification from the **foramen magnum** to the connection with the **preorbital plate.** This calcification occurs at both the inner and outer surfaces and extends laterally to the edges of the basal plate and ventral margin or the orbit.

The **palatoquadrates** are joined anteriorly by connective tissue; lateral to this union, each has a tall **orbital process** with a medially and posteriorly facing articular surface. The whole articular area is U-shaped and fits up around the braincase in front of the **basal processes.** The lateral aspect of the basal process connects through a thick pad of connective tissue with the medial surface of the palatoquadrate somewhat behind the vertical of the ascending process.

The palatoquadrate extends out and back to the angle of the mouth, where it articulates with the **mandible.** There is an upward flaring **adductor process** above the **articular condyle.**

The palatoquadrate of *Heptanchus* articulates with the cranium in two places: at the basal process and also with the **postorbital process.** The postorbital articular part of the palatoquadrate is identified as the **otic process,** or quadrate process. Two areas of articulation identify the **amphistylic** (both pillar) **style** of jaw suspension as opposed to the **hyostylic** (hyoid pillar supported) **type** of *Squalus.* The former is observed in the most primitive sharks, the latter in the more advanced forms.

The lower jaw is made up of the joined **Meckel's cartilages** and is short and massive. Associated with the jaws are **labial cartilages:** two with the palatoquadrate and one with the mandible. In *Heptanchus* all three appear to form a single Y-shaped piece.

The "hyomandibula" articulates with the posterior end of the cranium below the lateral head vein. In the other fishes the articulation is above the vein. The **hyomandibula,** or epihyal, of *Squalus* is a short irregular piece, distally bound ligamentously to the **palatoquadrate** and articulating with the stout **ceratohyal.** The latter in turn articulates with a slightly curved transverse plate, the **copula,** representing the fused **basihyals.** It is generally assumed that the **hypo** elements are missing in this group, although a vestigal one is found in the first branchial arch of *Scyllium* and in several arches of different rays. The assumption is based on the proposition that hypohyals continue the line of the **cerato** element forward and medially, while the **basi** elements tend to be single midline pieces extending posteriorly behind the tip of the lower arm of the arch.

There are five branchial arches in *Squalus* (seven in *Heptanchus* and *Chlamydoselachus*), each (from top down) with **pharyngobranchial, epibranchial, ceratobranchial,** and **basibranchial** components. The fifth arch is the exception, lacking a separate pharyngobranchial because of fusion with that element of the fourth arch. The pharyngobranchials extend posteriorly, and only the anterior part of the first one is attached to the cranium. The main attachment of these elements is to the spinal column.

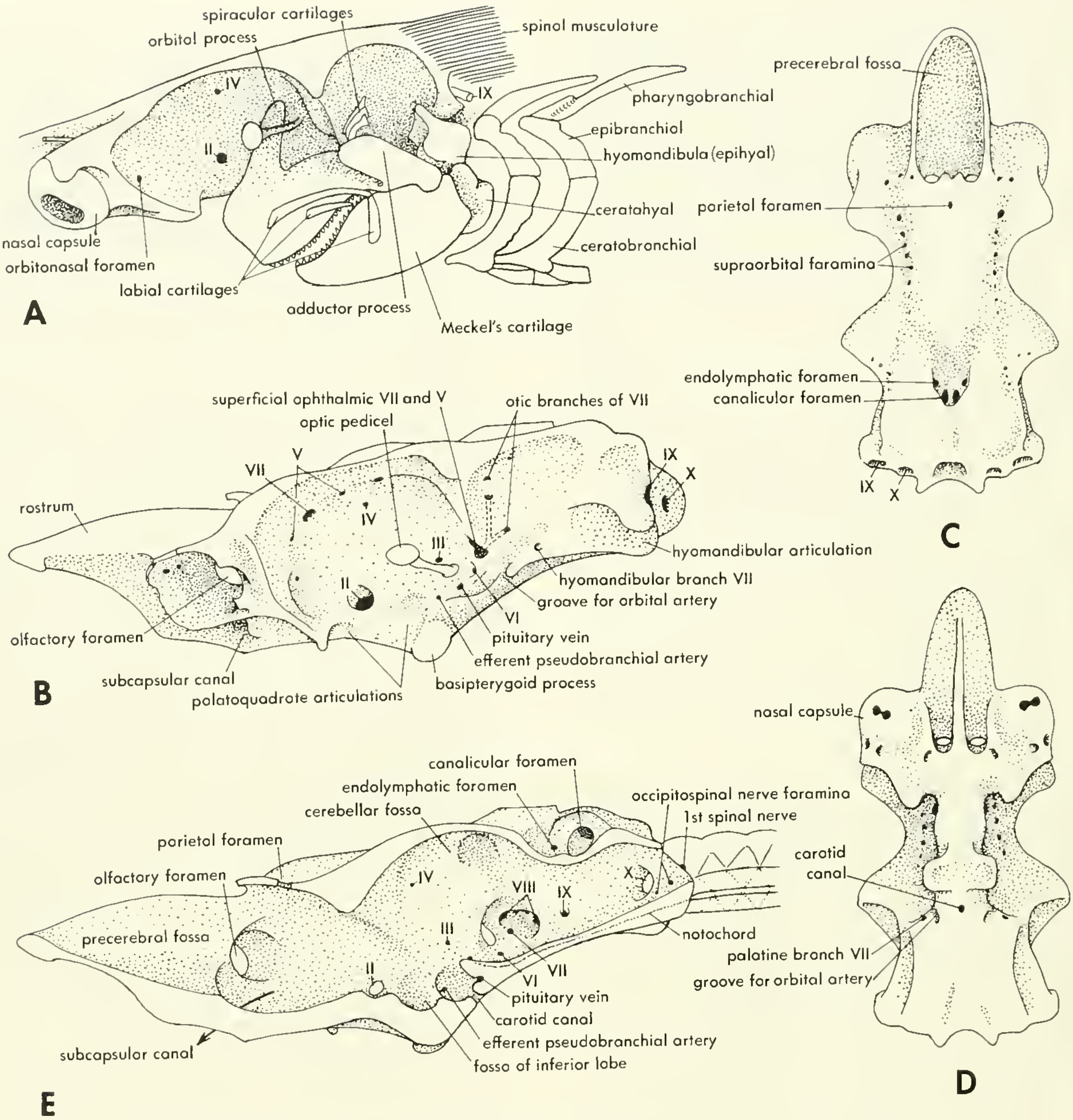


Figure 5-16. Head skeleton of the shark, *Squalus*. A, lateral view; B, lateral view of endocranium; C, dorsal view; D, ventral view; E, medial view of right half of endocranium.

EMBRYOLOGICAL DEVELOPMENT The development of *Squalus acanthias* has been described by many individuals (Figure 5-17). The difficulties of studying stages of development are commented on by Holmgren. Surveying the literature, one gets the impression that investigators have begun their accounts with the stage where the first cartilage appears. In reality, the appearance of the first cartilages is a rather late event in the development of the skull, which is already outlined in blastematic or mesenchymatic stages. Further, experience teaches that chondrification begins at very different stages in embryos of the same species. Because of this variability it is often difficult to line up stages in a continuous series with reference to the development of a particular part. Therefore a detailed comparison of embryos belonging to different groups of selachians must be more or less hazardous. A more general account, however, can serve the purpose of a comparative study.

The **parachordals** appear first, well behind the tip of the notochord and in contact with the notochord. These rods are extended laterally under the otic capsules. The **otic capsules** chondrify from **anterior** and **posterior vestibular centers.** These connect with the underlying **basiotic extension** of the parachordal. The **occipital arch** appears behind several of the hypoglossal roots and at first involves two pairs of centers.

The **orbital cartilage** arises as a part of the **pila antotica**; the former is perforated by the trochlear nerve and the pila is not attached basally. Separate **trabecular** and **polar car-**

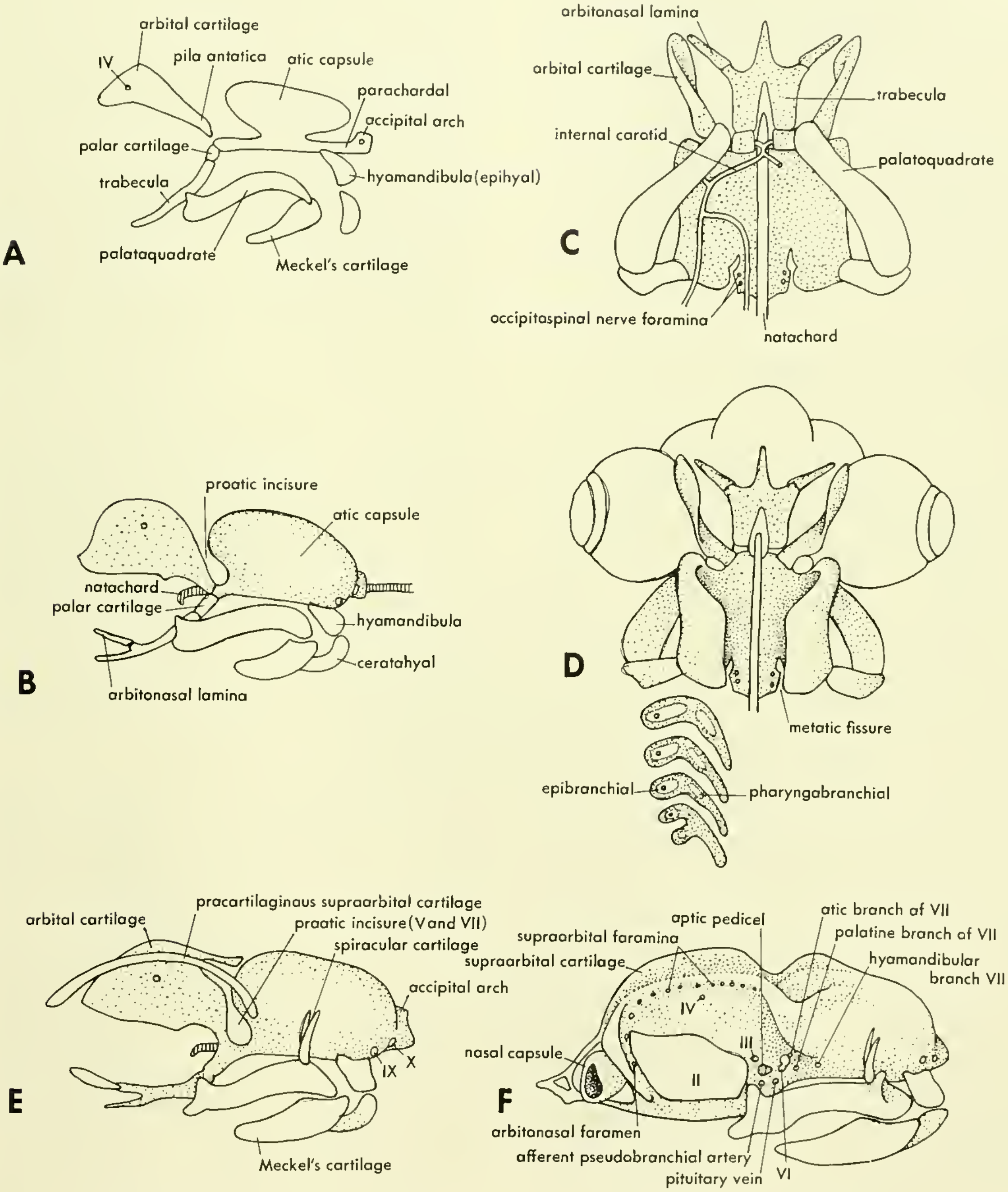


Figure 5-17. Development of head skeleton of *Squalus*. A, lateral view of 37-mm embryo; B, C, D, ventral, lateral, and dorsal views of 39-mm embryo; E, lateral view of 45-mm embryo; F, lateral view of 64-mm embryo. (After El-Toubi, 1949)

tilages appear ventral to the anterior ends of the parachordals, and behind these the anlages of the **palatoquadrate** and **Meckel's cartilage.** The jaws arise from a single mesenchymatous mass connected with the trabecula and the anlage of the hyoid arch behind it. The attachment of the anterior end of the palatoquadrate to the edge of the trabecula represents the basal process. With chondrification of the several elements, there remains a mesenchymatous otic process from the palatoquadrate up into the prespiracular area. This process lies lateral to the head vein and the facial nerve.

The **epihyal** chondrifies from below upward; ventrally it is in blastematic connection with the palatoquadrate—there is no symplectic. A semiseparate **pharyngohyal** center appears above the epihyal and fuses with it to form the **"hyomandibula."** In rays this center fuses with the otic capsule and forms the area of articulation of the epihyal; a large part of the epihyal is formed from the fused bases of the cartilaginous gill rays. Centers for the **cerato** and **basihyal** are also present.

The parts of the auditory capsule are now joined laterally and the capsule fused anteriorly with the underlying parachordal. The trabecula attaches to the polar cartilage, which in turn soon joins the parachordal. The **acrochordal** forms at the tip of the notochord and moves backward along the notochord, in a relative sense, until it joins the parachordals. The pila antotica joins the acrochordal laterally as well as fusing with the parachordal behind it. The trigeminal, abducens, and facial nerves emerge between this pillar and the otic capsule.

Between the otic capsules, the parachordals invade the sheath of the notochord. The occipital arch has two or three hypoglossal foramina penetrating it; there are separate foramina for one or two dorsal roots of the more posterior of these. One or two occipitospinal nerves pass out through the metotic fissure with nerves IX and X. A chondrification extends upward in the medial wall of the otic capsule, posterior to the auditory nerves. The completed capsule has an **endolymphatic foramen,** a **canalicular foramen,** and an **auditory** nerve **foramen** in its medial wall.

Anteriorly the trabeculae are joined by a plate from which a rostral process projects. Laterally there are processes from which separate **orbitonasal laminae** project dorsolaterally and anteriorly. The orbital cartilage arches forward and then down to attach to the trabecula by a **preoptic pillar** passing medial to the orbitonasal division of the profundus (V_1) and the superficial ophthalmic division of the facial nerve. The orbitonasal cartilage lies lateral to the preoptic pillar but soon fuses with it and the preorbital cartilage which appears in the mesenchymatous ring margining the orbit. **Preorbital** and **postorbital centers** appear in this ring and later they are joined by a **supraorbital cartilage;** the whole semicircle then fuses with the chondrocranium. The line of union is marked by the foramina of the branches of the superficial ophthalmic division of the facial nerve that serves the organs of the supraorbital sensory canal and the skin. A **posterior maxillary process** extends back from the ventral margin of the orbitonasal cartilage.

The **prootic foramen** is formed by an **orbitocapsular commissure** which is accompanied by a posterior extension of the supraorbital-postorbital band. From the pila antotica an extension divides the prootic foramen into upper and lower openings. The lower closes and the upper is divided by a commissure from the capsule into a trigemino-facio-abducens foramen and a posteroventral palito-hyomandibular foramen. The abducens foramen later separates from the others. The basal plate extends up between the hyomandibular and palatine nerves.

Anteriorly the **rostral process,** which represents the **nasal septum,** expands along its dorsal margin into a trough-like plate underlying a cavity, the **precerebral fossa.** This is filled with a gelatinous connective tissue and separated from the cranial cavity by a transverse membrane. The lateral margins of the precerebral fossa connect with the orbitonasal cartilage and with the **sphenethmoid commissure** of the orbital cartilage.

The orbit area is completed by closure of the large optic fenestra. Several foramina are formed in this closure: optic, oculomotor, efferent pseudobranchial, and pituitary vein. An optic pedicel arises in the connective tissue attaching the eye to the orbit wall. Ventrally the **hypophyseal fenestra** closes from in front back, involving a plate between the trabeculae. There is a **scleral cartilage** within the wall of the eye. Posteriorly the parachordals are interconnected by a thin sheet below the notochord. The notochordal sheath itself is chondrified.

The mesenchymatous **lateral commissure** gives rise to two small **prespiracular cartilages,** a transitory procartilaginous rod lateral to the palatine nerve, and a small extraotic cartilage which fuses to the capsule wall to form the canal for the otic division of the facial nerve.

The roof develops first from the **synotic tectum,** which expands forward and posteriorly. Behind the **endolymphatic fossa** a slim **posterior tectum** arises from the occipital arch, which is now attached to the otic capsule above the metotic foramen. Above the eyes, there are **orbital, paraphyseal,** and **epiphyseal tectal processes.** These join and expand until the roof is solid.

The upper and lower lip cartilages are derived from the blastema of the palatoquadrate; the posterior portion becomes the lower lip cartilage. The lower, small cartilage of the upper lip arises from the mesenchymatic area of attachment of the palatoquadrate to the trabecula. Posteriorly there is a small blastema lateral to the quadrate area. A mesenchymatous or chondrified intermandibular arises between the Meckel's cartilages but is later lost.

The shark lacks bone in its head skeleton, except for that in the basal plates of the scales, but it has been suggested that the mesenchymatous condensations giving rise to the orbit margin and labial cartilages are indeed remnants or forerunners of dermal bones. The labial cartilages appear to be comparable in their origin to the maxillary and dentary of other fish. The prismatic calcified cartilage of elasmobranchs is not primitive but clearly a highly modified hard tissue which cannot possibly be viewed as the forerunner of the enchondral bone observed in other fishes. From this it can be concluded that sharks may never have been extensively bony, either dermally or chondrally.

Holocephalan or chimaerid The living holocephalans belong to five genera: *Chimaera, Hydrolagus* (Figures 5-18 to 5-20), *Callorhynchus, Harriota,* and *Rhinochimaera.* Fossils of this group extend back to the Upper Triassic (*Squaloraja* and *Myriacanthus*). It has been assumed on the basis of the tubulodentine of the tooth plates (Figure 8-55) that these fishes are derived from the Bradyodont sharks dating back to the Upper Devonian.

Comparisons of the shark and chimaerid suggest that they have little in common. The differences in terms of *Hydrolagus* can be summarized as follows:

1. Palatoquadrate fused to the neurocranium from olfactory capsules to otic capsule (**holostylic style** of jaw suspension).
2. "Hyomandibula" only a slightly modified epihyal which does not articulate with the cranium; there is a separate posteromedially projecting pharyngohyal; there is no spiracle nor spiracular cartilages; there is a single external opercular opening on either side.
3. Precerebral fossa (or precerebral fontanelle) and capsular canals are lacking; nasal capsules are separated by nasal septum.
4. Posterior cerebral vein exists independently of the vagus.
5. Occipital condyles better marked.
6. Otic capsule lacks inner wall; a midline endolymphatic foramen opens through the cranial roof.
7. Ethmoid chamber present for myeloid tissue and passage of superior ophthalmic and profundus nerves.
8. Optic pedicel lacking.
9. Rostral cartilage present which supports spongy tissue of snout.

There is some agreement with the shark in features such as lack of bony jaws, chondrification of the notochordal

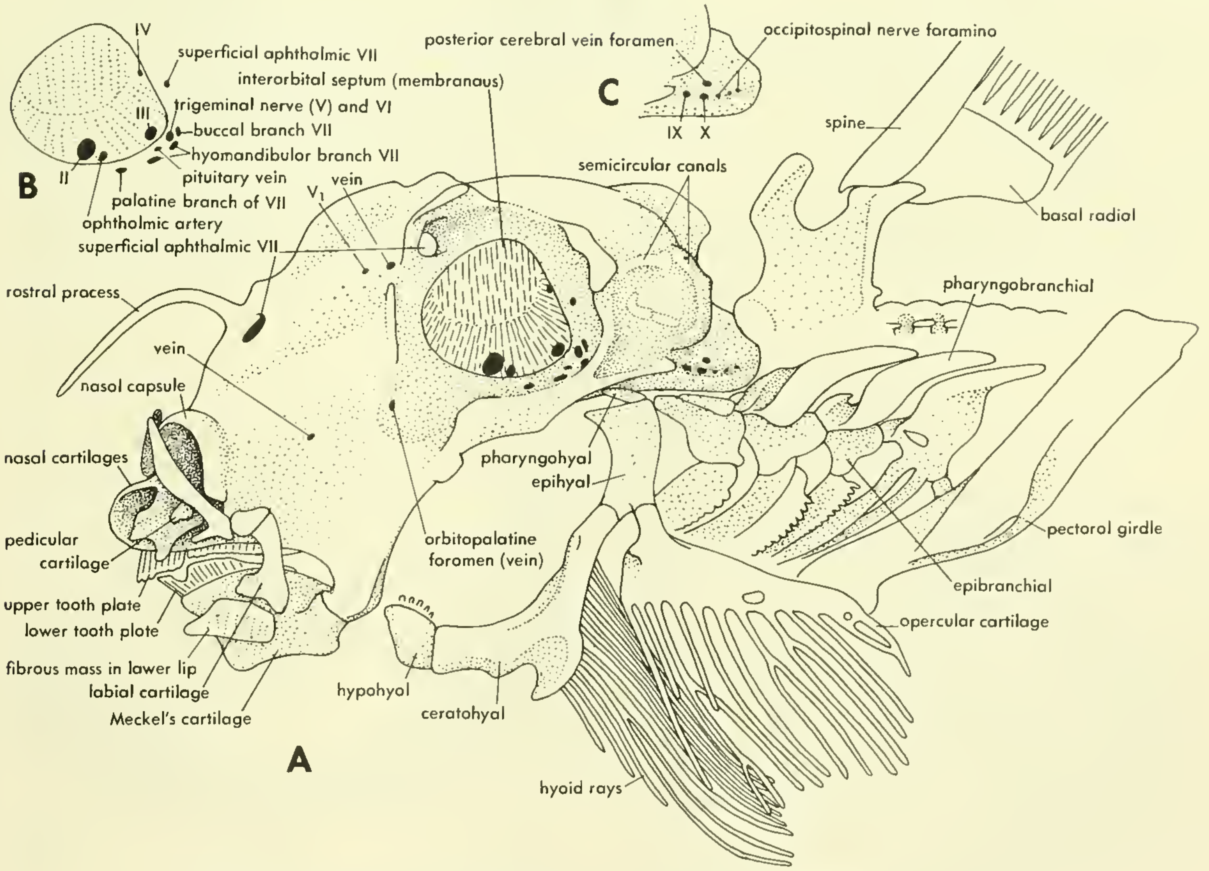


Figure 5-18. Head skeleton of *Hydrologus colliei.* A, lateral view of entire area; B, details of orbital foramina; C, labels for occipital foramina.

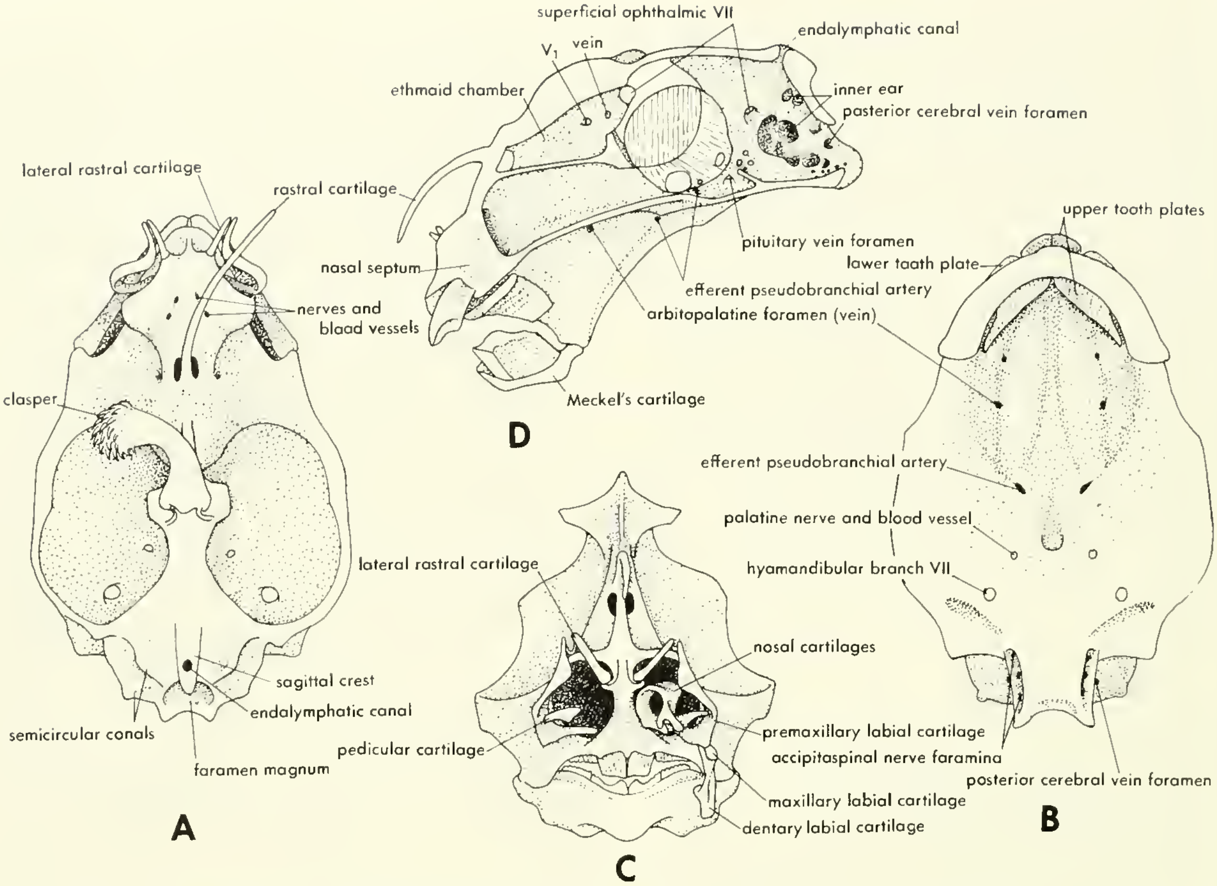


Figure 5-19. Cranium and lower jaw of *Hydrolagus*. A, dorsal view; B, ventral view; C, anterior view; D, medial view of right half.

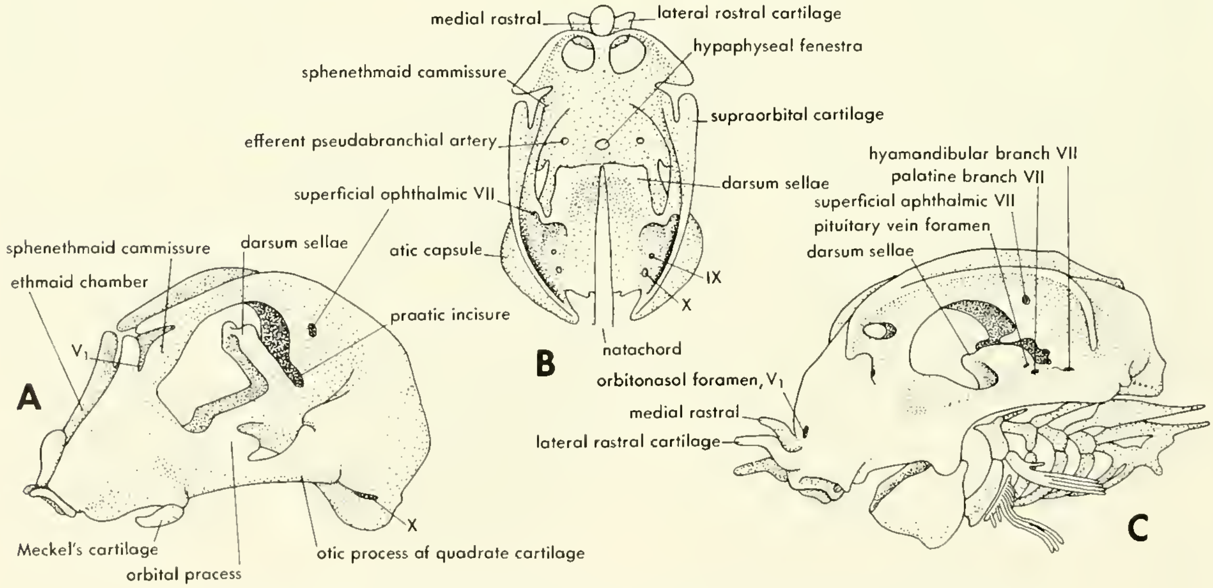


Figure 5-20. Stages in the development of the head skeleton of *Callorhynchus*. A and B, lateral and dorsal views of cranium and jaws of a 60-mm embryo; C, lateral view of head skeleton of 85-mm embryo. (After Schainsland, 1903)

sheath and constriction of the notochord in the basal plate, notochord reaching dorsal margin of dorsum sellae and projecting from it (at least in younger stages), dorsum sellae forming between ends of parachordals, epihyal not extending up lateral to head vein (no laterohyal involved), presence of orbital margin of cartilages, presence of nasal and labial cartilages, and separate posterior superficial ophthalmic foramen.

Acanthodians

The acanthodians are represented by spines and plates in Upper Silurian deposits, but it is not until Devonian strata that much of their structure is preserved.

The head (Figure 5-21) was covered by small scales with larger plates forming a **circumorbital ring.** The several **gill slits** opened separately behind folds; the most anterior fold or **operculum** was supported by **mandibular** rays. The **endocranium** had a large anterior orbit, little or no **ethmoid region,** and a large postorbital **oticoccipital section.** The endocranium was largely cartilaginous with subperichondral calcification in some species, and in others perichondral ossification shading into subperichondral calcification, which appears to be the more primitive condition. These ossifications included a pair of **exoccipitals** lying behind the vagus foramen. There was a **basioccipital** enclosing the dorsal aorta, and in front of this a **basisphenoid.** A **parasphenoid** sheathed the ventral surface and extended forward below the orbits. Its anterior end was associated with five small plates. The **postorbital process** was ossified and the processes of either side were joined by a section of ossified roof. There was a **lateral commissure** below the orbital process.

The **palatoquadrate** had **quadrate, metapterygoid,** and **autopalatine** centers of ossification. It articulated with the postorbital process and with a basal process of the parasphenoid. The two palatoquadrates were not joined anteriorly. The mandible consisted of an anterior and posterior ossification joined synchondrally. The articular may have

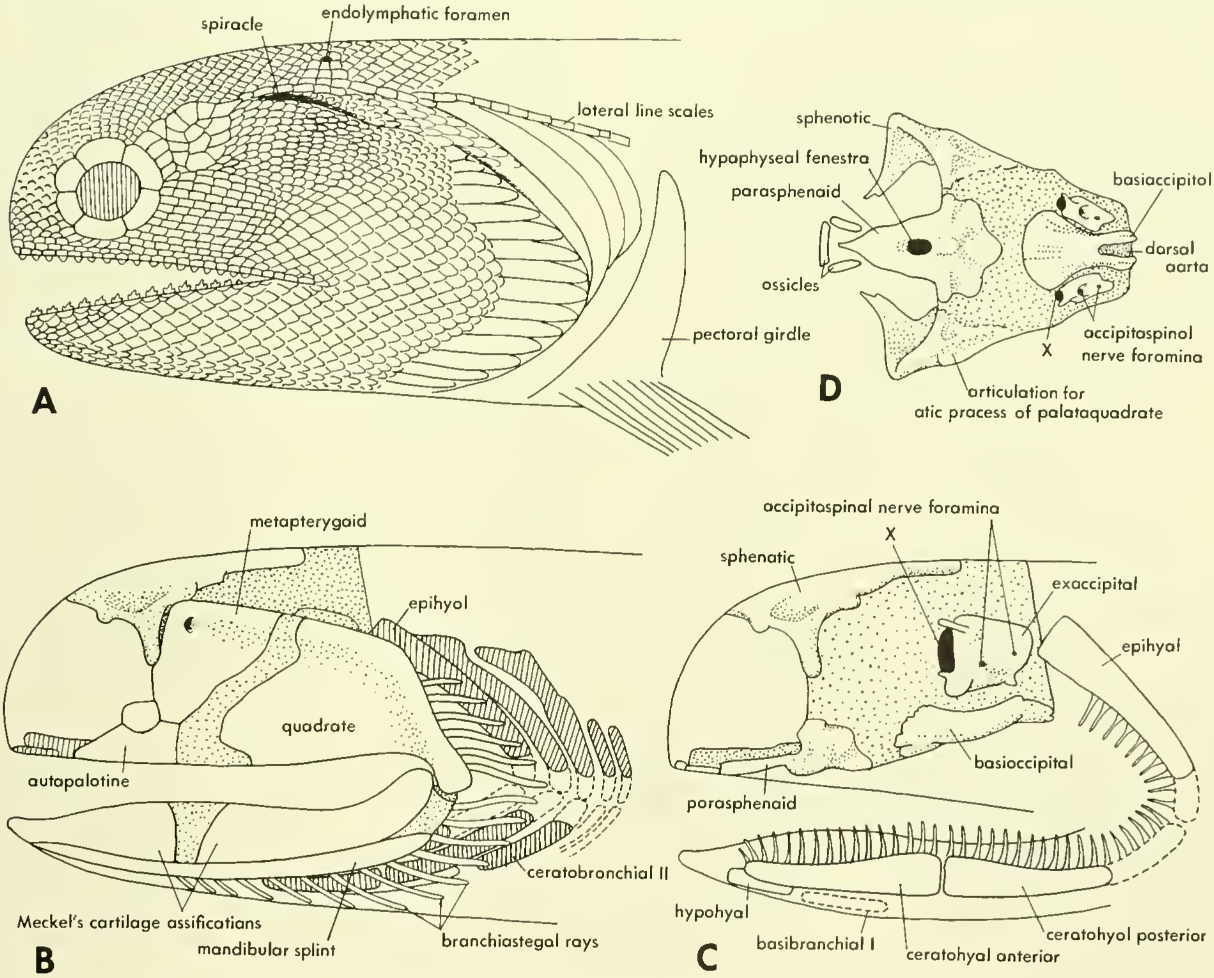


Figure 5-21. Head skeleton of *Acanthodes* sp. A, lateral view of head showing scales, circumorbital plates and operculum; B, lateral view of jaw elements, branchial skeleton, and endocranium; C, lateral view of endocranium and hyoid arch; D, ventral view of endocranium. (After Watson, 1937)

been separate. These ossifications were joined by a ventral band of perichondral bone. In some acanthodians the **mandible** ossified as a single unit and bore teeth. The palatoquadrate and mandible had rays extending into the opercular fold.

The **hyoid arch** was modified. The **epihyal** was quite broad (laterally compressed) at its dorsal end, which may have articulated with the posterior end of the cranium, and tapered to its ventral end. The ossification of hyoid, and branchial arches, was subperichondral. The ventral end of the epihyal cartilage articulated with the cartilaginous end of the ceratohyal. The latter was long and slim and abutted anteriorly against a long hypohyal, which in turn articulated with a small median basihyal. There is no evidence of a pharyngohyal.

There were three to five branchial arches. The more anterior arches with pharyngo, epi, cerato, and hypo segments; the more posterior arches lacked the pharyngo and perhaps the hypo segments. The pharyngobranchials were long and with distinct suprabranchial processes.

General observations The association of the acanthodians with the sharks is based upon such features as their dentition and the separate outer gill openings. The teeth are not unlike those of other fishes, while the gill openings are not truly comparable to those of the shark. The group is usually described as having a complete mandibular gill slit—a condition described by the term **aphetohyoidea.** In the shark this gill slit is reduced to the spiracle. On the basis of the course of the preopercular canal in *Acanthodes,* Stensiö (1947) assumed that these fishes had a spiracle and were not aphetohyoideans. *Hydrolagus* has a scarcely altered hyoid arch, yet lacks even a spiracle. Aphetohyoidean as used hereafter should be taken to imply an unmodified hyoid arch not involved in mandibular support.

Comparison of the shark palatoquadrate with that of the acanthodian gives no better agreement. The ossified parts of the palatoquadrate of this group are like those of the actinopterygian. The mandible is not like the shark's and there is the suggestion of dermal anchorage of the teeth, an anchorage lacking in the shark. The bony development in this group further supports separation from the sharks.

Arthrodires

Another group of fishes assumed to have some relationship with the sharks is the arthrodires. These are truly placoderms, so named because of the heavy dermal armor. The arthrodires are subdivided into a number of subgroups, some of which are shark-like. The euarthrodires (*Dunkelosteus, Kujdanowiaspis*) and the antiarchs (*Bothriolepis*) will be described although they are not particularly shark-like.

Euarthrodire In the euarthrodire (Figure 5-22), the cranial roof is thick and the plates closely joined. The roof is separated by a gap from the cheek and infraorbital bones. On the rear, outer margin of the roof is a knob and a large socket for the joint with the heavy pectoral girdle or trunk armor.

The pattern of the cranial roof has been compared with that of the osteichthian fishes (Table 5-2), but it seems best to use names which do not imply any homology with the plates of the Osteichthyes. The cheek was covered by a large

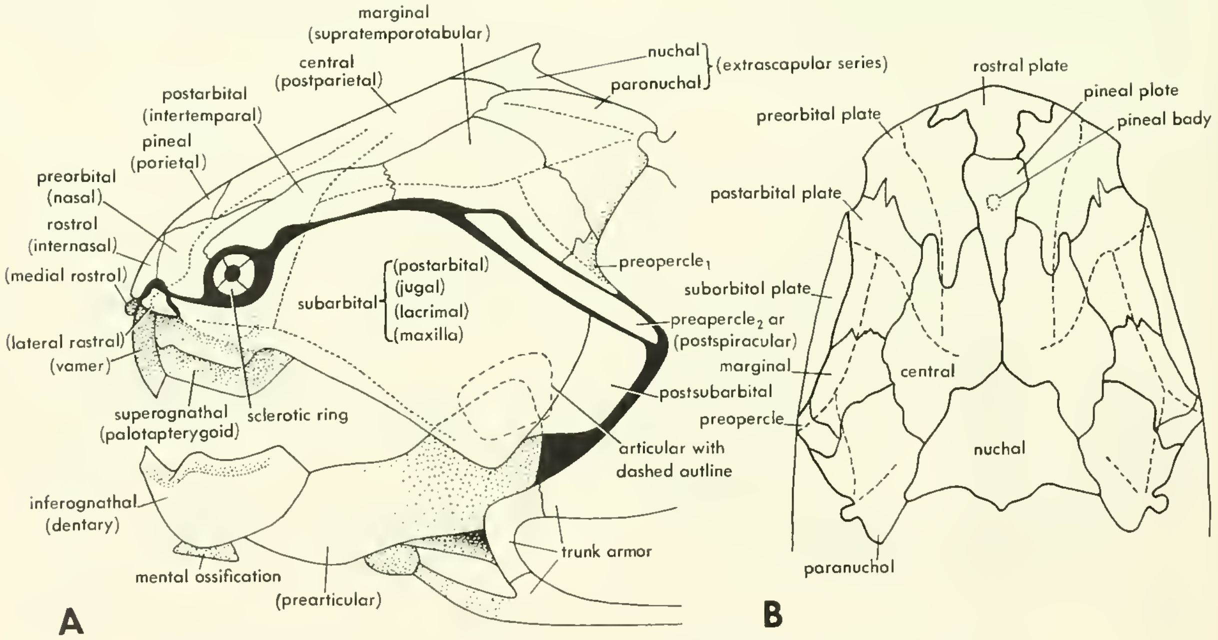


Figure 5-22. A, lateral view of head skeleton of *Dunklosteus terrelli;* B, dorsal view of *D. marsaisi.* (B after Lehman)

TABLE 5-2 SYNONYMY OF SOME OF THE CRANIAL PLATES OF THE EUARTHRODIRE AND THE HIGHER GNATHOSTOME

Euarthrodire	Higher Gnathostome
paranuchal and nuchal	extrascapulars
marginal	supratemporotabular
postorbital	intertemporal
preorbital	nasal
pineal	parietal
central	postparietal

suborbital plate which was grooved by the infraorbital canal. Behind the suborbital was a smaller **postsuborbital** and above this a **preopercle,** which was a long, slim, free plate. Anterior to the **infraorbital process** of the **suborbital** was a small **postnasal,** notched anteromedially by the nasal opening. The postnasal was free or incorporated into the shield. Both cheek and roof bore grooves marking the course of the sensory canals.

The upper jaw was formed by two **superognathal plates.** Teeth were present in the young but replaced by cutting edges in the adult. The superognathals have been identified as the vomerine and palatopterygoid plates and homologized with the tooth plates of the chimaerid. A free **palatoquadrate** was present and had **quadrate** and **autopalatine** ossifications.

The lower jaw was formed basically of a plate lying dorsolateral to **Meckel's cartilage** and anterior and medial to that cartilage posteriorly; this has been called the mixicoronoid or **inferognathal.** There were **articular** and **mental** ossifications in Meckel's cartilage.

The endocranium enclosed the brain cavity. It was mainly cartilaginous but was sometimes covered in various areas or entirely, inside and out along with all canals and hollows, by perichondral bone. Where the bone was well developed, endochondral trabeculae were within it. The **notochord** varied from unchanged to obliterated in the **basal plate.** The eye had a **sclerotic ring** of four bony plates. The **nasal capsules** were sometimes an integral part of the endocranium and sometimes separate.

The hyoid arch and branchial arches are not known, but it is assumed that these fishes were aphetohyoideans and operculate.

Antiarch Stensiö (1948) has described the antiarch *Bothriolepis* (Figure 5-23). The mouth was small and ventral, and the eyes were on top of the head along with the nasal openings. The head was somewhat flattened. These relationships suggest a sluggish, bottom living habit. The head articulated with the pectoral girdle, much as in the euarthrodire, except that the main socket was on the pectoral girdle. The cranial roof was joined with the cheek and much reduced in size. There was a spiracular opening above and behind the angle of the mouth. The jaws are suggestive of those of the euarthrodire. The endocranium was unossified except for one small, Y-shaped bone of unknown position. There were three **scleral plates** in the eye ring. The visceral skeleton is largely unknown, but there were several ventral perichondral ossifications associated with the hyoid arch.

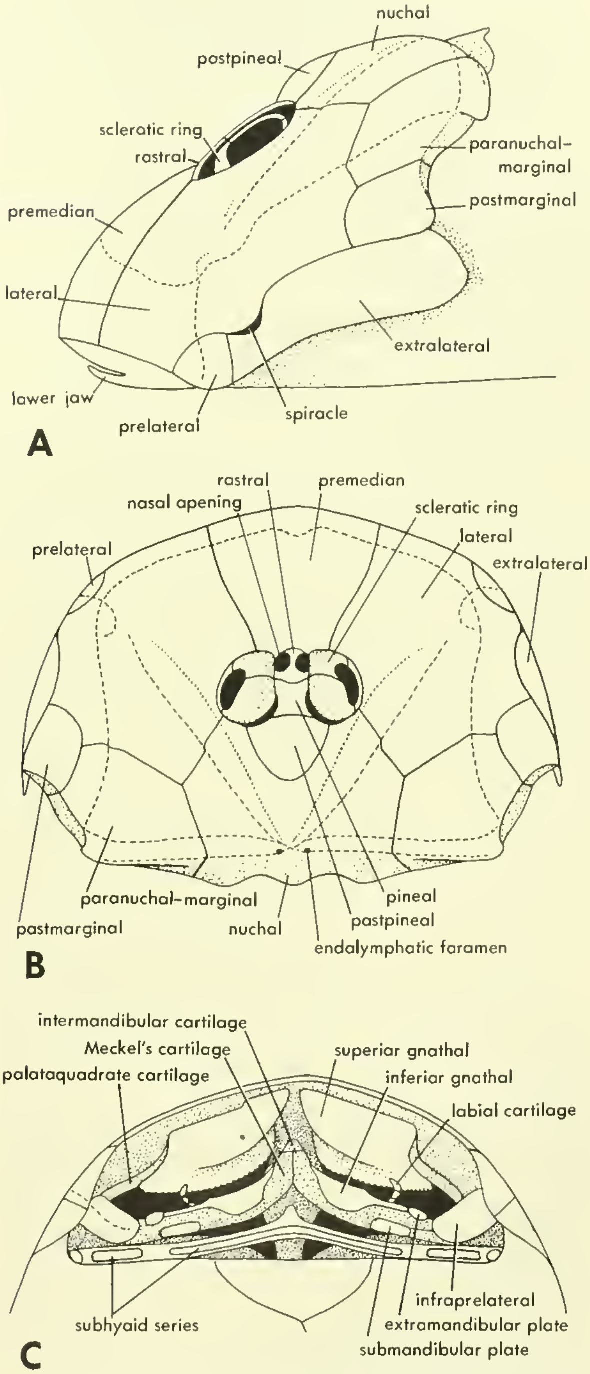


Figure 5-23. Head skeletan af *Bathrialepis canadensis.* A, lateral view; B, darsal view; C, ventral view. (After Stensiö 1931, 1948)

General observations The head skeleton of the antiarch only superficially resembles that of the euarthrodires. In view of the radical differences in design of the several subdivisions of arthrodires, it is quite possible that the acanthodians and sharks could be included in the same group. Such inclusion would be relatively meaningless in terms of comparisons with the osteichthian fishes. Even if the acanthodians and sharks are not included, the Arthrodira as a group is scarcely definable.

Comparisons of the shark type (with or without *Hydrolagus*) with the acanthodian or arthrodire is extremely difficult. Whereas the shark is characterized by lack of bone, the arthrodire is generally a heavily armored type—with a roof pattern having some resemblance to the osteichthyian. Detailed comparisons are not yet possible because of lack of information on these fossil groups.

Interrelationships at the base of the gnathostome fishes

The term **teleostome** has been used to identify actinopterygians and choanates having "perfect" or complete jaws, i.e. there is a premaxillary and maxillary margin to the upper jaw and a dentary margin for the lower jaw. These bones bear the main teeth or tooth rows. In contrast, the **plagiostome** mouth, meaning oblique or transverse, lacks this margin. As far as known, only the palatoquadrate cartilage is involved in the plagiostome upper jaw, and Meckel's cartilage in the lower jaw. The acanthodians and arthrodires may lie somewhere in between these two extremes, for they have vomer and palatopterygoid teeth and dermal jaw margins.

In terms of the branchial skeleton, the teleostomes differ from the plagiostomes. The pharyngobranchial extends forward and medially in the teleostomes and posteriorly and medially in the plagiostomes. Again they differ in the structure of the "hyomandibula" and the presence of a symplectic, or interhyal.

The number of branchial arches is generally five in both of these divisions; exceptions include several of the sharks which have six or seven. This increased number is probably due to the addition of slits rather than retention of a primitive number.

The number of segments in the branchial arches appears to be a constant. The hyoid arch of gnathostome fishes is assumed to be only a modified branchial arch. The aphetohyoidean is presumed to be more primitive than those types in which the epihyal is modified by participation in support of the lower jaw.

The basic branchial arch plan has been extended to the mandibular and premandibular arches by Jarvik (1954) in support of Gegenbaur's hypothesis. In this scheme, the palatoquadrate is seen to be a compound structure with autopalatine and quadrate subdivisions. The quadrate part is the epimandibula, and its ascending process (epipterygoid or metapterygoid) is the supramandibula. The otic process, comparable to the laterohyal, can be termed the lateromandibula. The trabecula is the pharyngo element. The premandibular arch has as its epi element the autopalatine, or processus pterygoideus. This part of the palatoquadrate lies anterolateral to the prespiracular groove and thus anterolateral to the diverticulum in the roof of the pharynx, which is interpreted as a vestige of the premandibular gill pouch. The orbitonasal lamina of the endocranium is the supra element, while the intermediate mesenchyme below the ethmoid region, which gives rise to the vomer, represents the pharyngopremandibula.

Supporting Jarvik's associations are the findings that, while the parachordals and polar cartilages are entomesodermal (i.e. of sclerotome or dermomyotome origin—see Chapter 7), the trabeculae are of neural crest origin or ectomesodermal (thought to be both ecto- and entomesodermal in sharks), like the various jaw and branchial arches.

Basically, the plagiostome agrees with the teleostome in most details of the endocranium and in the general course of development. The plagiostome differs in that the parachordals lie close to the notochord throughout their length; the notochord projects through the acrochordal or dorsum sellae; there is a strong angle between the parachordals and trabeculae; the palatoquadrates lack the autopalatine components and join below the trabeculae to form the upper jaw; there are circumorbital cartilages (or mesenchyme) and separate nasal cartilages (these may correspond to the paranasals of teleostomes); and a lateral commissure is missing or vestigial. These and other features indicate the basic dichotomy of the vertebrate stem into plagiostome and teleostome lines. However, in terms of ossification and probably in terms of dermal jaws and many of the other features considered above, the plagiostome and teleostome are probably only the extremes of a series represented in part by the acanthodians and arthrodires.

AGNATH FISHES

The jawless fishes, or agnaths, are presumed to be the most primitive of the vertebrates, preceding the gnathostomes in time and indeed giving rise to that group. The living agnaths, the cyclostomes, are considered relict species, highly specialized in their way of life—a way which has protected them from competition with gnathostomes.

Cyclostomes

There are two kinds of cyclostomes, the lampreys (represented by *Petromyzon*) and the hagfishes (*Myxine* and *Eptatretus*). Both have cartilaginous skeletons. They lack any trace of bone, and even the teeth are horny. These two types are so different that both should be considered. A description of these is difficult because the structural landmarks of the gnathostome are almost completely lacking or altered in interrelationships.

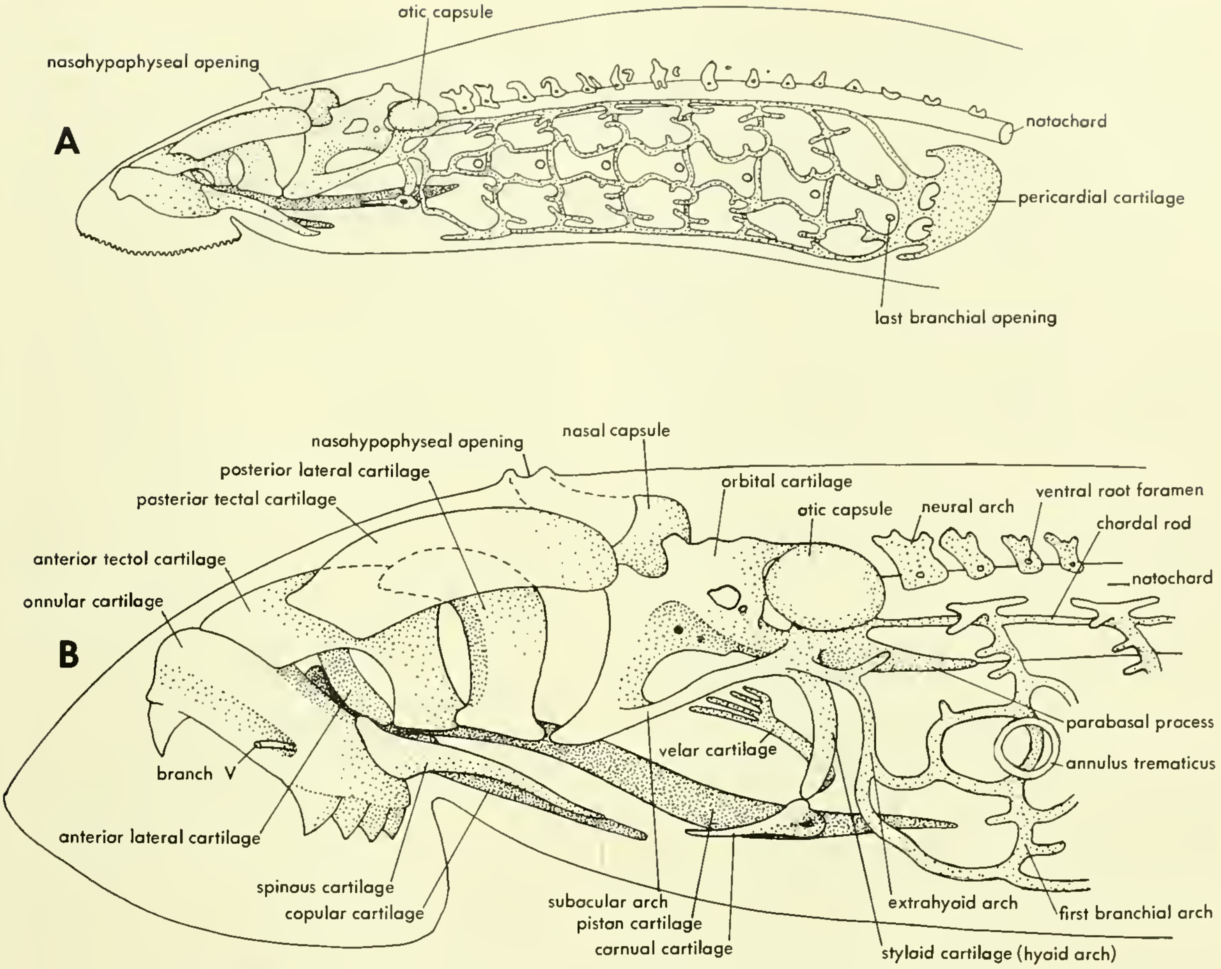


Figure 5-24. Head and visceral skeletons of the lamprey (partly after Marinelli and Strenger, 1954). A, entire head and visceral skeleton as seen in lateral view; B, anterior part, enlarged for detail, as seen in lateral view.

Lamprey The lamprey head skeleton consists of an **endocranium** and an extensive **"visceral" skeleton** (Figures 5-24, 5-25). The endocranium includes a single **nasal capsule**, paired **otic capsules**, and the side walls and floor of the cranial cavity. The otic capsules are joined above the cranial cavity by a **synotic tectum.** The **notochord** is much constricted between the otic capsules; it rapidly expands to its spinal proportions posteriorly. It is exposed in the floor of the cranial cavity and thinly covered ventrally by the **basis cranii.** The basal plate projects posteriorly along the notochord on either side. The anterior tip of the notochord is exposed at the posterior margin of the large **hypophyseal fenestra.** Anterior to the fenestra is a broad **basitrabecular plate** lying below the large midline nasal capsule.

Behind the neurocranium one or more of the **"occipital" arch** elements can be viewed as representing the occipital segments of the gnathostome head skeleton. The ninth and tenth cranial nerves exit behind the otic capsule, as does an occipitospinal nerve. The next segmental nerve perforates the base of the first neural arch.

The side wall of the neurocranium is joined to the otic capsule at three points: above, anteriorly, and ventroanteriorly. The dorsal opening formed by these connections is filled with connective tissue. The more ventral, larger opening is used by the trigeminal, abducens, and trochlear nerves. Anterior to this opening is a large optic foramen and just behind this a small oculomotor foramen; these may be confluent. Ventroanterior to the optic foramen is a small arterial (orbital or facial) foramen.

The otic capsule has a large **internal auditory fenestra** for the common root of the seventh and eighth nerves and above this a good sized **endolymphatic foramen.** The facial nerve leaves the eighth just inside the capsule and passes forward and downward through a small canal opening between the capsule and the cranial base just behind the trigeminal foramen.

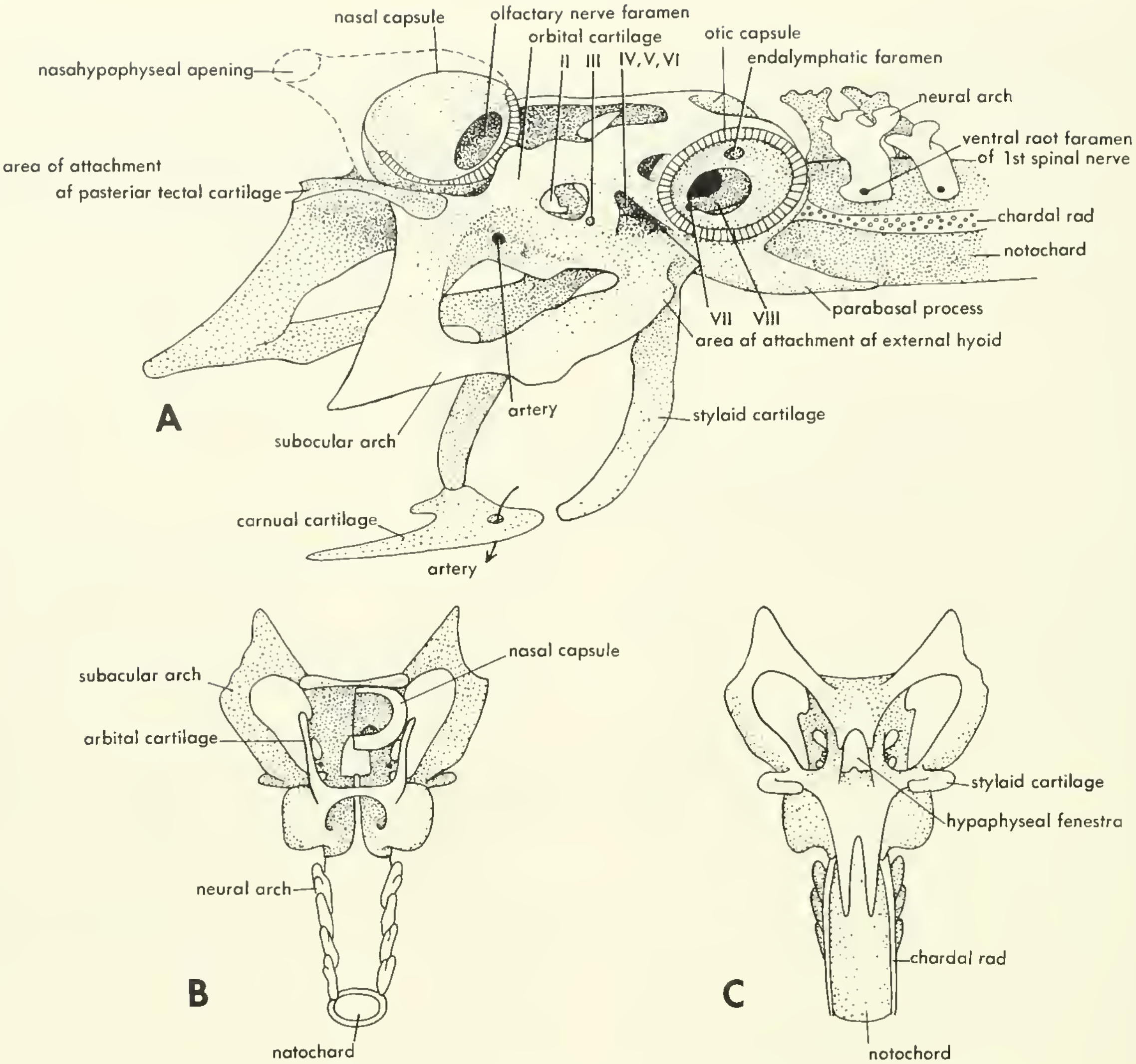


Figure 5-25. Endocranium of the lamprey. A, anterolateral view with part of nasal and otic capsules cut away; B, dorsal view with left half of nasal capsule removed; C, ventral view.

The nasal capsule is thin-walled and is separated from the rest of the endocranium. It encloses the posteroventral half of the **nasal sac** and is perforated by two large **olfactory foramina** separated by a rather thick strut.

Attached to the endocranium is a **subocular arch.** From this arch a **styliform** process extends down to the side of the pharyngeal cavity. Its tip is attached by fibrous cartilage to the **cornual cartilage** extending forward below the pharyngeal cavity alongside the **piston cartilage.** Medial to the styliform processes lie small **velar cartilages,** which join below the **pharyngoesophageal tube** to support the anteriorly projecting fingers of the velum.

The anterior end of the basitrabecular plate articulates with the **posterior tectal cartilage.** From the lateral margins of this, **ethmoid processes** extend ventrolaterally and slightly forward as part of the subocular arches. The distal end of the ethmoid process is joined by soft cartilage to the **posterior lateral cartilage.**

In front of and overlapped by the posterior tectal cartilage is an **anterior tectal cartilage.** This has bilateral **oral processes,** which extend posteriorly and down on either side to attach to the general tissue mass above and medial to the bases of the **spinous cartilages.** Just anterior to the oral processes lie the small **anterior lateral cartilages,** which are closely bound into the general supporting mass of the tip of the tongue apparatus.

The anterior tectal cartilage overlaps the annular cartilage of the oral sucker. The **annular cartilage** supports an anterior pair of teeth and a semicircle of eight posterior teeth. Posterolaterally spinous cartilages (stylets) extend backward from the annular cartilage. These spines lie to either side of the midline **copular cartilage** (Figure 5-26). This lies below the anterior end of the piston cartilage, which bears on its tip a medial **apical cartilage** and bilateral **supraapical cartilages.** The latter support the anterior and posterolateral **tooth plates** of the rasping apparatus.

The branchial skeleton is complex in form. It is composed of soft elastic cartilage, which in preserved specimens is darker than the cartilage of the mouth area and neurocranium. The arches are attached dorsally to a strip of soft cartilage extending along the side of the notochord and attached to the neurocranium behind the otic capsule. The basket is also attached by a band to the subocular arch just lateral to the base of the styliform process. The branchial skeleton is peculiar in that the arches are not divided into segments and in having epi and hypotrematic horizontal connectives and a pericardial basket enclosing the heart.

EMBRYOLOGICAL DEVELOPMENT In the lamprey, the branchial arches appear first and develop from front to back; they are well along when the neurocranium begins to form (Figure 5-27). The branchial bars are formed first in procartilage. Balfour in 1881 pointed out that these arches develop more superficially than those of gnathostomes. They lie lateral to the branchial blood vessels and nerves, not medial to them. Later in development the dorsal ends of the arches are extended forward and backward along the notochord as the chordal rod. Ventrally a midline connection also develops.

The **parachordals** are restricted to the otic and postotic region and seem to arise as anterior continuations of the **chordal rods.** The **trabecles** (including the polar cartilages) are derived from the first and second somites. They arise lateral to the notochord and anterior to the otic vesicle. Below the trabecles arise the **parabuccal rods,** which later connect to the posterior end of the trabecles and join across the midline by a mesenchymatous strand below the notochord and internal carotid arteries. These rods give rise to the velar skeleton. In the area where a rod joins the trabecle a **basitrabecular process,** or pedicle, extends outward from the latter.

The olfactory capsule is initiated by lateral cartilage centers. The subocular arch forms from a mucocartilage strand. Other bands of this material give rise to the styliform cartilage, the extrahyal band, and the mouth cartilages in general. The annular cartilage and the anterior lateral cartilage are derived in part by breakdown of larval musculature accompanied by mesenchymatous cartilage formation.

The later development of the head skeleton involves union of the trabecles anteriorly, through an ectomesodermal connective. An **orbital cartilage** appears which is anchored anteriorly by a **preoptic pillar.** The orbital cartilage later joins the otic capsule through an **orbitoparietal commissure** and the basis cranii through an **antotic pillar.** Still later, a weak **metoptic pillar** appears. The otic capsule has become cartilaginous and is perforated by the facial nerve.

Development of the definitive skeleton does not always follow directly from mucocartilaginous precursors. Some mucocartilage disappears without contributing to any skeletal element. Parts or entire elements are produced more-or-less directly from mesenchymatous condensations.

Hagfish The neurocranium of *Myxine* (or *Eptatretus*) is very incomplete (Figure 5-28). The **otic capsule** opens widely on its medial aspect for the auditory nerve and the endolymphatic duct, and is attached by **anterior** and **posterior basicapsular commissures** to a **parachordal rod** lying next to the **notochord** posteriorly and to the side of the large **hypophyseal fenestra** anteriorly. The rods are joined across the midline so as to enclose the tip of the notochord.

The parachordal rods are continued anteriorly as the **trabeculae,** which are widely separated at first by the hypophyseal fenestra but converge anteriorly to attach to the **nasal capsule,** above, and the **hypophyseal cartilage,** below. Ventrolateral to the trabecula is a **subocular arch** joining the otic capsule posteriorly. This posterior connective lies behind the facial nerve, the nerve passing ventromedial to it (in *Petromyzon* the nerve passes outside of the connective). The subocular arch extends down as the **visceral plate.** This has a large fenestra in it and lies lateral to the branches of the fifth nerve and medial to the distal part of the seventh. Both the external and internal divisions of the first branchial arch attach to the subocular arch at a point just below the otic capsule.

The subocular arch extends forward, past a connection with the posterior end of the trabecula, to form a midline **palatine commissure** with the arch of the opposite side. The palatine commissure lies below the olfactory capsule and the posterior end of the **subnasal cartilage.** There is a single, large, horny tooth, the **ethmoid tooth,** attached by a pad of

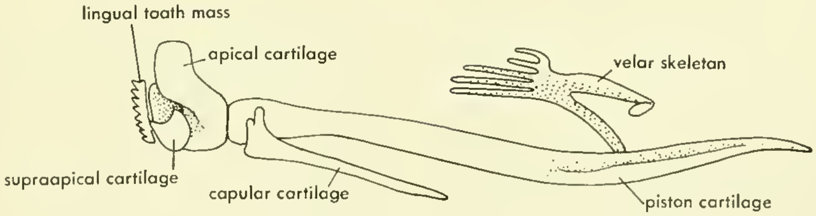


Figure 5-26. Skeleton of rasping organ as seen in ventralateral view.

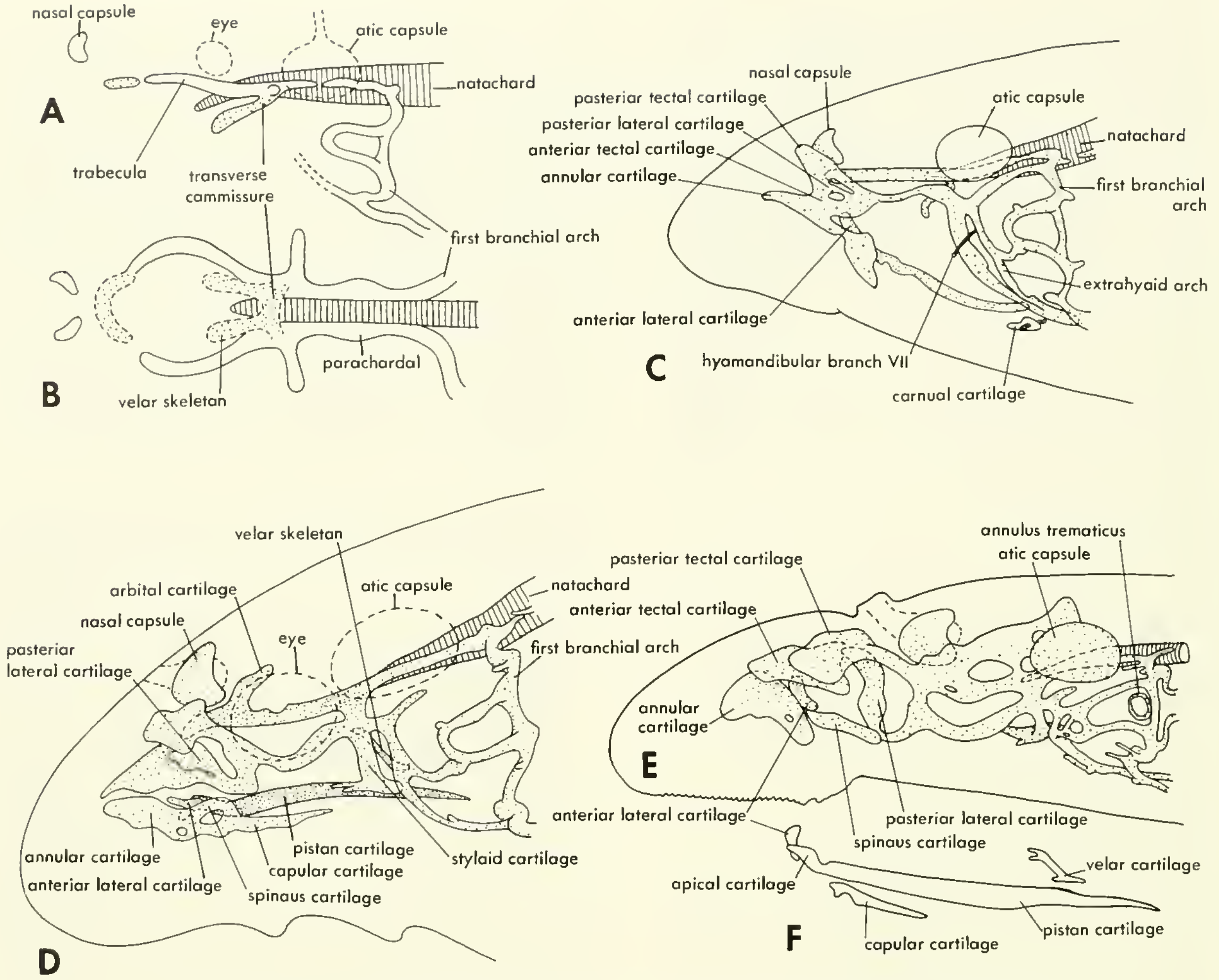


Figure 5-27. Stages in the development of the head skeleton of the lamprey. A, B, lateral and ventral views of 8 to 10-mm larva; C, lateral view of early metamorphic larva; D, lateral view of late metamorphic larva; E and F, lateral views of adult head and tongue elements. (After Johnels, 1948)

connective tissue to the ventral surface of this commissure. From the anterolateral angles of the commissure a **cornual process** extends out and forward.

Attached to the inner aspect of the subocular visceral plate by ligaments is a complex of several cartilaginous rods which extend back and medially into the velum. The velum lies between the opening of the **nasohypophyseal duct** into the mouth and the pharynx; it extends backward into the pharynx. Its margins roll and unroll so as to pump water from the mouth cavity into the pharynx.

The nasal sac and nasal duct are enclosed in a fenestrated **capsule** and a series of loops. Below these is a laterally compressed rod forking anteriorly into two **tentacular rods;** this is the subnasal cartilage. The posterior end of the subnasal cartilage lies just anterior to the tip of the hypophyseal cartilage. The latter underlies the hypophyseal duct and, about midway along its length, attaches to the trabecula of either side.

Below the endocranium is an extensive **tongue skeleton.** This is joined to the neurocranium through the external division of the first branchial arch. This arch attaches to the posterolateral angle of the **median lingual cartilage.** Anterior to this plate are two pairs of **anterior lingual cartilages —lateral** and **medial.** The medial pair is fused anteriorly. The anterior margins of the lateral plates give rise to rods which extend anteriorly. These divide distally into dorsal (nasal) and ventral (oral) tentacular rods. Posterior to the median basal plate is a midline, trough-shaped **posterior lingual cartilage** of soft white cartilage. Far back in the tongue musculature is a small ventral midline splint of cartilage.

Above the anterior plates is the **dental plate.** This is fenestrated and bears two rows of posteromedially curved teeth. When drawn forward, the tooth plate is inverted into the mouth opening; when drawn back, the rasping action results. The protractor muscles lies below the basal plates, the retractors above these plates.

The tentacles of the nasal and mouth openings are supported by cartilaginous rods. The ventromedial nasal tentacle of each side is supported by the subnasal cartilage, the dorsolateral nasal and the oral tentacle by the lingual apparatus, and the labial tentacle by a small independent rod.

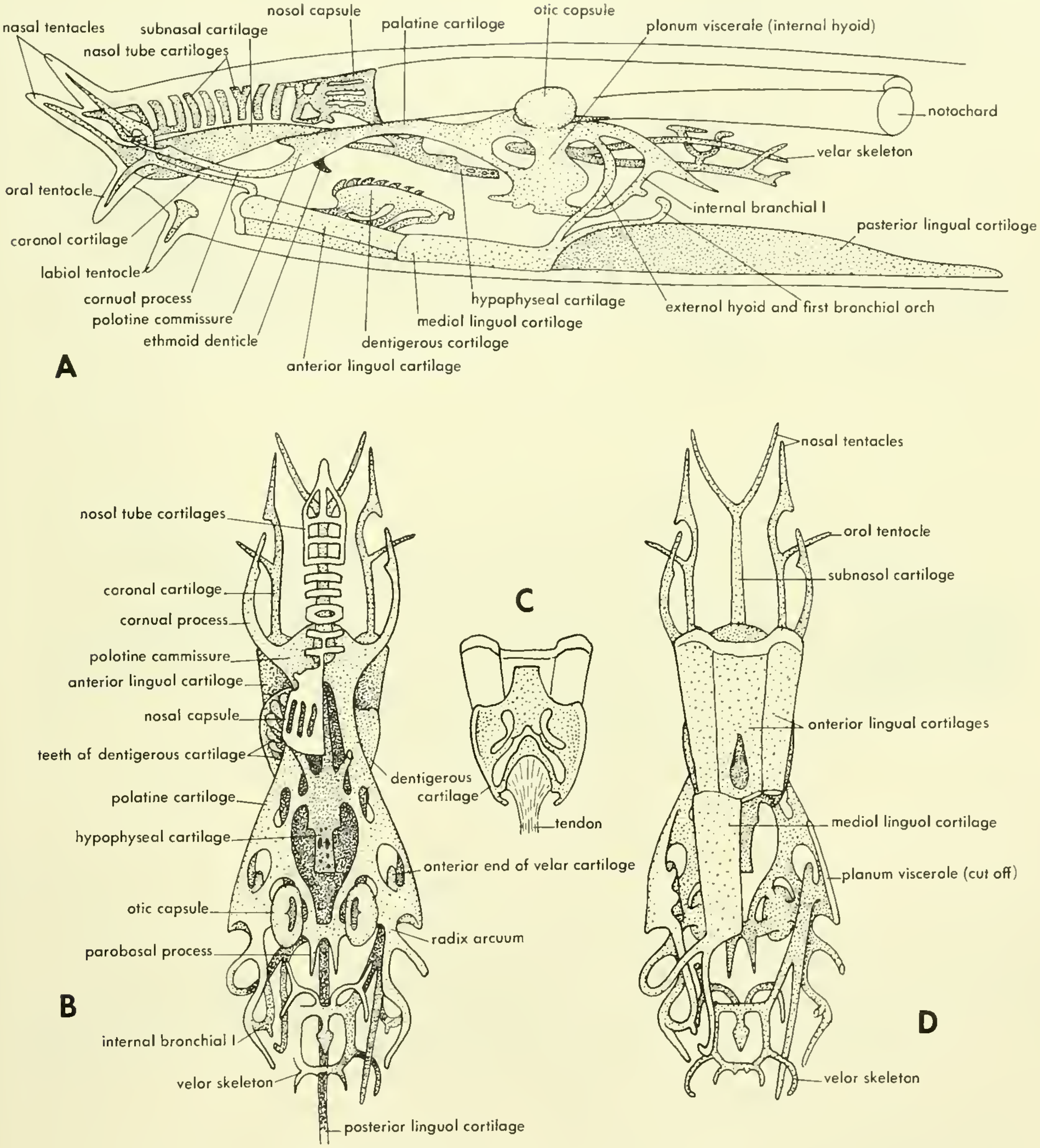
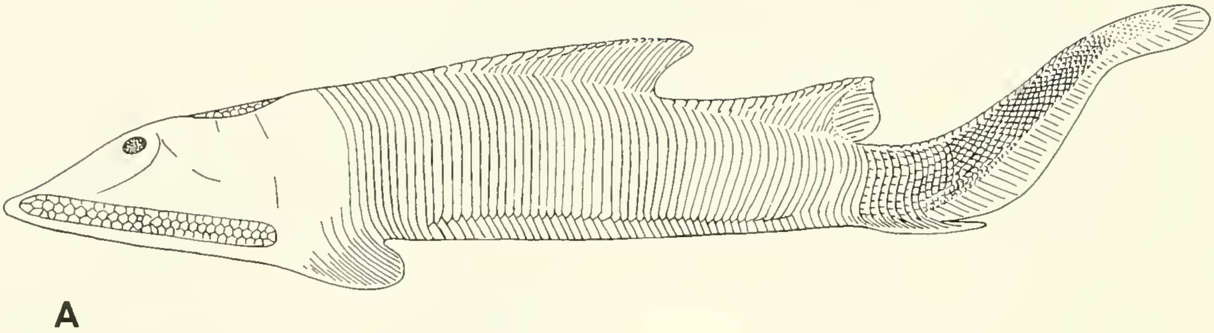


Figure 5-28. Head skeleton of *Myxine*. A, lateral view; B, dorsal view with right half of nasal capsule cut away; C, dentigerous cartilage lying above anterior lingual cartilages; D, ventral view with left posterior lingual cartilage cut away. (After Marinelli and Strenger, 1956)

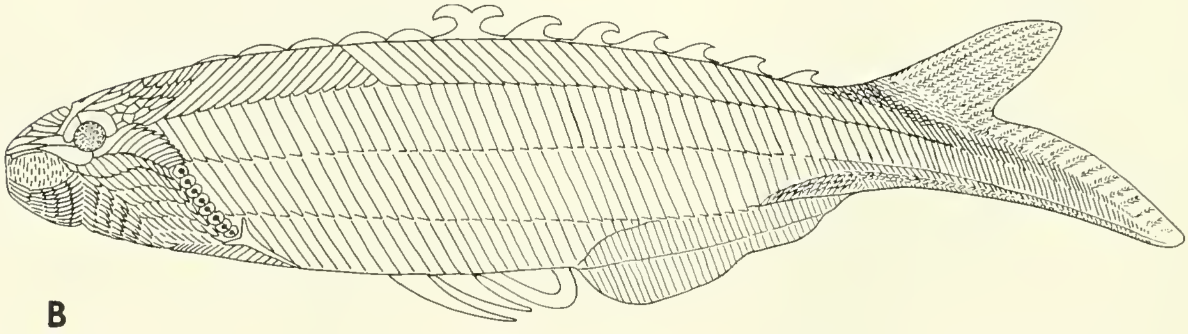
The branchial apparatus is restricted to the **external** and **internal divisions** of the **first branchial arch** and the ventral stub of the outer division of the second. Neither of these arches is closely associated with a branchial sac. The sac of the first arch may not even develop, whereas that of the second appears but is moved backward during development and then disappears. There is an irregular circlet of cartilaginous rod around the common posterior branchial opening of *Myxine;* that of the left side encircles the pharyngocutaneous duct as well.

The development of this type is only partly known. The general pattern is one of direct development to the adult condition. The primordia of the nasal capsule arise as upward processes from the anterior ends of the trabeculae. There are two cross connections between the trabeculae in front of the hypophyseal fenestra. The posterior one gives attachment to the hypophyseal cartilage and the anterior one disappears. Most interesting is the development of the internal and external arch elements.

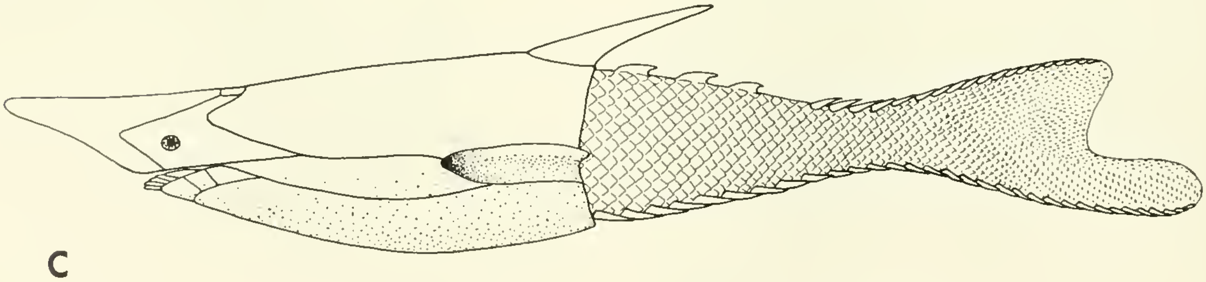
Holmgren described blastemas for paired palatoquadrates,



ACERASPIS



BIRKENIA



PTERASPIS

Figure 5-29. Lateral views of reconstructions of fossil agnaths: A, osteostracan, B, anaspid, and C, heterostracan. (Partly after Stensiö, Jarvik, and Romer)

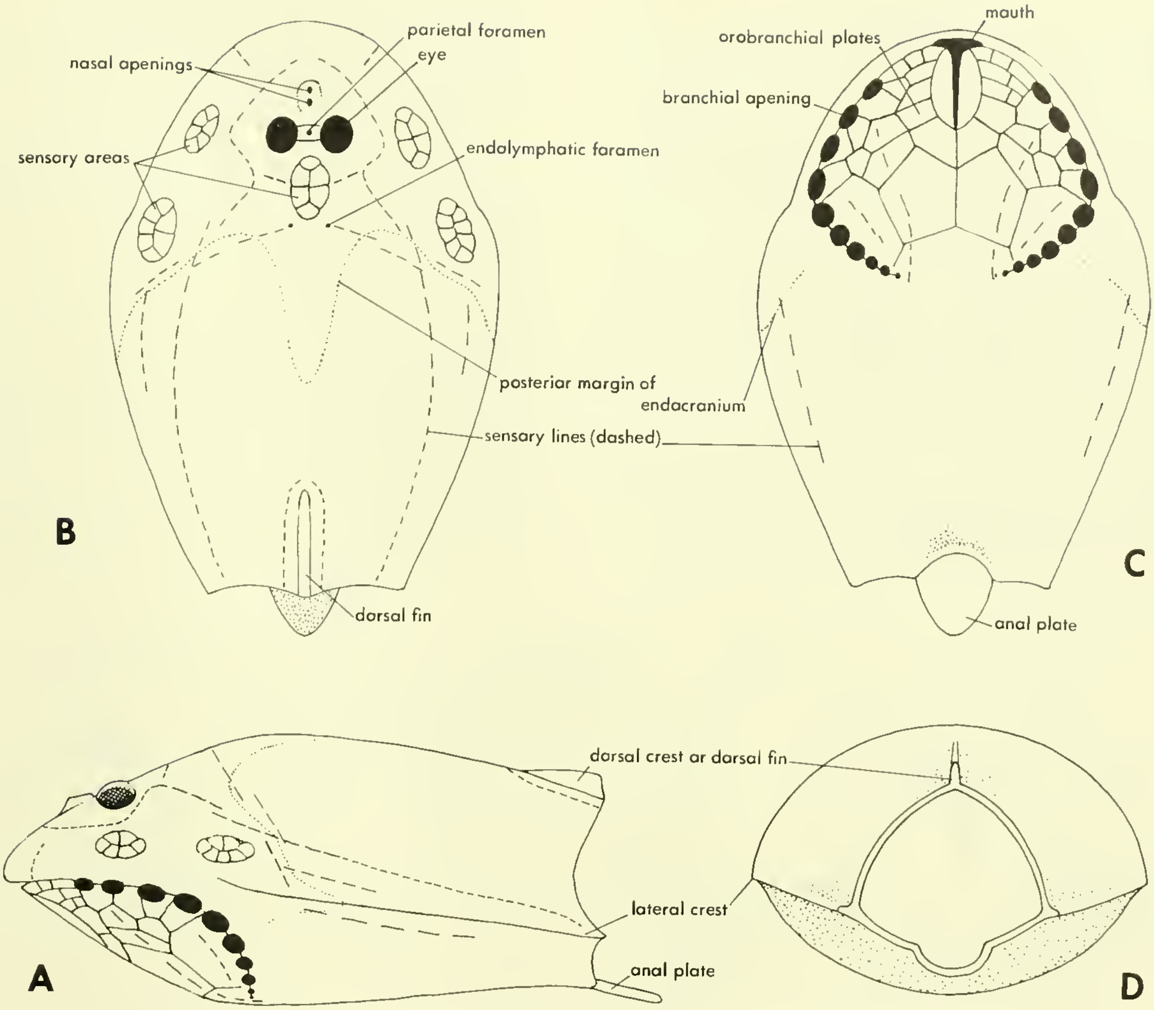


Figure 5-30. Cephalothoracic armor of *Trematapsis milleri*, an osteostracan. A, lateral view with main sensory lines indicated; B, dorsal view; C, ventral view; D, posterior view showing dorsal and lateral crests. (After Westoll, 1958)

joined anteriorly and bearing the ethmoid tooth; blastemas for Meckel's cartilages, extending downward from the posterior ends of the palatoquadrate condensations; and a true hyoid arch, inside the posterior margin of the subocular arch. The Meckel's cartilages later join to form the dental plate. The tongue base could represent an external series of elements related to Meckel's cartilages and/or the longitudinal elements joining the ventral ends of the visceral arches.

Comparisons of the lamprey and hagfish reveal some similarity but not the sort of agreement seen among the gnathostomes. Holmgren and others have drawn many parallels between agnath and gnathostome, but these at best are tenuous. The rasping tongues of both have been generally accepted as proof of common ancestry; yet in details these structures differ in the two types.

Fossil agnaths

The agnaths extend back in time to the Middle Ordovician. Those from that period are represented by bony bits of plates and occasionally larger imbricated areas. It is not until the Upper Silurian and Devonian that much is known of their structure. Three basic types have been described: heterostracans, osteostracans, and anaspidans (Figure 5-29). The best known are the osteostracans.

Osteostracan The osteostracan head skeleton was fused with the trunk armor, which extended variable distances back over the body to form a carapace. The earliest osteostracans were the tremataspids of the first part of the Upper Silurian (Figure 5-30). In these the solid carapace was interrupted above by openings for the eyes and by the pineal nasal organs. The nasal opening lay just anterior to the eyes; it was partly divided into anterior and posterior openings in the cephalaspids (Figure 5-31).

Behind the eye openings was a depression, closed above by a mosaic of small plates; this was the dorsal field. To either side were similar anterior and posterior lateral fields. Posteriorly the trunk part of the shield had a dorsal crest. Laterally the shield had small folds.

Ventrally, the mouth and pharyngeal area was open. The lateral and posterior margins of this ventral opening had ten notches, decreasing in size from in front backward, for the outer branchial openings. This area was covered in life by a mosaic of small plates, except for the mouth and branchial openings. The T-shaped mouth was in the anterior part.

The endocranium and visceral skeleton of the tremataspid is not well known but was probably like that of the more advanced cephalaspids, which have been described in detail (Figure 5-31). The endocranium and visceral skeleton were indistinguishably fused with each other and with the dermal carapace. They were in part identifiable as only perichondrally ossified. The degree of ossification varies from solid to superficial. The cranial cavity opened anteriorly into the nasal cavity, which opened to the outside. The inner ear was enclosed in a bony capsule, and, from the vestibular cavity, a number of canals radiate to the dorsal and lateral sensory fields. The walls of the cranial cavity were penetrated by many nerve and vascular foramina. The seventh nerve passed through the vestibular cavity. The bone of the endocranial margin was penetrated in the later forms, but not the tremataspids, by large venous sinuses. The notochord was much constricted, lying generally below the basis cranii in a groove but penetrating into the dorsum sellae. The tip of the notochord was not exposed in the sella. The endocranium extended posteriorly above the notochord into the root of the dorsal crest of the carapace, and it also extended back along the lateral margin.

The roof of the oral cavity was ridged between the gill pouches, of which ten pairs are generally indicated (11th

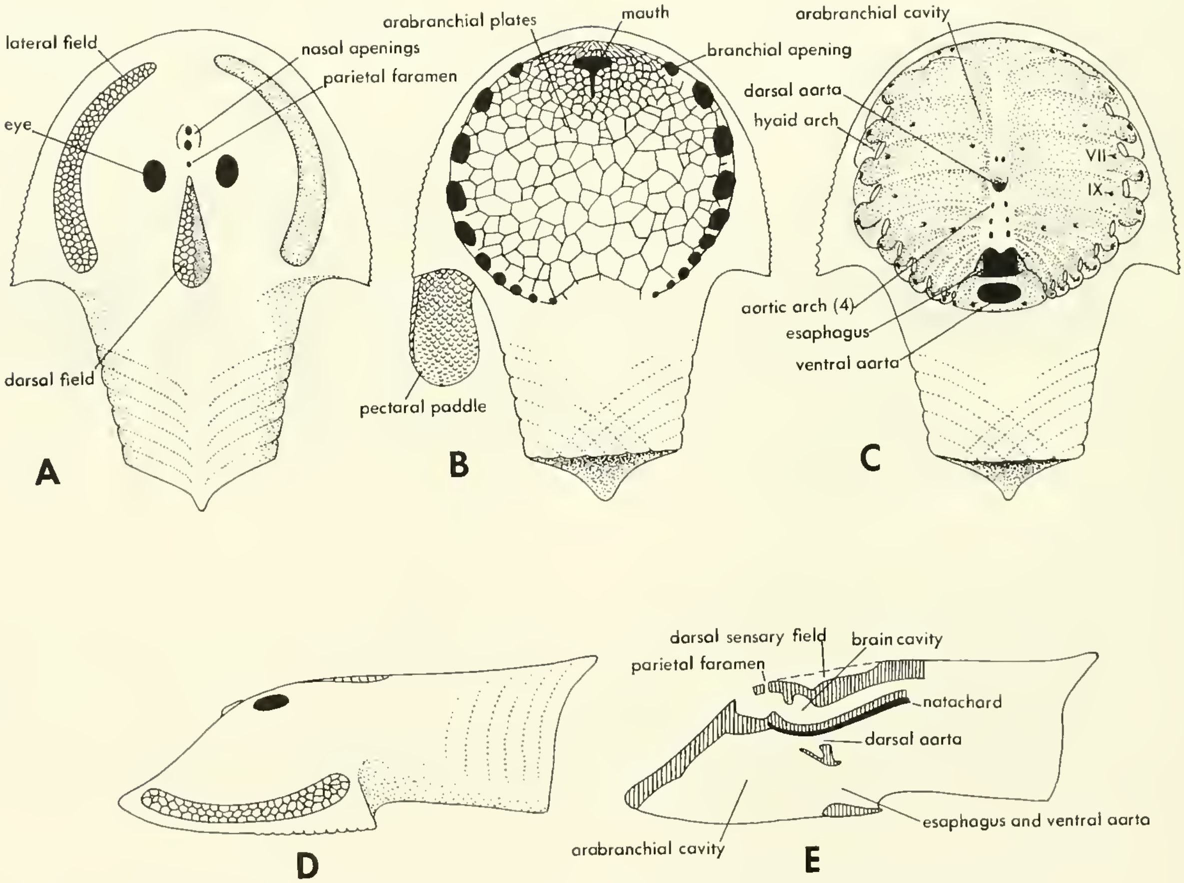


Figure 5-31. Cephalothoracic armor of cephalaspids and osteostracans. A, dorsal view of *Kieraspis*, B, ventral view with plates of orobranchial area and pectoral paddle as seen in *Hirella*; C, ventral view with orobranchial plates removed to show contours of bony roof of mouth; D, lateral view; E, sagittal section as seen in *Mimetaspis*. (After Stensiö, 1958)

vestigial). Posteriorly the pouches decreased in size, while the more anterior pairs were somewhat smaller in a gradient starting with the third or fourth pouch. The oral cavity extended down to the ventral wall of the carapace all around. It was perforated posteriorly by a large opening for the dorsal aorta, below which was a canal for the esophagus and below this, one for the ventral aorta. The esophageal and ventral aorta openings were sometimes confluent. There was no opening for a nasohypophyseal connection with the oral cavity.

There is no evidence of ventral endocranial elements nor of a tongue apparatus.

In many of the cephalaspids, there was a lateral spine extending back to either side of the trunk. Just inside of this spine was a lobe-like fin. The endoskeleton was exposed in the area of the base of this fin and is called the pectoral sinus. The walls of this sinus are perforated by vascular and nerve foramina.

The osteostracan type was peculiar in having mandibular, hyoid (spiracular), and eight pairs of branchial pouches, whereas in the lamprey, only the glossopharyngeal (first branchial) and vagus innervated pouches are present. In the hagfish, only vagus innervated pouches are present. A premandibular pouch has been postulated for the fossil forms but this does not agree with the nerve distribution. The pouches of the osteostracan were peculiar in that they extended further forward in the head, the more anterior ones lying well in front of the eye. The mouth was not suctorial.

Anaspid The anaspids are known only from faint outlines and impressions but appear to have been free-swimming forms with possibly a weakly suctorial mouth. The head of *Birkenia* (Figure 5-29 B) was covered by many small scales which were probably imbricated, not overlapped. The eye was surrounded by larger plates, and there was a perforated pineal plate in the roof between the eyes. Anterior to the pineal plate was a single nasal opening. Well behind and below the lateral eyes were eight gill openings. The mouth is not indicated in any of the fossils but is assumed to have been a vertical slit or oval. The round area in the cheek behind the mouth was perhaps related to a suctorial function.

No endoskeleton is known, although a tooth plate believed to belong to the tongue apparatus has been described for *Pharyngolepis*. The amount of dermal ossification varies from the scaled *Birkenia* to the nearly naked *Lasanius*. The arrangement of plates and scales does not suggest any basic pattern, and the number of gill openings varies from 6 to 15.

Heterostracan The earliest known vertebrates, those of the Middle Ordovician, are believed to have been heterostracans on the basis of the microstructure of their armor fragments (see scales, Chapter 8). The actual outline of these fishes is known from Upper Silurian and Lower Devonian species.

The head-trunk armor consisted of several distinct plates (Figure 5-32). The cornual plate may have extended as a pectoral fin. The mouth structure is poorly known but is described for a few species. The bilateral nasal openings probably lay just inside the mouth margin, and the hypophyseal pouch is assumed to have been in the roof of the mouth.

The endoskeleton is not known, but molds of the inner surface of the carapace show the positions of the gill pouches, the pineal organ, and the two semicircular canals of the inner ear. In its relation to the inner ear, the most anterior pouch was the hyoid, or spiracular. The pouches, varying in number from 7 to 14, all opened to the outside through a single port, well back on the side of the carapace. The endocranium was apparently cartilaginous and basically like that of a cephalaspid.

The drepanaspid (Figure 5-33) had the same pattern of plates as the typical pteraspid, but the dorsal and ventral plates were surrounded by an area of small polygonal units. The carapace was not sharply delimited from the tail.

In other heterostracans, such as the poraspid, the dorsal and ventral plates were fused to form single elements above and below; the eye no longer opened through an orbital plate but rather through a notch in the margin of the dorsal shield. The branchial plate remained separate or was fused to the dorsal shield. The earliest heterostracan, the astraspid, has the entire carapace made up of a mosaic of small polygonal plates. In the drepanaspid there is evidence of the fusion of these to form the large plates of the pteraspid.

Stensiö has compared the head structure of the pteraspid with that of the myxinid, but the fossil material does not support some of his assumptions, such as those regarding the nasohypophyseal duct and the occurrence of tentacles on the mouth margin The two semicircular canals of the inner ear disagree with the condition in the hagfish. Thus, the position of the myxinid is not clarified by these comparisons.

General observations The armored condition of many of the fossil agnaths has been viewed as peculiar in the light of the naked living forms. The single-piece carapace of some fossils also presents questions as to growth. It is assumed that the younger stages were naked or had small denticles in the skin and that the armor was acquired with full growth.

Among the heterostracans, the poraspids acquired their armor when fully grown, but the pteraspids developed their plates at ever earlier points in their life history, and the individual plates increased peripherally in size. The earliest heterostracan, the astraspid, was covered by a mosaic of small plates and thus had no restrictions as to growth. Similarly, the anaspid appears to have developed its dermal scales and plates early in its life history, and the increase in size of these dermal elements was accomplished by marginal growth.

One can conclude that the most primitive agnaths were naked or were covered with a shagreen of small denticles (like the shark, *Squalus*) and that plates or a solid carapace

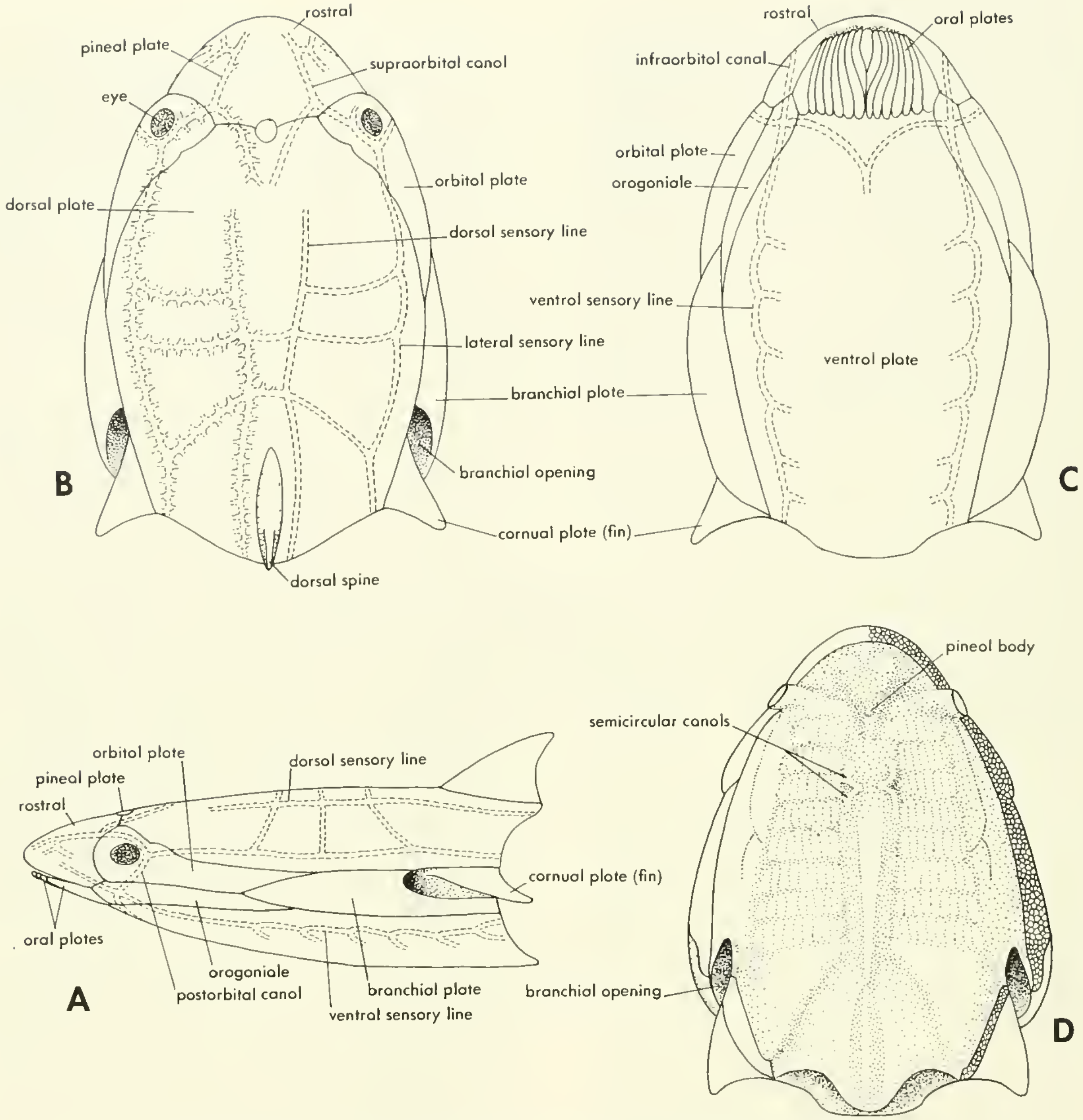


Figure 5-32. Structure of Cephalothorax of *Simopteraspis primaevo*, a heterostracan. A, lateral view with main sensory canals shown; B, dorsal view; C, ventral view; D, dorsal view of cast of internal surface of bony armor. (After Stensiö, 1958)

were acquired by the fusion of small denticles into polygonal plates and these into larger units. Not all agnaths tended to develop a dermal skeleton and of those that did, the time and sequence of fusion were variable. If a solid carapace was to be formed, this was held off till full growth was achieved. It the tendency was to develop supporting (or protective), shaped plates, these appeared increasingly earlier in the life cycle to perform their functional service over a longer period. Acquisition of plated or solid armor was sometimes followed by reduction and fragmentation into the constituent polygonal units, or into the denticular subunits of the latter.

Evolution of the agnaths The variations observed in the fossil agnaths suggest a very early radiation of types, two of which, the petromyzontid and myxinid, have come down to the present. The position of the nasohypophyseal opening on the top of the head in the osteostracan and anaspid suggests relationship with the lamprey. The position of this opening at the tip of the snout in the myxinid, along with the general separation of cranial and branchial skeletons suggest as close a relationship between the hagfish and lamprey as with the heterostracan. The many differences in structure of the hagfish as compared with the lamprey suggest that the two living lines arose at the time of the primary radiation of the agnaths, or shortly thereafter.

The relationship of agnath to gnathostome is hard to decide. Johann Müller (1839), the first student of the myxinid type, decided that the "Bauplan" of the marsipobranchs (pouch-gilled fishes) was different from that of the gnathostome. In the pre-Darwinian period, such a decision could be made without serious difficulties, but this explanation was unacceptable to the evolutionists. Cole (1905) was able to account for the lack of jaws and the lack of similarity to the gnathostome "type" by identifying the head skeleton of the myxinid as a functional neomorph, that is, a skeleton developed in this type to meet its own needs.

The theory of Gegenbaur, that the gnathostome jaws were developed from anterior gill arches, saw in the agnath a stage preceding that of the gnathostome. There is little evidence of visceral arches being involved in the mouth area of the agnath—the evidence is more apparent in the gnathostome. In spite of the difficulties, many comparisons have been drawn between the mouth parts of these two groups. If the blastematic condensations observed by Holmgren, a recent contributor to this problem, are equated to palatoquadrate, Meckel's cartilage, and hyoid arch, then there is evidence of gnathostome jaws in this agnath group. A correlation of parts with jaws, whether following Holmgren's views or those of Ayers (1921, 1931), leads to the conclusion that the gnathostome structure preceded the agnath.

Deriving gnathostomes from agnaths, or the reverse, necessitates the formation of many tenuous homologies accompanied by lengthy and often obscuring explanations. The following summary of views regarding the visceral skeleton indicate this. As early as 1832, Rathke suggested that the branchial arches of the lamprey were homologous with the extrabranchials of sharks. Balfour in 1881 expressed the same opinion. However, Huxley (1875–76), Parker (1883), and Howes (1891–92) considered that the visceral arches in cyclostomes and gnathostomes were homologous. Dohrn (1884) tried to show that the superficial position of the branchial arch of *Petromyzon,* as compared to that of sharks, was to be regarded as a secondary phenomenon—merely a shift in relationships—and that, consequently, no objection could be raised to homologization. Against Dohrn's opinion, Goette (1901) stated that the branchial arch of the lamprey was fundamentally different from that of the gnathostome because of its superficial position. Sewertzoff (1916–17) endeavored to trace the origin of gnathostomes and cyclostomes back to a common ancestor from which both styles could have evolved—evolution from a common ancestor demanded homology in his opinion. Neumayer (1938) agreed with Sewertzoff, while Allis (1923–24) tried to homologize cranial elements of cyclostomes with extra visceral elements in gnathostomes. Damas (1944) stated

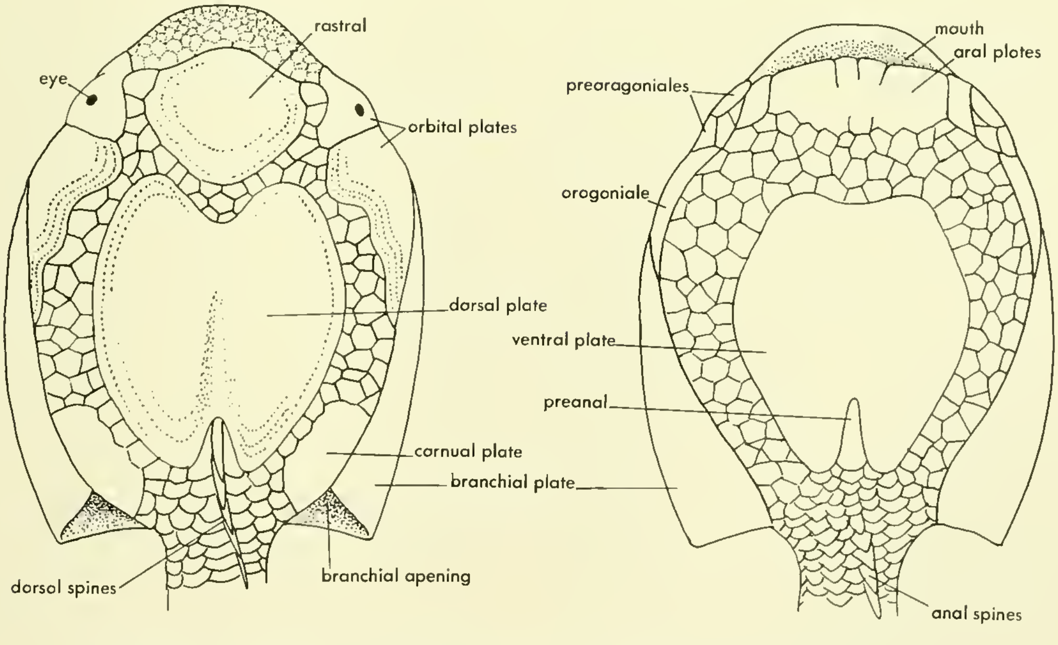


Figure 5-33. Anteriar part of bady af *Drepanospis gemuendensis* as seen fram abave, left, and below, right. (Mainly after Obrutschev, 1943)

that, on account of the embryological facts, the branchial arches of the two groups were not homologous. Holmgren (1942–1946) showed that internal as well as external arches may exist in the embryo of the hagfish. If such is the case, then a part of the branchial skeleton is homologous with that of the gnathostome.

In view of these opinions, it can be assumed that the common ancestor of both agnaths and gnathostomes had an elementary head skeleton from which both types developed through modification of existing parts, additions, and deletions. It may be that the common ancestor had not yet developed a cartilaginous branchial skeleton, and that these two types represent divergences resulting from different functional needs. It seems quite unlikely that the gnathostome style was derived from the known agnath, or vice versa.

RESUMÉ OF THE HEAD SKELETON

In summary, the head skeleton is an important guide to the understanding of the major subdivisions of the vertebrates. On the basis of this area of structure, the agnath can be separated from the gnathostome. These appear to be two independently developed types of head skeletons; neither was probably derived from the other. The gnathostome type can be broken down into subdivisions in each of which a skeletal system was developing at the time of its origin. The endocranium was already partly formed in the stem type so that there are only minor variations of a basic theme in the several lines. Dermal covers for the head appeared independently in each line. One of these, the osteichthian, early in its dermal shield development, gave rise to the actinopterygians, choanate fishes, and amphibians. This stem type was close to the ancestral acanthodian and arthrodire.

The tetrapod plan is largely a derivative of the osteichthian line. The tetrapod stem gave rise to three modified patterns: mammal, reptile, and living amphibian, each of which shows reduction in the number of bones along with other specializations. The systematic position of the stem tetrapod cannot be based on similarity to any of the three living derivatives. The stem type has arbitrarily been called amphibian simply because of its way of life, laying eggs in water and having a larval stage.

6

The Vertebrate Body Skeleton

Having observed some of the variations of the head skeleton and derived from these certain generalizations relative to the basal radiation of the vertebrate type, the rest of the skeletal system can now be studied. The goals of this examination are the same as those in the previous chapters; specifically these are to learn about the body skeleton and its range of variation in the several kinds of vertebrates, and to evaluate this variation in terms of its contribution to the over-all problem of the evolution (phylogeny) of the vertebrates.

THE VERTEBRAL COLUMN

Mammals

Although vertebrates get their name from the bony vertebral column, not all of them have such a column. It is perhaps best developed in the mammal. In this group, it can be divided into a number of segments: **cervical, thoracic, lumbar, sacral,** and **caudal.** These regions are quite apparent in a mounted skeleton, and the terms are defined in the following description.

The cervical, or neck, vertebrae are distinguished from the other vertebrae by their lack of ribs and by having a **vertebral** (artery and vein) **foramen** (transverse canal) in the base of the **transverse process.** The first two cervicals are highly modified and are called the **atlas** and **axis.** There are usually 7 cervicals, but there are exceptions to this number; the manatee has 6, while certain sloths have 6, 8, or 9.

The thoracic vertebrae bear **ribs** and usually number 12 to 14. The least number is 9 in the whale *Hyperoodon,* and there are as many as 20 or 21 in *Hyrax.*

The lumbar vertebrae lack ribs and the transverse processes are drawn out, down, and forward. The number is variable, depending in part on the number of thoracics. The lumbars complete the presacral series, which usually consists of 27 vertebrae.

The number of sacrals, those fused vertebrae that support the pelvic girdle, is 2 or 3 (5 in man, of which two contact the ilia). The transverse processes of these vertebrae along with the ventral rib heads (costal centers of ossification) are expanded and contact the ilium of the pelvic girdle. Vertebrae of the lumbar or caudal series may fuse to the sacral series, thus accounting for variations in the number. The number of caudals is most variable, being least in man with 4, and nearly 50 in the pangolin, *Manis,* and the insectivore, *Microgale.*

Description of vertebrae is difficult because of the functional modifications shown in each of the segments of the column and the transitional forms between them. Using the cat or the opossum as representatives, the several kinds can be examined (Figure 6-1).

In the cat but not the opossum, the atlas has broad flaring transverse processes that are perforated basally by the vertebral foramen. This bone is a ring that encloses not only the **neural canal,** containing the spinal cord, but also the **odontoid process** of the next posterior vertebra, the axis. Dorsoanteriorly the ring is pierced by bilateral **atlantal foramina.** There is no neural spine. Posteriorly the ring has large hollowed articular areas for the axis and anteriorly even larger, more deeply hollowed areas for the occipital condyles of the skull. In a young kitten, the atlas is observed to be formed from three ossification centers: two **neural arches** and a ventromedial **intercentrum.** An intercentrum is missing in some marsupials (wombat and kangaroo); it is a small nodule in the Tasmanian Wolf (*Thalacinus*), and is well developed in the opossum. Loss of this intercentrum can be considered a specialization.

The axis (or **epistropheus**) is a compound bone with a crest-like **neural spine** above. At the posterior end of the crest are bilateral and ventrolateral facing **postzygapophyseal** articular surfaces. The term **"zygapophysis"** is derived from the Greek words *zygos* or *zygon* which refers to yoking or joining, and *apophysis* meaning an outgrowth or process. Most of the various processes and articular areas of the vertebrae have names involving the use of *apophysis.*

Below the neural canal of the axis is a relatively flattened **body,** or "centrum," which has a flat, slightly dorsally directed posterior articular surface. **Centrum** is generally used to identify the body of the vertebra, but it is also used to identify one of the ossification centers involved in verte-

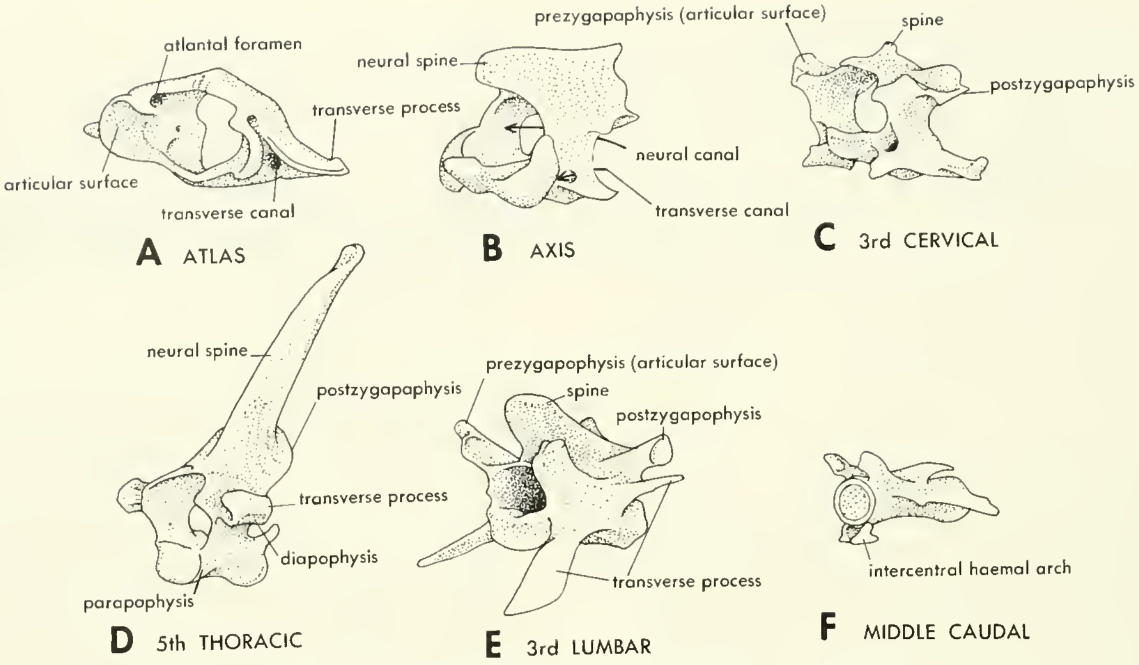


Figure 6-1. Some of the vertebrae of the cat as seen in anterolateral and slightly dorsal view.

bral construction. In the case of the mammal, the body is usually formed from the centrum (and its epiphyses); therefore, the terms can be interchanged, although the former term is less ambiguous. In some animals (or individual vertebrae—see account of axis below) the body is not formed entirely from the centrum; it includes the intercentrum. In other animals the body may be largely intercentral in origin or it might not be known whether centrum, intercentrum, or both, are involved. In these situations, body and centrum are not synonyms.

Anteriorly the base of the neural arch and the body of the axis have broad, somewhat laterally directed articular surfaces for the atlas. Between these surfaces is the fingerlike odontoid process. The transverse process is small, posterolaterally directed, and perforated at its base by the vertebral foramen.

In the young animal, six ossification centers are apparent: bilateral neural arches meeting dorsally to form the crest or spine and forming the postzygapophyses, the transverse processes, and most of the atlas articular pads; and four midline bones forming the body, which, from behind forward, are the epiphysis, centrum, and intercentrum of this vertebral segment, and the centrum of the atlas forming the odontoid process. The articular surface for the atlas involves both the atlas centrum and the base of the neural arches of the axis. The anterior tip of the odontoid process may also include the centrum of a pro-altas vertebra.

The third cervical is like the rest of the cervicals in having a dorsal spine, both pre- and postzygapophyses on the neural arch, and transverse processes drawn out and back, each with a vertebral foramen through its base (the foramen is lacking in the seventh cervical of the cat and in many other animals). The anterior margin of the transverse process is drawn out forward and medially so as to lap inside the posterior end of the transverse process of the axis. This overlapping is better marked in the opossum and is related to muscle attachment rather than articulation of vertebrae. The seventh cervical lacks the forward extension of the transverse process and, in the cat, only the dorsal root of the process is present.

In the young animal, each cervical arises from five ossifications: there is a pair of **neural arches,** which meet dorsally, extend upward as a dorsal spine (particularly evident in the opossum), and basally form the transverse processes; and below them is the **centrum,** with its separate **anterior** and **posterior epiphyses.**

The **thoracic** vertebrae have tall **neural spines** with **pre-** and **postzygapophyses** lateral to the **neural canal.** The **transverse process** of either side has a single root above the vertebral artery and distally has an articular facet for the dorsal head of the rib, the **diapophysis.** The posterior margin of one body and the anterior margin of the next posterior body form the socket for the ventral head of the rib, the **parapophysis.** As one progresses posteriorly through the thoracic series, the neural spines slant more posteriorly and become shorter. The pre- and postzygapophyses become reduced to facets. The prezygapophysis facet faces dorsally at the anterior base of the spine, and that of the postzygapophysis faces ventrally at the posterior base. The transverse process becomes more and more anterior in position on the body and bulkier on the posterior vertebrae of this series. The transverse process has a distinct posterodorsal muscular process, which, on the lumbar vertebrae, becomes separate, lying ventrolateral to the postzygapophysis.

In their development, the thoracic vertebrae arise from five ossification centers: bilateral **neural arches**, which bear the zygapophyses, transverse processes, and the articular facets for the two heads of each rib; and the **centrum** with its two **epiphyses**.

The **lumbar** vertebrae have an anteriorly directed neural spine and large pre- and postzygapophyses. The transverse process is lacking, but its posterior process is well developed. In its development, this type of vertebra is like the thoracic.

There are three **sacral** vertebrae in the cat; the most anterior one is the main support for the **pelvic girdle**. The **transverse process** of this anterior sacral is very thickened and distally spread out to suture with the **ilium**. The second sacral has a thick transverse process that joins in supporting the ilium. The third sacral is not involved. In their development, the sacrals are like the thoracics, except the transverse process of the first sacral includes a secondary center, a **costal** or **rib element**, arising below it, and forming much of the articulation with the ilium.

The **neural canal** continues posteriorly through the first seven **caudals** and then is lost. The **pre- and postzygapophyses** are present, as are anterior and posterior extensions of the **transverse process**. The fourth to ninth caudals have small **"hemal arches"** enclosing the caudal artery and vein. These arches are directed forward and serve for muscular attachment. Further posteriorly, the hemal (or haemal) arch is represented by bilateral splints.

Embryological development The terminology of the parts of the developing vertebra is quite confusing, because it is based on that of Gadow, who originally applied it to fish vertebrae. Extrapolation from fish to mammal has not been at all successful.

In the course of the development of the mesoderm, somites are formed (Figure 6-2). These are segmental blocks (readily observed in whole mounts of embryo chicks) lying to either side of the **neural tube**. These blocks develop a small central cavity, the **myocoel**, which is a fissure separating the somite into an outer **dermatome** and an inner **myosclerotome**, or **myotome**. From the ventromedial aspect of the myotome, cells move downward and medially toward the **notochord**. From these cells the **sclerotomes** of the more advanced embryo form.

The sclerotomes also show a segmental arrangement; the cells are densest near the myotome and the middle of the segment and more diffuse toward the notochord and the **intersegmental fissures**. Observed in frontal section (as in the 10-mm pig), these mesenchymatous masses are separated by intersegmental fissures, or **intersclerotomic fissures**, in which the **segmental arteries** lie medial to the larger segmental veins. These blood vessels extend upward, from the parent vessels, to either side of the notochord.

Somewhat later, the **intrasegmental** or **sclerotomic fissures** appear, marking the division of the sclerotomes into anterior or **cranial**, and posterior or **caudal** halves, the **sclerotomites**. These fissures are by no means complete nor conspicuous. In the 10-mm pig, they are apparent, as is also the trend for the caudal part of each sclerotome to appear more dense than the anterior or cranial sclerotomite. The

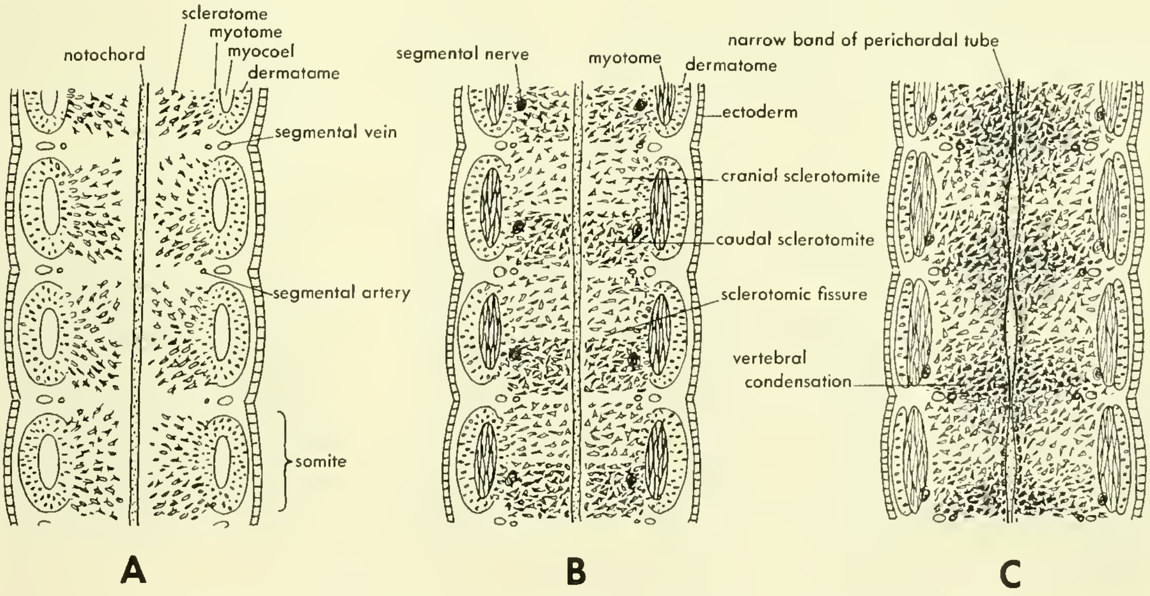


Figure 6-2. Three early stages in the blastematic origin of the vertebrae in the mammal. (After Patton, 1958)

intersclerotomic (inter—referring to between) and the intrasclerotomic (intra—referring to within) fissures disappear, but the position of the former is marked by the segmental blood vessels, while the ventral ramus of the segmental nerve runs down through the caudal sclerotomite. The notochord remains small in the mammal and never has a distinct sheath.

Mesenchyme of the sclerotomes eventually encloses the notochord and forms a tube of irregular thickness around it (Figure 6-3). An indistinct **perichordal tube,** made up of fusiform cells oriented so that they encircle the notochord, is formed within the sclerotomal tissue; elsewhere the irregular mesenchyme cells persist. An **intervertebral disc** is now apparent which is much denser than the mesenchyme in front of or behind it. This condensation extends laterally along the myotomic septum as the **blastematic** rudiment of the **rib.** Exactly what this transverse condensation represents is hard to say, but it is assumed to be the condensed caudal sclerotomite plus a little of the cranial sclerotomite in front of it. The light band, the primary centrum, plus the posterior part of the dark band, gives rise to the **blastema** of the **centrum.**

Chondrification appears first in the middle of the primary centrum and encloses the notochord as a **vertebral ring.** From this **center,** chondrification spreads throughout the entire centrum. At the same time, the neural arches chondrify separately as do the proximal ends of the ribs. The neural arches and ribs were primarily associated with the dense intervertebral disc but now attach to the more anterior part of the primary centrum (Figure 6-4).

The neural arches, are joined by a blastema to either side of the neural canal, which when chondrified forms the post- and prezygapophyses of adjacent vertebrae.

With formation of the completed cartilaginous vertebra, the dark intervertebral band is narrowed and now lies on the plane between the ventral nerve rami of the segment and somewhat anterior to the original position of the intrasclerotomic fissure. As this dark band narrows, the fibrous intervertebral disc is formed from it.

Endochondral ossification centers appear in the arches, then in the centrum and ribs. The centers grow outward to form the definitive, or fully developed, structure. The epiphyses of the vertebral body appear late, following the elimination of the notochord within the centrum. Their appearance is followed by fusion of the arches dorsally and then with the centrum. The centrum is pierced dorsally, and just medial to the roots of the neural arches, by bilateral, large **nutritive foramina.**

General observations Among mammals the vertebral column shows a wide range of variation but it is always divisible into segments: cervical, thoracic, etc. In its ossification the mammalian centrum is distinctive in that the bone arises endochondrally and in that there are epiphyses on the ends of the centrum. Of interest is the fusion of the centra of the first and second vertebrae to form the body of the axis; this is accomplished without the intercession of epiphyses. The posterior end of the definitive axis centrum has an epiphysis. Epiphyses are present only in the caudal series of the monotremes, and are lacking throughout the column in Sirenia.

Between the vertebrae are intervertebral discs. The intervertebral disc may be little more than connective tissue binding succeeding vertebral bodies, or it may be a distinct pad of fibrous connective tissue, as in man. In this connective tissue, there is sometimes a nucleus pulposus, a mass of vacuolated cells representing the remains of the notochord.

Reptiles and bird

A variety of reptiles, alligator, lizard, and Sphenodon, will be examined along with the bird. The bird, as a modified archosaur, is in most respects a reptile and as such is described here.

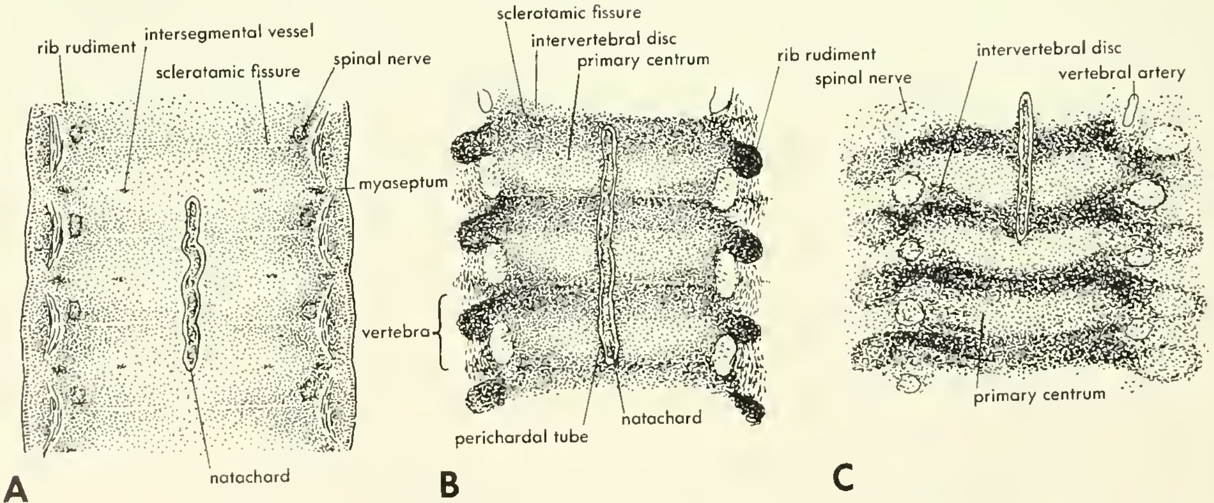


Figure 6-3. Blastematic stages af vertebrae in the human. (After Sensenig, 1949)

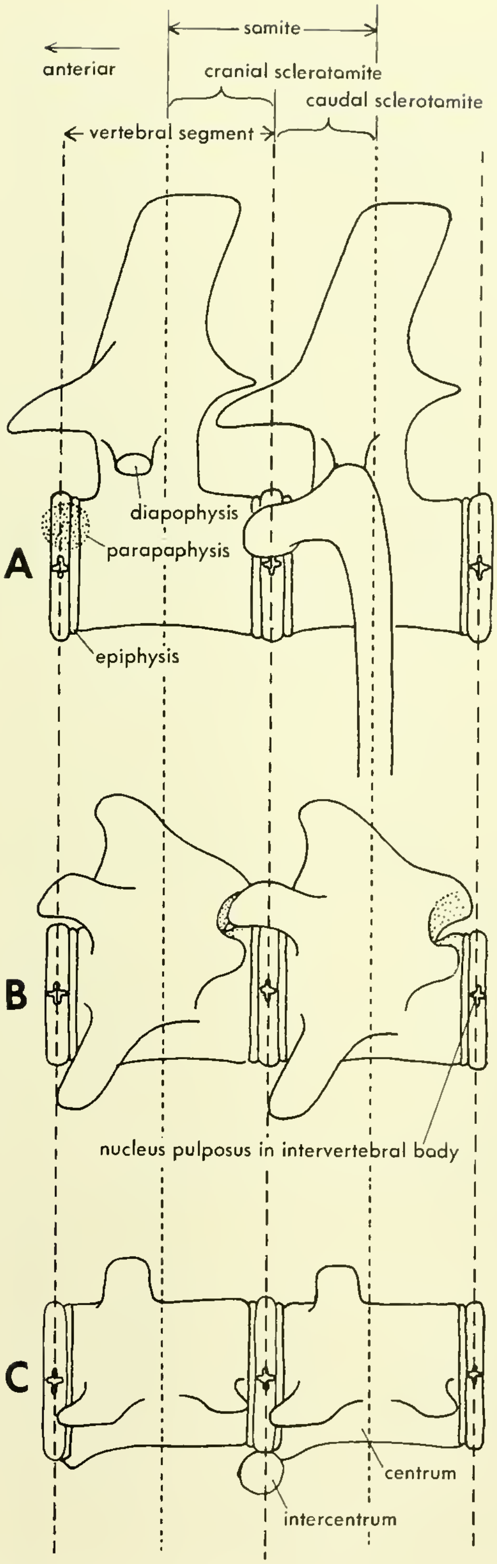


Figure 6-4. Sclerotomic composition of mouse vertebroe. (After Remone, 1936)

Alligotor The vertebral column of the alligator is observed to be segmented much as in the mammal. There are 9 **cervical** vertebrae; 8 of these have small ribs attached to them, while the ninth has a large rib. There are 8 **thoracics** bearing **ribs** which are attached through ventral segments to the membranous or bony **sternum.** The last cervical has a long rib, but this is not attached ventrally. There are 2 **lumbars** with short ribs and 4 without ribs, plus 2 sacrals, and about 40 **caudals.**

The **atlas** (Figure 6-5 G) is composed of 3 units, 2 **neural arches** and an **intercentrum.** The arches do not meet dorsally but are articulated with the fused neural arches of a **preatlas vertebra,** which lies in contact with the back of the skull. The neural arches of the atlas articulate through the **postzygapophyses** with the **axis.** The **intercentrum** of the atlas has splint-like and separate ribs extending back on either side.

The **axis** is composed of the second cervical plus the fairly distinct centrum of the first (suture line evident). The first centrum, or **odontoid process,** is partly enclosed by the ring of the atlas and partly exposed behind that ring, where it bears a two-headed rib on either side. The axis has a large **neural spine** with **pre-** and **postzygapophyses.** Its **tranverse process** is much reduced, the dorsal head of the rib apparently having been transferred to the odontoid process. The posterior articular surface is a ball that fits into the socket surface (procoelous) of the third cervical. In the development of the axis, a second intercentrum is not observed in the young alligator or caiman.

The third to ninth **cervicals** are much alike having strong **neural spines, pre-** and **postzygapophyses,** and **transverse processes** articulating with the dorsal head of the short **ribs.** The neural arch is separated from the body by an indistinct suture. The body has a distinct **parapophysis** for the ventral head of the rib, and there is a ventrally projecting **hypapophysis.** All the vertebrae, except the first 2 cervicals, the last presacral, the sacrals, and the first caudal are procoelous, that is, they have a socket anteriorly and a ball posteriorly.

The **thoracic** vertebrae are like the cervicals generally, but have a broader **dorsal spine** and broad, flat **transverse processes.** The ribs all appear to be two-headed, but only the first two articulate with the **diapophysis** of the transverse process above and the **parapophysis** below. The others have both heads jointed with the elongate transverse process. The most posterior ribs have only a single head. The first three thoracics, along with the last cervical, have **hypapophyses** of decreasing length.

The **lumbars** show a continuation of the slight changes observed in the thoracics. The **sacral** vertebrae have relatively short **transverse processes,** closely sutured to thickened **rib heads.** The rib head is also sutured to the body of the vertehra along a line from the tip of the transverse process to the general position of the parapophysis. There are 2 such ribs on either side that suture to the **ilia** of the **pelvic girdle.**

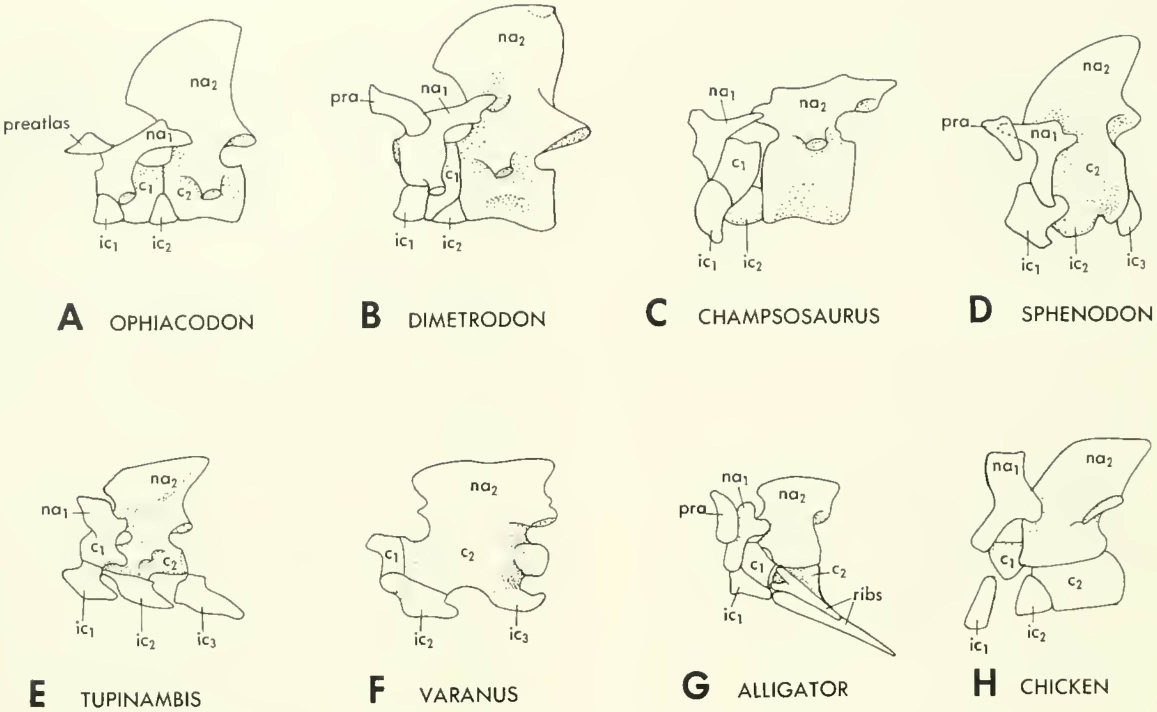


Figure 6-5. Anterior vertebrae of reptiles and birds showing their modifications for articulation with the skull.

The **caudal** vertebrae are like the lumbars, but with more slender processes. **Neural arches** are present along with **neural spines** on each vertebra right to the tip of the tail. The first two caudals are without intercentra, the third has a small **intercentrum** in the form of a **hemal arch** and **spine.** The fourth has a large hemal arch and spine, while succeeding vertebrae, nearly to the tip of the tail, have similar, progressively smaller arches and spines. The **transverse processes** decrease in size posteriorly and disappear at about the middle of the tail.

In their ossification centers, the vertebrae of the crocodilian are much like those of the mammal. The neural arch remains separated from the centrum by a faint line, the **neurocentral suture,** even in grown animals. The vertebrae of this type differ from those of the mammal in lacking epiphyses and in having the parapophysis on the centrum rather than on the intervertebral disc and the margins of adjacent vertebral bodies. On the basis of the alligator, the costal centers of ossification of the mammalian sacrals are seen to be ventral rib heads.

Lizard In *Tupinambis* or *Iguana,* the vertebral column is much like that of the alligator, except that any trace of the neurocentral suture is lacking. The number of cervicals is 6 or 8, depending on how one defines this region. On the basis of short ribs, it is 6; on the basis of full ribs joined to the sternum, it is 8. Using the latter definition, 2 long ribs occur on this first part of the column which do not have direct connection with the sternum. In the alligator there is one such large rib, that on the ninth cervical. The first 7 or 8 vertebrae (cervicals) have **intercentra;** those of *Tupinambis* appear to be functional **hypapophyses,** closely sutured to the centrum.

There is no preatlas (Figure 6-5 E,F). The **atlas** is composed of 3 separate pieces in the adult which form a ring with a wide suture between the tips of the neural arches. The **axis** is formed of the fused first and second centra, and is nearly fused to the large second **intercentrum.** The first centrum forms the blunt **odontoid process,** lying partly within the ring of the atlas. The axis has both **pre-** and **postzygapophyses** and a strong **neural spine.**

The third **cervical** has a transverse process, but no rib, while the fourth may have a short rib.

From the fifth vertebra on, the ribs are of increasing length. The heads of the ribs are broad with a slight constriction between dorsal and ventral parts, but they are not "two-headed." There is no vertebral canal through the base of the transverse process. The **prezygapophyses** of the third cervical and more posterior vertebrae have an accompanying overhanging **zygosphene.** The flange of the **postzygapophysis** of the next anterior vertebrae is grasped between the zygasphene and the prezygapophysis. The cavity around the dorsal articular surface of the inner flange of the postzygapophysis is called the **zygantrum.** The articular surfaces should be identified as the pre- and postzygapophyses.

There is no evident lumbar series, for all of the vertebrae between the cervicals and the 2 sacrals bear ribs. Since the thoracic and lumbar series are not distinct, these vertebrae collectively are called **dorsals.** About 6 dorsals have ribs connected with the **sternum.** Behind these complete ribs, the ribs shorten in a graduated series until the last presacral (the 24th or 25th vertebra), which has only a nubbin, is reached. The complete ribs, and those behind them, are distinctly single-headed, and lack an uncinate process. All of the dorsal (thoraco-lumbar) vertebrae have wide neural spines, and distinct pre- and postzygapophyses.

There are 2 **sacrals** supporting the **pelvis,** and nearly 50 **caudals.** From the fourth caudal to nearly the tip of the tail, each vertebra has a Y-shaped **hemal** or **intercentral arch** (caudal chevron). This arch articulates with the intervertebral gap. The caudal vertebrae have tall **neural spines** tapering down and disappearing at about two-thirds of the length of the tail. **Neural arches** with **pre-** and **postzygapophyses** continue back nearly to the tip of the tail. The anterior caudal vertebrae have long **transverse processes** that double about one-third of the way back along the tail and take part in the formation of a vertical **breakage line** in the middle of the **body.** About half way along the length of the tail, the transverse processes disappear, but the breakage lines occur to the tip of the tail. The vertebrae, with the exception of the atlas and axis, are procoelous—hollowed in front, but with a bulging articular surface behind (Figure 6-10).

Tuatara The neural arches of Sphenodon do not retain the line of suture with the body as in the alligator, and an intercentrum is present between all of the vertebrae. There are 8 cervicals, unless one excludes the last, which bears a large rib. This rib, however, is without a costal segment attaching to the sternum.

There is a small **preatlas** neural arch to either side in the ligament joining the **atlas,** a ring of 3 pieces, to the skull (Figures 6-5 D, 6-6). The atlas neural arches do not meet dorsally. The body of the **axis** has the expected composition; its **centrum** is fused with its **intercentrum,** with the centrum of the first cervical, and, perhaps, with the centrum of the preatlas (Figure 6-9). The third cervical has a **transverse process,** but no rib. There is a two-headed, connective tis-

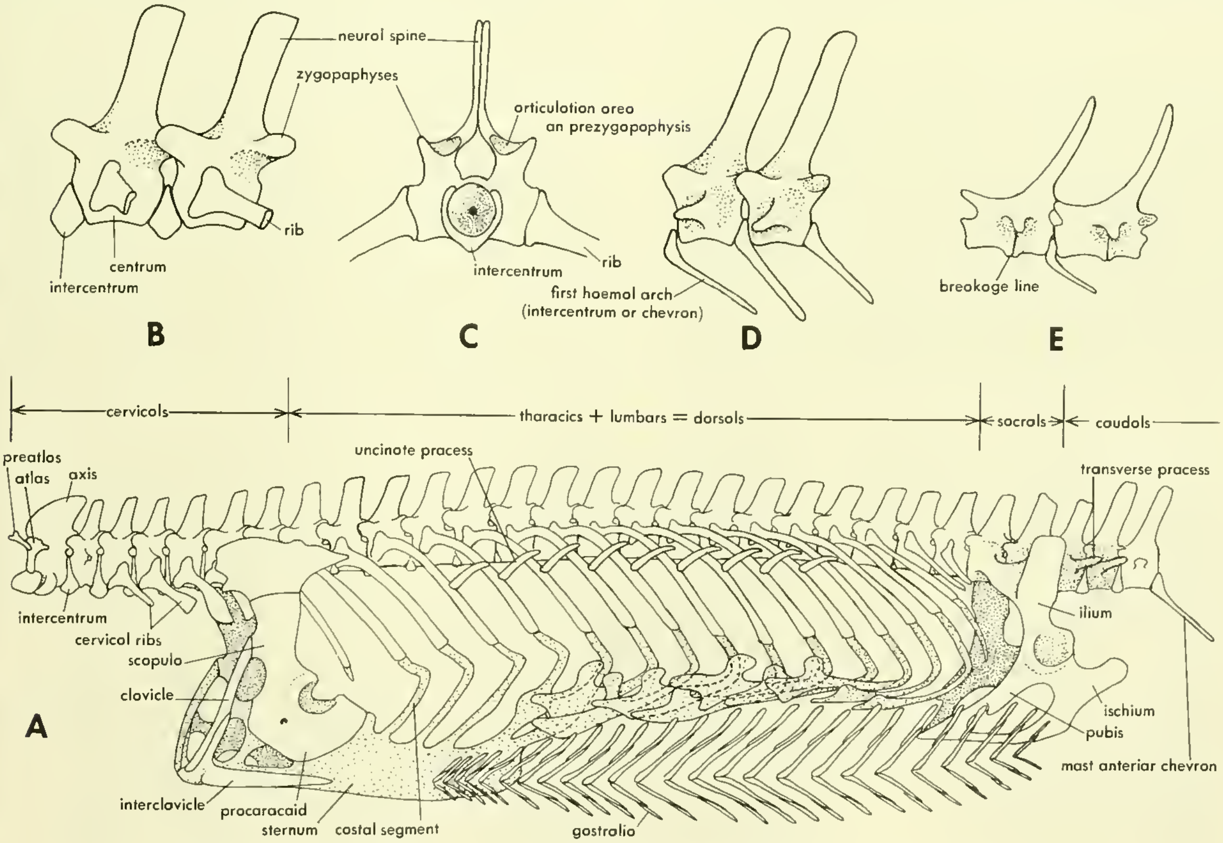


Figure 6-6. Body skeleton of Sphenodon. A, vertebral column, girdles, and ribs with the gastralia rotated somewhat to produce a more ventral view; B, lateral view of two dorsal vertebrae with intercentra and ribs; C, anterior view of dorsal vertebra; D, lateral view of two anterior caudal vertebrae; E, two middle caudal vertebrae.

sue, rib in the embryo. The third cervical has a free intercentrum. The fourth to last cervicals have ribs of increasing size. The rib of the fourth cervical may be distinctly two-headed, the **capitulum**, or ventral head, nearly touching the intercentrum. The more posterior ribs have but a single dorsal (**tuberculum**) head, which articulates increasingly further back on the vertebral body.

As there are no lumbar vertebrae, a series of **dorsals** completes the **presacral** part of this column (Figure 6-6). All of the presacral vertebrae with the exception of the first 3 cervicals have ribs. Five or six of the ribs are complete with **costal segments** attaching to the **sternum**, while 8 or 9 more have large irregular costal expansions associated with the **gastralia** covering the abdominal area. Three more incomplete ribs complete the presacral series of 25 vertebrae. The ribs have **uncinate processes** like those in the bird.

There are 2 **sacrals** similar to those of the lizard, and 29 **caudals**; the fourth and succeeding caudals, nearly to the tip of the tail, have an **intercentral** arch (chevron bone). The tail is like that of the lizard even to the breakage line in the middle of the vertebral bodies of its terminal half (Figure 6-6 E). The neural arches (without a spine) continue to the next to the last vertebra.

EMBRYOLOGICAL DEVELOPMENT The development of the vertebrae of Sphenodon appears to follow the same pattern as in the mammal or bird (Figure 6-7). **Sclerotomes** form and divide into **sclerotomites**; the posterior sclerotomite unites with the anterior sclerotomite of the next posterior segment to form a vertebral segment. Within the sclerotomic tissue, a **perichordal tube** of circularly arranged cells is formed around the **notochord**, and this is subdivided into **intervertebral** and **vertebral rings** (Figure 6-8); the former has more irregularly arranged and less spindle-like cells and is joined with the **rib** and **neural arch blastemas.**

In chondrification, **centrum** blocks are formed (Figure 6-7, 6-9) and are separated by connective tissue penetrating inward from a line around the middle of the intervertebral ring. The neural arches and ribs chondrify separately, and the rib joins the vertebra on the base of the neural arch.

Ossification begins perichondrally (or perhaps subperichondrally) in the neural arch, then in the vertebral centrum (Figure 6-9) and the proximal part of the rib.

The vertebrae remain amphicoelous (Figure 6-10), that is, hollowed at both ends. The open ends of adjacent vertebrae hold a ball-like intervertebral body with a remnant of the notochord in its center. The intervertebral body is reduced to little more than a disc between some vertebrae. In the centrum the notochord first chondrifies and then becomes ossified. It is completely eliminated in the odontoid process.

Growth of the centrum and arch is probably a matter of periosteal (membranous) extension outward accompanying chondral ossification. Bony extension at the articular ends is a matter of endochondral ossification.

In describing the vertebrae of reptiles, the form of the articular ends of the vertebral bodies is frequently referred to (Figure 6-10). The **amphiplatyan** vertebra is seen in the mammal (that is, both articular surfaces of the centrum are flat), the **procoelous** vertebra in the lizard and alligator, and the **amphicoelous** vertebra in Sphenodon. Some lizards have the articular surfaces just reversed: that is, the front articulation is convex and the hind articulation is hollowed. This condition is called **opisthocoelous.** The cervical vertebrae of turtles are remarkable for the diversity of their joints. The usual pattern is one in which the second and third cervicals are opisthocoelous, the fourth **biconvex,** the fifth and sixth procoelous, the seventh amphicoelous, and the eighth biconvex, that is, rounded at both ends or just the opposite of amphicoelous. In some cases, the articular

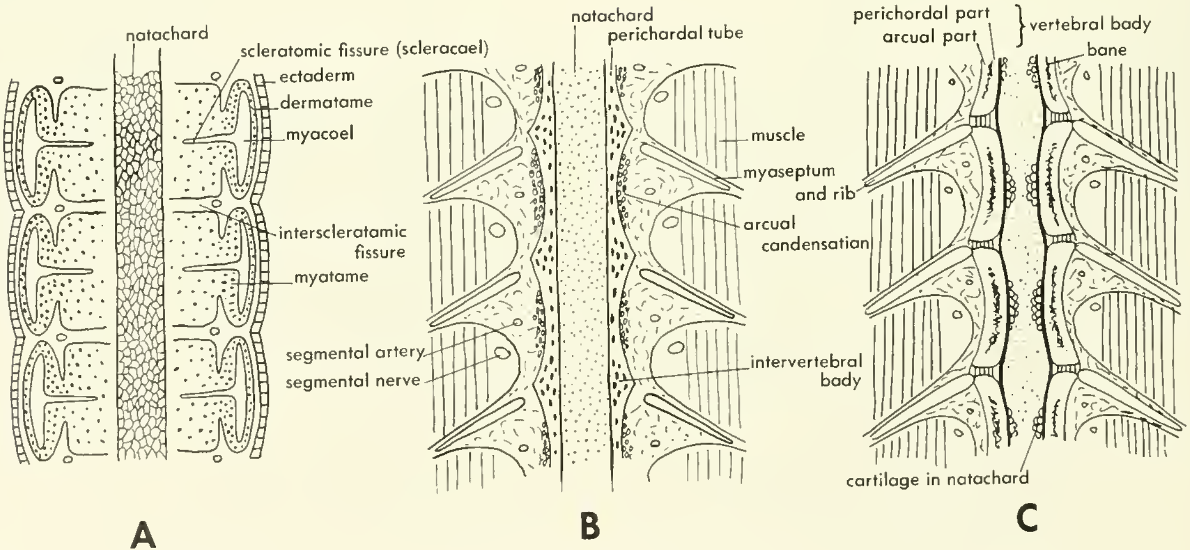


Figure 6-7. Three diagrammatic stages in the somitic origin of vertebrae and ribs in Sphenodon.

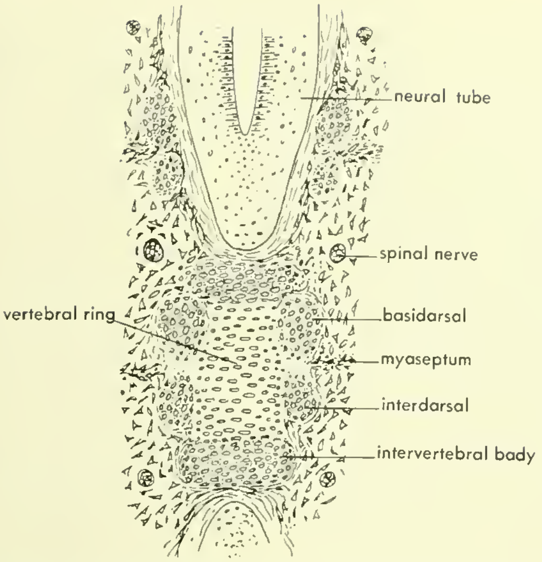


Figure 6-8. A frontal section through a developing vertebra of Sphenodon showing the blastemic condensations believed to be present and which are identified by Gadow's terms. (After Schauinsland, 1906)

surfaces are double (double convex, concave, or asymmetrical); this is called **ginglymoidy.**

Bird The vertebral column of the bird has a marked specialization of segments. There are 13 to 15 cervicals (up to as many as 25 in the swan), 6 to 7 or more dorsals (several of which may be fused), many sacrals, and a short series of caudals (6 to 7) ending in a **pygostyle** (or terminal structure) made up of several fused caudals (5 to 6).

There is no preatlas vertebra (Figure 6-5 H). The **atlas** is ring-like and the **axis** is like that of the lizard. The third **cervical** has a short rib fused to the diapophysis and parapophysis. The more posterior cervicals have free ribs, increasing in length up to that of the first thoracic. The last cervicals and first **thoracics** have **hypapophyses.** The thoracic vertebrae bear large, two-headed ribs with **uncinate processes.** The **parapophysis** is little more than a facet on the line of juncture of the neural arch and body.

Of the many vertebrae in the **synsacrum** (10 to 15), none can be identified as the sacrals, although in the developing embryo two or more of these near the **acetabulum** (socket for the femur) appear to be the original sacrals. The vertebrae of the synsacrum have separately ossifying dorsal and ventral rib heads lying lateral to the body, and these support the greatly elongated **ilia** of the **pelvic girdle.**

The **caudal vertebrae** have long **transverse processes; intercenta** are present and fused to the anteroventral margins of the more posterior members of this series. The pygostyle represents about five fused vertebrae, the most anterior of which is fairly distinct.

In its vertebral column, the bird shows much shortening as compared with the alligator or lizard. The shortening of the caudal series and elimination of the lumbar series (incorporated into the synsacrum) is particularly interesting. While the trunk and body are short, the neck is long. The cervical series is elongated by the apparent process of moving the pectoral limb posteriorly. Shortening of the body thus appears to involve lengthening of the neck segment at the expense of the dorsals and shortening of the caudal segment. In birds and alligators, the number of presacral vertebrae is about the same.

EMBRYOLOGICAL DEVELOPMENT In its early stage, as observed in a 96-hr chick (serial sections), the **notochord** is proportionally much larger than in the mammal. It lacks a distinct sheath and is enclosed in a continuous mass of **sclerotomic mesenchyme,** more concentrated laterally, less concentrated near the chord. The posterior **scleromite** is the more dense. The cranial and caudal sclerotomites are separated at first by an intrasegmental fissure. Around the notochord, a distinct **perichordal tube** of circularly arranged fusiform or spindle-shaped cells is formed (Figure 6-11 A). This tube is constricted into vertebral segments by the massing of mesenchyme cells in the intervertebral area. The cells of this area are now denser than those of the vertebral ring and are more irregularly disposed. The notochord is dilated in the vertebral rings.

As finally developed, the blastematic precursor of the vertebral includes 2 pairs of dorsal **arcual masses** in which the polygonal (procartilaginous) cells are concentrically arranged

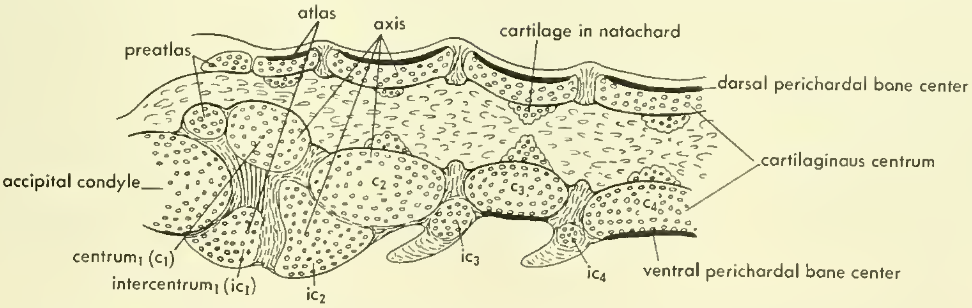


Figure 6-9. A sagittal section through the anterior vertebrae of an embryo of Sphenodon showing their cartilaginous precursors, and the first ossification.

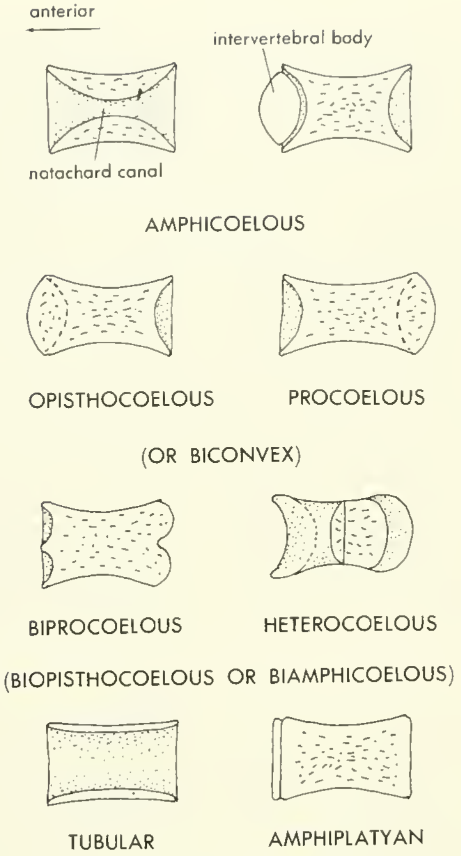


Figure 6-10. Diagrammatic representation of the various articular surfaces and types of "centra" of vertebrae as seen in sagittal section, with exception of heterocoelous type which has only the left posterior half cut away.

and a pair of similar bilateral ventroanterior nodules. These have been likened, respectively, to the basidorsals and interdorsals above, and to the basiventral of one vertebra combined with the interventral of the next anterior vertebra below (see Figure 6-8 of Sphenodon and Figure 6-12). This ventral pair of compound nodules forms the connective tissue intercentrum of the adult vertebra. The blastema of the rib is continuous with the basidorsal-interdorsal bulges, and extends out into the septum between the myotomes. Within the centrum itself, the cells are concentrically arranged (around the central axis of the notochord). The arrangement of cells in the centrum is apparent in both cross and frontal sections. It is best marked at the center of the vertebral body around the notochord and less clearly marked outward and toward the ends of the centrum.

Chondrification begins in the vertebral ring, and as procartilage extends through the invertebral rings. The resulting **tube** becomes segmented into **vertebral blocks** by movement of connective tissue into the intervertebral regions. The vertebral blocks are by now cartilaginous. The intercentra of the first and second cervicals and of the posterior caudals chondrify separately in the procartilaginous tube. Those of the caudal vertebrae later fuse with the centrum of their respective vertebra.

The neural arches chondrify at about the same time, the cartilage extending upward to enclose the neural canal, and laterally as transverse processes. The arches of adjacent vertebrae meet above the spinal ganglia to form pre- and postzygapophyses. The neural arches soon fuse with the centra. The ribs chondrify from separate centers.

Ossification follows much as in the mammal. Centers appear at the base of the neural arch, in the centrum, and in the ribs. Ossification in the centrum is peculiar in that first

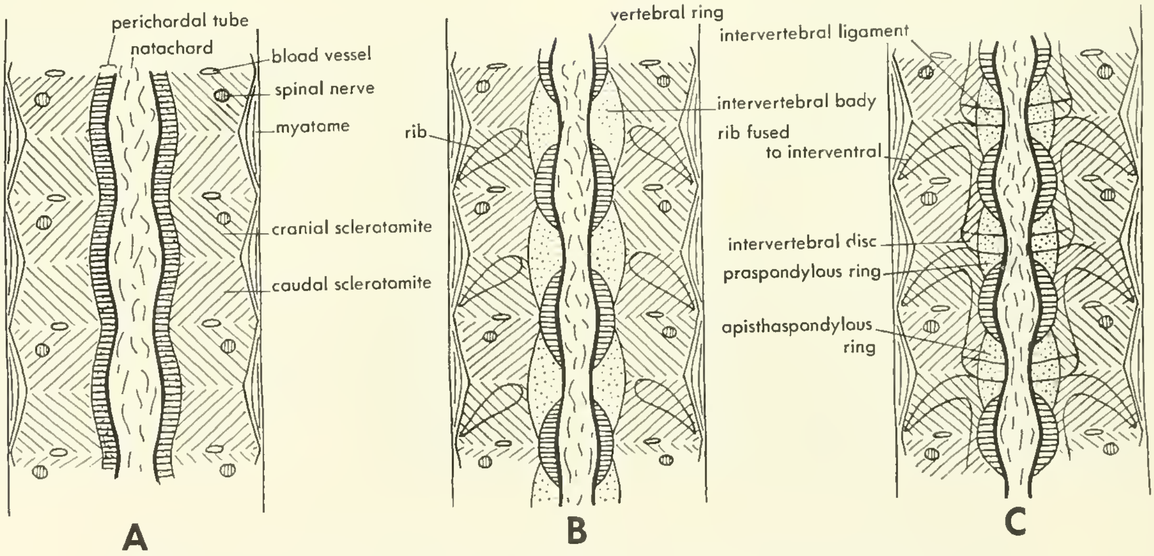


Figure 6-11. Diagrammatic stages of development of bird vertebrae as described by Piiper (1928).

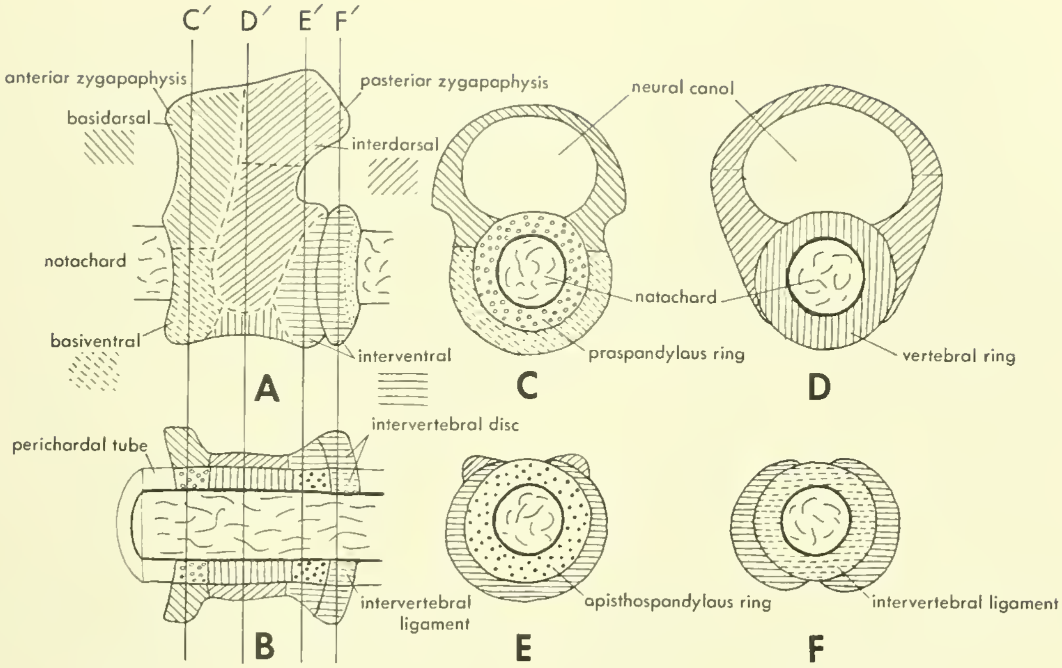


Figure 6-12. Composition of bird vertebra in terms of Gadowian elements said to be indicated by blastematic condensations. A, lateral view; B, frontal section of vertebra; C to F, cross sections at levels C′ to F′ of A.

a dorsal and a ventral plate are formed (perichondral or subperichondral). These plates are soon joined by a vertical pillar, perforated by the much constricted notochord, through the cartilage of the centrum. When arch, centrum, and rib are well formed in bone, fusion takes place between arch and centrum. There are no epiphyses.

In later development of the centrum, the notochord is constricted to a remnant which then disappears. Between the vertebrae the notochord is also constricted and obliterated. The articular surfaces of the (movable) vertebral bodies are of a **heterocoelous** type (Figure 6-10), that is, having a transverse, saddle-shaped surface in front and a vertical, saddle-shaped surface behind.

Fossil reptiles and amphibians Traced back in time, the reptilian type shows the intercentrum becoming a regular feature and increasing in size. The body of the vertebra (or centrum) becomes amphicoelous, articulating with ball-like intercentral masses in which the notochord plays a part. The spool-like body now becomes perforated by the notochord, which is constricted but remains intact (except, perhaps, at the joint between the head and vertebral column). We have now arrived back in time to the Pennsylvanian genus *Cephalerpeton;* the Permian amphibian-reptile *Seymouria* (Figure 6-13); or the Pennsylvanian-Permian forerunners of the mammal, the primitive Pelycosaurs.

Among the early amphibians (Figures 6-14 to 6-17), an extension of this pattern is observed with further reduction of the size of the central and intercentral blocks or arcs, and evidence of their bilateral origin. Exactly what the stem type was like is difficult to say. The most primitive amphibian known, the ichthyostegid (Figure 6-16), has the same type of vertebra as the crossopterygian fish (Figure 6-25). Because of this similarity, it is generally supposed that this is the basic type. Figure 6-18 shows a presumed radiation of the several types, and Table 6-1 lists the terms (adjectives) used to describe them.

The use of vertebrae in a classification seems impractical at first glance. For example, among reptiles the lepospondylous type appears to be but an ontogenetic or phylogenetic stage in what is, or was, a continuum. From fossil amphibians, it is suggested that the trend was toward the stereospondylous type (whether from a rhachitomous or embolomerous source). In the stereospondylous vertebra, the intercentrum forms much, or all, of the adult vertebral body. The lepospondylous amphibian *Megamolgophis* (Figure 6-17) has the parapophysis apparently on the intervertebral connective tissue, suggesting that in this group the centrum alone remains and the intercentrum is lost. This lepospondylous type resembles, but is even more advanced than, the amphibian type leading to the reptile. To penetrate this question of vertebral structure a bit deeper, the living amphibians will be examined.

Amphibians

Salamander *Cryptobranchus* and *Necturus* are much alike in terms of the vertebral column. There are 19 presacrals in

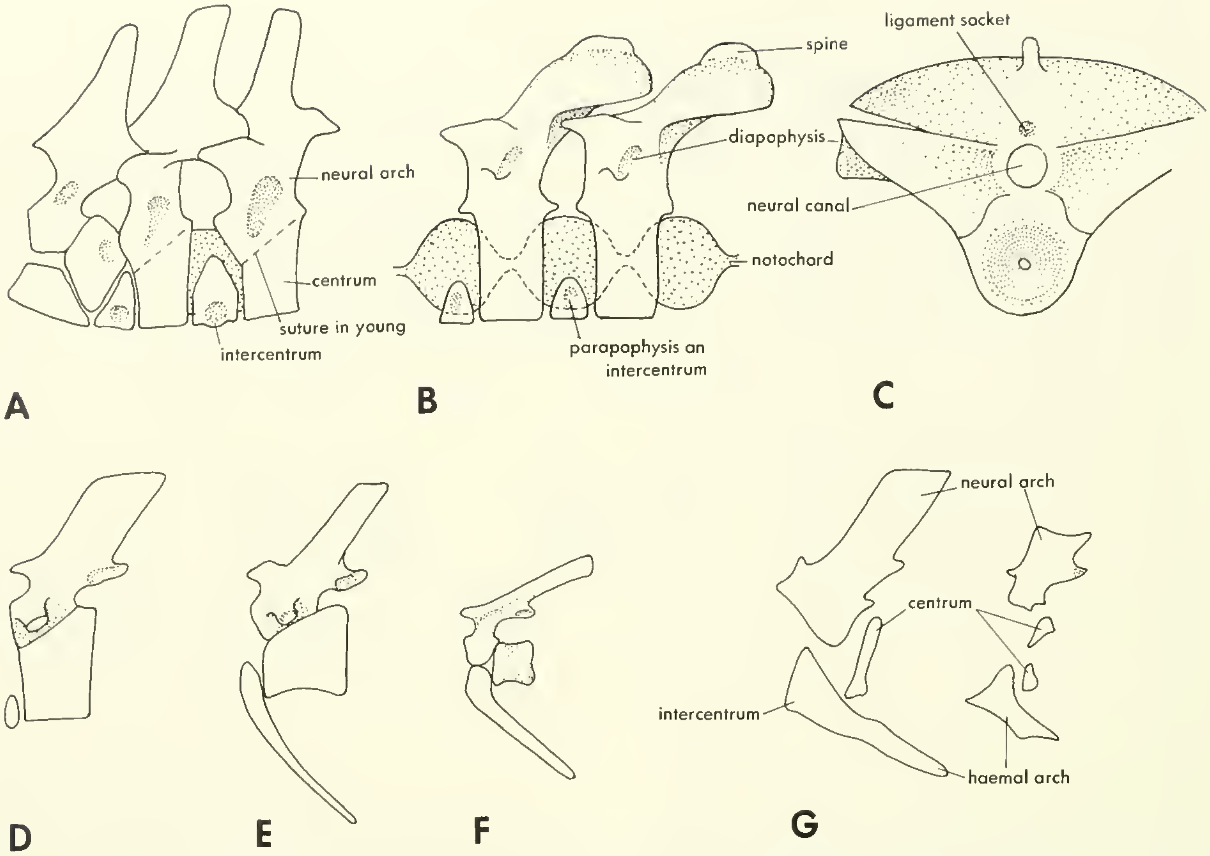


Figure 6-13. A–F, variation of vertebrae within the column of *Seymouria* and the separation of component parts. A, atlas, axis, and 3rd cervical; B, two dorsals; C, anterior view of a dorsal; D–F, 2nd, 8th, and 23rd caudals. G, component parts of vertebrae as seen in the caudal region of *Archegosaurus*, an eryopsoid amphibian. (A to F after Watson, 1919, and White, 1939; G after Goodrich, 1930)

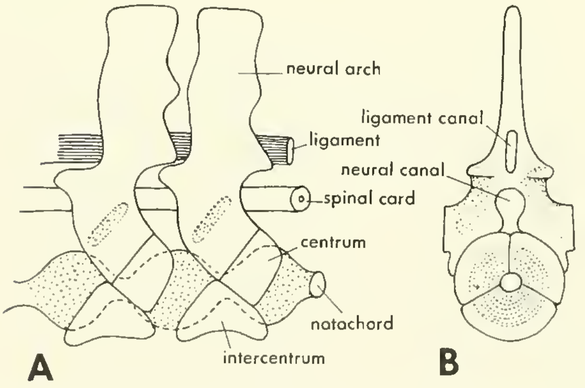


Figure 6-14. Dorsal vertebrae of the fossil amphibian *Eryops* in lateral view, A, and as seen from behind, B. (After Williston)

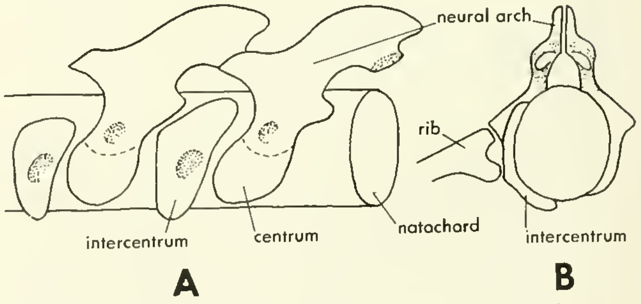


Figure 6-15. Dorsal vertebrae of Upper Pennsylvanian branchiosaur, *Amphibamus.* (After Eaton, 1959, and Gregory, 1950)

Cryptobranchus and 18 in *Necturus;* only the first presacral in each lacks a rib. The first vertebra articulates with the skull through 3 facets; its body has a rounded **odontoid process** which lies between the occipital condyles of the skull and bears a facet on its tip, while what appears to be **transverse processes** bear hollowed facets for the occipital condyles. There is a low **neural arch** with strong **postzygapophyses.** The second and succeeding vertebrae, back to the third caudal, bear single-headed ribs. The rib-bearing vertebrae are quite uniform. They have low **neural arches,** distinct **pre-**

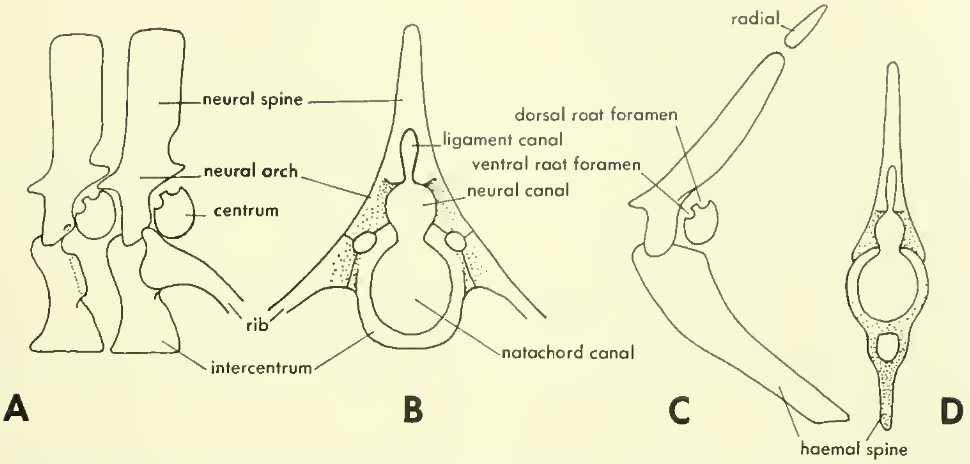


Figure 6-16. Vertebral structure of an ichthyostegid. A, two dorsals as seen in lateral view; B, anterior view of dorsal; C, lateral view of caudal; D, anterior view of caudal. (After Jarvik, 1952)

and **postzygapophyses** and long, posterolateral **transverse processes.** These processes are pierced at their base by an **arterial canal** in *Necturus.* In some amphibians the ribs are two-headed with what appears to be, but is not, a vertebral canal. There are no hypapophyses.

There is one **sacral** with a thickened down-curving rib which supports the **ilium** of the **pelvic girdle,** and there are 15 to 25 **caudals.** The second and succeeding caudals have **hemal arches** fused to the center of the vertebral body. The transverse processes of the first three caudals bear small ribs.

Frog There are only 9 vertebrae and a urostyle in the column of the frog. The first vertebra has bilateral articular facets for the occipital condyles of the skull, and a medial, **odontoid process** which extends forward between the condyles. There is a low **neural arch** with a slight spine and postzygapophyses. The second vertebra has broad **transverse processes,** as do the succeeding ones. The processes of the ninth vertebra, the sacral, attach to the ilia. These processes represent both rib and diapophysis. **Pre- and postzygapophyses** are well developed in the second though the eighth vertebrae, as are short, **neural spines.** There are no hypapophyses. With the exception of the first, next to the last, and last, the vertebrae are **procoelous.** The last vertebra is convex anteriorly with a biconvex posterior surface; the next to the last is biconcave. The **urostyle** is a long splint which, posteriorly, is tubular for the remnant of the notochord.

In its ossification, this column resembles the amniotes. The neural arches bear the transverse processes and unite with the body, which at first is tubular. The body appears as a crescent of bone above the notochord and spreads down and around the notochord to form a tube. The first ossification thus appears as an epichordal center. This is as far as ossification proceeds in some anurans (*Bombinator, Xenopus*).

The urostyle is formed around the expanded posterior region of the notochord. Dorsally, there are at least three pairs of neural arches involved, while below the notochord, a single midline splint extends back. This splint is the ventral, perichondral ossification of the hypochordal cartilage. This cartilage lies in the perichordal tube, not in the notochord sheath as has been suggested. The vertebral centra of the urostylar vertebrae appear late and complete the structure observed in the adult. The neural parts of the urostyle form the dorsal crest of the adult bone. No caudal vertebrae as such are formed in the frog; much of the tail of the tadpole is supported only by the notochord, its sheath, and the thick perichordal tube of sclerotomic cells which is stiffened by the cartilaginous hypochordal rod in the urostylar area.

Embryological development The development of the amphibian type of vertebra has been described by many but much confusion remains. In the early stages of the frog or salamander (see Chapter 7), the neurula, distinct dermatomes, and myotomes have not yet appeared, but there is an indistinct mass from which these parts develop.

The myotome lies close to both the neural canal and the

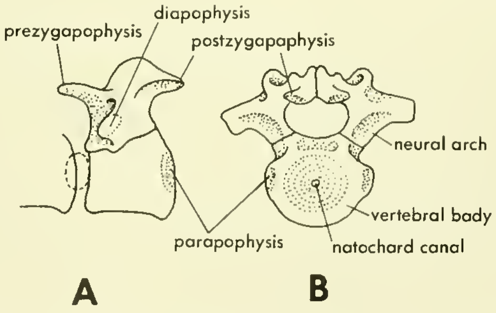


Figure 6-17. A lepospondylous vertebra of *Megamolgaphis* as seen in lateral and anterior view. (After Pivteaux, 1955)

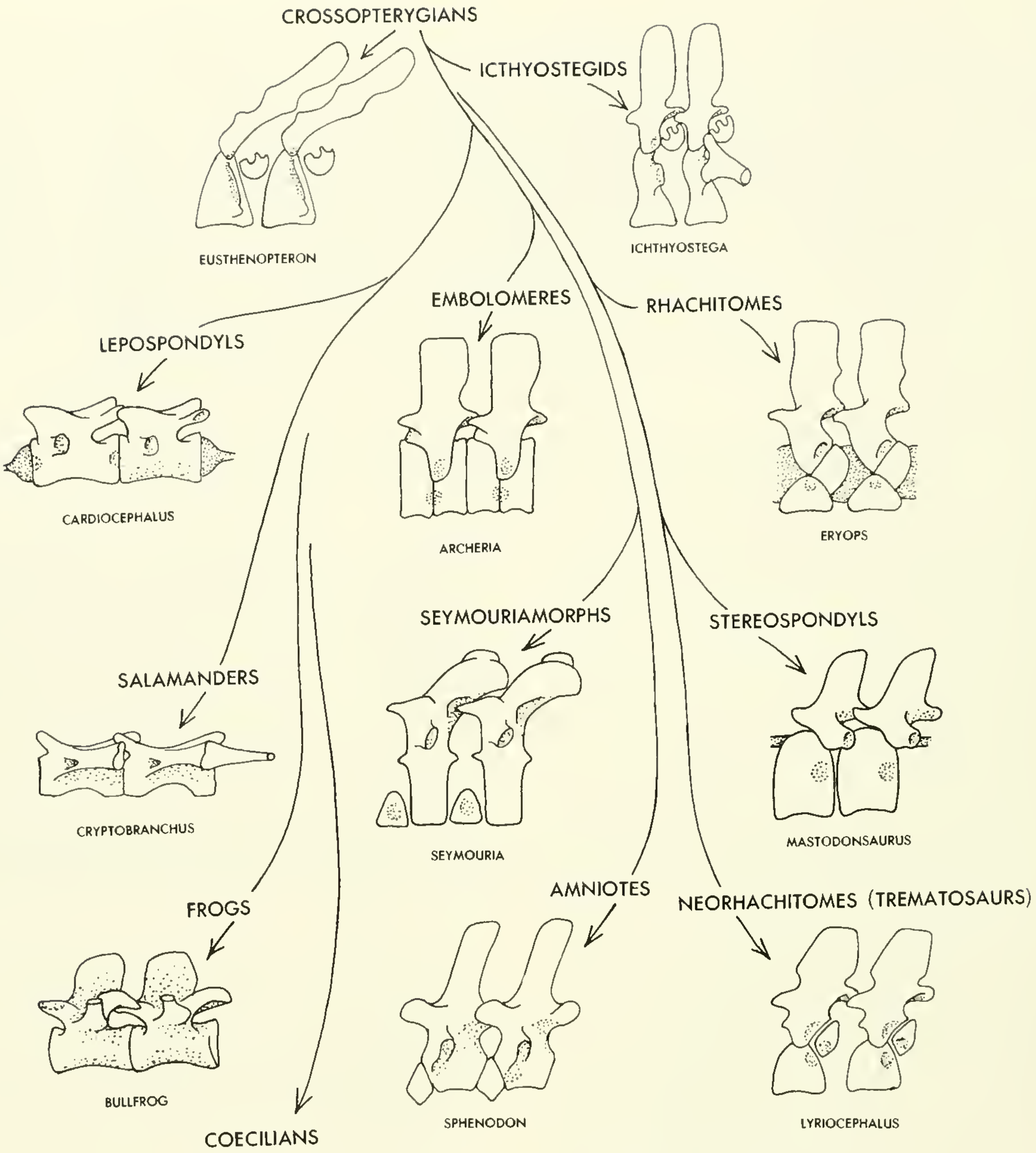


Figure 6-18. The phylageny of vertebral types as suggested by Williams (1959).

notochord. The sclerotome, having a thickness of only one or a few cells, is very restricted. The close relation of muscle to notochord is explained by the fact that the larva is soon to swim actively.

Because the sclerotome is so restricted, intrasegmental clefts cannot be detected. The first evidence of the skeleton is the appearance of the procartilaginous neural arches in the sheath of the neural canal. These arches extend up from the notochord on either side of the neural tube. Their bases lie in contact with a perichordal tube of cells. The perichordal tube is thickest in the intervertebral areas, where it forms an intervertebral ring of circularly arranged fusiform cells. This ring is thickest at the line of junction with the myoseptum (Figure 6-19). The myoseptum extends up and back along the neural arch and, in the caudal region, down and back along the hemal arch.

As development progresses, the intervertebral ring becomes cartilaginous and constricts the notochord (Figure 6-20). Ossification and chondrification appear at about the same time in the thin vertebral rings of the perichordal sheath. Externally the vertebral rings become bony, but the inner cartilage is continuous with the interverte-

TABLE 6-1 TERMS, ADJECTIVES, USED TO DESCRIBE THE VARIOUS KINDS OF VERTEBRAL STRUCTURE IN TETRAPODS

Temnospondylous *temno* or *tamno,* to cut; *spondylos,* vertebra

Vertebra consisting of several parts; formerly designated as having the arch separated from the body as opposed to stereospondylous. Several of the following more specific terms are now used in place of temnospondylous.

Rhachitomous *rhachis* or *rhachites,* spine, of the spine; *tomos,* cut or section

Referring to the "cut up" spine, or having two pairs of arch components. The body is in two parts; a larger anterior intercentrum and a smaller posterior centrum. The latter is the second "arch" component.

Embolomerous *embolos,* object thrust in; *meros,* a part

Referring to the separate and equally, or nearly equally, developed intercentrum and centrum. Literally another part thrust in.

Stereospondylous *stereos,* solid; *spondylos,* vertebra

Referring to a vertebra with a single body composed entirely or essentially of the intercentrum. The neural arch may be detached (Figure 6-18, *Mastodonsaurus*).

Lepospondylous *lepis* or *lepos,* a scale; *spondylos,* vertebra

Referring to shell-like or husk-vertebrae—a type of vertebra that does not extend beyond an amphicoelous stage and has a notochordal perforation through the body. This type includes the primitive or neotenic frogs, and salamanders. The vertebra may be **holospondylous,** all in one piece, or the neural arch may be detached as in the adelospondylous type (see below).

Phyllospondylous *phyllon,* leaf or leaf-like; *spondylos,* vertebra

Referring to the shell-like (perichondrally ossified) disconnected pieces of an otherwise rhachitomous type. An example is *Amphibamus* (Figure 6-15).

Adelospondylous *adelos,* concealed, not known; *spondylos,* vertebra

Vertebrae with a detached neural arch as in *Lysorophus;* otherwise, a lepospondylous type.

Neorhachitomous *neos,* new or recent

A rhachitomous type approaching the stereospondylous by reduction in size of the centrum component. The term applies to a late group of amphibians of rhachitomous ancestry.

Holospondylous *holos,* whole or entire; *spondylos,* vertebra

Each vertebra consists of a single piece whether it is solid or husk.

bral cartilages. As development proceeds, the middle of the vertebra becomes quite constricted and cartilage may invade the notochord (Figure 6-19 A); the ends of the vertebral body flare out around the intervertebral cartilage.

In the caudal region of the salamander, the hemal arches appear below the neural arches and become attached to the body. A circlet of connective tissue grows into the intervertebral cartilage to form the joint. A ball-like intervertebral body may be separated by this connective tissue, thus forming an amphicoelous joint; the greater part of the intervertebral cartilage can remain attached to the more posterior vertebral body to form an opisthocoelous articulation or to the anterior vertebral body to form a procoelous joint. In some species the intervertebral body appears to be split equally between the vertebrae.

A separate supradorsal cartilage forms in the neural arch above the neural canal. This gives rise to the pre- and postzygopophyses as well as to the short spine. The ribs appear as separate chondrifications as do the "rib bearers." The origin of the rib bearer in the various salamanders suggests that it is a compound structure of both dorsal and ventral rib heads. The definitive rib, whether two-headed or not, is not entirely comparable to the reptilian rib, which is basically a dorsal one with its capitular head derived from the ventral rib. The ribs of Urodela and Anura are thought to be dorsal ones, the ribs of the Apoda ventral ones.

General observations The vertebral body of the amphibian forms between intervertebral rings very much as it does in the previous groups (Figure 6-21). Whereas the reptile or mammal vertebral body lies generally behind the rib, that of the amphibian projects well in front. This suggests that the intercentrum was incorporated into the body or, perhaps, that the body is of intercentral rather than central origin. The craniovertebral articulation of the amphibian is quite distinctive.

Choanate fishes

Dipnoan In recent dipnoans, vertebral bodies are not developed, although cartilaginous blocks occur in the tail region (Figure 6-22). "Centra" have been observed in the Devonian fossil forms, *Dipterus* and *Rhynchodipterus,* but the details of these are not known. Jarvik (1952) has described the vertebral bodies of two kinds of dipnoans from the uppermost Devonian of Greenland. One of these, *Soederberghia* or form *A,* is like *Rhynchodipterus,* the other, *Jarvikia* or form *B,* resembles the fossil genus *Fleurantia* in external shape. In these forms, no arcualia (neural or hemal arches) have been seen; however, long ribs occur in form *A.*

The vertebral bodies of form *B* (Figure 6-23) have been sectioned (by grinding), but their detailed histological structure was not revealed. There is evidence of concentric layering of trabecular material around the central axis (notochord axis). The tissue may have been bone, but more probably, was calcified cartilage.

The vertebral bodies are amphicoelous, those of *A* being pierced by a narrow notochordal canal. In *B,* the canal is lacking, and there are paired dorsolateral and ventrolateral openings, which probably were occupied by the cartilaginous arcualia (or arches). The form of the body in *B* suggests invasion of the notochordal sheath by sclerotome cells. This is supported by observations of the development of the

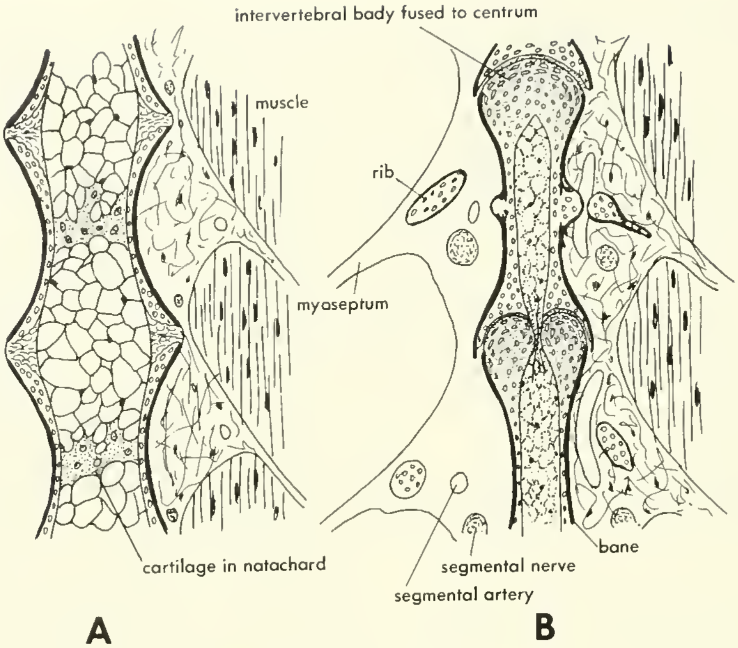


Figure 6-19. Developmental stages of vertebrae in *Siredon*, a salamander. (After Schauinsland, 1906)

living dipnoans *Neoceratodus* or *Protopterus.* In these, the cartilaginous neural and hemal arches rest on a thin perichordal tube of connective tissue enclosing the notochord. Cells of this perichordal tube penetrate the outer membrane of the notochord, the elastica externus, and convert the underlying fibrous layer of the notochord sheath into a cellular one. The notochordal sheath of the fossil species *B* apparently was expanded outward to form the body, with the result that the cartilaginous bases of the arches became embedded. The enclosed notochord was also constricted and eventually eliminated.

It seems quite possible that the **chordospondylous** or chordocentrous ("centrum" or body, formed from notochordal sheath) vertebra observed here, represents an extreme modification in one line of dipnoans, whereas others such as *Fleurantia,* also of the Upper Devonian, lacked vertebral bodies and had only ossified arculia similar to those which are largely cartilaginous in living dipnoans. The ribs of dipnoans are of the ventral type, that is, each is formed along the line of contact of the somatopleure (lining of body cavity) with the myoseptum in contrast to the basically dorsal rib of the amniote which is formed along the intersection of horizontal septum and myoseptum.

Actinistian The coelacanths are much like the dipnoans. In fossil forms only, the neural and hemal arches are indicated. *Diplurus* and *Undina,* a late Triassic form of small size, have short pleural, or ventral, ribs like those of the dipnoan, while *Latimeria,* the living form, lacks ribs. *Latimeria* (Figure 6-24) has cartilaginous neural arches and intercentra, and the neural spine and adjacent part of the arch are ossified; in the fossil forms both the dorsal and ventral arches were ossified. In *Latimeria,* the notochord has a thick fibrous sheath and the interior vacuolated cells have disappeared, leaving a fluid-filled cavity. The thickness of the sheath suggests infiltration by connective tissue cells, but this has not been described. Anteriorly, the perichordal tube is indistinct,

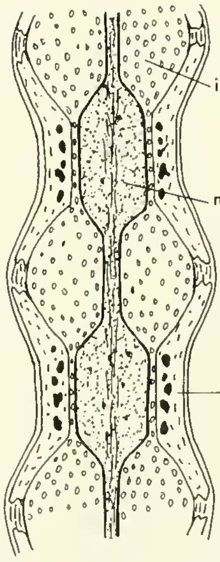


Figure 6-20. Late developmental stage of *Ascaphus*, a frog. (After Ritland, 1955)

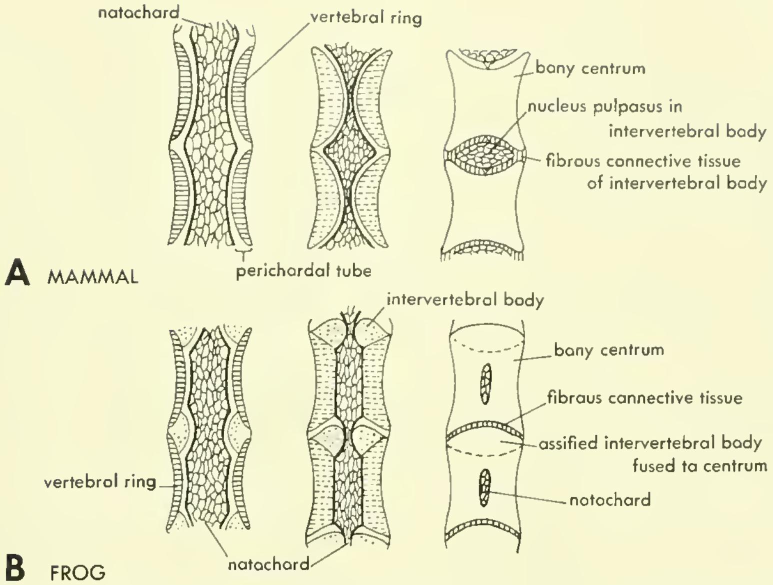


Figure 6-21. Vertebral as compared with intervertebral constriction of the notochord as observed in the mammal, A, and the frog, B. (After Remane, 1936)

but in the caudal region it is thicker and the dorsal and ventral arch components become joined by a connective tissue band.

Rhipidistian The vertebral column of *Eusthenopteron* is well known (Figure 6-25). In this type, the notochord is essentially unconstricted. There is a pair of large intercentra which extend nearly around the notochord, with only a short gap separating the dorsal ends. The neural arch rests on the upper ends of the intercentra. Behind the base of the neural arch of either side, is a small interdorsal (or interneural) arch which is notched along its anterodorsal margin for the roots of the spinal nerve. The arrangement of parts is much like that in the ichthyostegid amphibian (Figure 6-16), and the similarity is carried even further in that a short rib articulates along a line beginning low on the intercentrum and ending on the ventral margin of the neural arch. The rib is, however, single-headed.

The crossopterygians and some of the dipnoans seem to have essentially the same sort of vertebral column. That of

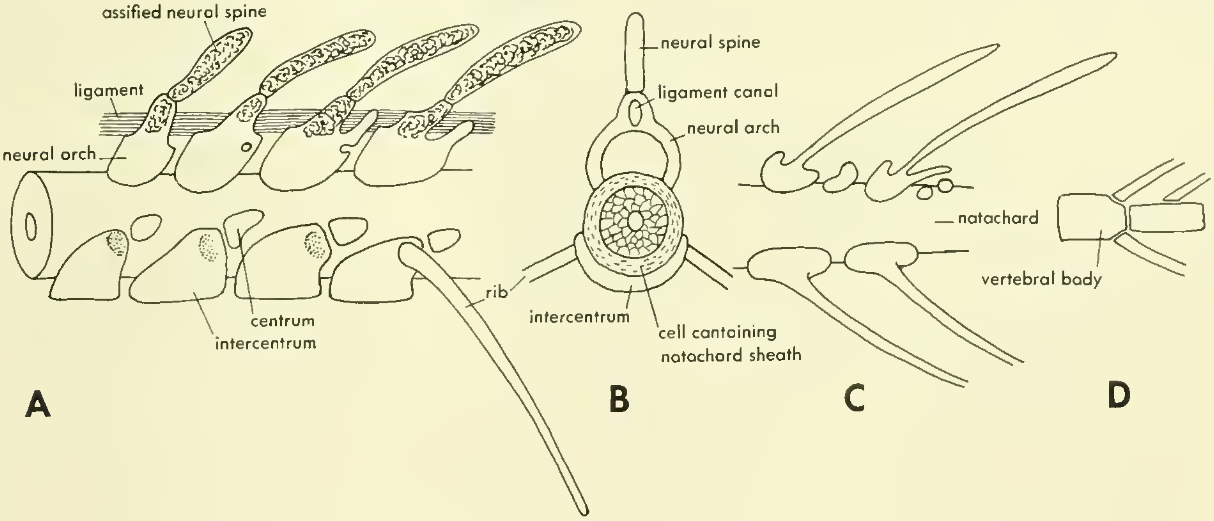


Figure 6-22. Vertebral structure of *Neoceratodus*. A, lateral view of thoracic (dorsal) vertebrae; B, end view of thoracic; C, lateral view of anterior caudals; D, posterior caudals. (After Remane, 1936)

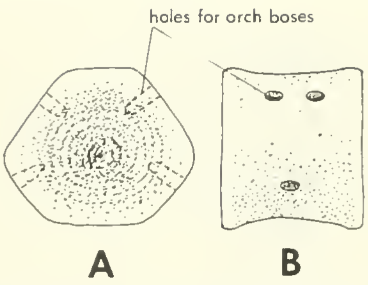


Figure 6-23. Vertebra of Upper Devonian dipnoan, *Jarvikia arctica* as seen in end, A, and side view, B. (After Jarvik, 1952)

the osteolepiform crossopterygian is most like the ichthyostegid amphibian in terms of elements and interrelationships of parts. It is possible that the rhachitomous type of the amphibian was derived from a rhachitomous fish. The problem of the difference in ribs—the dorsal type in *Euthenopteron* as opposed to the ventral type in the dipnoan or coelacanth—can be accounted for by modifying the view of Naef (Figure 6-73) that both ventral and dorsal ribs are involved in the dorsal rib of the amphibian. The only remnant of the ventral rib is the capitular head.

Actinopterygian fishes

Teleost The teleost, as represented by the salmon or perch, generally has a holospondylous vertebra, that is, a one-piece vertebra. The term is generally used in describing fish vertebrae, but there is no special term for vertebrae having separate parts. The most anterior trunk and the posterior caudal vertebrae of the salmon or the first vertebra of the perch have the neural arch sutured to the body (Figure 6-26). The body is hour-glass shaped and amphicoelous. The notochordal canal is constricted to a narrow passage at the center of the body. The bone forming the body is spongy except around the intervertebral swelling of the notochord.

The neural arches of the anterior 20 to 25 vertebrae of the salmon have double neural spines. Those of the perch fuse at the tip. The neural arches of the posterior dorsals and caudals of the salmon have the two halves fused. In the salmon, the anterior neural arches (first 20 to 25 vertebrae) are separate from the bodies, whereas, in the perch, only that of the first vertebra is separate. In the salmon, these free arches have their bases fitted into sockets. In the same regions, there are calcified supradorsals between pairs of arch components and lateral to the longitudinal ligament. The supradorsals suggest the interneural connective from which the pre- and postzygapophyses of the higher forms arise. The neural arches of the perch have anterior and posterior **basal processes** which overlap those of adjacent vertebrae to form intervertebral articulations (Figure 6-26 D).

In the salmon, the parapophyses of the anterior trunk vertebrae are fitted into sockets of the body, and bear a strong, ventral rib. Above the rib and attached by a ligament is a small dorsal rib. In the perch, only the ventral rib is developed. The parapophysis of a middle, trunk vertebra of either the perch or the salmon has a strong lateral process extending out anterior to the rib attachment. In a posterior succession, these processes become longer and more ventrally directed, and the rib articulation moves farther out on them (Figure 6-40). In the anal region, these spines are transformed, first, into the base of the hemal arch, and then into the entire hemal arch including the hemal spine.

The parapophyses of the most anterior vertebrae of the perch are much reduced in size and are situated high up on the side of the body. They are fused with the body and neural arch. In the caudal region of the perch, the bases of the hemal arches form a series of articulating processes (**hemosphenes**) between the vertebrae.

EMBRYOLOGICAL DEVELOPMENT In development, the notochord of the teleost is at first large and unconstricted. The myotomes lie very close to either side. There is little

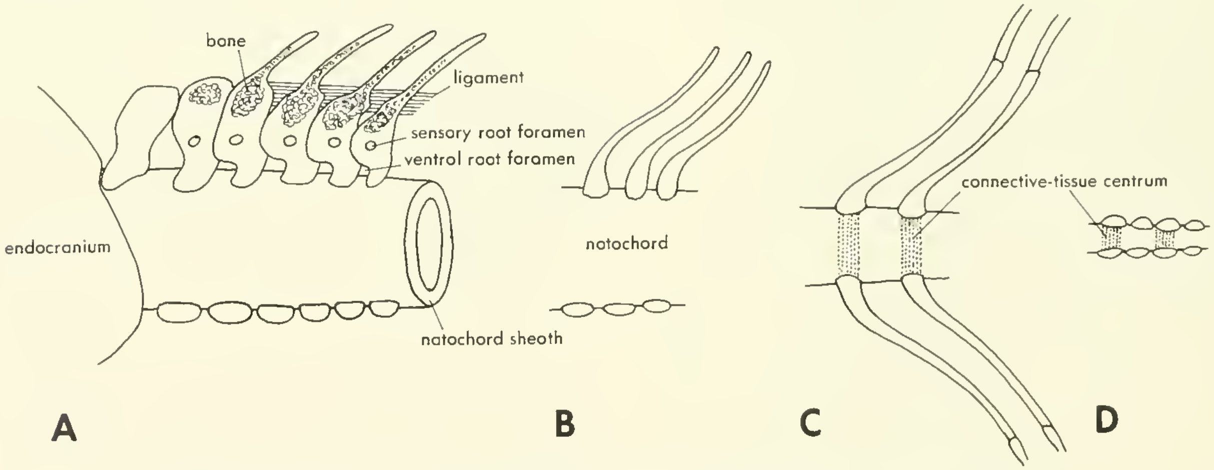


Figure 6-24. Vertebral structure of *Latimeria*. A, anterior end of column; B, midthoracic region; C, anterior caudal region; D, posterior part of column. (After Millot and Anthony, 1958)

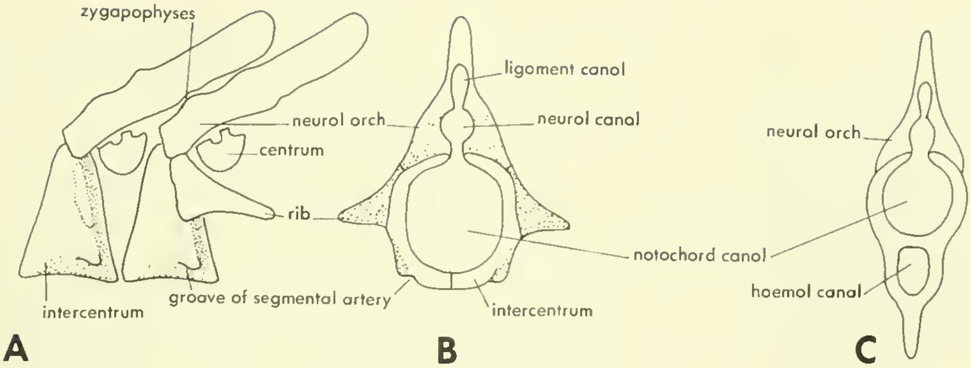


Figure 6-25. Vertebral structure of *Eusthenopteron*. A, lateral view of two thoracic vertebrae; B, anterior view of a thoracic; C, anterior view of a caudal vertebra showing neural and hemal arches. (After Jarvik, 1952)

sclerotome material, and this is mainly in the region of what is to become the neural arch. The notochord has a distinct sheath with fibrous and external layers. The first evidence of the skeleton is the appearance of the neural arches followed by the hemal arches. The cartilaginous dorsal and the ventral arches, or arcualia, lie in contact with the notochord, and a perichordal tube encloses their bases (Figure 6-27). These arches lie mainly in front of the myoseptum, but extend partly into the area behind the myoseptum. In some cases, a secondary procartilaginous center is observed behind the ventral arch center. This interventral center unites with the anterior arch. The vertebral body ossifies without a cartilaginous precursor in the perichordal connective tissue enclosing the bases of the arches. The dorsal arch, ossifying perichondrally, generally fuses to this body. The ventral arch unit forms the parapophysis of the hemal arch, ossifies perichondrally, and fuses to, or remains separate from, the body. In the process of development, the notochord is constricted within the body and eventually is reduced to a strand of tissue. There is a large ovoid intervertebral mass of connective tissue and notochord in the adjacent ends of the amphicoelous vertebrae.

In teleosts, the notochord may be much constricted, or only slightly so. In some teleosts (*Clupea* and *Lebistes*), the outer part of the notochordal sheath ossifies, but this is, probably, not usually the case. The notochord is, as a rule, modified in terms of its internal structure; there are large internal spaces, or strands and patches of denser tissue.

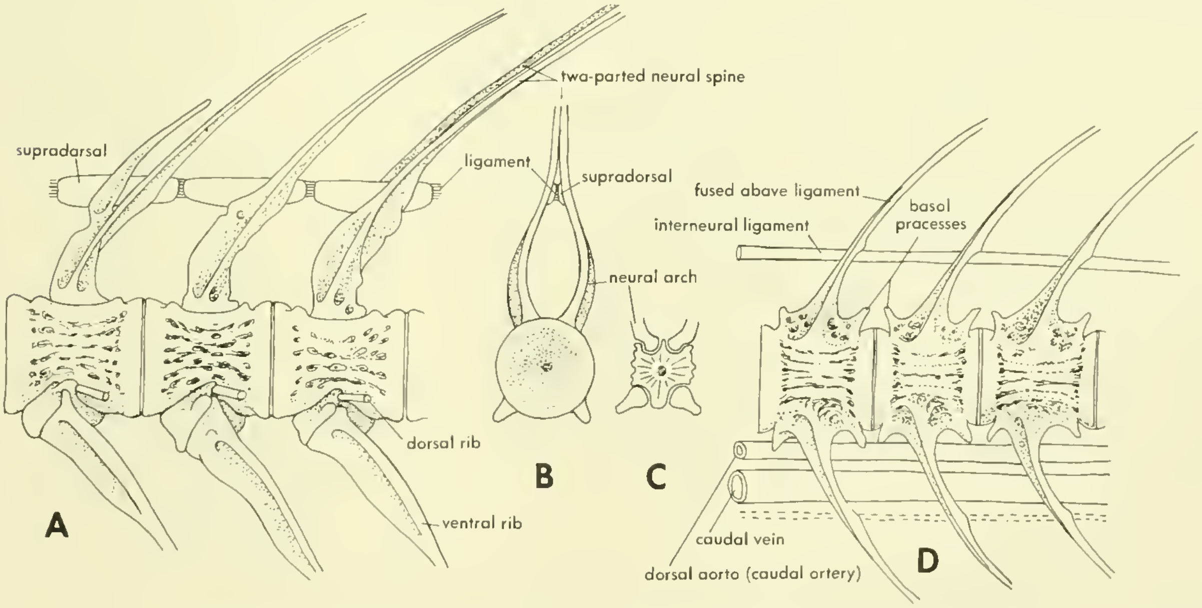


Figure 6-26. Vertebral structure of a salmon (Blue-Backed Salmon). A, lateral view of anterior trunk vertebrae; B, anterior view of a trunk vertebra; C, cross section through the middle of the centrum of a trunk vertebra showing the roots of the arches; D, caudal vertebrae as seen from the side.

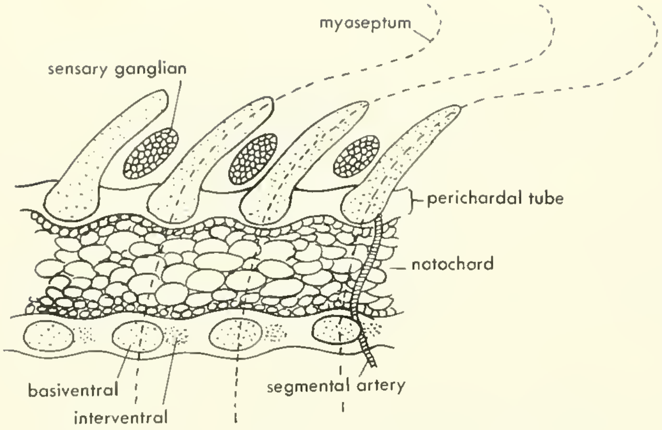


Figure 6-27. Early stage (25 mm) of vertebral formation in the salmon showing cartilaginous neural and central elements.

Amia In *Amia,* the vertebrae are short, amphicoelous spools, with the exception of the first, which is opisthocoelous (Figure 6-28). The neural and hemal arches remain separate from, and are not rooted in, the body. The first few (5 to 7) neural arches have detached neural spines, and the first few hemal arches (10 to 12) also have detached spines. Each vertebral body has a parapophysis for the pleural or ventral rib (there is no rib on the first vertebra) or, in the caudal region, a short parapophysis for the separate hemal arch. The parapophyses are not converted into the hemal arches—rather the head of the rib appears to have this fate.

The relationship between the neural (and hemal) arch and the body is of interest, particularly in the caudal region where there is one set of dorsal and ventral arches to two bodies, a situation identified as **diplospondyly.** This situation is analogous to the embolomerous condition observed in amphibians. Anteriorly, the arches of the trunk vertebrae lie above the joints between the bodies. In the anterior caudal region, the neural arch has this relationship while the parapophysis tends to be slightly posterior on the body. As one progresses posteriorly in the examination of these vertebrae, one finds suddenly that the neural and hemal arches have been moved back one vertebral body and now attach to the middle of that body (Figure 6-28 C). In the most posterior caudal region, many peculiar relationships exist between arch and body, suggesting random association of parts. The question now becomes, "What are the parts involved?" The embryological development of these vertebrae may reveal this.

EMBRYOLOGICAL DEVELOPMENT In the early stages of development of *Amia,* a dorsal and a ventral arch appear (Figure 6-29), and the myoseptum is attached near the posterior margin of these rudiments, which lie along an oblique line, the dorsal behind the ventral. As the neural arch extends upward (or the hemal arch down), it becomes independent of the myoseptum, which now curves posteriorly to the top of the next posterior arch. The dorsal arch is curved; its base extends dorsoposteriorly, while its upper part is nearly vertical. Between the basal and vertical segments of the arch, a break develops: first as a region with little intercellular material in the procartilage, and then as a purely connective tissue gap between two cartilaginous parts. This transition occurs at a total length of 15 to 17 mm.

There are now two dorsal elements: the base of the arch

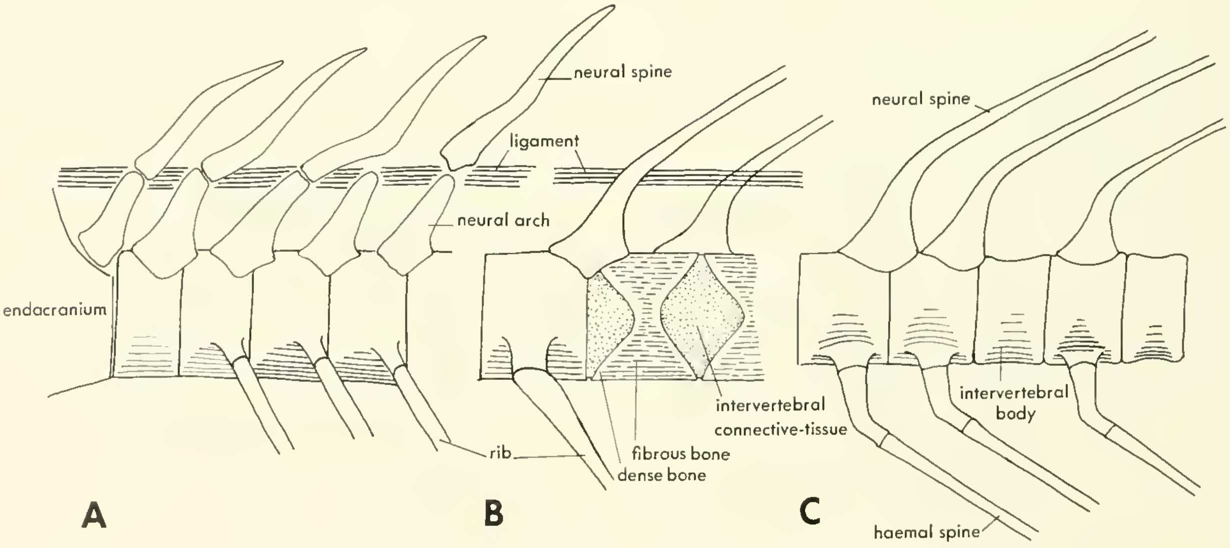


Figure 6-28. Vertebral structure of *Amia.* A, anterior end of column as seen from the side; B, middle trunk vertebrae, two cut in sagittal section to show amphicoelous nature; C, caudal vertebrae showing transition to diplospondyly.

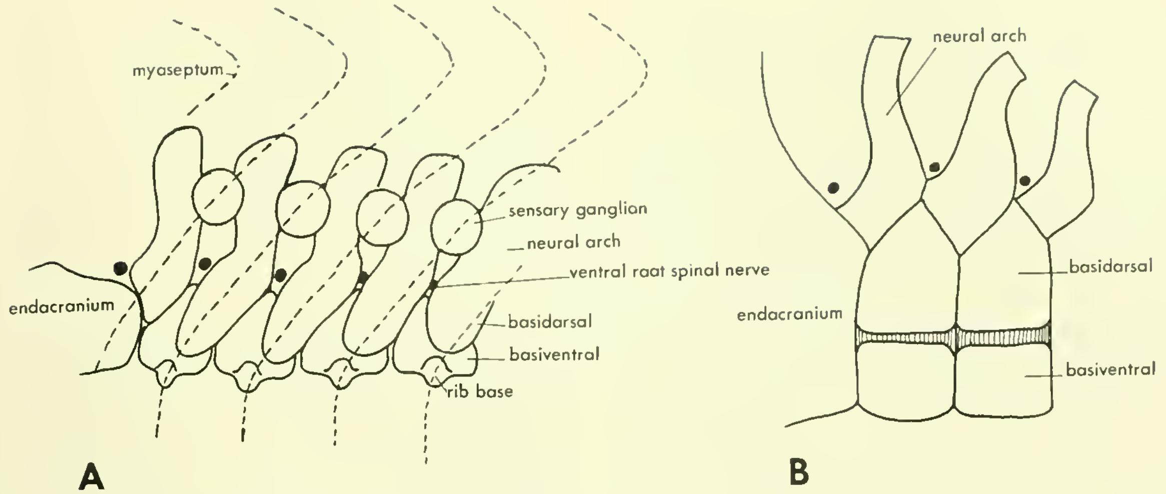


Figure 6-29. Cartilaginous precursors of the vertebrae as seen in larvae of *Amia*. A, 15 mm and B, 30 mm. (B after Schauinsland, 1906)

and behind this, the rest of the original arch. The now posterior neural arch rests on the notochord, and in part overlaps the anterior element. In the caudal region, the same process occurs with the hemal arches, so that the original ring-like vertebral body now lies in front of a new ring bearing the arches; this produces the diplospondylous condition.

The structure and development of the vertebral body in *Amia* is much the same as that observed in the teleost. However, cartilaginous components of the arches are involved, as well as the perichordal mesenchyme enclosing them. Ossification appears to spread from the bases of the arches into this mesenchyme (Figure 6-30). The differences observed involve inclusion of cartilage supplied by the arch bases, and in the transposition of the neural spine. The neural arches (and hemal arches in the caudal region) are displaced into the position of the interdorsal and interventral. The notochord is constricted by the development of the body and finally segmented into intervertebral parts.

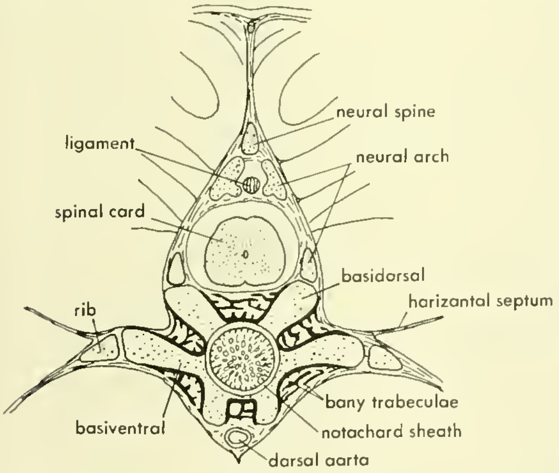


Figure 6-30. Cross section of an ossifying trunk vertebra of a 60-mm specimen of *Amia*. (After Goodrich, 1930)

Lepisosteus *Lepisosteus* has a very different course of development for its vertebrae, which are opisthocoelous. The neural arches are fused to the body and end at the dorsal ligament. Below this ligament is a supradorsal element for each arch.

In the early stages, dorsal and ventral arches are present. Posterior to the bases of these arches a cartilaginous ring forms around the notochord. It is possible that this relationship is achieved by the forward displacement of the arches. This intervertebral ring constricts the notochord, as does the larger, now developed vertebral ring associated with the arches. With ossification of the body in the perichordal tissue and arch bases, the intervertebral ring becomes divided by an ingrowth of connective tissue to form the ball and socket joint between adjacent vertebrae.

The supradorsal cartilages appear at the sides of the dorsal ligament and then fuse below it. The neural spines arise from separate centers and remain distinct through life. The ribs develop separately from the parapophyses; posteriorly, the parapophyses plus the rib centers form the hemal arches. In ossifying, the neural arch is first (perichondral); bone spreads from its base into the perichordal mesenchyme of the body. The base of the ventral arch ossifies separately from the rib or hemal arch and soon joins the dorsal arch base. From these arch centers, ossification spreads back through the body to the intervertebral joint. Ossification penetrates and displaces the cartilage of the joint and eventually eliminates the notochord remnant.

The hemal arch ossifies separately, but gives rise to the hemal spine. It remains articulated with the parapophysis in the adult. The neural spine always remains separate from the neural arch, but the neural arch is, from the beginning, fused with the body. The parapophyses of the ventral arches also ossify in connection with the body The neural arches are nearly articulated through the supradorsal cartilages, thus approaching a pre- and postzygapophyses condition.

***Acipenser*, the sturgeon** The adult vertebral column of the sturgeon (Figure 6-31 or *Polyodon*, Figure 6-32) is formed around an essentially unconstricted notochord with a fairly thick sheath. Dorsally and ventrally, in the anterior part of the column, there are two pairs of cartilaginous elements per segment. A large anterior neural arch extends down and partly around the notochord. Behind the neural arch, a small interdorsal element lies in contact with the notochord, behind and below the ventral (motor) root of the spinal nerve. The interdorsal element may be divided into two pieces. Ventrally, there are large bilateral elements which give rise to the parapophyses, and, behind these, smaller interventral elements. The latter may be divided into dorsal and ventral parts. Ventrally, the dorsal aorta and **hypochord** (subchordal rod) are enclosed in a canal. The hypochord is retained even in the adult and hangs down into the aortic canal; usually it is displaced to the left side (Figure 10-46).

The neural arches are ossified dorsally. There is a dorsal longitudinal ligament between their ends; below these ends, and above the neural canal, the arches lie in contact. Above the neural arch is a separate bony neural spine. The pleural ribs are ossified.

In development, the first structures are the cartilaginous (or procartilaginous) dorsal and ventral arches. As development progresses, the more posterior part of the dorsal arch, below the ventral root of the spinal nerve, becomes separated and chondrifies as the interdorsal. The same process takes place in the ventral arch—a gradual separation of a postvertebral artery portion of the expanded ventral arch.

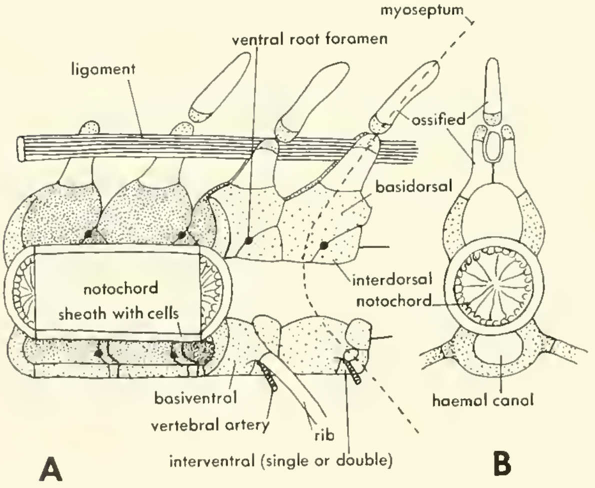


Figure 6-31. Vertebral structure of the sturgeon, *Acipenser*. A, lateral view of the anterior trunk vertebrae with one half of the two most anterior vertebrae cut away; B, anterior view of a trunk vertebra showing the neural and haemal canals.

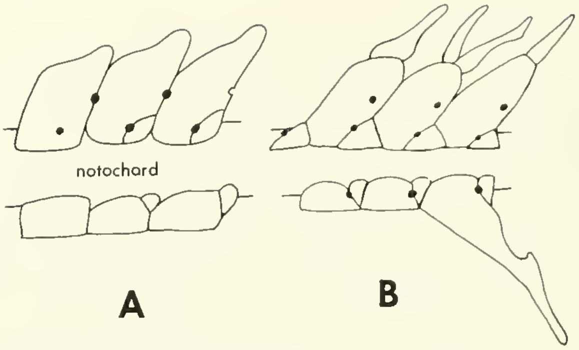


Figure 6-32. Lateral views of trunk, A, and transition from trunk to caudal vertebrae, B, in *Polyodon*. (After Shauinsland, 1906)

Thus, few "arcualia" are formed which, in the case of *Amia*, do not have the simple relationship to the myo- and horizontal septa (Figure 6-33) suggested by Gadow or others. The origin of these parts as observed in *Amia* or *Acipenser* does not suggest that primitively four centers were present, rather it seems more likely that there was a subdivision of two basic parts into four as an adjustment to the folding of the myomeres. There is no evidence of discrete perichordal centers such as the **pleurocentrum** or **hypocentrum** of Figure 6-33.

Palaeoniscoid Some support for considering the subdivision of the primitive arch as a secondary event is given by the vertebrae of palaeoniscoids such as *Pteronisculus* (Figure 6-34) and *Australosomus* (Figure 6-35); these are like the vertebrae of the living palaeoniscoid *Acipenser* or the brachyopterygian *Polypterus* (Figure 6-36). However, in the tail of *Pteronisculus*, four elements are present, and in *Australosomus*, the dorsal arch of each thoracic vertebra is subdivided into an anterior arch and a posterior interdorsal element as in *Acipenser*.

It is of interest to note that the palaeoniscoids generally lacked a vertebral body; *Australosomus*, however, had a thin ring of calcified or partly ossified tissue. The nature of this ring, and the separate arches, suggests invasion of the notochordal sheath by mesenchyme cells followed by calcification, or ossification. In *Acipenser*, some mesenchyme cells enter the notochordal sheath, as in the Dipnoi.

The above observations suggest a sequence of events. First, a dorsal and ventral arch chondrified, and some support was derived from thickening of the notochord sheath by cell invasion and calcification The latter support was replaced by further arch development in an anteroposterior direction along the notochord, followed by subdivision into anterior and posterior parts for flexibility. Ossification of the arches followed with extension into the perichordal mesenchyme. This system was then replaced by direct perichordal ossification apart from the arches. The extreme is *Lepisosteus*, in which the vertebral bodies are solid, much like those of some amphibians.

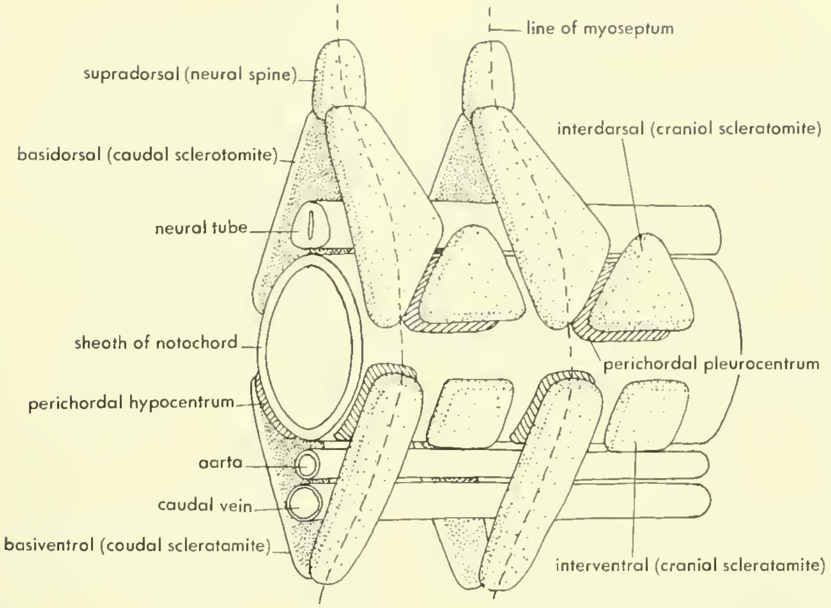


Figure 6-33. Components of a typical vertebra as described for the shark by Goodrich. (After Hyman, 1942)

Chondrichthyes and agnaths

Support for the primitive nature of four arcualia per segment comes primarily from the agnaths. In this group, the notochord sheath has an outer elastica externus and a distinct fibrous layer, but it not invaded by cells. Only cartilaginous "neural" arch elements occur, and, except at the anterior end of the column, there are two of these per segment, one in front, and one behind the ventral root of the spinal nerve (Figures 5-25 A, 6-37). The dorsal nerve root lies behind the posterior element. Ventral arch elements are found only caudally where a skeletal mass encloses the end of the notochord and the neural and hemal canals. From this mass, radials extend out to the thin margin of the caudal fin.

Fossil agnaths lacked ossified vertebral elements, although they may have had cartilaginous ones.

Shark Support for the four-arcualia concept comes also from the vertebral structure of the Chondrichthyes. In *Squalus* (Figure 6-38), there are two pairs of units above and below the notochord. In the course of development, the anterior dorsal unit, or neural arch, which at first lies in front

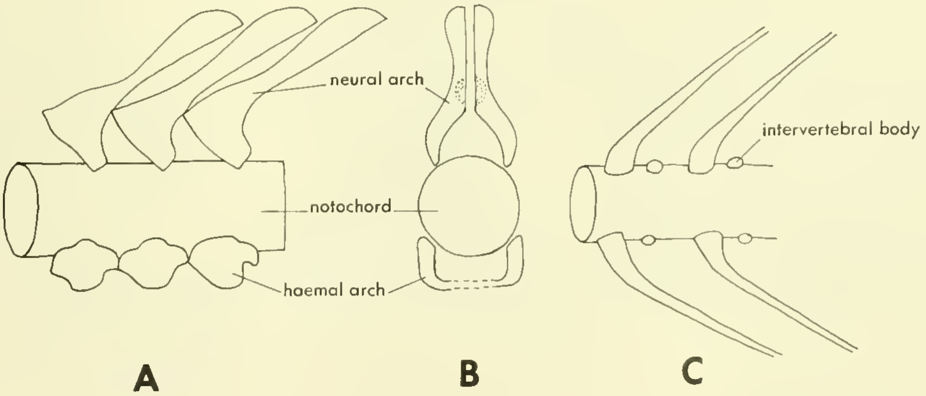


Figure 6-34. Vertebral structure of *Pteronisculus*. A, thoracic vertebrae in lateral view; B, thoracic vertebra as seen from in front; C, anterior caudal vertebral elements in lateral view. (After Nielsen, 1942)

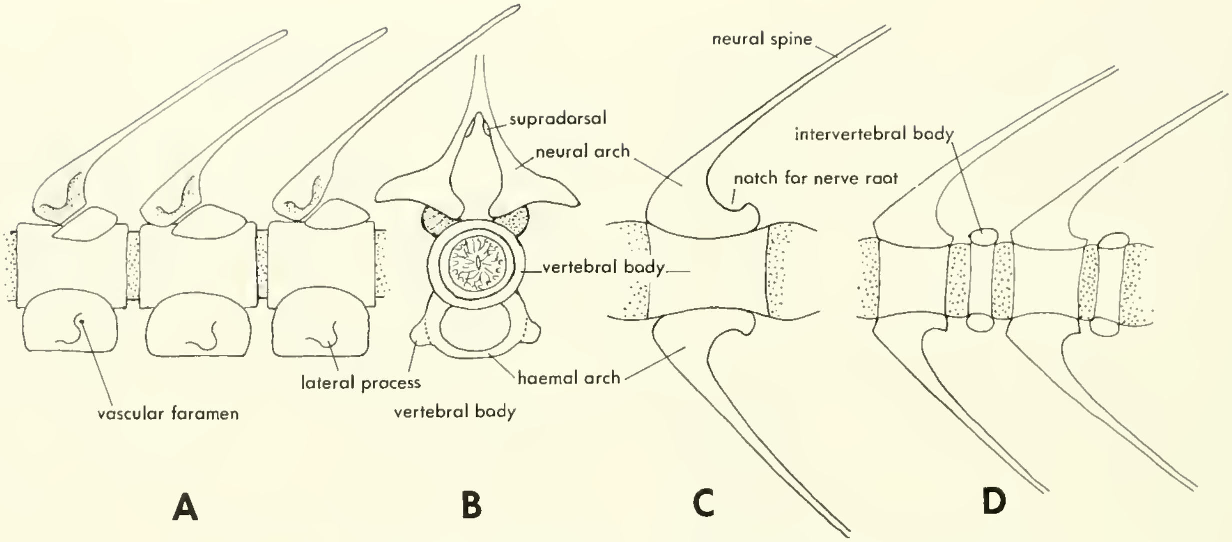


Figure 6-35. Vertebral structure of *Australosamus.* A, thoracic vertebrae in side view; B, thoracic vertebra as seen from in front; C, anterior caudal vertebra; D, posterior caudal vertebral elements. (After Nielsen, 1942)

of the ventral root of the spinal nerve, encloses that root. The posterior dorsal element, the interdorsal, has a similar history in regard to the dorsal root. In the definitive vertebra, the neural arch is continuous with the vertebral body, as is the parapophysis supporting the dorsal ribs. The vertebral body consists of expanded and chondrified notochordal sheath and perichordal tissue.

In the formation of the body, the outer elastic membrane of the notochord sheath ruptures and mesenchyme cells move into and through the fibrous layer. Later, the fibrous layer is chondrified as is the outer perichordal layer. Chondrification accompanies constriction of the notochord and is followed by local calcification. Numerous patterns of calcification and even body formation are observed in different sharks.

The posterior ventral element remains separate from the body, as does the posterior dorsal one. In the tail, diplospondyli may occur. The ribs arise in connection with the parapophyses, and only after chondrification do they become separate.

Holocephalon *Hydrolagus* (Figure 6-39) resembles the shark in having two pairs of dorsal elements, but differs in having the ventral pairs of irregular numbers and size: sometimes two

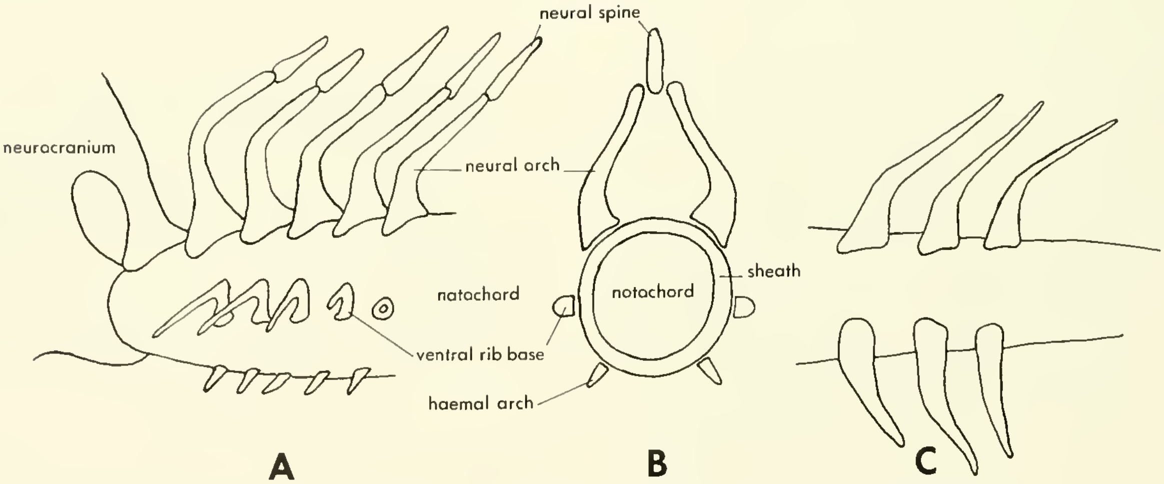


Figure 6-36. Vertebral components of larval *Polypterus.* A, anterior end of column in lateral view; B, anterior view of components of a trunk vertebra; C, caudal elements in lateral view. (After Budgett, 1901–1903)

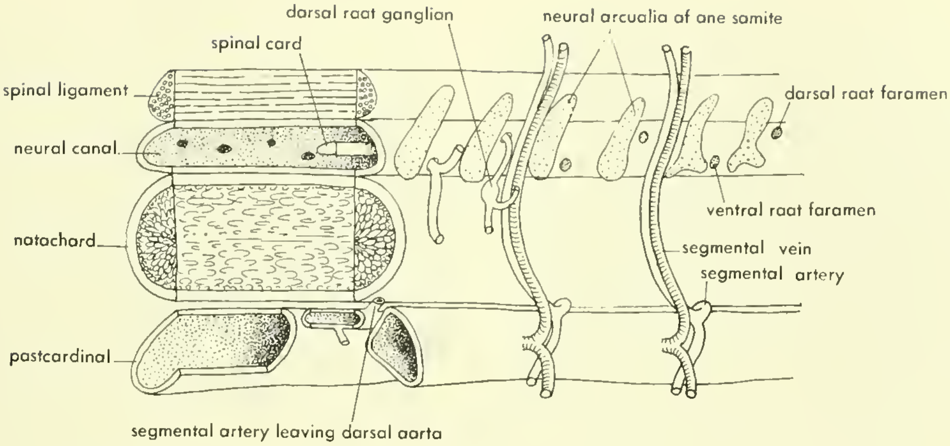


Figure 6-37. Vertebral elements of an adult lamprey, *Petromyzon marinus*, in relation to other structures. (After Goodrich, 1930)

per segment, sometimes extending a segment and a half, and, to confuse things even further, the elements of a pair may be of different sizes. Dorsal and ventral elements are separated from each other by a thin perichordal layer of connective tissue. The interdorsal arch lies behind the ventral root foramen, while the dorsal root foramen, is at its apex. The neural arch has a slight diapophysis and its ventral point marks the position of the myoseptum.

The "vertebrae" of *Hydrolagus* lack bodies. However, the sheath of the unconstricted notochord is invaded by rings of sclerotomic cells which later calcify. Such rings are lacking in *Callorhynchus*.

The anterior end of the column of *Hydrolagus* is fused into a single block which supports the dorsal fin and its spine. The units in this anterior piece are somewhat shortened. This anterior section articulates with the cranium by way of a heterocoelous surface on which the notochord is constricted to a fine strand.

The relationships of dorsal elements to nerve roots in the embryo suggest the agnath but do not resemble the situation observed in other groups. It is quite possible that this nerve-arcualia relationship is indeed basic, but there is no convincing evidence to support the assumption.

The manifold evidence of specialization—the many variations of structure in different sharks and rays, and the anterior section of the column of *Hydrolagus*—warns against considering the vertebral type of the Chondrichthyes as primitive. The same remark applies to the lamprey.

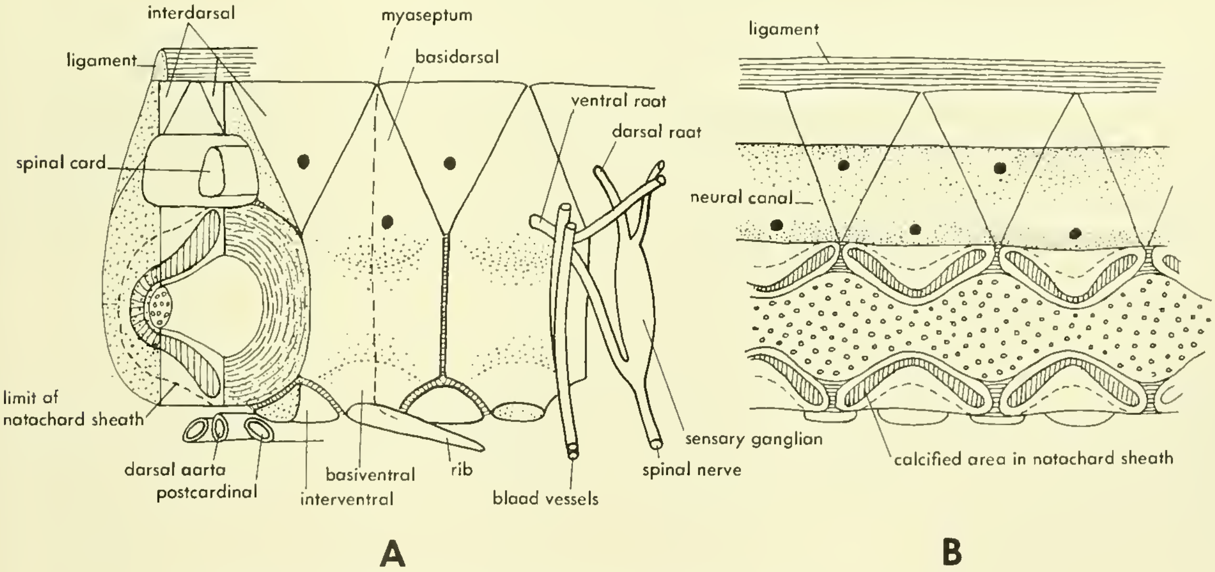


Figure 6-38. Vertebral structure of the shark *Squalus*. A, in lateral view, anterior vertebra cut obliquely; B, median sagittal section. (After Marinelli and Strenger, 1959)

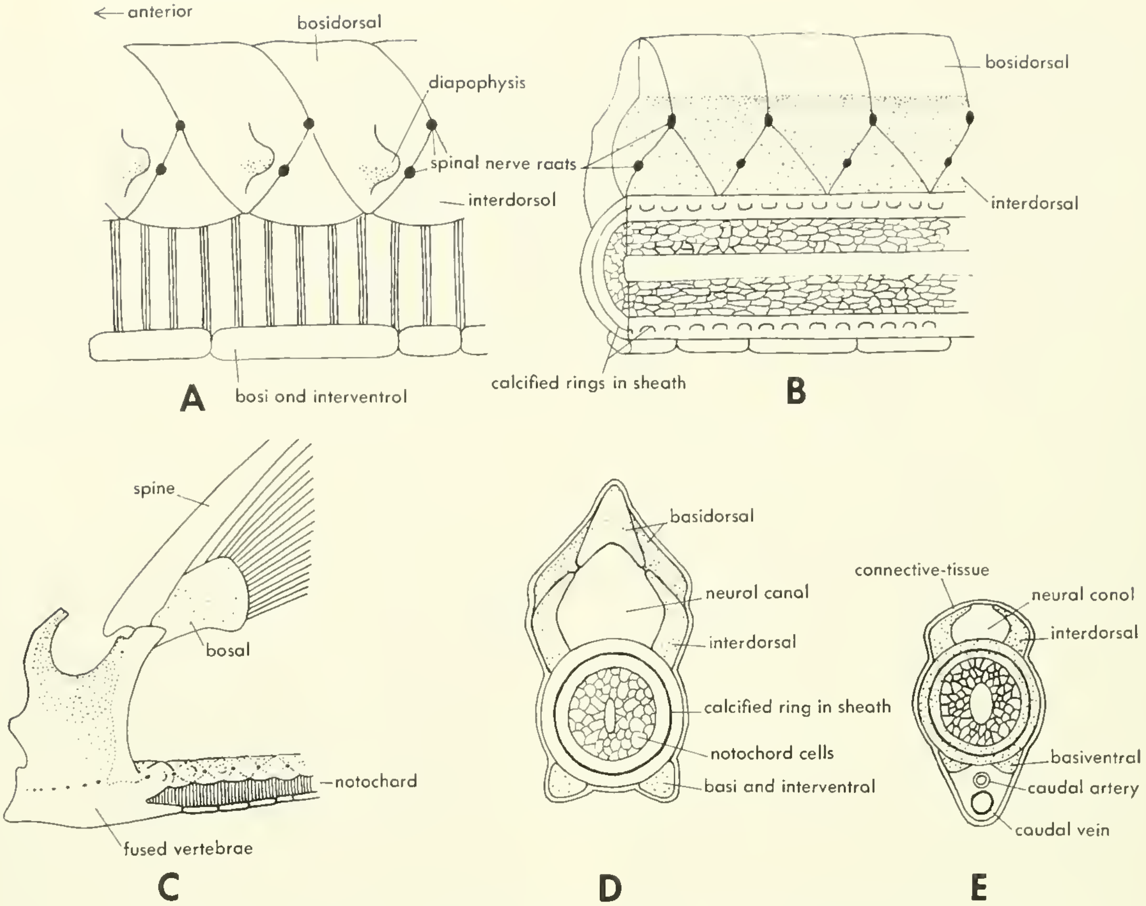


Figure 6-39. Vertebral structure of the chimaerid, *Hydrolagus colliei*. A, lateral view of thoracics; B, median sagittal section of thoracics; C, anterior end of column with base of dorsal fin; D, cross section of column in trunk region; E, cross section of column in tail region.

General observations on vertebrae

In spite of the conflicting evidence, it seems best to conclude that four pairs of elements (two pairs related to the myosepta and two pairs of intermyoseptal elements for anticompression aid) occurred in primitive forms. From these, the solid-walled neural canals of chondrichthians were developed as well as the open neural canals of teleostome fishes. In teleostomes, the myosepta elements tended to fuse with the interseptal structures, and this was associated with the formation of the vertebral body.

The vertebral body rose differently in each of the groups examined. It can be assumed that the tendency for mesenchymal invasion of the sheath was common to choanates (Dipnoi), actinopterygians, and chondrichthians. The vertebral body of the shark represents one direction of evolution, that of the osteichthian fishes, another. Discrete pleuro- and hypocentral centers are lacking.

In the fishes, the arches rest on the notochord, and they are thus rooted in the perichordal tissue; whereas, in amniotes, these arches chondrify away from the notochord (which is much reduced in size and thus makes room for increased perichordal tissue) and appear to lie outside the body. Although this difference is one which seems scarcely worthy of mention, there has been much concern over whether the vertebral body is **"archicentrous"** (developed from the arches) or **"autocentrous"** (developed separate from the arches).

MEDIAN FINS

Median fins include the **dorsals,** the **caudal,** and the **anal**—these are structures limited to fishes or at least specialized aquatic forms. The tetrapod groups are not involved in this discussion although it can be noted that whales have dorsal fins and **caudal flukes.** Similar fins were present in the ichthyosaur reptiles (also mosasaurs and others) with the difference that the caudal flukes of the whale are fleshy transverse planes, while the tail of the aquatic reptiles was like that of a fish.

Dorsal and anal fins

In actinopterygian fishes there is a great variety of fin structures and fin arrangements. The dorsal fin may be preceded by a series of **spines**, as in the perch; this fin may be divided into two parts or it may be continuous with the caudal fin. The salmon has a small **"adipose"** fin between dorsal and caudal. This small fin seems to be a new structure peculiar to some of the teleosts. The skeletal support of the dorsal fin or its parts is fairly simple. **Radials** extend upward from the spinal column toward the fin, and on the ends of these there are one or two **basal elements** which support the **fin rays** or spines (Figure 6-40). The anal fin is similarly constructed.

In the more primitive (fossil) actinopterygians, there was a single dorsal fin, an arrangement retained in *Acipenser* (Figure 2-3) or *Lepisosteus* (Figure 2-4). This style is obscured in *Amia* (Figure 2-4) where the dorsal extends much of the length of the body, and in *Polypterus* (Figure 2-5) where many **finlets** replace the usual dorsal fin. These finlets occupy much the same space as the dorsal fin of *Amia,* but there is no gap between them and the caudal fin. Most actinopterygians have a simple anal fin, but sometimes it becomes continuous with the caudal or is subdivided into finlets.

In the choanate fishes (Figure 2-18), there were two dorsals, the more posterior one generally the larger. There was a single anal in the same position as that of the actinopterygian. *Latimeria* (Figure 2-6) has brought this pattern down to the present, differing in that the anterior dorsal is the larger. These fins in the rhipidistian or actinistian have large, plate-like basal structures, with or without radials, in lobe-like extensions of the body resembling those of the lateral fins (Figure 6-41). The dipnoans retain the simplest relationship between basal, radial, and fin ray.

The Chondrichthyes (Figure 2-2) generally have two dorsals but the most primitive living genera (*Chlamydoselachus, Heptanchus, Hexanchus*) have only one. This exceptional condition may be due to secondary loss of one fin, or evidence of both patterns of dorsal fins in sharks. The known Devonian species of sharks (Figure 2-15) had two fins and this suggests that loss has occurred in these primitive living genera. The Holocephalans have two dorsals; the second is long and low in *Hydrolagus.* The skeletons of these fins are complex in the shark, resembling those of the lateral fins or being simply a jumble of closely packed cartilaginous elements. The anterior dorsal of *Hydrolagus* has a

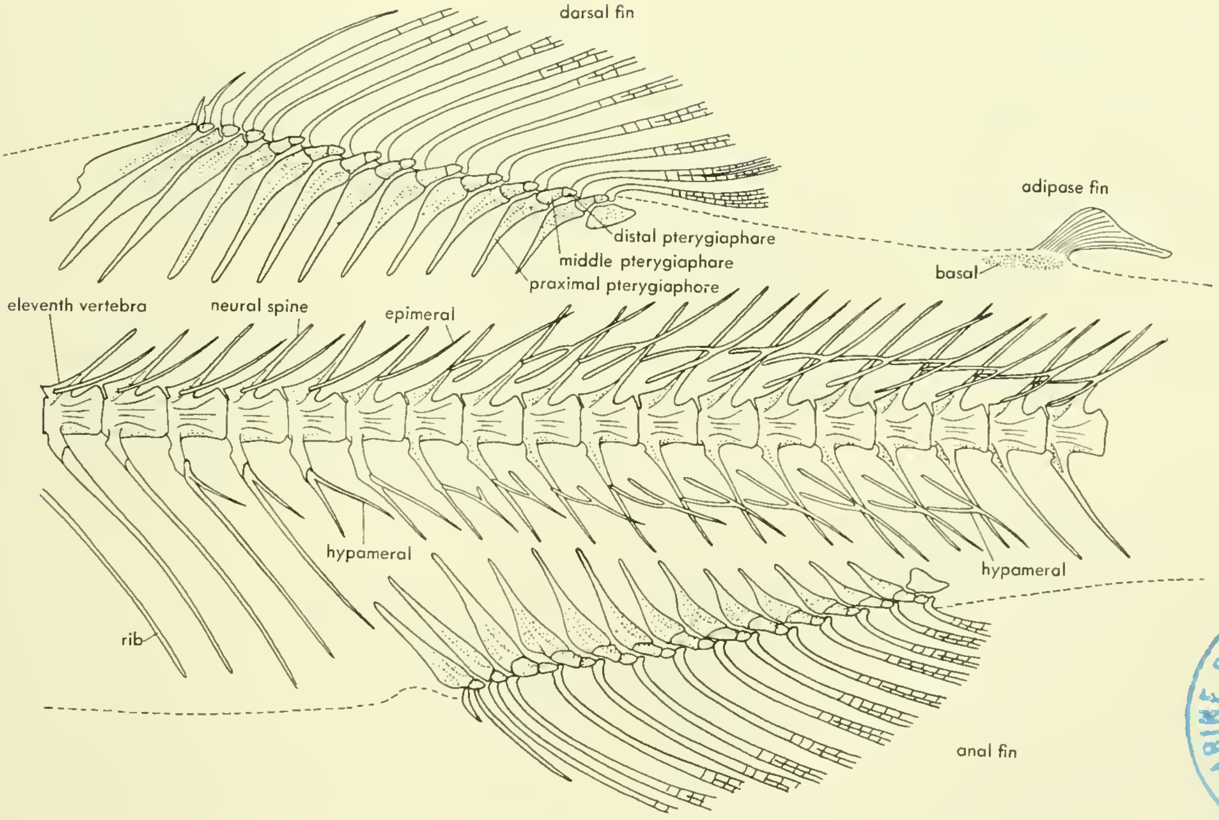


Figure 6-40. Middle region of vertebral column of a lantern fish, *Lampanyctus leucopsarus,* along with skeletons of the dorsal and anal fins.

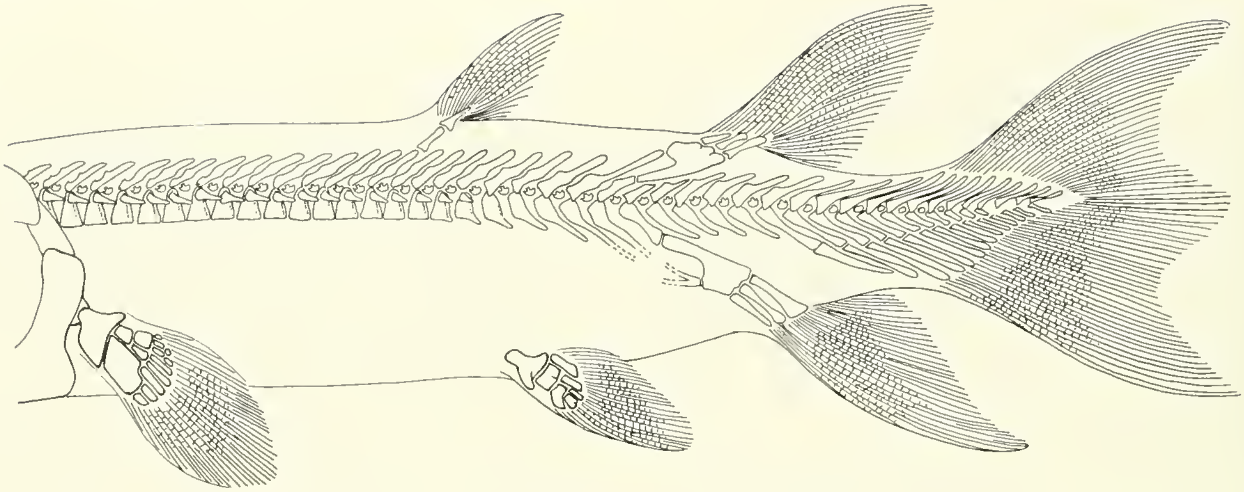


Figure 6-41. Vertebral column and fins of *Eusthenapteron.* (After Jarvik)

massive basal plate with a large anterior spine (Figure 6-39 C). The posterior dorsal has simple basals with no apparent radials. Having spines in front of the dorsal fins is typical of many sharks, living and fossil. In *Hydrolagus* only the anterior dorsal has a spine and this is very large (Figure 2-2).

In the living cyclostomes (Figure 2-1), median fins are not distinct; the caudal fin fold extends far forward suggesting that dorsal and anal fins are, in effect, only specialized parts of the tail fin itself. In some fossil agnaths (*Pteraspis*), a dorsal spine was present in the position of a doral fin (Figures 2-13, 5-28). The tail in the Heterostraci generally had dorsal and ventral rows of large scales. Some of the Osteostraci are assumed to have had two dorsal fins, while others had only a single posterior dorsal. These fins were preceded by a series of large scales or a spine. Although there were no anal fins, the ventral margin of the caudal fin is assumed to have been extended out to either side. Anaspids had a row of dorsal scales and an anal fin; *Endiolepis* is described as having a distinct dorsal as well as an anal fin. The anal fin of some anaspids was preceded by a spine.

Caudal fin

Because the caudal fin is an important contributor to forward thrust in swimming, it is well developed in most fishes. The design of this fin is related to the habits of its possessor.

In actinopterygian fishes, several tail shapes are observed and are described by special terms (Figure 6-42). Sometimes more than just the shape of the fin is involved in the use of these terms, which are built around the Greek word *kerkos* meaning tail. The nature of the end of the spinal column enters into this descriptive grouping. In the following account it is to be understood that **dorsal** (**epichordal**) and **ventral** (**hypochordal**) **fin folds,** above and below the tip of the spinal column, may be involved in the formation of the caudal fin. These folds must be differentiated from the posterodorsal and anteroventral lobes of the ventral fin fold which make up the apparent caudal fin (Figure 6-44). The term "lobe" is used variously in referring to the fleshy base of a fin and to a division of that base or of the ray-supported fin.

In most actinopterygians the tip of the spinal column is bent upward, and this upturned part is associated with a **urostyle** and **hypural plates** (Figure 6-43). There is no apparent dorsal fin fold; only the ventral fold is developed and this may have two equal lobes; this type is identified as **homocercal** (Greek *homos*—common, same, alike). In some teleosts the homocercal form has been retained, but the terminal upturned portion of the spine has been largely or completely done away with (cod, tuna). Another type has the upturned tip of the spinal column elongated and straightened out. The ray-supported fin is a marginal extension above and below this elongated tip. Such a tail, occurring in some deep sea fishes, is identified as the **isocercal** type (Greek *isos*—equal, similar, in this case referring to the dorsal and ventral fin folds). Reduction of the terminal part of the spine is sometimes accompanied by reduction of the fin itself to a vestige without equal lobes. Such a fin on a rounded caudal lobe or peduncle, in which the axial skeleton is truncated and without hypurals, is identified as the **gephyrocercal** type (Greek *gephyra*—a bridge or intermediate).

In the primitive actinopterygian the tail is strongly **heterocercal** (Greek *heteros*—other, different), as in *Acipenser* or *Polyodon* (Figure 6-44). The dorsal fin fold is lacking or represented by **fulcra** (spines). The ventral fin fold has a longer posterodorsal than anteroventral lobe. *Polypterus* has the tip of the spine slightly upturned, with a small urostyle but without distinct hypurals and without an upturned fleshy lobe; this can be described as an **abbreviated homocercal** tail. *Amia* and *Lepisosteus* have retained the upturned fleshy caudal lobe but have developed only the anteroventral lobe

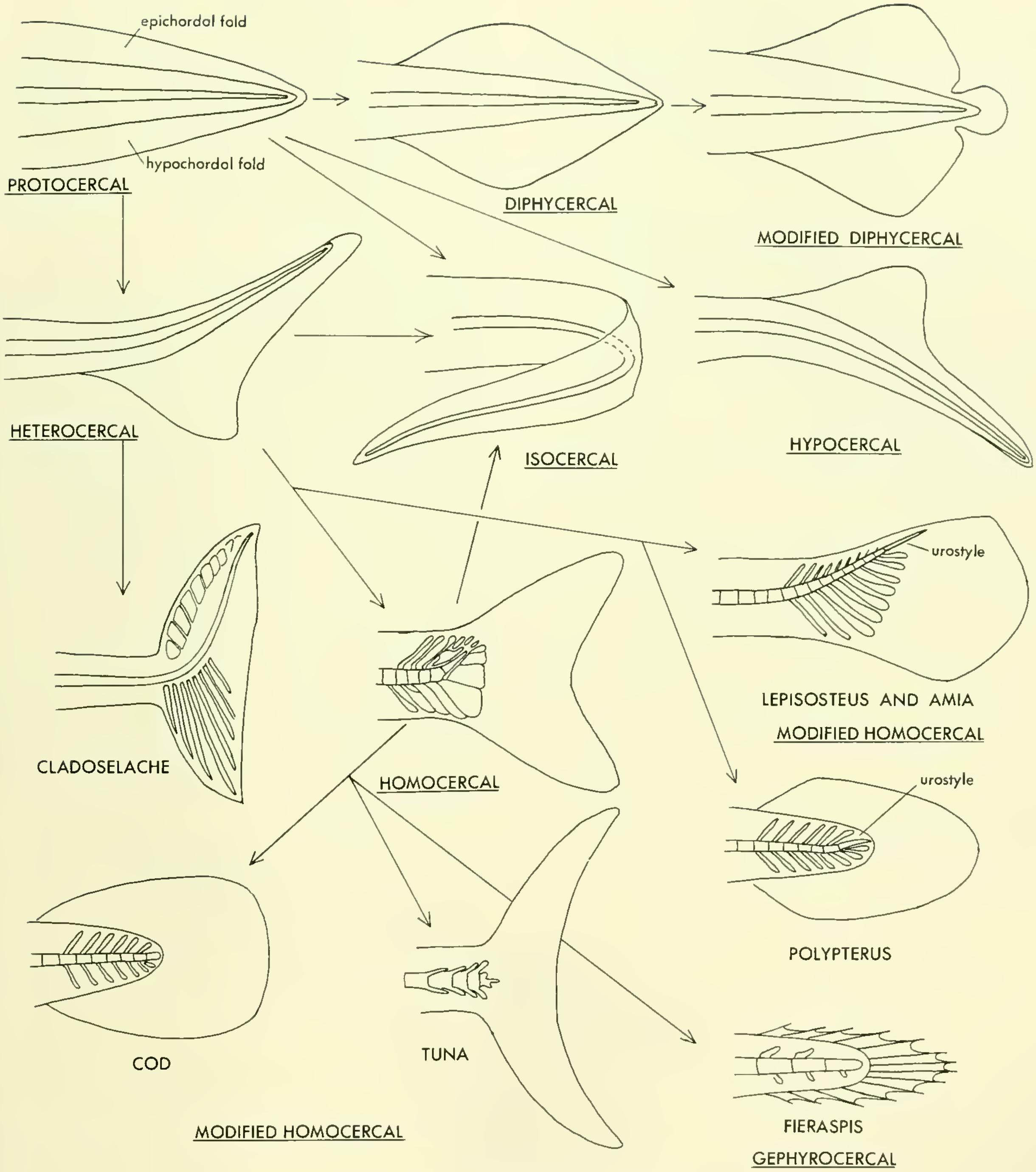


Figure 6-42. Evolution of tail fins in fishes.

of the originally heterocercal tail; this is also an abbreviated homocercal type.

In the dipnoans the tail ranges from that of the living lungfishes, a **protocercal** type (*protos*—first, primary) in which the ray-supported part of the fin is limited to the margins, back in time to the heterocercal tail of *Dipterus* or the protocercal tail of *Phaneropleuron,* which has a separate anal, or *Uronemus.* Among crossopterygians there are those which are **diphycercal** (*diphyes*—double) or modified diphycercal (*Eusthenopteron*), but most are heterocercal. Actinistians are, as far as now known, modified diphycercal; that is, with the caudal fin divided into dorsal, ventral, and terminal lobes. It is likely that some earlier actinistians (than the Upper Devonian *Diplocercides*) had a **protoheterocercal** tail, that is, one with a reduced but evident epichordal fold.

The primitive tail form is assumed to have been protocercal, the caudal fin continuous with the dorsal and anal fins. A protoheterocercal type then developed in which the dorsal and anal fins were separate, and from his came the heterocercal and diphycercal types. The embryological development of the caudal fin suggests this same phylogeny. Most of the early fishes were heterocercal. From this, by reduction of the upturned caudal fleshy lobe, came the homocercal type as well as some of the isocercal types and other modifications. The homocercal type in its turn has been converted to isocercal, abbreviated homocercal, or gephyrocercal.

These same tail types are observed outside the osteichthian array. Among the chondrichthians, the tail is usually heterocercal, occasionally isocercal, as in *Chimaera* or *Chlamydoselachus*. The fins of the sharks, and shark-like fishes, appear to be comparable to those of the osteichthian fishes, differing mainly in the type of supporting rays (see Chapter 8).

The living agnaths are protocercal in appearance but without ray-supported fins. It has been suggested that the early larvae of the lamprey have a slightly **hypocercal** or down turned tip to the tail (*hypos*—under, beneath, less than). The continuous posterior dorsal and caudal fin of *Petromyzon* has been likened to the caudal fin of the anaspid straightened out. Among fossil agnaths the osteostracans were heterocercal, while the anaspids were hypocercal. The heterostracans were originally protocercal, while more advanced types were hypocercal.

This wide variation of form seen in agnaths has been related to habit. The heterocercal tail tends to elevate the head, while the hypocercal form does just the opposite. Feeding off the bottom is aided by a hypocercal tail, while mid-water swimming of a heavily armored type is aided by the heterocercal type.

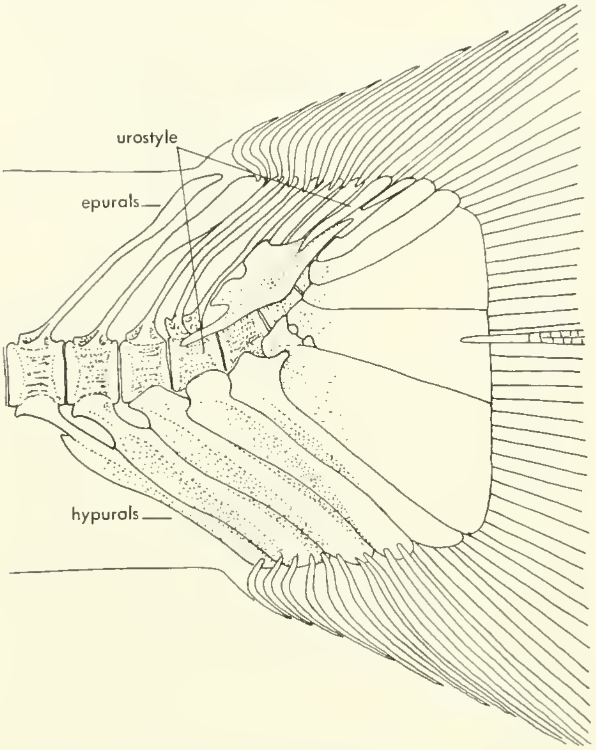


Figure 6-43. Details of structure of the homocercal tail of a salmon (Blue-backed Salmon).

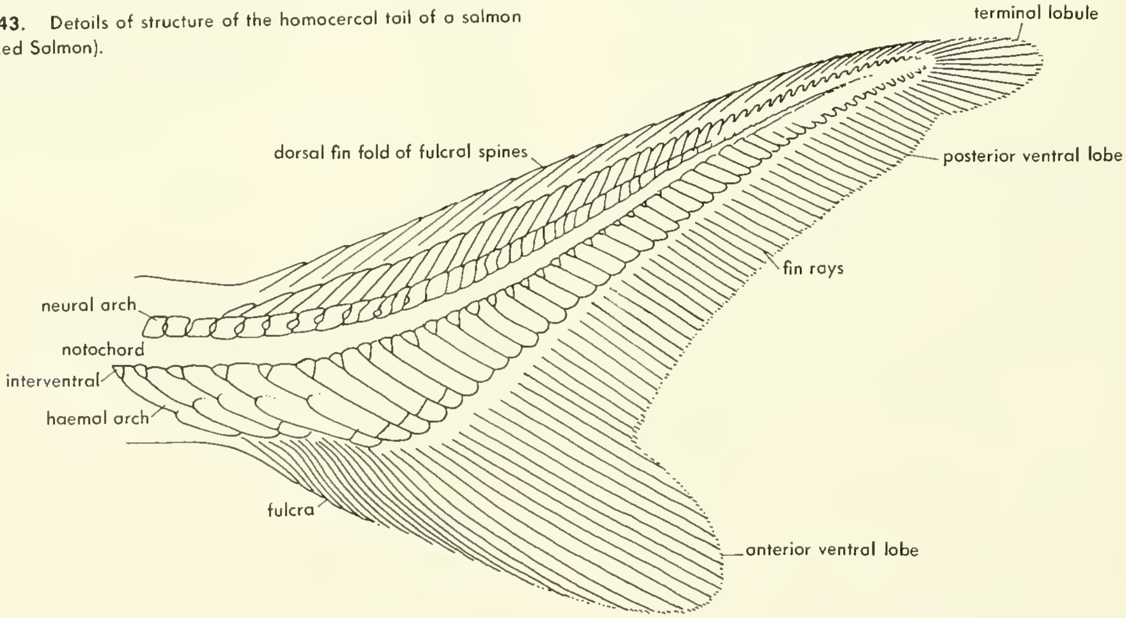


Figure 6-44. Details of structure of the heterocercal tail of a sturgeon (*Acipenser fulvescens*).

Agnath medial fins appear to be at best only parallelisms to those of other fishes. Fin rays as such are never developed.

BILATERAL APPENDAGES

Most vertebrates have two pairs of appendages, a pectoral and a pelvic pair. These appendages and the girdles which support them can now be described following the same sequence set up in the earlier chapters.

Mammal

Pectoral appendage The girdle of the pectoral limb consists of the **scapula,** its **coracoid process,** and the **clavicle** (Figure 6-45). In the cat the coracoid process is small, but that of the opossum is conspicuous and shaped somewhat like a crow's beak, from which it gets its name. The coracoid process of the opossum arises from a separate ossification center which remains distinct even in the adult. The monotreme (Figures 6-48, 6-72) has these three parts but they are more strongly developed, and in addition it has a **precoracoid** and **interclavicle.** An interclavicle may be indicated in some placentals (rabbit Figure 6-72). Of these bones the clavicle and interclavicle are dermal.

The limb consists of a basal element, the **humerus,** which articulates in the **glenoid fossa** formed by the scapula and coracoid. Distally this basal element articulates with the **radius** and **ulna;** the latter is extended past the joint as the **olecranon.** Distal to these forearm elements are the **carpals,** of which there are usually eight; occasionally a **centrale** occurs. In man (Figure 6-46) these carpals are given names somewhat different from those of comparative anatomy. These names are listed in Table 6-2.

Beyond the carpals are the **metacarpals** and the **phalanges.** Each **digit** has several **phalanges** from which the formula 2–3–3–3–3, starting with the number in the first digit (the thumb), can be derived. This formula is common to man, the cat, the opossum, and the monotreme—if one counts the claw bearing element of these animals as one of the phalanges.

The limb and its make-up of bones varies according to its use. The extremes are the flipper of the whale and the forelimb of the horse. In the whale the number of digits is usually reduced and the middle digits may have many phalanges. In this type of limb the basal element (humerus) and the forearm are shortened. In the horse the middle (third) digit and its metacarpal are much elongated, the second and third metacarpals are vestigal, while the first and fifth are lost. Among marsupials reduction in the number of digits also is observed among kangaroos.

Several features of interest are observed in this limb. Most of the bones have **epiphyses.** The carpals lack these and there are no epiphyses on the proximal ends of metacarpals II to V. This situation is matched in the opossum with the difference that the distal epiphyses of the radius and ulna remain distinct in the grown animal, whereas those of the cat or man are indistinguishably fused into the ends of these bones.

In man there is a small **sesamoid bone** (type of bone formed in a ligament or tendon) below the joint between the metacarpal and proximal phalanx of the thumb. At this joint of each of the five digits of the opossum, there is a pair of sesamoids. The opossum also has a small **prepollex ossicle** on the inner margin of the carpus at the radius-radiale joint. In the make-up of the carpus, there is only slight variation: the monotreme differs from the opossum or cat in lacking the intermedium.

Pelvic appendage The girdle of the pelvic appendage in the human or cat consists of three elements which fuse to form the **innominate bones** of either side. These three components are the (dorsal) **ilium,** the (ventroposterior) **ischium,**

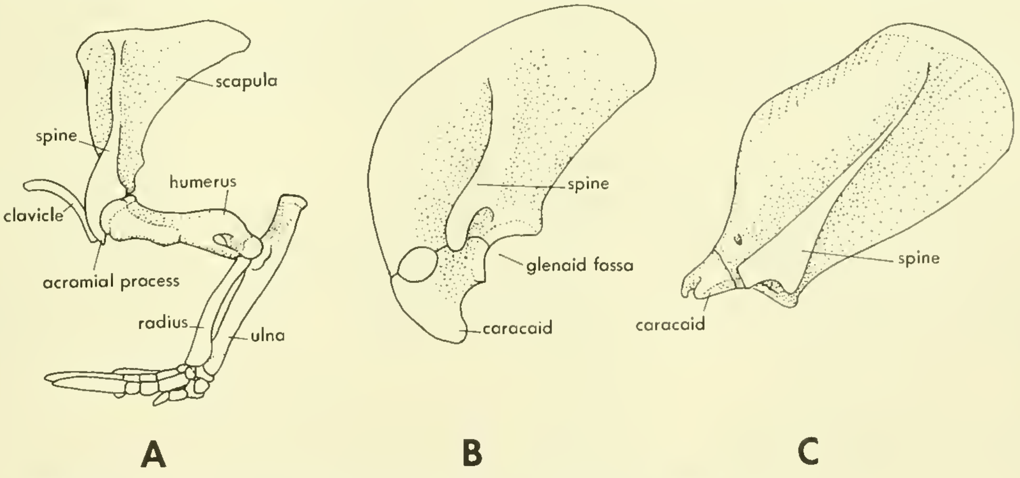


Figure 6-45. Pectoral girdle and limb of mammal. A, forelimb of Armadillo; B, scapula and coracoid of sloth; C, scapula and coracoid of opossum.

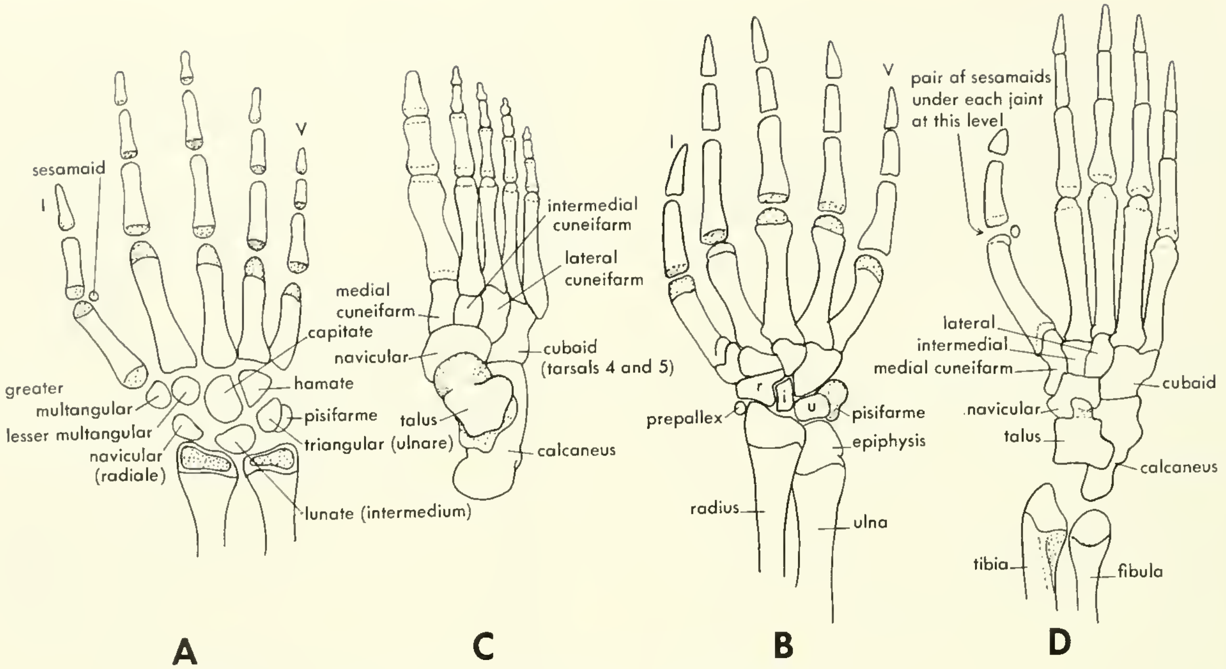


Figure 6-46. Manus, A and B, and pes, C and D, of man and the opossum.

and the (ventroanterior) **pubis** (Figure 6-47). Where these elements come together, there is a deep socket, the **acetabulum,** into which fits the **head** of the basal limb bone, the **femur.** The pubis and ischium are partly separated by a large round **obturator foramen.** The form of the pelvic girdle of the cat and the opossum is very similar except that in the opossum the suture lines between the elements are evident. In addition, there is a bone, the **marsupial bone,** which extends forward from the anterior margin of the pubis. This bone appears to support the body wall and the marsupium, the pouch in which the young are suckled.

In the monotreme the pelvis is similar to that of the marsupial. Presence of the marsupial bone in these two groups suggests its presence in their common ancestor, although such a bone is not known in the therapsids. It therefore appears to be a neomorph, and perhaps is an independently acquired parallelism in the two groups—a slight marsupial fold is observed in the female Echidna.

The pelvic limb, like the pectoral, has basal **stylopodial,** middle **zeugopodial,** and distal **autopodial** segments. The basal element in the thigh (stylopodium) is the femur, while the tibia and fibula form the middle segment or shank, the zeugopodium. The autopodium is subdivisible into a basal series of tarsals, the **basopodium,** a series of metatarsals in the **metopodium,** and the digits which form the **acropodium.** The names applied to the various tarsals are indicated in Table 6-3.

The pelvic limb is remarkably constant in its elements. The foot of the opossum or monotreme is much like that of man, and there is also close agreement in their **epiphyses.** Again, as in the forelimb, the second to fifth metatarsals, like the tarsals, lack epiphyses. The epiphyses of the distal

TABLE 6-2 SYNONYMY OF NAMES APPLIED TO THE BONES OF THE WRIST REGION, THE CARPALS, OF TETRAPODS

Man (N. A.)	Other Texts	Used in This Description
scaphoideum	naviculare manus	radiale
lunatum	—	intermedium
triquetrum	triangular	ulnare
pisiforme	—	pisiforme
(centrale)	—	centrale
trapezium	greater multangular	carpale I
trapezoideum	lesser multangular	carpale II
capitate	—	carpale III
hamate	—	carpales IV–V

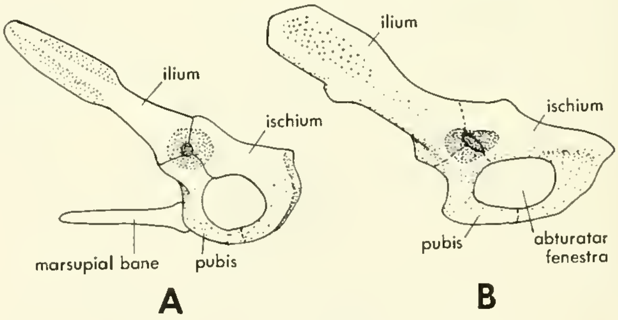


Figure 6-47. Pelvic girdles of opossum A, and cat, B.

end of the tibia and tarsus of the opossum remain distinct, as do those of the other long bones of the limb.

The function of the **fibulare** is of interest; it extends down and back to form the heel. In the anterior limb, the **pisiforme** has the same function. The fibulare of the mammal is peculiar in that it does not articulate with the fibula. The **astragalus** is apparently a compound bone as is observed in the primitive reptile. This will be discussed later.

TABLE 6-3 SYNONYMY OF NAMES APPLIED TO THE BONES OF THE ANKLE REGION, THE TARSALS, OF TETRAPODS

Man (N.A.)	Other Texts	Used in This Description of Mammal	Used in This Description of Reptile and Amphibian
talus	astragalus	astragalus	tibiale intermedium proximal centrale
calcaneus	fibulare	fibulare	fibulare
naviculare	centrale	centrale	centrales
medial cuneiform	—	tarsale I	tarsale I
intermediate cuneiform	—	tarsale II	tarsale II
lateral cuneiform	—	tarsale III	tarsale III
cuboid	—	tarsale IV–V	tarsale IV–V

In comparing the anterior and posterior limbs we find that they are very similar in the units composing them. This similarity represents a kind of serial homology which must be entirely or in part functionally determined.

Reptile and bird

Pectoral appendage In Sphenodon or the lizard, the girdle consists of three dermal elements: the **clavicles** of either side, jointed with a median **interclavicle** (Figure 6-48). The chondral elements of either side include a dorsal **scapula** fused with a ventromedial **procoracoid**. The use of procoracoid here will be explained when fossil reptiles are examined. The scapula generally has a process (the acromion process of the mammal spine) that extends out to the

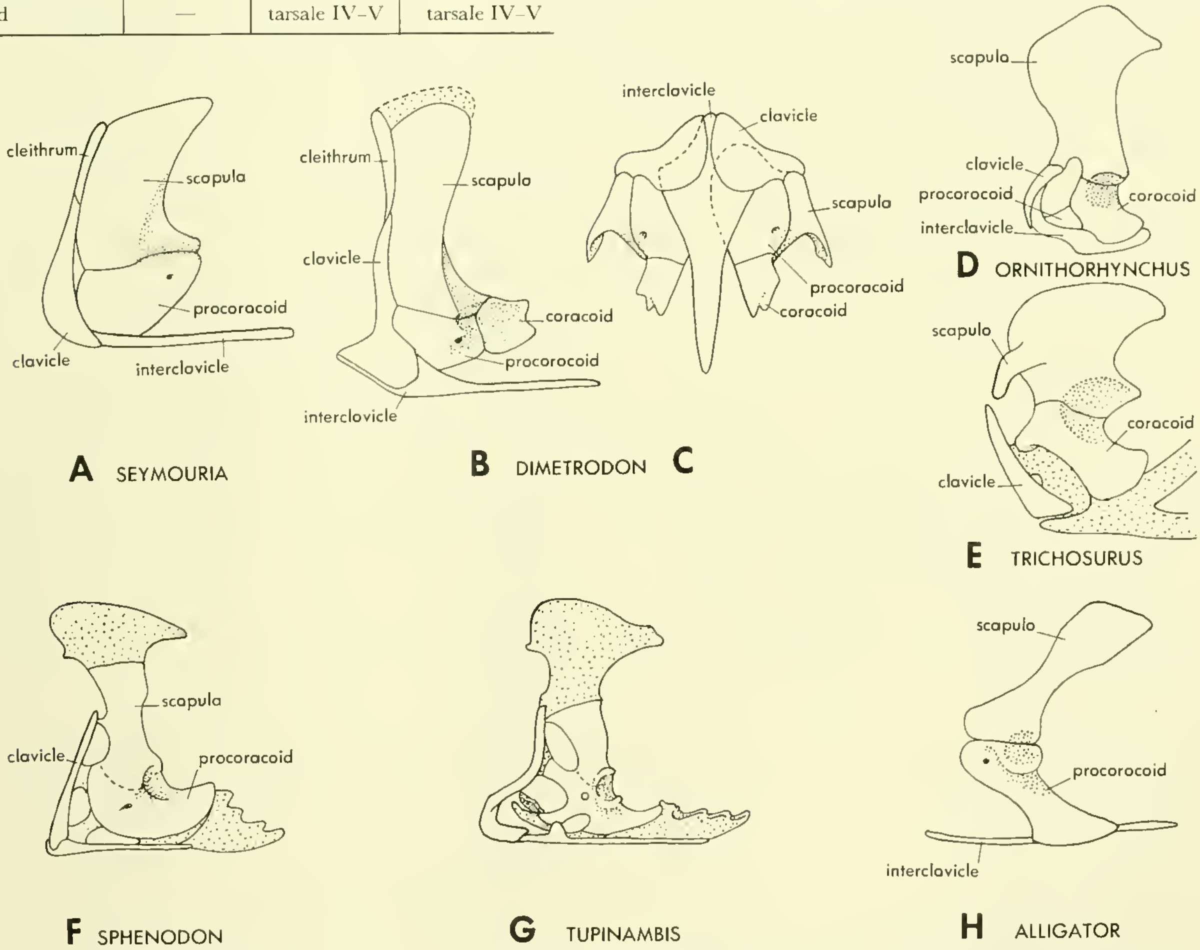
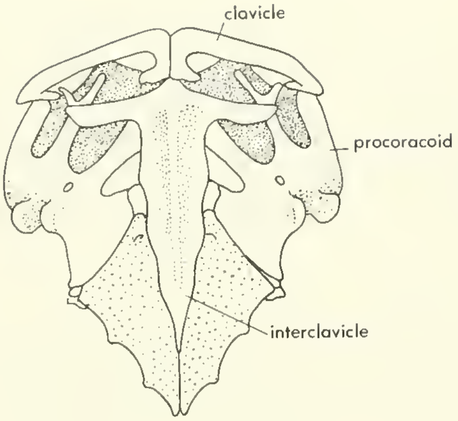
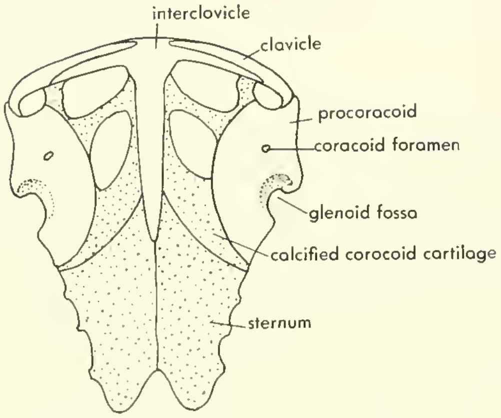


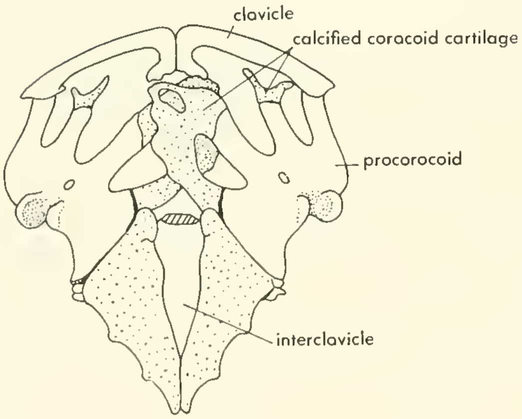
Figure 6-48. Pectoral girdles of reptiles and mammals as seen in lateral and ventral views (C). A, *Seymouria;* B and C, *Dimetrodon;* D, *Ornithorhynchus;* E, *Trichosurus,* a shrew; F, Sphenodon; G, *Tupinambis;* H, *Alligator.* (A, B, C after Romer, 1956; D; after Vialleton; E, after Broom)



A TUPINAMBIS



B SPHENODON



C IGUANA

Figure 6-49. Ventral views of pectorol girdles of *Tubinambis*, A, *Sphenodon*, B, and *Iguana*, C, Part of interclavicle of *Iguana* removed to show cartilaginous extensions of the procoracoid.

clavicle. Above the scapula there is a cartilaginous **suprascapula,** which may bear the **clavicular process.**

The cartilage in which the scapula and procoracoid ossify extends well beyond these bones: dorsally, anteriorly, and ventromedially. Anterior to the procoracoid, the cartilage is fenetrated; the number, size, and shape of the openings is variable. Ventromedially the cartilages overlap, the left above the right or just the opposite. The amount of overlap is small in Sphenodon, considerably more in the lizard *Tupinambis* (Figure 6-49). The procoracoid ossifications, perforated by the **supracoracoid foramen,** approach the midline interclavicle but do not reach it.

The girdle of the alligator differs in lacking the dermal elements and in having simple outlines for the scapula and procoracoid. The latter articulates with the anterior end of the sternum (endochondral).

The bird, as a modified archosaur, is much like the alligator but retains the clavicle. The clavicles of either side are fused ventromedially to form the furcula. The interclavicle as a dermal element is lacking, but the keel of the sternum is perhaps a modified remnant of this bone. The scapula is long and blade-like, while the procoracoid is large and ventromedially expanded where it articulates with the sternum. The procoracoid may be notched or perforated by the supracoracoid foramen. The ventromedial angles of these bilateral bones may overlap at the midline.

Among fossil reptiles there are two kinds of pectoral girdles (Figure 6-48). The two-element type, lacking a true coracoid, is found in the intermediate amphibian-reptile, *Seymouria;* the three-element type, with both procoracoid and coracoid along with the scapula, in the pelycosaurs (*Dimetrodon*) and some other early reptiles such as the captorhinids. The presence of a single ossification in the coracoid region of primitive amphibians, and perhaps some of the earliest reptiles (*Petrolacosaurus*), may have been due to fusion of coracoid and procoracoid. Living amphibians do not help with this question since the salamander has only a "scapular" center, while the frog has only scapular and procoracoid centers, as do some of the actinopterygian fishes.

The pelycosaur (three-element) type of pectoral girdle can be followed through the therapsid (mammal-like) reptiles to the mammals, whereas most of the reptiles, including all of the living kinds, and birds, are found to stem from the two-element type. This difference between two lines of early reptiles agrees with what has already been observed in the head skeleton and is made more meaningful by the observed intermingling of these types in the earliest known reptiles.

The pectoral limb of the reptile is much like that of the mammal but differs in several respects (Figure 6-50). The lizard has one or two centrales in the middle of the carpal area, and there is a sesamoid plate in the tissues below the carpals. A vestigial intermedium is observed in *Tupinambis.* In Sphenodon there are two centrales and an intermedium.

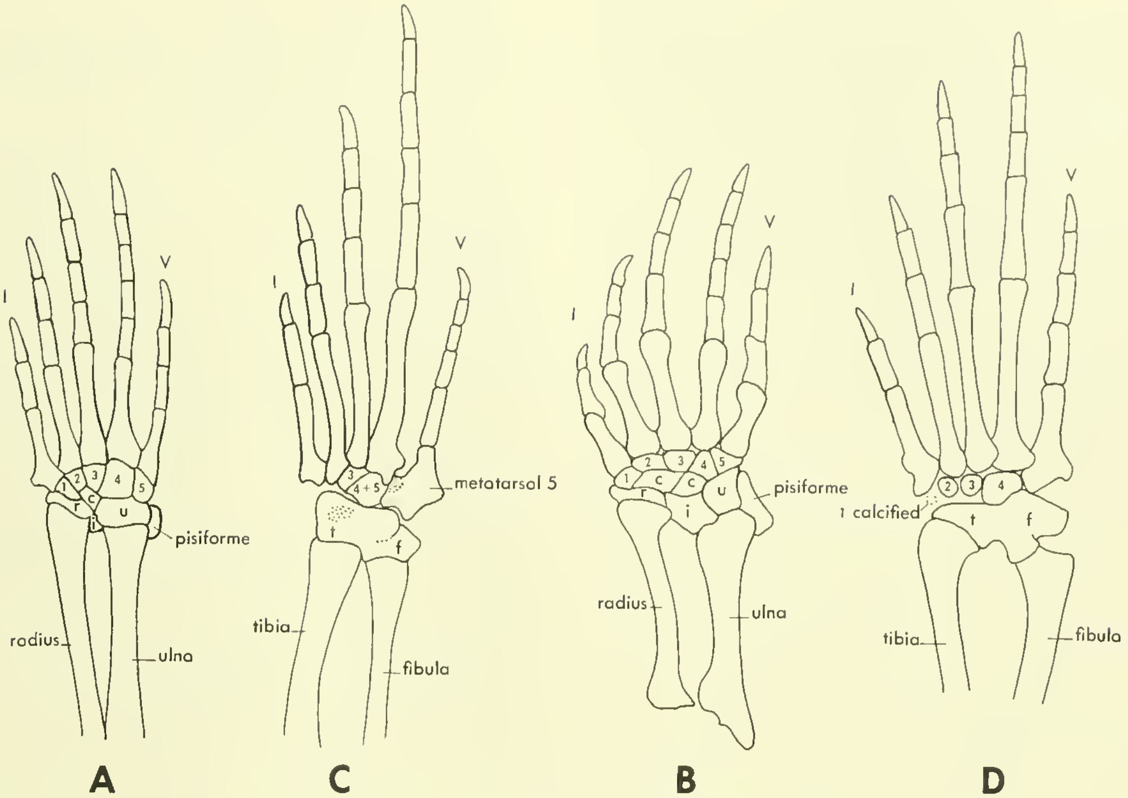


Figure 6-50. Manus and pes of *Tupinambis*, A and B, and Sphenodon, C and D.

The structure of the carpus in the early reptiles is not clearly revealed, but a captorhinid and the pelycosaurs (Figure 6-51) are quite like Sphenodon. *Seymouria* appears to have had at least one centrale. The number of digits was five in these reptiles, and the phalangeal formula was 2–3–4–5–3.

Among later reptiles, including the living types, a reduction in the number of carpals or digits has occurred. The alligator lacks an intermedium and has only three distal elements. Carpals I and II tend to fuse, and carpals III and IV are joined from the beginning of ossification. The pisiforme is much reduced. The ichthyosaurs had paddles or flippers like the whale and in these the number of phalanges is even greater than in the mammal—all five digits are involved in this polyphalangy.

An extreme of the reptile type is observed in the bird, where the carpus includes only a radiale and ulnare and the digits are reduced to three. It has generally been assumed that the remaining digits were one, two, and three—a fourth vestigal digit was also known. Several embryological studies suggest that in fact the well-developed digits are two, three, and four, with five in a vestigial state.

Pelvic appendage The pelvic girdle of the reptile as observed in *Sphenodon* or *Tupinambis* has three elements nearly

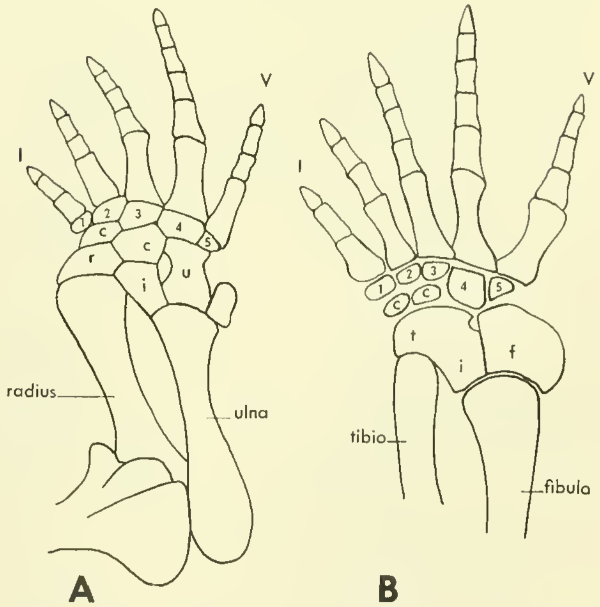


Figure 6-51. Manus and pes of a pelycosaur, *Ophiacodon*. (After Romer, 1955, 1956).

fused or quite fused in the region of the **acetabulum** (Figure 6-52). There is a large **obturator fenestra,** but the ends of the ischium and pubis do not join to close this gap. The **pubis** is pierced near the acetabulum by an **obturator foramen.** The **ilium** is blade-like, nearly vertical in *Sphenodon,* sloping down and forward in *Tupinambis.*

In the primitive reptile or amphibian, the pubis and **ischium** were broad plates, jointed to one another across the ventral midline; the ilium was a dorsally directed plate of variable shape. The pubis was pierced by an obturator foramen.

In the pelycosaur line (*Ophiacodon* and *Dimetrodon*), the obturator fenestra lies near the acetabulum, the bones meeting ventromedial to this fenestra. In the bulk of the reptiles, the obturator fenestra appears to have formed by a gradual separation of pubis and ischium, first near the midline, then with progressive increase in size until the fenestra approached the acetabulum. The medioventral ends of the pubis and ischium may now secondarily approach each other. Since these types of obturator fenestrae appeared late in time, they serve to mark the two lines of reptiles.

Extremes of the reptile type are observed in the crocodilian and in the bird. The pelvis of the bird has an anteroposteriorly drawn-out ilium with the pubis and ischium directed posteroventrally. The obturator fenestra is a long, thin fissure between these latter bones; the anterodorsal end of the fenestra serves as the obturator foramen. In the primitive bird the ischium and ilium are not connected posteriorly, but in more advanced types this has been achieved.

The pubis of the alligator is not perforated by an obturator foramen, and it resembles the marsupial bone of the monotreme or marsupial, perhaps having much the same function as that bone. It does not participate in the formation of the acetabulum, whereas that of the bird does.

The pelvic limb parallels the pectoral limb, but in the lizard or Sphenodon it shows even greater reduction in the number of tarsals. The centrales are missing as is the first tarsal in Sphenodon and the first and second tarsals in *Tupinambis* or *Iguana.* In the lizard or Sphenodon, tarsal IV is much enlarged and V is missing. The fifth metatarsal is peculiar in that it appears to be fused with its distal tarsal or has extended into the position of that tarsal. This peculiarity is generally typical of living reptiles and was used by Goodrich to identify the true reptiles as opposed to the pelycosaur-mammal line. In the Eosuchia a fifth distal tarsal may be present (*Youngina*) or absent (*Tangasaurus*) and the fifth metatarsal is not hooked. In the pelycosaurs a fifth metatarsal is present in the early forms, lost in the later ones, but the pattern of the mammal is already indicated. The fifth metatarsal is never hooked.

The phalangeal formula is usually the same as for the manus: 2-3-4-5-4. In the alligator, the fifth digit is reduced to its metatarsal; its formula is 2-3-4-5-0.

In the bird, the number of digits is reduced to four, the

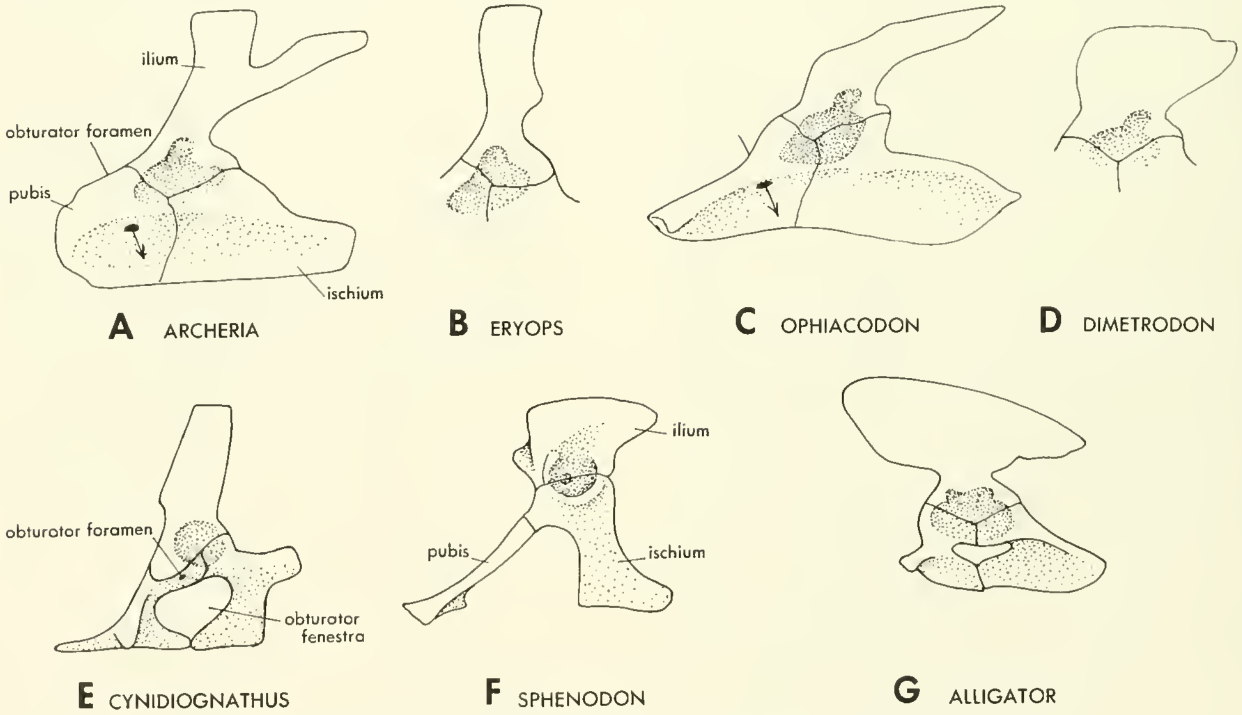


Figure 6-52. Pelvic girdles of amphibians and reptiles as seen in lateral view. A, *Archeria,* an anthracosaur; B, *Eryops;* C, D, the pelycosaurs, *Ophiacodon* and *Dimetrodon;* E, *Cynidiognathus,* a therapsid; F, *Sphenodon;* G, Alligator. (A, B, C, D, E after Romer, 1955)

first (the hallux) being directed backward. Three metacarpals and a number of tarsals are fused into a tarsometatarsus. The situation observed in the bird is approached in some of the bipedal dinosaurs.

Amphibia

Pectoral appendage The pectoral girdle of *Cryptobranchus* and *Necturus* is quite similar (Figure 6-53). It is largely cartilaginous with a distinct anterior process and overlapping **procoracoid plates.** There is a **scapular ossification** which reaches down to the **glenoid fossa** but not beyond it. In some salamanders, the scapula extends beyond the fossa to include the **supracoracoid foramen.** It does not extend much behind the glenoid fossa in any. There is a large **supracoracoid cartilage** above the scapula. There are no dermal elements involved.

The frog in contrast has a remnant of the **cleithrum,** which secondarily extends perichondrally over the outer surface of the suprascapular cartilage, and a **clavicle,** which is associated with a clavicular cartilage anterior to the large supracoracoid fenestra. The so-called **omosternum** probably represents a converted remnant of the **interclavicle,** which is now associated with a calcified cartilaginous mass.

The scapular ossification lies above and anterior to the glenoid fossa with the large suprascapula above it. The procoracoid ossification extends ventromedially from the glenoid fossa; it lies behind the supracoracoid fenestra. The procoracoid cartilages fuse at the midline in the Bullfrog in a **"firmisternal union."** In some anurans these cartilages overlap posteriorly and are joined only anteriorly. When the procoracoid cartilages overlap, the omosternum is entirely cartilaginous or, as an extreme, it is missing (*Ascaphus*). The sternum of the Bullfrog is ossified, while in those frogs, which have the procoracoids overlapped, it is cartilaginous. The evolutionary sequence is usually described as from **arciferal** (with the procoracoid cartilages overlapped) to firmisternal—actually the reverse seems to be indicated both within the frogs (more united, and ossified, in the Bullfrog than *Ascaphus*) and in terms of amphibians in general. In the early amphibians the procoracoid bones or the procoracoid areas of the scapulocoracoids were probably firmly connected to the broad interclavicle; with reduction of the interclavicle the procoracoids were extended by cartilages which tended to overlap.

In the anthracosaur *Pteroplax* (Watson, 1926), the most primitive amphibian known—primitiveness being based on the connection between the girdle and the skull as in the fish, the girdle has a series of dermal elements and a single scapulocoracoid ossification. This girdle contrasts strongly with that of *Branchiosaurus,* in which the clavicle and cleithrum are reduced to splints and only a scapular ossification, lying above the glenoid fossa, is known to occur.

Consideration of the pectoral girdle in amphibians indicates that there has been a continual reduction of the dermal components. The broad dorsal expansion of the cleithrum has been replaced by the cartilaginous supracoracoid. Reduction of the interclavicle resulted in loss of direct contact with the scapulocoracoid ossifications and was accompanied by the overlapping of the extensions of the procoracoid cartilages. It is also suggested that in the frogs, the interclavicle has been replaced by a cartilaginous omosternum, which in the Bullfrog is perichondrally ossified, on its ventral surface.

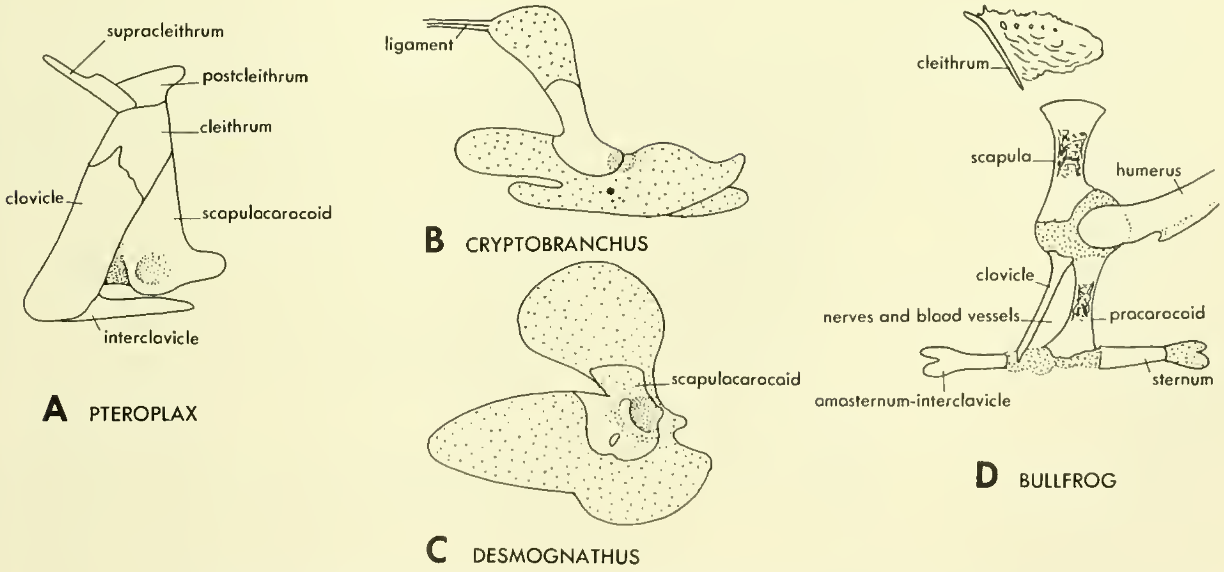


Figure 6-53. Pectoral girdles of amphibians as seen in lateral view. A, *Pteroplax*, an anthracosaur (after Watson, 1926); B, *Cryptobranchus*; C, *Desmognathus*; D, Bullfrog.

The scapulocoracoid ossification probably has always had scapular and procoracoid centers, although these sometimes become so closely associated (as indicated by *Ascaphus*) as to appear to be one. In the heavily ossified forms, such as *Pteroplax*, or in the early reptile *Petrolacosaurus*, these two centers are lost in the fused element of the adult. Young specimens would probably show these centers.

The occurrence of three bones in this girdle suggests the origin of a new center posterior to the glenoid fossa. The occurrence of three centers in several types of early reptiles suggests a parallel origin in the different groups. The two-center type has been carried down to the present in frogs, living reptiles, and birds, while the three-center type has come down through the synapsids to the mammals.

The pectoral limb of living salamanders is quite simple in its structure; this can be viewed as secondary simplification since it goes along with reduction in the number of digits. Reduction has gone slightly further in *Necturus* than *Cryptobranchus* with the loss of the fifth distal carpale (Figure 6-54). The digital formula of both is 0–2–2–3–2. The frog has the radius and ulna fused and the carpals highly modified. The salamander and frog agree in having only four digits, the first having been lost.

The presence of four digits (or less) in the forelimb extends far back in the history of these groups and into the earliest known amphibians: the branchiosaurs and microsaurs. *Eryops*, a large and presumably modified type, appears to have had only four digits in the manus (Figure 6-55). Holmgren (1949) suggested that the four-digit forelimb of the amphibian evolved independently from the archipterygium. It is generally assumed that the four-digit limb was derived by loss of the fifth digit.

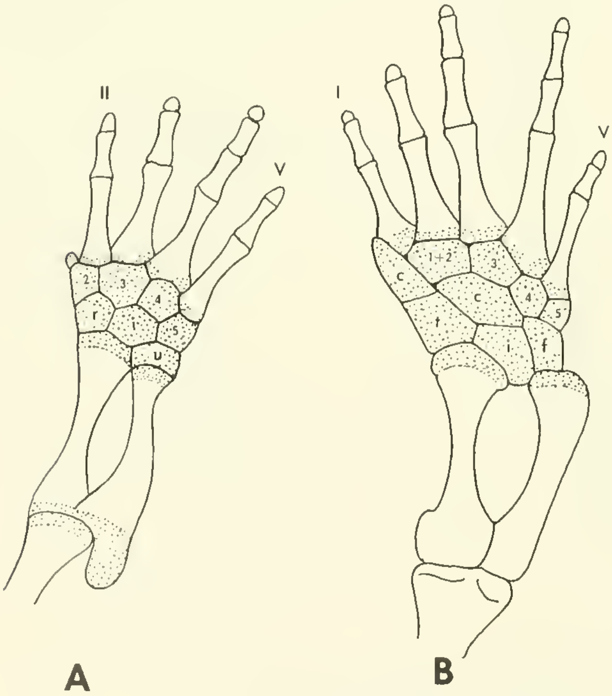


Figure 6-54. Manus, A, and pes, B, of *Cryptobranchus*.

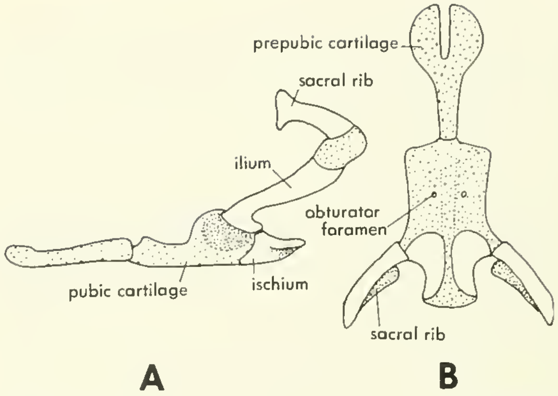


Figure 6-55. Pelvic girdle of *Cryptobranchus* as seen in lateral, A, and ventral, B, views.

The original number of digits was apparently five, with an additional **prepollex** extending down from the radiale (as in *Eryops*) and a **postminimus,** perhaps represented by the pisiforme. The basic five-digit plan is shown by *Seymouria* and the early reptiles.

Pelvic appendage The pelvic girdle of living amphibians consists of two ossifications and an extensive and forward extending cartilaginous plate; attached to this is a separate anterior process, the epipubis (Figure 6-55). Above the acetabulum is the ilium, while below and behind it is the ischium. A pubic ossification is lacking. In fossil forms, the pelvis includes a pubis, which in its form is similar to that of the primitive reptile. In the early amphibians the three units tend to be fused, and suture lines are obscured or lacking.

The pelvic limb of *Cryptobranchus* (Figure 6-54), and many salamanders, has been conservative in its structure; it has retained five digits. There are only four in *Necturus*. The carpals fan out from the end of the fibula in a way suggestive of the speculations relative to the origin of the ancestral limb from the archipterygium of the fish (Figure 6-61).

In fossil amphibians, five digits are known for the pes (foot) of the rhachitomous type *Trematops* (Figure 6-56). Again in *Trematops* we see the archipterygial pattern but note that there are several centrales rather than the single one of *Cryptobranchus*, also there is a distinct prepollex. The carpals and tarsals of some amphibians are ossified.

General observations Whereas the **manus** (hand) of the amphibian is modified as compared with that of the primitive reptile, the **pes** is less modified than that of the reptile. In the primitive captorhinid reptile (Figure 6-56), three elements coalesce—the intermedium, tibiale, and a proximal centrale—to form the astragalus. Although this appears to be the phylogenetic origin of the astragalus, in ontogeny it

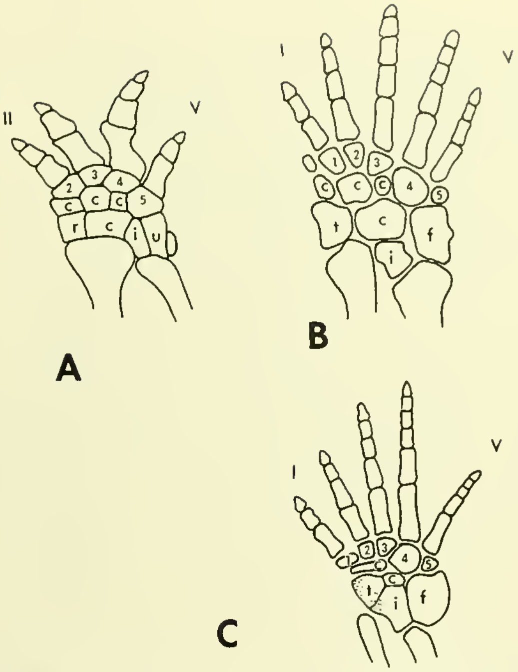


Figure 6-56. Manus of *Eryops*, A, and pes of *Trematops*, B, a rhachitomous amphibian; and *Captorhinus*, C, an early reptile.

ossifies from what appears to be the tibial center. This modification of the hind limb of the reptile—it is the front limb of the amphibian which is most changed—suggests a difference in limb use. The hind limb becomes the main source of power in the reptile line, leading to bipedalism in some.

Choanate fishes

Pectoral appendage The pectoral girdle of the crossopterygian fish consists of six dermal elements. From above down they are the **posttemporal,** the **supracleithrum,** the **postcleithrum** (or anocleithrum), the **cleithrum,** the **clavicle,** and a small medial **interclavicle** (Fig. 6-57). The first two elements bear the sensory canal connecting the lateral line of the body with the temporal canal of the head. The postcleithrum varies in its relationships from a part of the girdle arc to a more posterior element overlapping the cleithrum-supracleithral joint. The chondral part of the girdle is not well known but is assumed to have a dorsal scapular extension, an anteroventral and medial clavicular portion, and a tubercle for the articulation of the fin.

The actinistian agrees fairly well with this. In *Latimeria* (Figure 6-58) the supracleithrum and interclavicle are lacking and an **extracleithrum** has been added. The extracleithrum appears to be an element unique to this group. The most dorsal unit is perhaps the postcleithrum; however, its exact homology must remain in doubt. In *Latimeria* the fin support process of the **scapulocoracoid** is partly (perichondrally) ossified. This ossification can scarcely be equated with either the scapula or the procoracoid. In *Diplurus* this element has the relationship of a supracleithrum, but in *Latimeria* it could easily be the postcleithrum since it lies deep in the tissues and is not connected with the cranium. It may be that both elements were present and there has been variation in retention.

The dipnoan as represented by *Protopterus* (Figure 6-59) or *Neoceratodus* has a highly modified girdle that lacks the posttemporal, supracleithrum, and interclavicle. The postcleithrum is a bifurcated splint lying in the ligament joining the

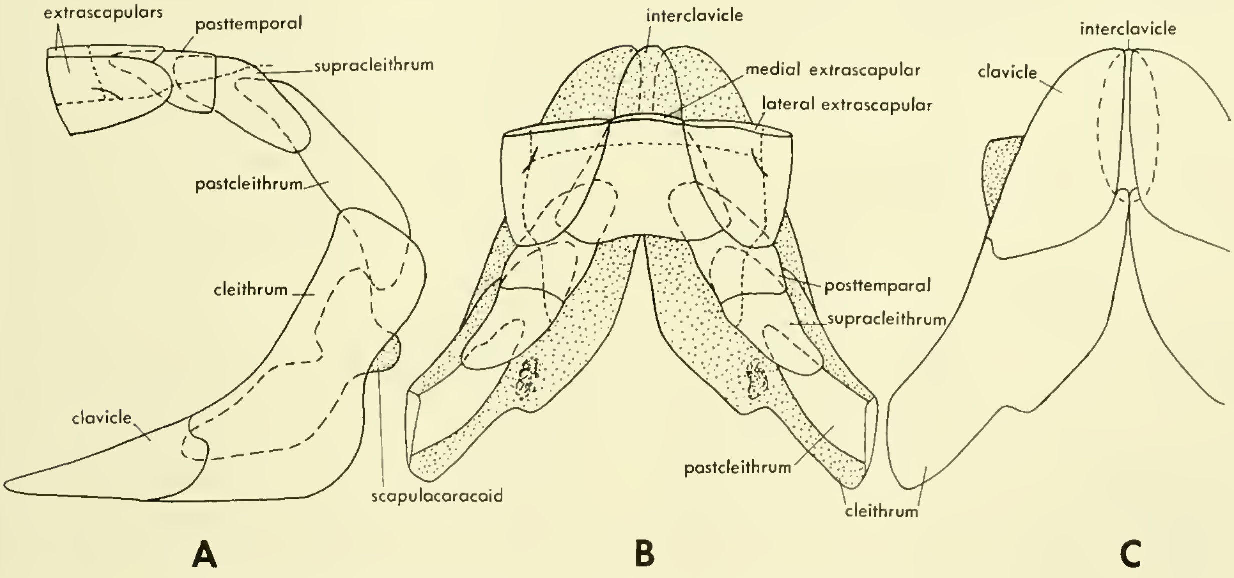


Figure 6-57. Pectoral girdle of *Eusthenopteron* as seen laterally, A, from above, B, and from below, C. (After Jarvik, 1944)

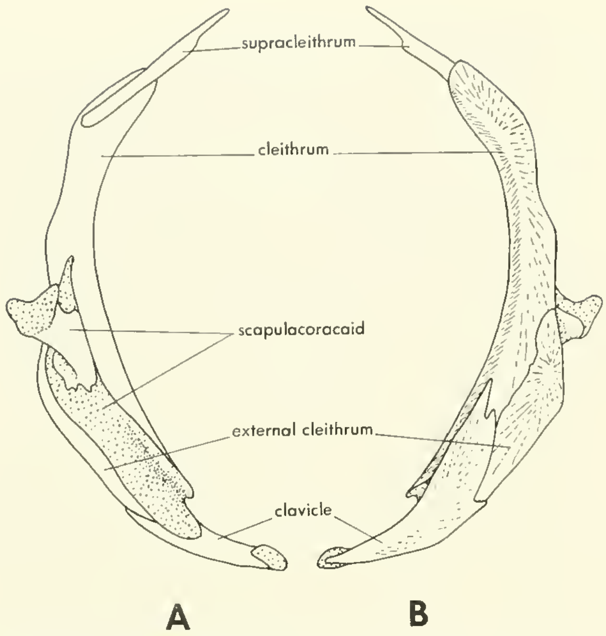


Figure 6-58. Pectoral girdle of *Latimeria*. A, lateral view; B, medial view of left half of girdle. (After Millot and Anthony, 1958)

girdle to the posterior margin of the cranium, lateral to the exoccipital bone. The cleithrum is much reduced, while the clavicle extends from near the dorsal end of the cleithrum to near the ventral midline. The cartilaginous scapulocoracoids are small and joined across the ventral midline of their clavicular processes.

Of particular interest is the fact that the scapulocoracoid articulates with and is partly supported by a massive **rib** attached to the occipital segment of the head. Articulation is through a cartilaginous process of that rib. Whereas this head rib is very large, the first two ribs following it are not ossified in *Protopterus;* the first trunk rib is that of the third segment behind the head. In *Neoceratodus* these first spinal ribs are present but smaller than the head rib.

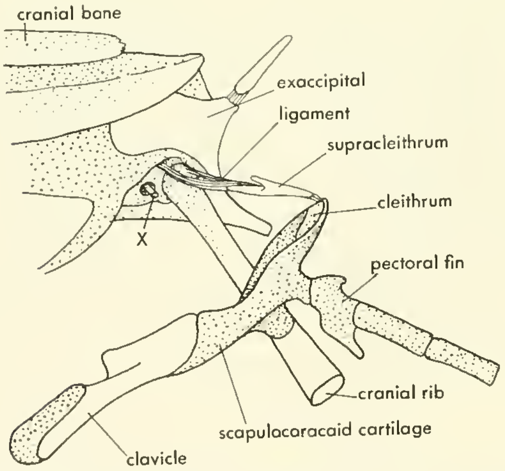


Figure 6-59. Pectoral girdle of a dipnoan, *Protopterus*. The ventroanterior end of the girdle has been pulled outward.

The choanate fishes all agree in having a fin with an extensive fleshy lobe. Possession of such a lobe is described by the term **Sarcopterygii** (from Greek *sarkos*—flesh; *pteryx* or *pterygos*—wing, fin, feather). The choanates are effectively identified by this term as well as by having internal nares. In view of the lack of agreement as to whether the dipnoans have internal nares, Sarcopterygii is perhaps a better term.

The crossopterygian fin (*krossoi* or *krossotos*—fringe or fringed) is generally assumed to be ancestral to the five-fingered (**pentadactyle**) limb of the tetrapod. The fins of rhipidistians are not well known; generally they are represented by that of *Sauripterus* or *Eusthenopteron.* The actinistian can be represented by *Latimeria,* while the dipnoan *Neoceratodus* has perhaps the closest approach to the ancestral type (thickest, shortest lobe) of that group.

The common feature of these fins is the fanned arrangement of parts from a single basal element (Figure 6-60). The skeleton of the fin of *Neoceratodus* appears to be an attenuation comparable in some ways to that observed in flippers of reptiles and mammals. The lack of a ray-supported fin in the dipnoan agrees with this conclusion.

In *Neoceratodus* we see a central axis for the fin with rays extending out on the preaxial and postaxial sides. This condition has been described as a biserial archipterygium. Gegenbaur assumed that the **archipterygium** (*archi*—first or primitive), as exemplified by *Neoceratodus,* was the primitive type. In contrast, the fin of the rhipidistian is almost a uniserial archipterygium; only reduced postaxial rays are present. The central axis of the rhipidistian fin is not so well defined as that of the lung fish. The latter is most likely specialized in the direction of a flipper rather than a fin.

Derivation of the tetrapod limb from a fish fin, or **ichthyopterygium,** is most easily achieved by starting with the fin of a rhipidistian. Several descriptions of the way in which this might have happened have been published (Figure 6-61). It does not seem worthwhile to speculate on how the archipterygium was converted to a **cheiropterygium** or **cheiridium** (*cheir*—hand; *idion*—diminutive suffix) since several possible paths could be followed in this conversion.

Pelvic appendage The pelvic limb and its girdle in choanates are variable just as was the pectoral (Figure 6-62). The girdle consists of bilateral elements with a dorsolateral projecting **iliac process,** a medial **ischial process,** and a forward **pubic process.** The girdle of the dipnoan is peculiar in that the two parts are fused at the midline. Thus there is a resemblance to the amphibian; this similarity, when taken along with the great reduction of the cleithrum and the lengthening of the clavicle in the pectoral girdle, gains some importance.

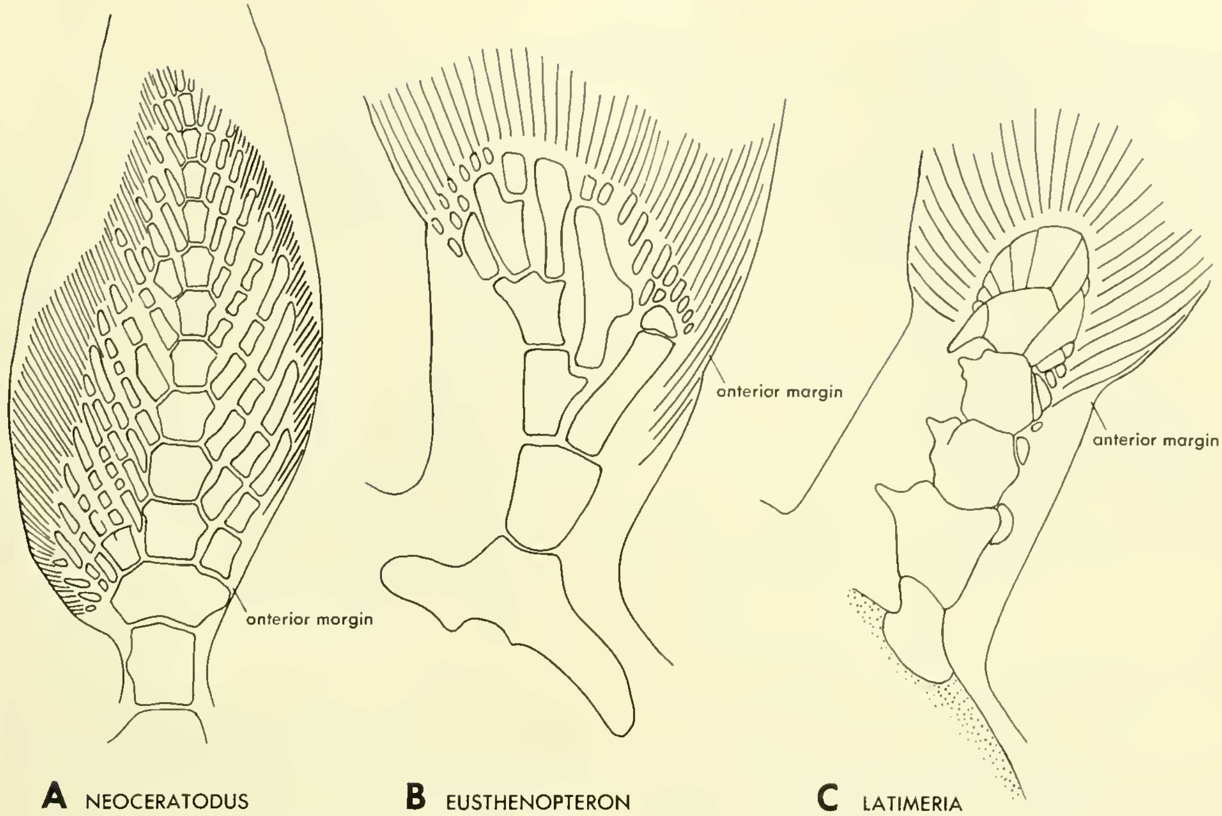


Figure 6-60. Pectoral fins of choanate fishes as seen in dorsal view. A, *Neoceratodus;* B, *Eusthenopteron;* C, *Latimeria.*

Actinopterygian fishes

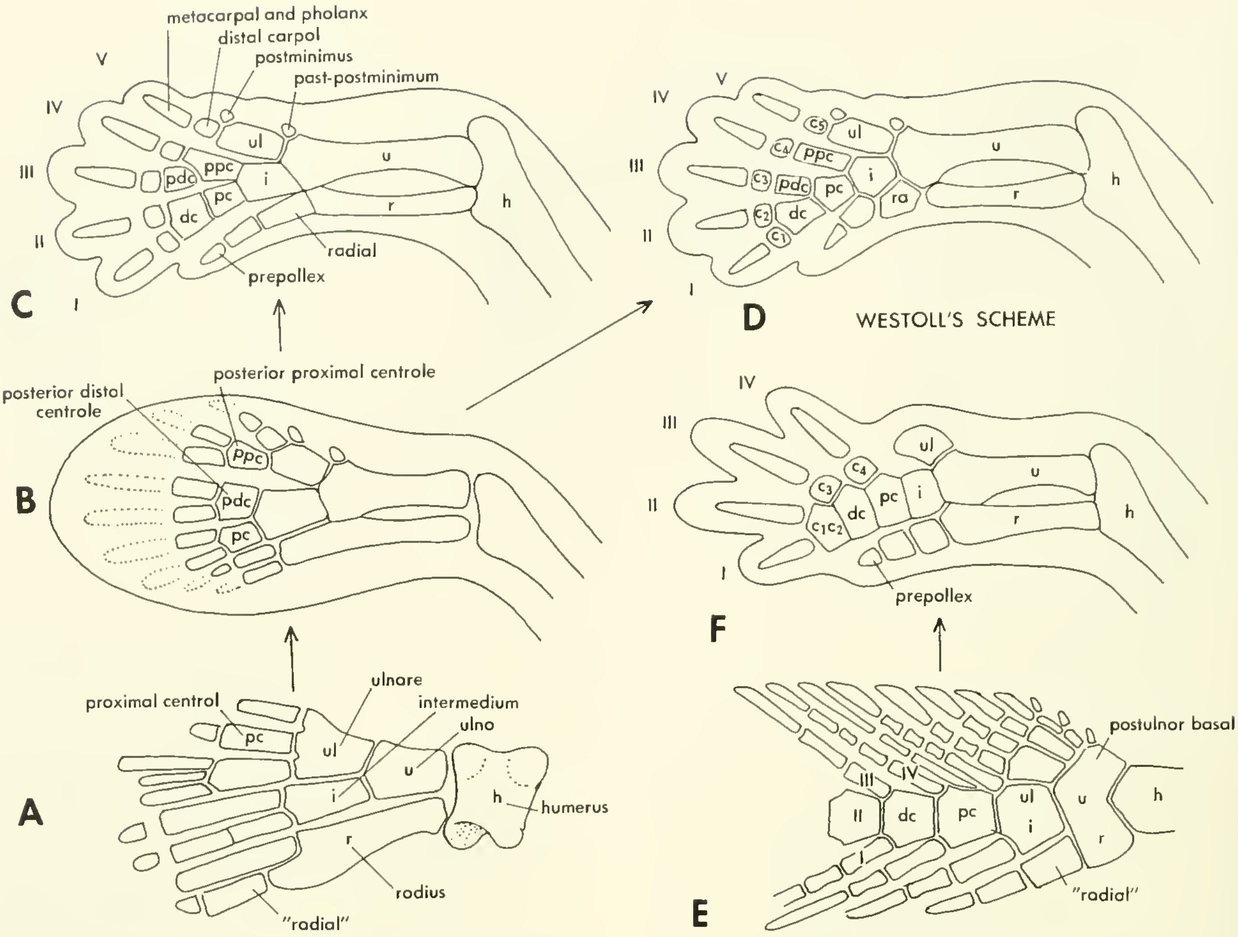
Pectoral appendage The pectoral girdle of the primitive members of this array is essentially like that of the crossopterygian except that an interclavicle is usually lacking (Figure 6-63). There is generally a **posttemporal,** a **supracleithum,** a **postcleithrum, cleithrum,** and **clavicle.** The clavicle is present in *Polypterus* and *Acipenser* but lacking in other living forms. An **interclavicle** is present in *Acipenser* (and *Scaphirhynchus* but not *Polyodon*), where it lies dorsal to the line between the clavicles (Figure 6-64). The clavicular process of the scapulocoracoid cartilages meet above it.

A postcleithrum is present in the primitive forms but lacking in the teleosts generally. In *Polypterus* or *Lepisosteus* the postcleithrum is associated with a line of scales along the posterior margin of the girdle. In the salmon a thin postcleithral scale may be present and below this a second large scale (as in *Polypterus*). Below this are one or two elongated **postpectorals** lying in the fold of skin between the basal lobe of the fin and the body (Figure 6-64). Two postpectorals are generally present in teleosts, one above the other. The postpectorals are new structures unique to the teleosts.

The **scapulocoracoid** is cartilaginous in *Amia* and fairly complex in form (Figure 6-64). That of *Acipenser* is similar but more massive and with a ventral process passing down inside the ventral fin musculature. Also, the ventral muscles which fan out the fin are separated by a cartilaginous pillar from those drawing the fin toward the body. There is thus an inner and outer ventral process. The salmon is like *Acipenser,* except that it has only the inner of these ventral processes; also it has three ossifications in the scapulocoracoid: a (dorsolateral) **scapula,** which supports the radials of the fin, a (ventroanterior) **coracoid,** and a (dorsomedial) **mesocoracoid.** The perch differs from the salmon in lacking the mesopterygoid cartilage and bone. *Polypterus* is like the perch in having only two ossifications but the coracoid lacks any ventral process.

The fins are supported by a number of **radials.** That of the anterior (dorsal) margin of the fin is the largest and generally cartilaginous; it resembles a **propterygium** (Figure 6-66). The number of radials varies. In *Amia* and *Acipenser* they are associated with a **metapterygium.**

The fin of *Polypterus* is peculiar in that both pro- and metapterygia are present. These are long rods separated by a cartilaginous **mesopterygium** in which there is an oval ossification. The radials lying distal to the mesopterygium are more numerous than in the other fishes. There are two series of radials, proximal and distal. This type of fin has a



HOLMGREN'S SCHEME FOR NON URODELE

HOLMGREN'S SCHEME FOR URODELE

Figure 6-61. The origin of the tetrapod pectoral limb (cheiropterygium) from the fin of a choanate fish (ichthyopterygium). A, bones of fin of *Sauripterus* or *Eusthenopteron;* B, hypothetical intermediate stage toward tetrapod; C, basic tetrapod pattern of elements (except for urodeles) as derived by Holmgren from intermediate stage; D, alternate to C as proposed by Westoll; E, *Neoceratodus* fin as possible ancestor to the Urodele type pattern, F, as proposed by Holmgren.

distinct fleshy basal lobe, not as large as that of a sarcopterygian but intermediate between that group and the actinopterygian. On the basis of its fin, *Polypterus* has been placed in a distinct group called the **Brachiopterygii** (*brachii*—upper part of arm, thus having arms).

Pelvic appendage The pelvic girdle of the teleost (Figure 6-65) consists of a pair of pelvic bones associated with a cartilaginous core which is T-shaped: the shaft extends forward and represents the **pubis,** the lateral part of the cross piece represents the **iliac process,** and the medial one the **ischial process.** There is a distinct resemblance to the girdle of the choanate, except that the iliac and ischiac processes are not apparent in the definitive bony structure.

The girdle of *Lepisosteus, Amia,* or *Polypterus* is very similar. Here the cross processes are maximally reduced. In *Acipenser* the base of the fin is attached along much of the length of the **pelvic cartilage.**

The pelvic fins are generally comparable to the pectoral. *Polypterus* is peculiar in that the pelvic fin has radials much like the pectoral fin of other fishes, or like the pelvic fin of *Acipenser.* This suggests that the pectoral fin of *Polypterus* is specialized. The reliance on the pectoral fins in much of the ordinary swimming of this fish supports this view.

Chondrichthyes

Pectoral appendage The pectoral appendage of the shark (Figure 6-66) is peculiar first for its lack of any dermal elements in the girdle and second for the size and development of the cartilaginous scapulocoracoid which supports the fin. The scapulocoracoid of *Squalus* has a small separate "supra-

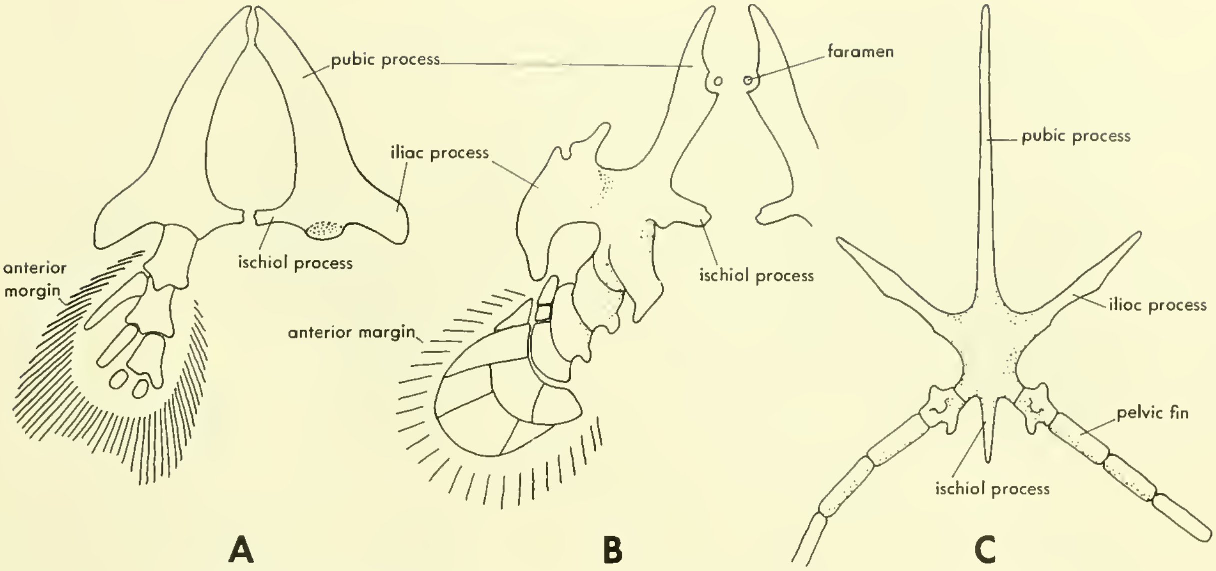


Figure 6-62. Pelvic girdles and fins of choanate fishes as seen in ventral view; A, *Eusthenopteron;* B, *Latimeria;* C, *Protopterus.*

scapula" extending medially from its dorsal end. *Chlamydoselachus* also has this element. In many sharks such a piece is lacking; the scapulocoracoid merely tapers to a point. The scapulocoracoids are joined ventrally through a separate piece of cartilage which has been compared with the sternum. The presence of this median piece cannot be detected in the adult.

The base of the fin is generally built around three elements: a **propterygium,** a **mesopterygium,** and a **metapterygium.** From these numerous radials extend out. The variations in shark fins are multitudinous but generally there are three basal units as in *Squalus.* Occasionally only two are present, the propterygium being absent (*Heterodontus*). In fossil sharks this "uniformity" is lost; *Cladoselachus* and *Cladodus* appear to have only the metapterygium (Figure 6-67).

A most peculiar fossil "shark" is *Pleuracanthus* (Figure 6-67), which has a suprascapular element and a biserial archipterygial type of fin. A similar but much shorter and rounder fin is observed in *Chondrenchelys.*

The presence of both broad-based and concentrated fins (the **archipterygium**) in sharks and shark-like fishes suggests that there was considerable experimentation with a newly developed structure and that in the sharks, as represented by the living fauna, only a single basic type has come down to the present.

The pectoral appendage of *Hydrolagus* (Figure 6-66) is comparable to that of the shark. The scapulocoracoids are more broadly joined ventrally and the base of the fin lacks an evident mesopterygium. The radials are longer and separated by gaps like those of an actinopterygian. This type of appendage and girdle fit well into the fossil array suggesting that the chimaerid pattern is independent of that of the present day sharks.

Pelvic appendage The pelvic fins of the shark (Figure 6-66) are quite similar to what we have seen in other fishes. The puboischial processes meet at the midline and fuse; there is a slight iliac process anterior to the fin base. In *Chlamydoselachus* there is a broad medial plate between the fins. In *Squalus* the radials are arranged at an angle along the metapterygial element and behind the propterygial unit. In males of *Squalus,* and sharks in general, there is a **clasper** extending back from the metapterygial element (see Goodrich, 1930, Figure 165). The pelvic fin, except for the clasper, appears to represent a less highly developed fin than the pectoral—it remains at a more primitive structural level, like the pectoral fin of *Hydrolagus.*

In terms of its pelvic appendage, *Hydrolagus* is quite distinctive and unmatched among the sharks or among other fishes for that matter. The pelvic girdle is like the pectoral girdle in having a large iliac process extending upward in the lateral body musculature. There is a strong puboischial process ligamentously joined to the opposite pelvic element at the ventral midline. Attached to the puboischial process is a clasper which is normally sheathed in a pouch anterior to the base of the fin. This anterior clasper has several hooked denticles on it. The fin itself articulates with a distinct process. At its base is a large element with pro- and metapterygial processes. Articulating with the posterior end of the metapterygial process is a posterior clasper involving two units of the metapterygial stem; the more posterior of these is forked.

The presence of a posterior clasper in male sharks and

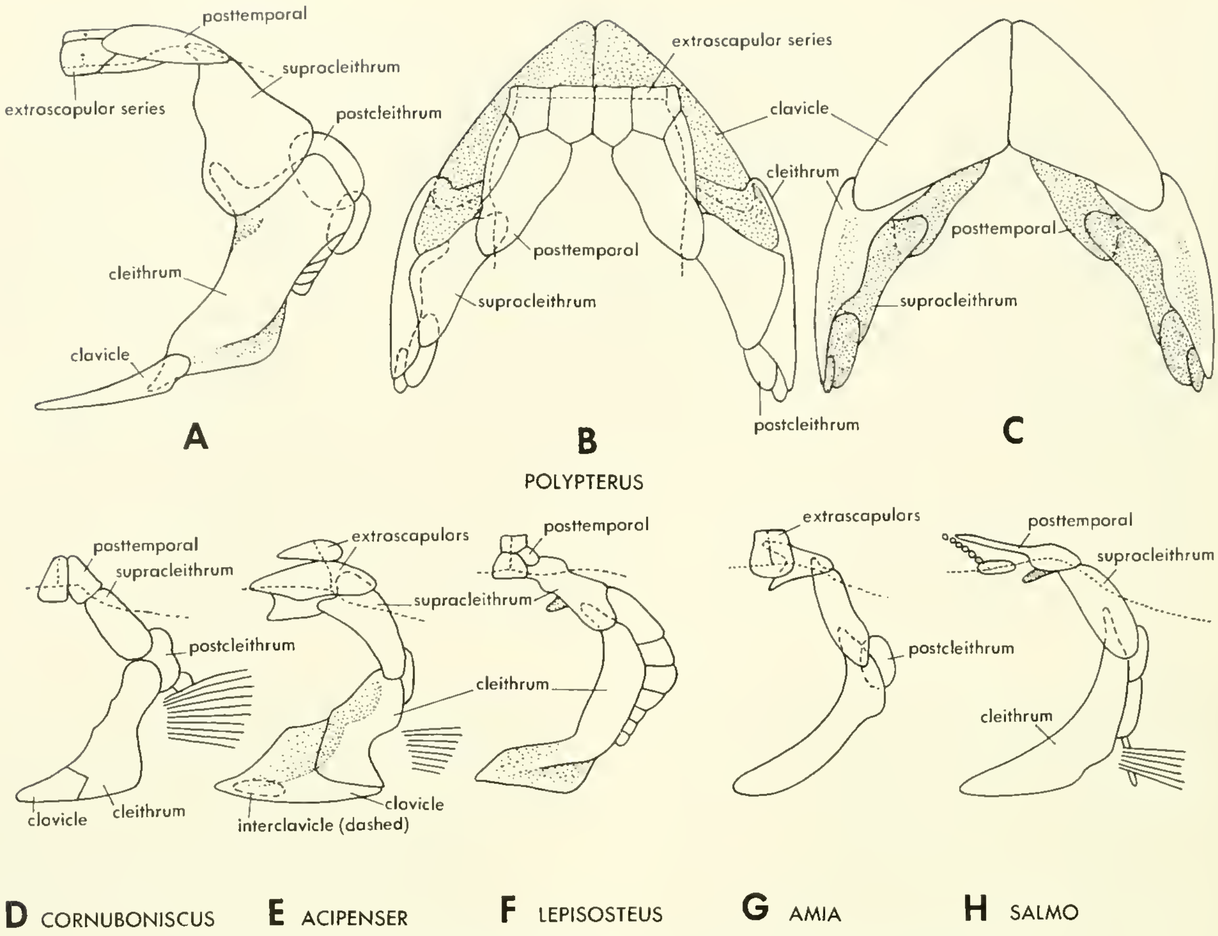


Figure 6-63. Pectoral girdle of actinopterygion fishes. A, B, C, lateral, dorsal, and ventral view of *Polypterus;* D, lateral view of *Cornuboniscus budeusis,* a palaeoniscoid; E, *Acipenser fulvescens;* F, *Lepisosteus;* G, *Amia;* H, *Salmo.* (A, B, C after Jarvik, 1944b; D, after White, 1939)

chimaerids has been cited as an important linking feature. The presence of an additional anterior clasper in the chimaerid and a clasper on the head, viewed along with the variety of structure of the type of clasper observed in sharks, suggests parallel development rather than common ancestry.

Other fishes

The Acanthodii, arthrodires, and agnaths had fins that are of particular interest since they appeared to be parallelisms to those already discussed. The pectoral girdle of acanthodians has a scapular ossification above the pectoral spine and a coracoid ossification below it (Figure 5-21). The fin has a small basal lobe; there is a large spine in front and behind this a membrane (Figure 6-68). In the base of this fin, a few cartilaginous elements have been observed. The pattern of these elements is only poorly known but suggests a concentrated condition, with the elements radiating back and outward from the base of the spine. The acanthodians are also of particular interest because there were more than two pairs of spines in some of them. This multiplicity of appendages is unique (Figure 2-15).

The arthrodires had an extensive trunk armor, in part corresponding to the dermal pectoral girdle of other fishes (Figures 6-69, 6-70). There is a **posttemporal, supracleithrum, postcleithrum, cleithrum, clavicle,** and **interclavicle** (paired or single), as well as a **dorsal medial plate, postventrolateral plates, spinal, ventral cleithral,** and **medial ventral plates.** This trunk armor is much reduced in some types, extensive in others. Inside of this armor is a cartilaginous **scapulocoracoid** extending ventromedially, as a clavicular process, to contact or join its opposite across the midline. There is no particular scapular process and when pectoral spines are present there is a cartilaginous core (see Stensiö, 1959).

The direction of evolution in the group has been difficult to decide upon. Stensiö suggested that the primitive condition was one with a broad-based fin. This type could follow

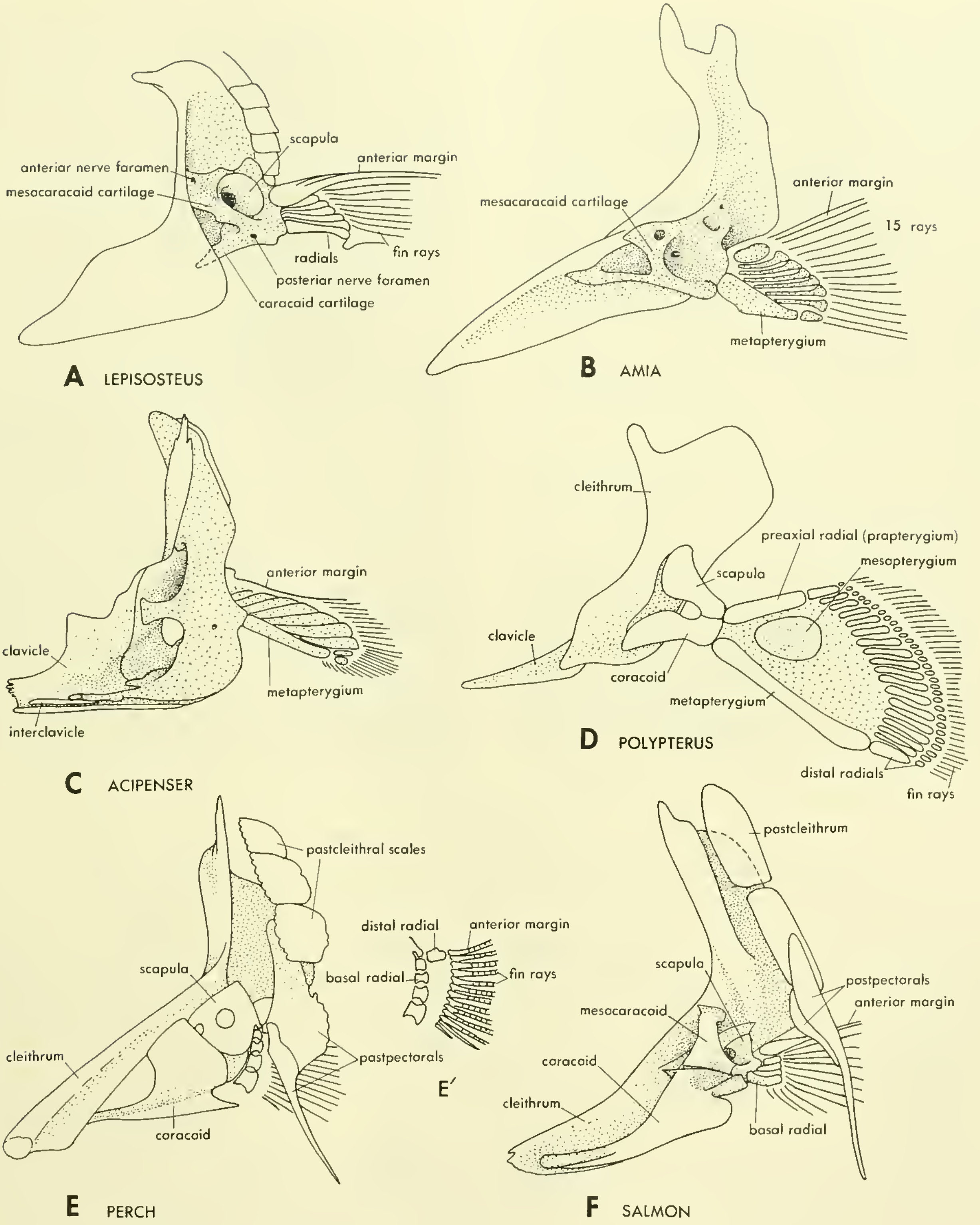


Figure 6-64. Medial aspect of the pectoral girdle and base of limb showing variations in scapulocoracoid development. A, *Lepisosteus;* B, *Amia;* C, *Acipenser;* D, *Polypterus;* E, *Perca* (Perch); E′, details for base; F, *Salmo.*

several lines of modification. One line acquired an anterior spine, and, through continued basal concentration, the spine alone remained and increased in size. The jointed limb of the antiarch is a modified spine.

Westoll (Figure 6-71) has documented a rather different sequence beginning with rather heavily armored types with long spines and no fins, to types with reduced spines and small fins, to types lacking the spine but with a large fin. The fin of the antiarch is a derivative of the primitive spined conditon (Figure 6-72). Westoll bases his opinion on the sequence of appearance of forms in the fossil record; however, it is doubtful that the record is so good as to prove this order. There is some doubt that heavily armored types are primitive; they are undoubtedly more easily preserved. Stensiö's sequence is more in agreement with the fin-fold theory and the embryological development of fins as observed in sharks. However, what is true for the sharks may not apply to arthrodires, since it has already been observed that these two groups are quite distinct.

Pelvic fins are presumed to be among the several pairs observed in acanthodians and are known in at least one arthrodire, *Coccosteus decipiens.* In this form there is a strong iliac process with an expanded ventral margin from which extends a broad-based fin.

Fossil agnath fishes reveal something as to the origin of fins. In the earliest osteostracans, slight ventrolateral folds are present (Figure 5-31), then spines appear projecting out from this fold, and gradually cephalic horns are formed (Figure 5-32). Behind these large cephalic horns a flap-like fin developed in some of the later types. Heterostracans developed slight pectoral spines but no lateral fins (Figures 5-28, 5-29). The anaspids (Figure 5-28) and living cyclostomes are finless. The former may have scales forming a fin fold ventrolaterally and this fold may have an anterior spine.

Thus, within the several fossil groups, the origin of fins as parallel developments for stabilization in swimming or even resting on the bottom can be observed. The need for stabilization devices was probably related to the development of armor. In each group it is possible that a spine preceded the fin and that a movable fin with cartilaginous basal elements followed. These general observations are a part of Westoll's (and many others') conclusion as to the sequence in arthrodires. The process of development of the shark fin is not necessarily primitive, and certainly Gegenbaur's archipterygium with its complex skeleton cannot be viewed as primitive since it is neither accompanied by a "spine" nor broad-based.

As regards the origin of paired fins, a part of the above agrees with the fin-fold theory proposed by Balfour, Thacher, and Mivart. This theory holds that the lateral fins are essentially comparable to the median ones (their skeleton derived from the stiffening radials). The origin of the girdle involves bracing extensions from the base of the fin and utilization of overlying dermal elements to strengthen these. This type of fold is not a biproduct of an anterior spine. A fin fold of this type is observed in Amphioxus.

An alternate theory, that of Gegenbaur, which assumed that the girdles were gill arches—the pelvic fins having migrated far back on the body—and that the fin was a development from the rods of the branchial rays, is not supported by any of the facts presented here. The scapulocoracoid of the arthrodire or shark is far from being a gill arch, nor does its relationship to the trunk armor support its being a gill arch. Connection of the pectoral girdle to the head is through dermal elements rather than chondral, and there is no ventral connection between visceral and pectoral skele-

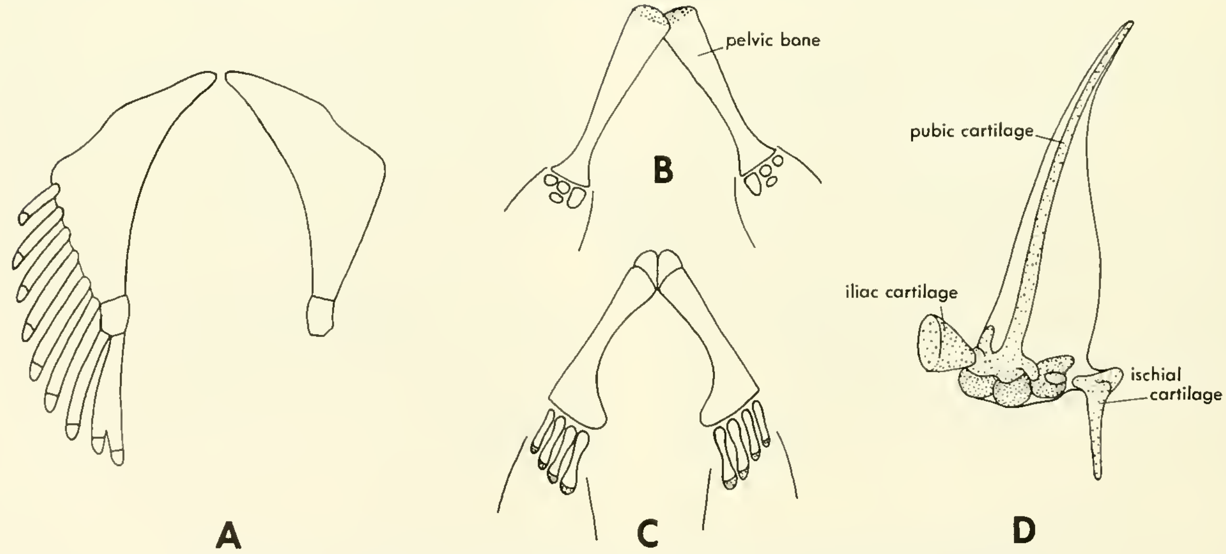
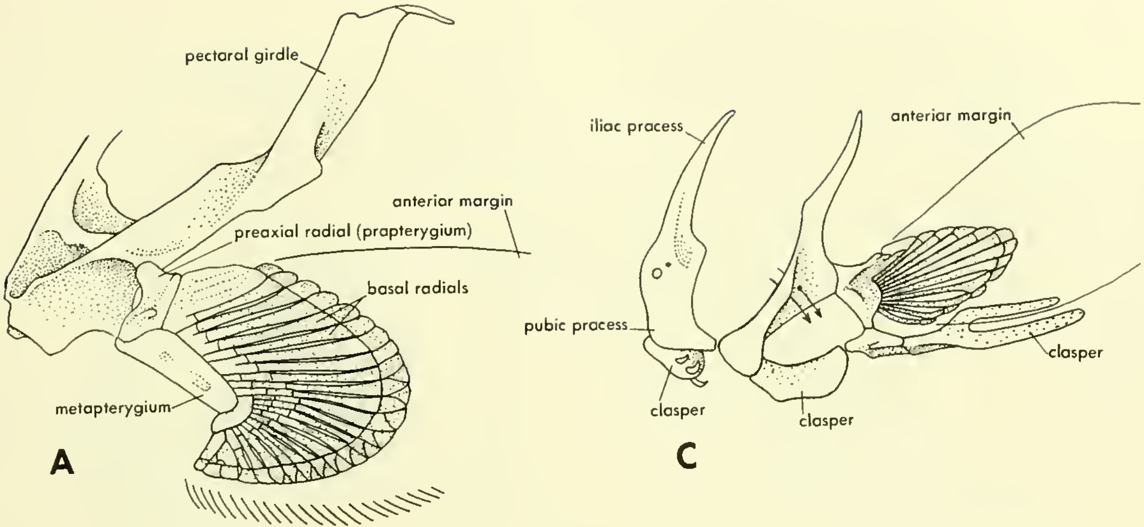
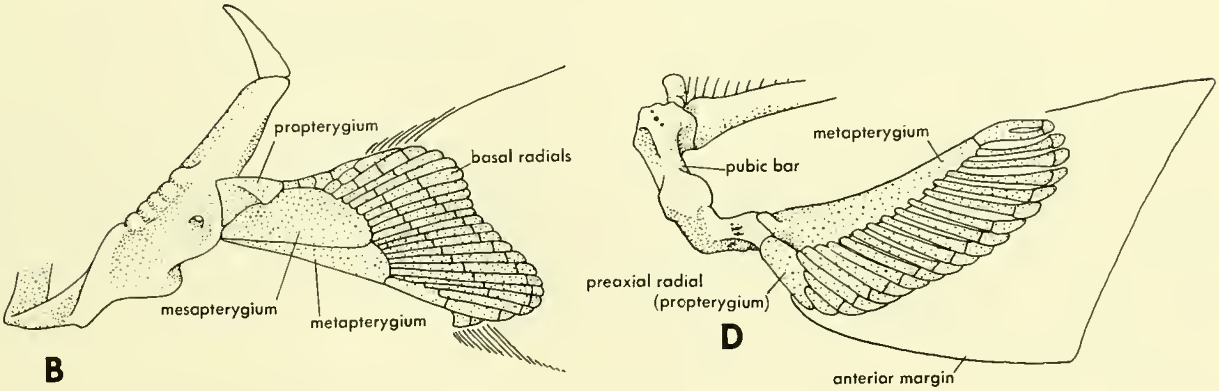


Figure 6-65. Ventral views of the pelvic girdles and fin bases of Actinapterygians. A, *Acipenser;* B, *Polypterus;* C, *Amia;* D, *Lampanyctus.*



HYDROLAGUS



SQUALUS ACANTHIAS

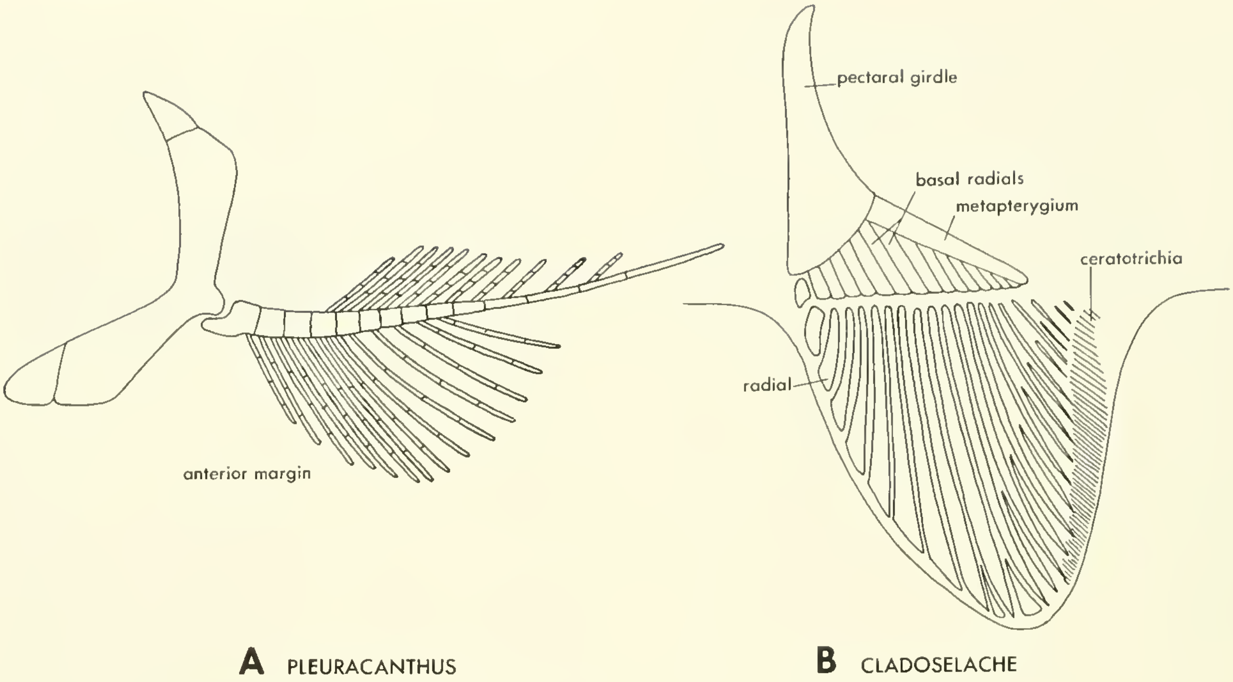
Figure 6-66. Pectoral and pelvic girdles and fin bases of *Hydralagus*, A and C, and *Squalus*, B and D.

tons. The branchial arches are formed from ectomesoderm; this is an origin not even suggested for the scapulocoracoid. The resemblance between girdle and arch is superficial and misleading. The crowning difficulty is the position of the pelvic girdle, which only secondarily, as in some teleosts, becomes closely associated with the head and pectoral girdle.

RIBS AND STERNUM

The ribs have already been mentioned in regard to the vertebral column but a summary is desirable. There are two main questions with regard to these structures: (1) what is their relationship to the vertebrae and (2) do all vertebrates have comparable ribs? The answer to the first question can be derived from the observation of the continuity between the connective tissue sheaths of the neural tube and notochord, the somatopleure of the body cavity, the dorsal, ventral, and horizontal septa, and the myosepta. This basic interrelationship suggests that, like the neural and ventral arches, the rib is just a part of the stress reaction. Unlike the neural or hemal spines, which secondarily lose their myoseptal relation due to the folding of the myomeres, the rib retains this relationship.

In some of the fishes, ribs arise at the intersection with the horizontal septum as well as along the somatopleure-myoseptum union. Those of the horizontal septum are the dorsal ribs, those of the somatopleure the ventral or pleural ribs. The points of attachment of these two ribs are not fixed but are related to the form of the body cavity. If this cavity extends up around the ventral half of the centrum,



A PLEURACANTHUS **B** CLADOSELACHE

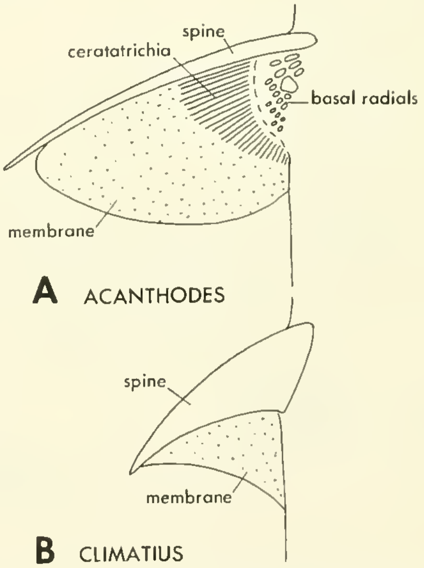
Figure 6-67. Pectoral girdles and fins of fossil sharks. A, *Pleuracanthus;* B, *Cladoselache.* (A after Goodrich, 1930; B after Dean, 1909)

the point of attachment is high on the centrum. The parapophysis may then act as the point of attachment of both dorsal and ventral ribs, as it does in the salmon. It might be assumed that originally there were separate points of attachment for each of these ribs, the parapophysis serving the dorsal rib and the hemapophysis serving the ventral rib, as in *Polypterus.* Such a view finds no support in the fossil record; the parapophysis appears to be the only constant process whether it serves dorsal or ventral rib or both. The hemapophysis has apparently become associated with the ventral ribs in *Polypterus.* Certainly, the ventral ribs are related to the hemal arches in the tail in fishes. In the teleost the elongated parapophysis appears to be modified into that arch; the dorsal rib has similar relationship in the tetrapod.

Another problem is defining parapophysis as opposed to rib. This can only be solved by assuming that the point of articulation is a variable, mechanically determined thing and that the parapophysis of an amphibian is quite different from that of a mammal.

The various groups of vertebrates can be characterized by their ribs. The Chondrichthyes have dorsal ribs or no ribs (*Hydrolagus*). Actinopterygians in general have well-developed ventral ribs and less-developed or vestigial dorsal ones. In addition, many teleosts have intermuscular bones distinct from the ribs.

The choanates appear to have had both types of ribs; pleural ribs are developed in dipnoans and actinistians but replaced in rhipidistians by dorsal ribs. However, the dorsal ribs of the rhipidistian have acquired a diapophysis connection with the neural arch. This suggests that Naef's assumption of the compound nature of the tetrapod rib may apply (Figure 6-73). It is possible that the ventral head is the remnant of the ventral rib, while the rib body is of the dorsal type with a secondarily acquired new capitular head on the neural arch. In the actinistian, it could be assumed



A ACANTHODES

B CLIMATIUS

Figure 6-68. Pectoral fins of acanthodians. A, *Acanthodes* (Lower Permian); B, *Climatius* (Lower Devonian). (After Watson and Westall)

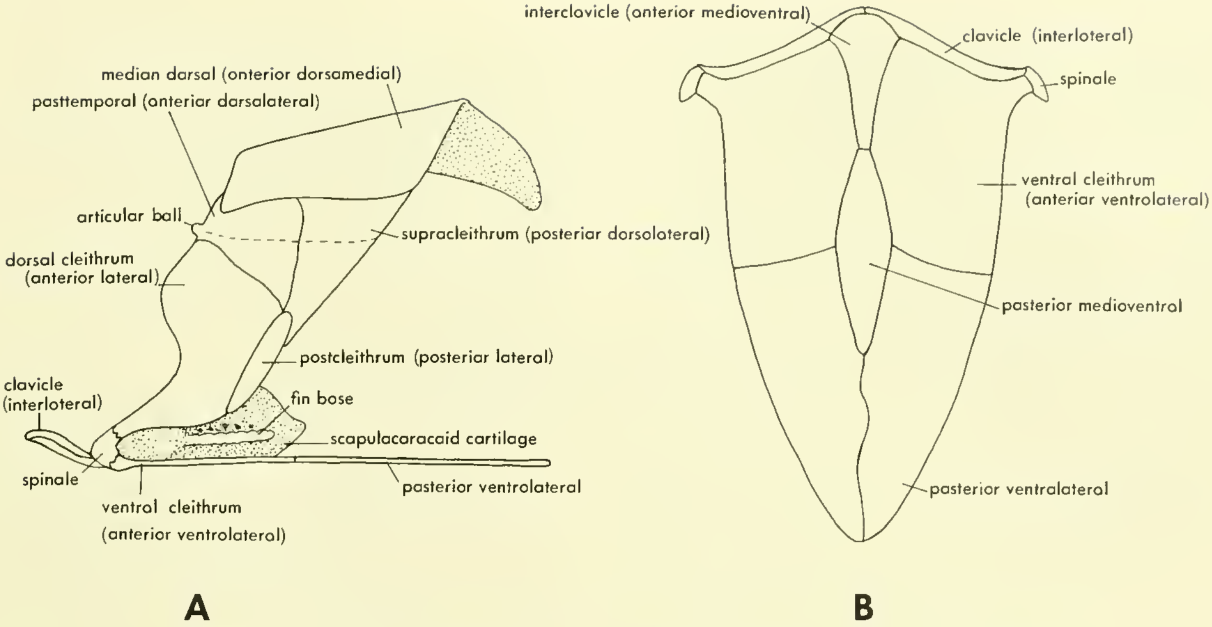


Figure 6-69. Lateral, A, and ventral, B, views of trunk armor of *Dunkelosteus terrelli.* (In part after Westoll)

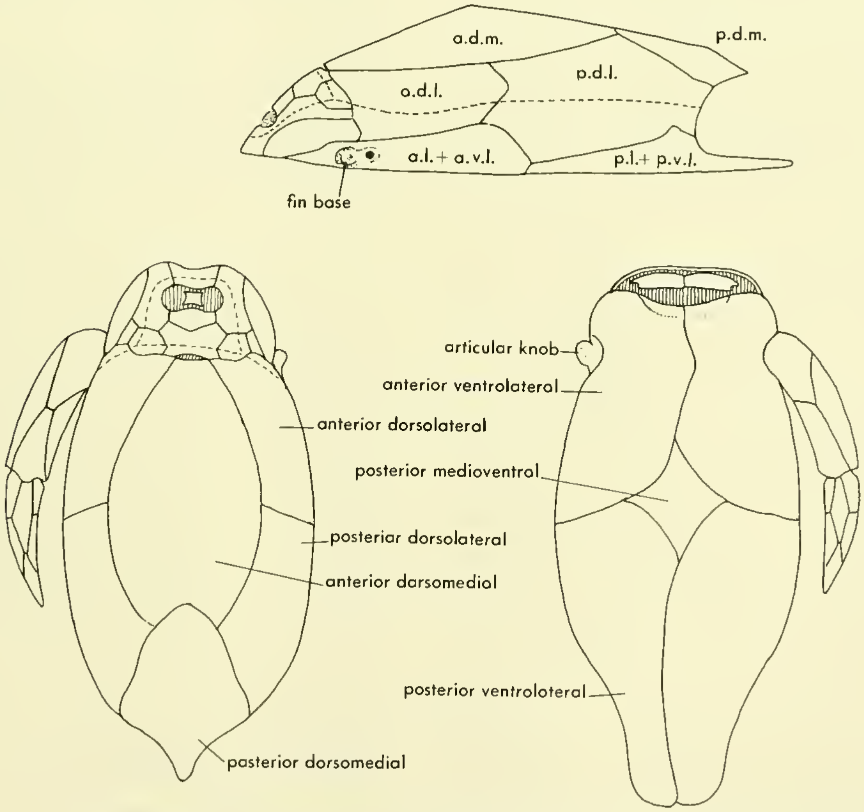


Figure 6-70. Anterior part of body of *Asterolepis maxima*, an antiarch. (After Traquair)

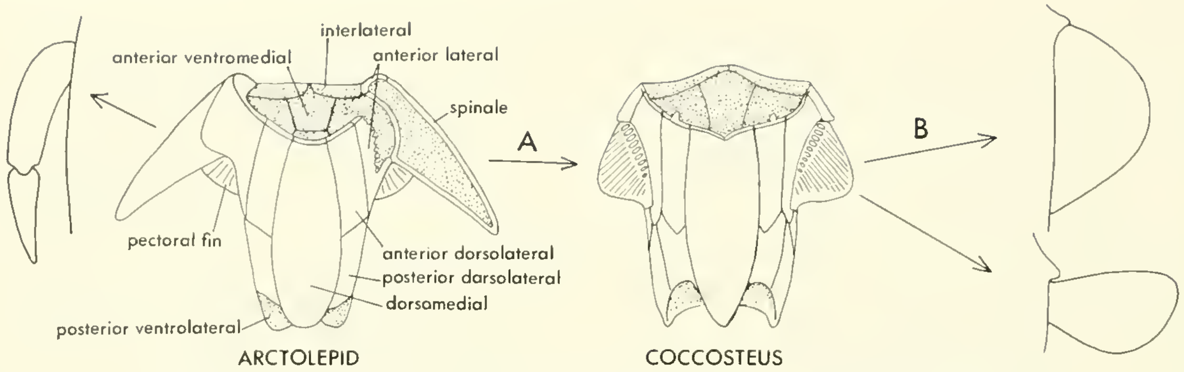


Figure 6-71. Evolution of trunk armor as suggested by Westoll (1958). Reversing direction of arrows A and B gives the sequence proposed by Stensiö (1959).

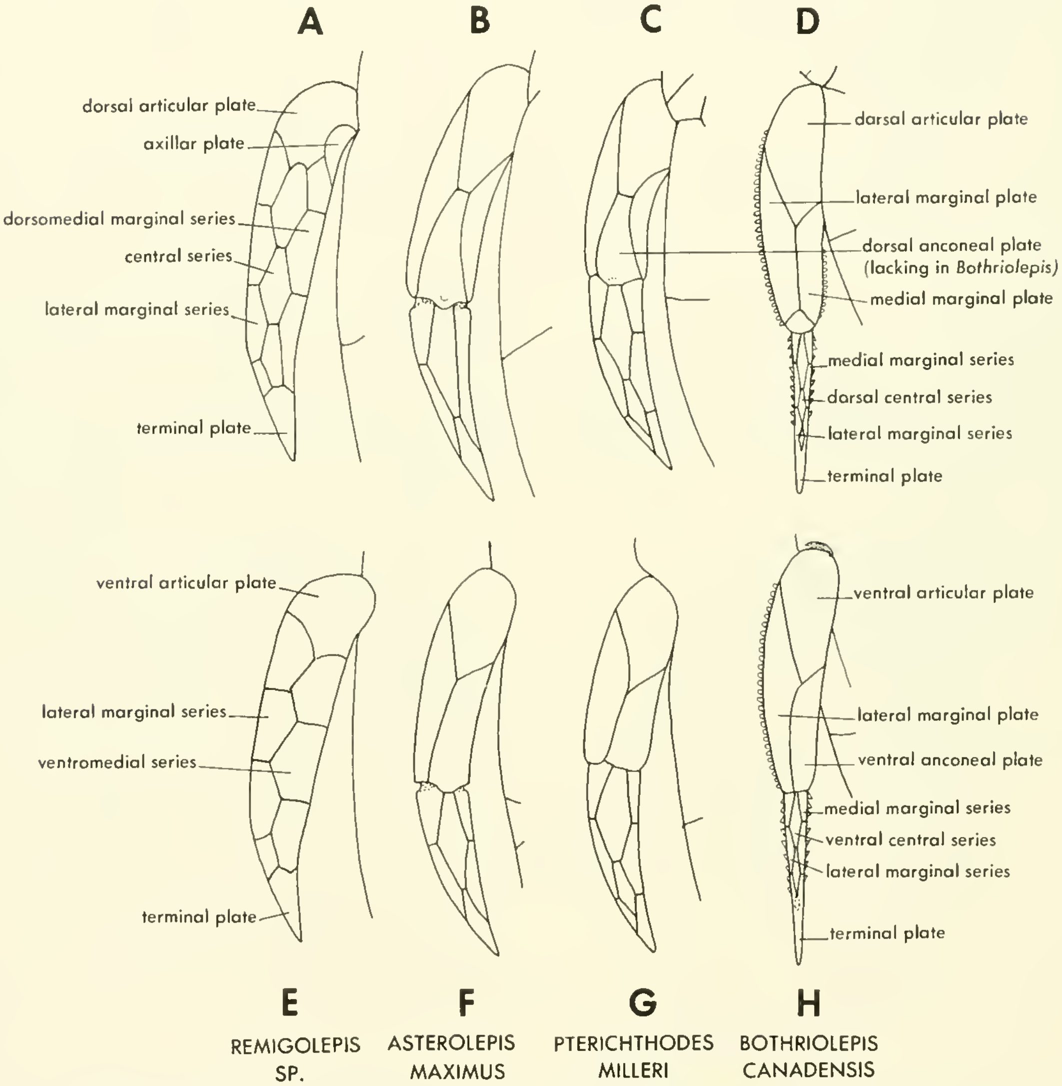


Figure 6-72. Dorsal and ventral views of the pectoral fins of *Remigolepis*, A and E, *Asterolepis*, B and F, *Pterichthodes*, C and G, and *Bothriolepis*, D and H. (After Stensiö, 1948)

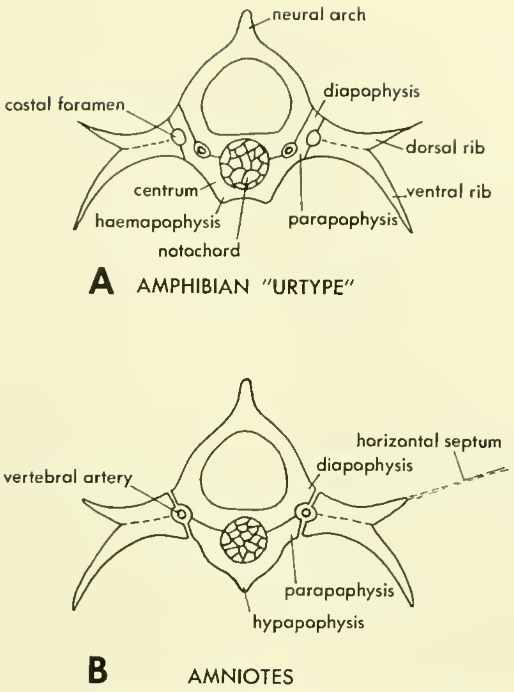


Figure 6-73. Dorsal and ventral ribs and their relationships to the centrum and neural arch in the primitive amphibian vertebra, A, and the typical amniote vertebra, B. (After Naef, 1929)

that there is evidence of reduction of the ventral ribs—*Latimeria* has none. With reduction of the ventral rib, dorsal ones appeared, and in *Eusthenopteron* there are very short dorsal ribs, retaining only the base of the ventral one as their ventral head. In the primitive amphibian there are well-developed, two-headed ribs.

Among tetrapods the costal or ventral segments of the ribs were acquired along with the sternum. At first, the sternum appears to have been a medial plate for the rib attachment, much like that observed in living salamanders and some frogs (arciferous), as well as reptiles; in mammals it is a line of separate ossified units. The sternum in the embryo develops as an expansion of the medial ends of the costal rib blastemas formed along the line of contact of the myosepta with the dermis (Figure 6-74). Paired blastemal strands appear and fuse to form the definitive structure made up of anterior manubrium, which may include an interclavicle component, the line of sternebrae between the ends of the ribs, and the posterior xiphisternum or metasternum. The sternum of the bird is of special interest because of its broad plate-like form with a deep keel. In some birds there are three or more distinct ossification centers, a pair of centers in the region of the procoracoid articulation, and one in the keel. The latter is probably of interclavicular origin. In the chicken there are five centers, two bilateral pairs and a keel center.

In amniotes, ribs and sternum enclose a well-defined thoracic cavity which in the mammal functions in respiration; in other amniotes, these rib walls function in support of the body, which frequently lies pressed against the ground. In aquatic forms or small types such as the living amphibians, the ribs are not important for support but are utilized in the functioning of the axial musculature.

Support and protection of the body cavity in the creeping primitive forms was aided by ventral scales and gastralia. The latter are present in the alligator and Sphenodon. Gastralia (Figure 6-6) mark the reptile level of differentiation and are presumed to be developed from the rows of bony, ventral scales present in the early amphibians. These ventral rows of scales are well marked and fish-like in the small branchiosaurs.

Support for the posterior part of the body cavity is given also by the forward-projecting plate of cartilage in *Cryptobranchus* (Figure 6-55), the pubis of many reptiles, and the marsupial bones of monotremes. Each of these seems to be an independent response to a common problem.

RESUMÉ OF THE BODY SKELETON

The vertebrate body skeleton tells essentially the same evolutionary story as the head skeleton, clarifying some areas while being less useful in others. In terms of "vertebrae," it is evident that some sort of column was forming in

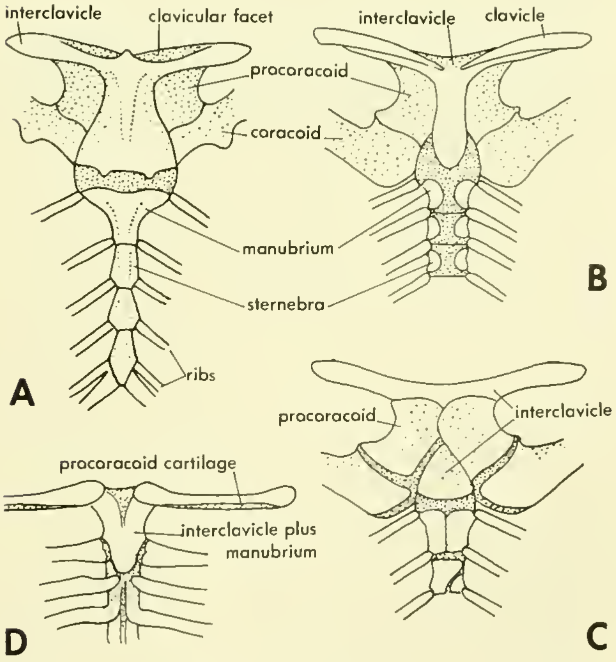


Figure 6-74. The interclavicle in mammals. A, ventral view of sternal area of *Ornithorhynchus;* B and C, ventral and dorsal views of sternal region of a half grown Echidna; D, ventral view of sternal region of 18-day rabbit in which the cartilaginous manubrium supports the clavicles much as the interclavicle of more primitive forms. (A, B, C after Parker in Remane, 1936)

the earliest vertebrate. Perhaps only cartilaginous neural or hemal arches were present and the notochord had a thick supporting sheath. Whether the agnath and gnathostome lines share any common vertebral features is open to argument, the two neural arches and spines per segment of the agnath are suggestive of the two arcualial elements per segment of the gnathostome. These, however, may be parallelisms.

Vertebral evolution in the gnathostome appears to have involved a basal radiation into chondrichthian, osteichthian, and perhaps other lines. It is possible that in the osteichthian group several kinds of vertebrae were produced and served to give greater support to the notochord. There is a question as to whether the vertebral "spools" of some Devonian dipnoans can be compared with the vertebral elements of other choanates or for that matter whether the vertebral body of the actinopterygian is comparable to that of any other group.

The evolution of the vertebral column within the tetrapods is a better story but one cannot be certain which came first, the embolomerous or the rhachitomous type. Occurrence of the latter in the osteolepiform is not proof that it is the ancestral type. Again the fact that the stereospondylous (intercentrum largely) and reptilian (centrum largely) types of vertebrae can best be derived from an embolomerous type (or the proto-rhachitomous type, of Romer), with intercentrum and centrum about equally developed, does not mean that this was the ancestral form.

The primitive vertebra of the tetrapod was temnospondylous and tended to become holospondylous, following a number of pathways. The tendency among vertebrates thus has been to develop a bony vertebral column and this end has been achieved in a variety of ways. Ways which are not as yet fully understood.

In fin structure the agnath is separated from the gnathostome and in each of these groups are seen the beginnings of lateral fins. In each group there were apparently several, and sometimes parallel, pathways leading to the origin of lateral fins. Among gnathostomes separate lines are more evident but the pattern of evolution cannot be strictly defined from the fossil remains. It is possible that lateral fins arose either from membranes behind spines or from fin folds.

Among the Osteichthyes there are two patterns of fin structure, both of which are paralleled among the Chondrichthyes; these characterize the actinopterygians and choanates. The origin of the tetrapod limb from the fin of the latter appears to be a relatively simple step. Although these two types of fins probably arose independently, the similarities of the pectoral girdles suggest common ancestry. The pectoral girdle thus becomes a strong point in the demonstration of relationship between these two kinds of fishes. A rather distant relationship with the Osteichthyes is suggested by the trunk, armor of Arthrodires; this reinforces the relationship suggested by the cranial roof patterns.

In summary, the gap between agnath and gnathostome is as well defined here as in the head. The Chondrichthyes are quite distinct from the osteichthian line both in terms of their vertebral column and in the fin skeleton. The actinopterygian, choanate fish, and tetrapod lines are well marked but seem to share a basic ancestry. As in the case of the head, the vertebral column and fin skeletons were forming at the time of origin of these several lines. The gap between choanate fish and amphibian is more apparent here perhaps than in the head skeleton.

7

Embryogenesis of the Chordates

Embryology contributes much to an understanding of adult anatomy and therefore to comparative morphology. In the preceding chapters, the developmental aspects of the skeletal system were reviewed; in each of the following, the embryological contributions will be described. Embryogenesis, the early stages of development before highly differentiated tissues have been achieved, should be described separately for two reasons: to assess its contribution to the history of the vertebrates and to serve as a reference base for the accounts of later events.

THE EGG

It will not be necessary to review the production of sperm cells and ova, for the details of **meiosis** and **gametogenesis** (**maturation**) are fully described in texts of histology, cytology, and genetics.

The **ovum** is considered a cell, but differs from most cells in its developmental potential and in its relatively large size and contained yolk. In those with little yolk, the nucleus is central and the yolk is evenly scattered in the **oöplasm** or the cytoplasm of the egg cell. As the amount of yolk is increased, it tends to sink down, shifting the clear area of oöplasm enclosing the nucleus upward. During maturation the nucleus is near the surface and by its divisions two **polar bodies** are produced. The first of these polar bodies may divide into two. In eggs with a great deal of yolk, the nucleus lies in a dorsal patch of oöplasm. A top and underside to the egg cell are indicated either in terms of the position of the polar bodies (**polocytes**—Figure 7-1) or by the separation of yolk and oöplasm. At the top is the **animal pole,** at the bottom the **vegetal pole.**

The surface of the ovum is generally covered by a thin membrane described as the **vitelline membrane.** Outside of this there is a **chorion** (zona pellucida), secreted by the **follicular cells,** which nourish and help produce the ovum (the corona radiata of the follicular ovum). Outside of the chorion may be layers of jelly, as in the frog, or a **zona radiata.** These are actually a part of the chorion. There are many different viewpoints about the nature of the membranes enclosing the ovum and the terminology used to describe them.

The amount of yolk is important in determining the kind and path of development (Figure 7-1). **Isolecithal** or hololecithal eggs are those in which the yolk is small in quantity, fine grained, and evenly scattered throughout the egg—except for the area surrounding the nucleus. In some, yolk is more concentrated centrally (**centrolecithal**). Isolecithal eggs are small in size and divide readily into cells when development begins. Since the yolk is not prominent, they might be described as **alecithal.** Eggs with more yolk, distinctly concentrated at the vegetal end, are described by the term **mesolecithal.** Eggs with a great deal of yolk and with a thin germinal disc on top are described as **telolecithal.** Sometimes telolecithal is used for any degree of vegetal yolk concentration.

An egg with little yolk must either receive nutrition from the maternal animal, as in the case of the human, or it can produce a very small larva which must soon begin to feed in order to grow. An egg with a larger amount of yolk can develop to a later stage or a more complete stage; the larva is larger and better prepared to fend for itself when its yolk supply is exhausted. In the case of the chicken or the reptile, with a very large telolecithal egg, the young are hatched nearly fully differentiated and fairly large in size. In the case of the bird, with some parental care, they quickly become independent.

The amount of yolk also determines the type of cleavage or division. An egg with little yolk cleaves rapidly and completely. As the amount of yolk increases, the difficulty of cleavage increases, and in a large telolecithal egg part of the yolk mass never becomes intracellular.

Since there is every gradation between the essentially alecithal egg and the teleolecithal egg, it is difficult to apply these terms and it is not uncommon to have different terms applied to the same egg. Since the type of cleavage is tied to the type of egg, the terms of cleavage are also difficult to define, and perhaps, are redundant.

Complete and rapid division of the egg is described by the term **holoblastic** (Figure 7-2). The resulting cells of several cleavages can be **equal** to each other in size or **unequal.** This dichotomy of equal versus unequal is rather

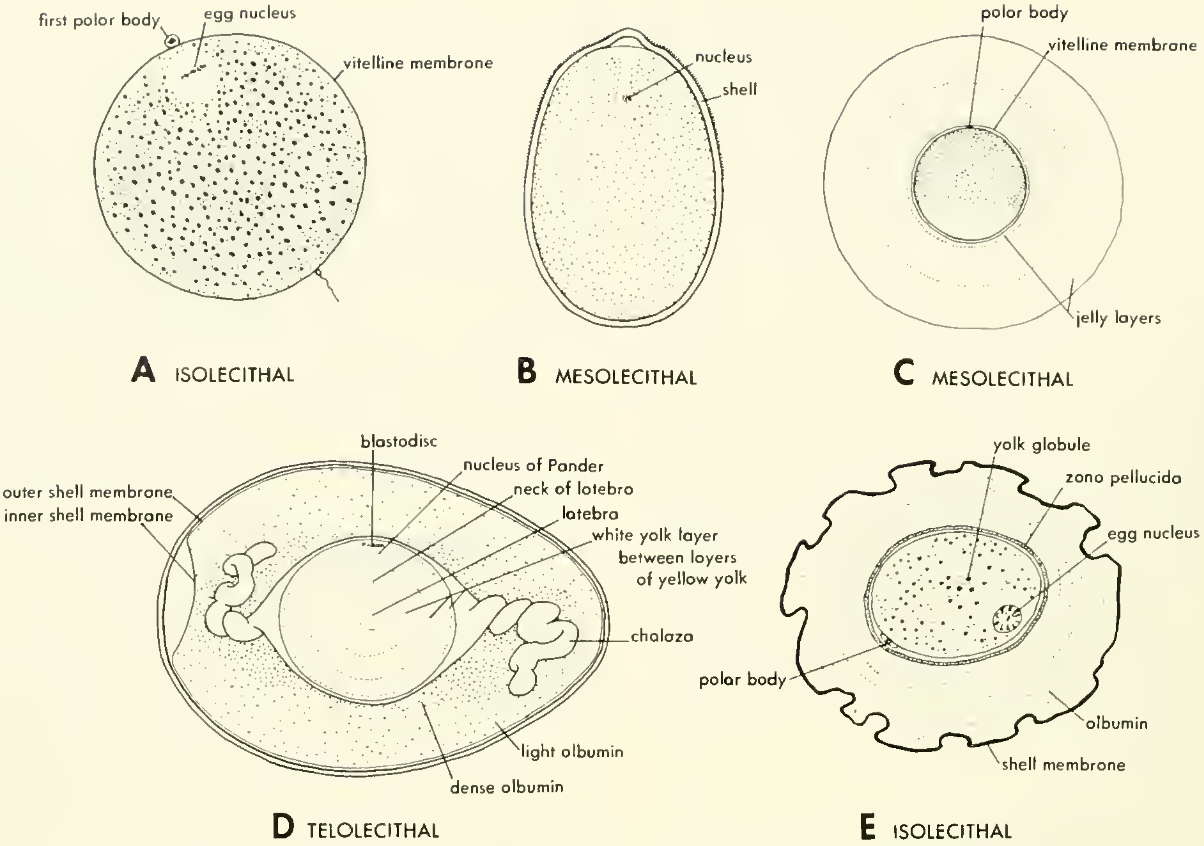


Figure 7-1. The general form of the chordate egg. A, the isolecithal egg of amphioxus; B, mesolecithal, shelled egg of the lamprey; C, mesolecithal, jelly-coated egg of frog; D, extreme telolecithal egg of the chick with accessory materials and shell; E, isolecithal egg of the opossum which retains something of the structure of the shelled egg of the monotreme. (A, C after Huettner, 1949; B after Nelsen, 1953)

misleading in that the cells at the vegetal pole are always larger than those at the animal pole; the difference then is a matter of judgment. When there is a great discrepancy in the size of the resulting cells, one speaks of **macromeres** versus **micromeres.**

When the egg is of a teleolecithal type, the cleavage is described as **meroblastic** (Figure 7-9). The terms **discoidal** and **superficial** describe the extremes of this division type. The first refers to extreme telolecithal eggs with a cytoplasmic or **germinal disc** on the top to which the cleavages are restricted. Superficial refers to a less yolky egg in which the cleavages, at first only surface events, gradually extend through to the vegetal pole (Figure 7-12). The discoidal type is observed in the hen or reptile egg; the superficial type occurs in some fishes.

CLEAVAGE, GASTRULATION, ORGANOGENESIS

For a better understanding of the early stages of development of chordates, some of the details of several types can be compared.

Amphioxus The ovum of Amphioxus is small and **isolecithal** or hololecithal (Figure 7-1 A). The **nucleus** and its enclosing **oöplasm** is displaced toward the **animal pole.** This results in the first **meiotic** division of the nucleus, with a **polar body** lying at the animal pole. The egg is covered by a thin **vitelline membrane,** and outside of this lies the polar body (polocyte).

The eggs are shed into the water at a time when the males are shedding sperm. Fertilization occurs by penetration near the **vegetal pole** by a single sperm cell. As a result of this penetration, a **perivitelline membrane** forms beneath the vitelline membrane, and, as a result of loss of water by the ovum, these two membranes, now fused, lift off the egg surface to form a **perivitelline space** (Figure 7-2). These two membranes combined are identified as the **fertilization membrane.**

The male **pronucleus** (from the sperm) moves upward through the egg and meets the female pronucleus moving downward. The two fuse (or lose their separate identities) above the center of the egg and set up the first division spindle. Cleavage is **holoblastic;** the first cleavage plane se-

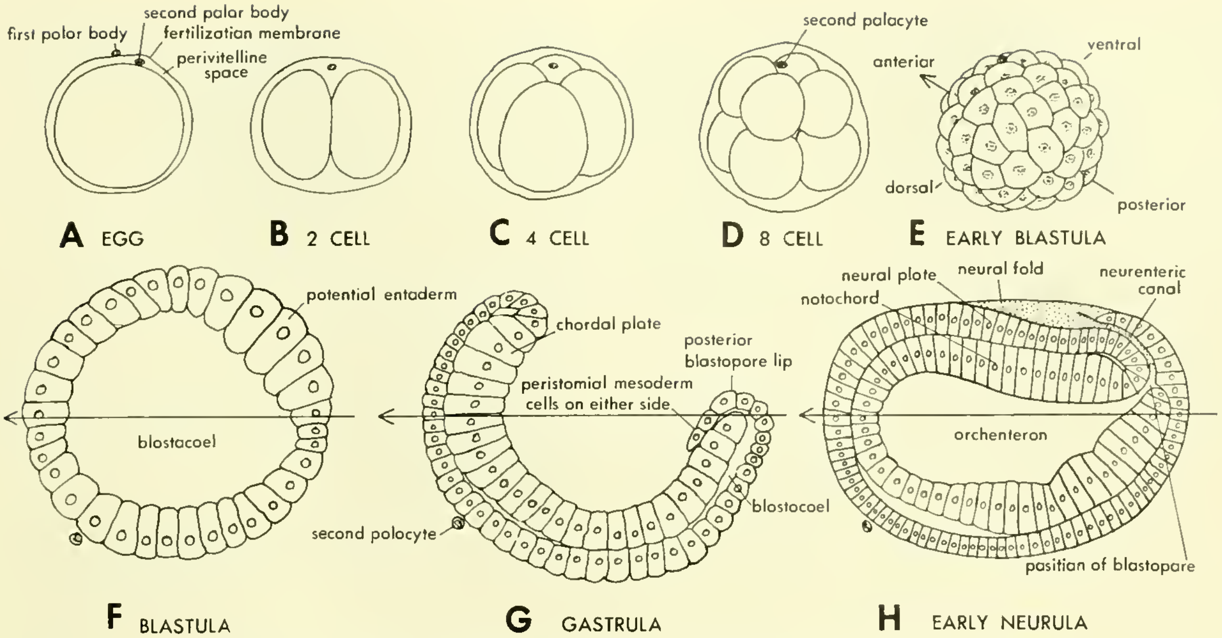


Figure 7-2. Cleavage and gastrulation as observed in amphioxus. A, fertilized egg with two polar bodies; B, 2-cell stage; C, 4-cell stage; D, 8-cell stage; E, late cleavage with axis of larva indicated by arrow; F, blastula in sagittal section, axis indicated by arrow and ventral side down; G, gastrula; H, early neurula. (After Conklin)

parates the egg into right and left halves, and the second is at right angles to the first. They intersect below the polar body.

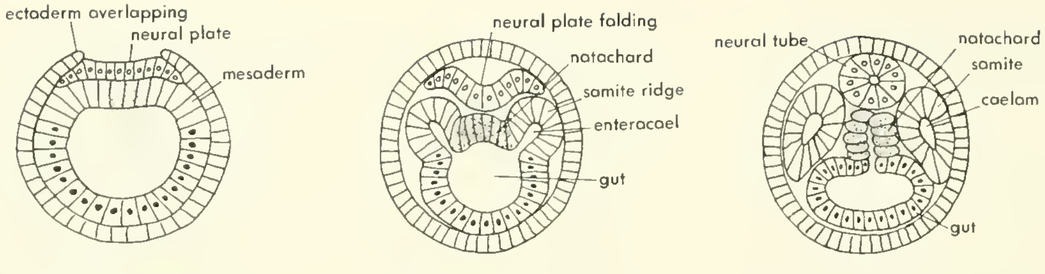
The third cleavage plane, a synchronous division of each of the four cells, is usually an equatorial one separating each cell into top and bottom halves, but it may be a meridional one. The top cells are slightly smaller than the bottom cells. After this, there are vertical cleavages of each dorso-ventral pair of cells followed by an essentially synchronous horizontal **cleavage** of each of the resulting 16 cells. At this stage, there are now 32 cells. By the 32-cell stage, cleavages have become asynchronous, and the cells of the top half are noticeably smaller than those below.

The resulting **blastula** is a hollow ball of cells. The cavity is the **blastocoel** with a wall a single layer of cells thick. As the blastula develops, it flattens ventrally (at the vegetal pole) and this area gradually **invaginates**; that is, it appears to be pushed into the more rapidly dividing hemisphere of the animal region. The process of **gastrulation** also involves some outgrowth of the rims or lips of the **blastopore.** As the process continues, the blastopore constricts to a small opening.

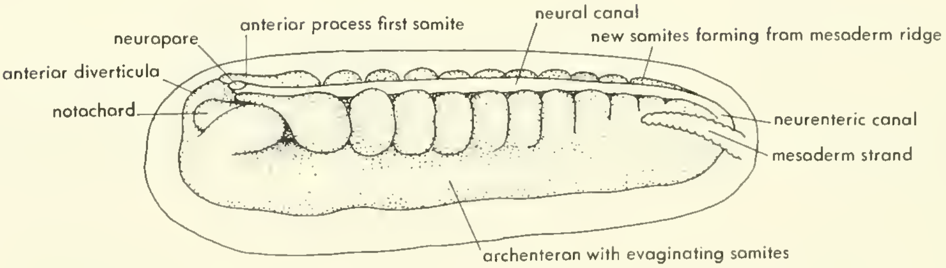
When completed, the **gastrula** is a two-layered structure with an internal cavity, the **archenteron,** which opens to the exterior through the small blastopore at the posterior end. The polar body marking the original animal pole now lies ventroanteriorly in the region of the head. A **neural** or medullary **plate** differentiates on the dorsal surface of the gastrula and begins to sink down, starting from the **dorsal blastopore lip** (Figure 7-3 A). It is overgrown by the margins of this plate, beginning with the ventral blastopore lip. The crescent-shaped margin of ectoderm moves medially, while its posterior margin moves forward and dorsally (Figure 7-2 H). Concurrently, the margin extends more anteriorly as the medullary plate begins to sink in this region. The larva is now called a **neurula.**

The neural plate thus differentiates from back to front and is overgrown by ectoderm from back to front. The plate, now covered by ectoderm, rolls up laterally to form a tube from back to front. As a result of this action, the blastopore is closed, but the archenteron is connected with the exterior through the **neural canal** and the **anterior neuropore.** The cavity of the neural tube is connected with the gut by the **neurenteric canal** (see Figure 7-7 K).

The entoderm is composed of somewhat larger cells than the ectoderm since it is derived from the large cells of the vegetal half of the blastula. The dorsal part of this entoderm is derived by involution of cells from the outside. The dorsal wall of the archenteron underlying the neural plate and tube now begins to form bilateral outpocketings or **pouches** at the anterior end of the neurula (Figure 7-3 B). The first of these pouches lies somewhat behind the anterior end and new pairs arise serially behind it (Figure 7-3 D). Between these pairs of pouches, the roof of the archenteron forms the **notochord,** which arises as an evaginated groove; the edges of the entoderm move towards the midline below this grooved plate. The notochord and coelomic pouches are of apparent entodermal origin in this group.



A EARLY NEURULA **B** NEURULA **C** LATE NEURULA



D LATE EMBRYO

Figure 7-3. Development of neural tube and mesoderm in Amphioxus. (After Nelsen, 1953, and Huettner, 1949)

Anterior to the first coelomic pouches, bilateral dorsal diverticula appear (at a stage of about six pairs of pouches) and extend upward next to the notochord (Figure 7-3 D). The left one, located on the median line in front of the gut, forms the **preoral pit** opening to the surface of the body on the left side. The right one lies above it but below the notochord and forms the **rostral coelom.**

As the animal develops, it becomes pointed anteriorly, expanded in the pharyngeal region, and tapers to a thin posterior end with a small caudal fin. An oval **mouth** opens through the left body wall into the anterior end of the **pharyngeal cavity** (Figure 7-4). The first **pharyngeal opening,** or fenestra, appears ventrally and to the right, and is the most anterior of what is to be the series of the left side. Other fenestrae arise behind, and these tend to become more ventral in position. Fourteen openings appear before the right-side series begins to form. With the appearance of eight openings on the right side, the fenestrae shift around toward their final position. The first and the last five of the left-hand series close up, equalizing the numbers of the two sides.

While the pharyngeal fenestrae are appearing, the **endostyle** (Figures 1-4 A,B and 7-4) begins to form in the roof of the pharynx. At first, it is a nearly transverse bilobed thickening, then it is V-shaped with the apex posterior, and finally an anteroposterior band. This structure shifts with the pharyngeal fenestrae at metamorphosis to its midventral position.

In the right wall of the pharynx, anterior to the first fenestra, a vertical groove invaginates to form a tube which dorsally remains open to the pharynx but ventrally closes and opens to the exterior near the anteroventral margin of the mouth. This organ, the **club-shaped organ,** is of unknown function and disappears with the appearance of the right row of fenestrae; it has been equated with a pair of slits.

At about this stage, **metapleural** folds appear (Figure 1-4), with that of the left side before the right. These folds, grow-

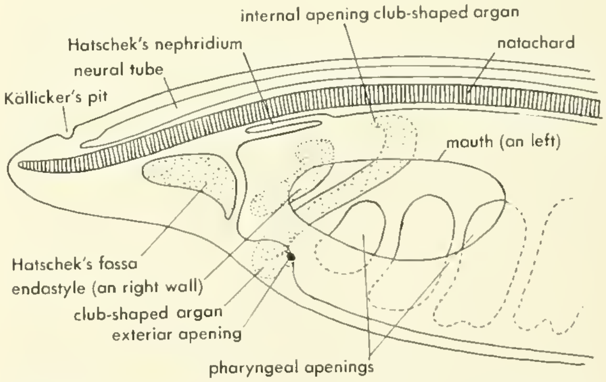


Figure 7-4. Anterior end of larva with 11 (left) pharyngeal openings. (After Goodrich)

ing down around the ventral surface of the animal, form the **atrium** (Figure 14-1). The atrial cavity expands up around the pharynx to either side as the folds meet below.

The adult mouth is formed during metamorphosis by appearance of a **buccal depression** (perhaps the stomodeum), extending anteriorly from the margin of the primitive mouth, and by the outgrowth of the posterior margin of the mouth to form the membranous ventral and lateral walls bearing the **marginal cirrae.** The **buccal funnel** comes to lie directly below the **rostrum** and leads back to the anteriorly facing mouth set in a muscular **velum. Languets** grow out from the velar margin. The **ciliated pit of Hatschek** (Figure 1-3) now lies in the roof of the funnel and from it extends a ciliated tract, the **wheel organ.** The pit also gives rise to a band of **solenocytes** (Figures 1-2, 1-3), lying just to the left of the notochord, whose duct opens into the pharynx just behind the velum. At the end of the metamorphosis, there are eleven pairs of pharyngeal fenestrae. The branchial openings increase in number, and each is subdivided into anterior and posterior halves by the downgrowth of a **languet** from the dorsal margin. There are about ninety pairs of openings in the adult, each subdivided vertically by a languet and horizontally by a number of bars, the **synapticulae.**

The **liver** arises as a diverticulum from the gut behind the pharynx and grows forward on the right side. The **anus** opens far back to the right of the caudal fin. The atrium opens midventrally about two-thirds of the way back. The notochord extends nearly to the tip of the rostrum. In the early stages of its development—cleavages, gastrulation, and neurula formation, Amphioxus resembles the tunicate very closely (Figure 7-5).

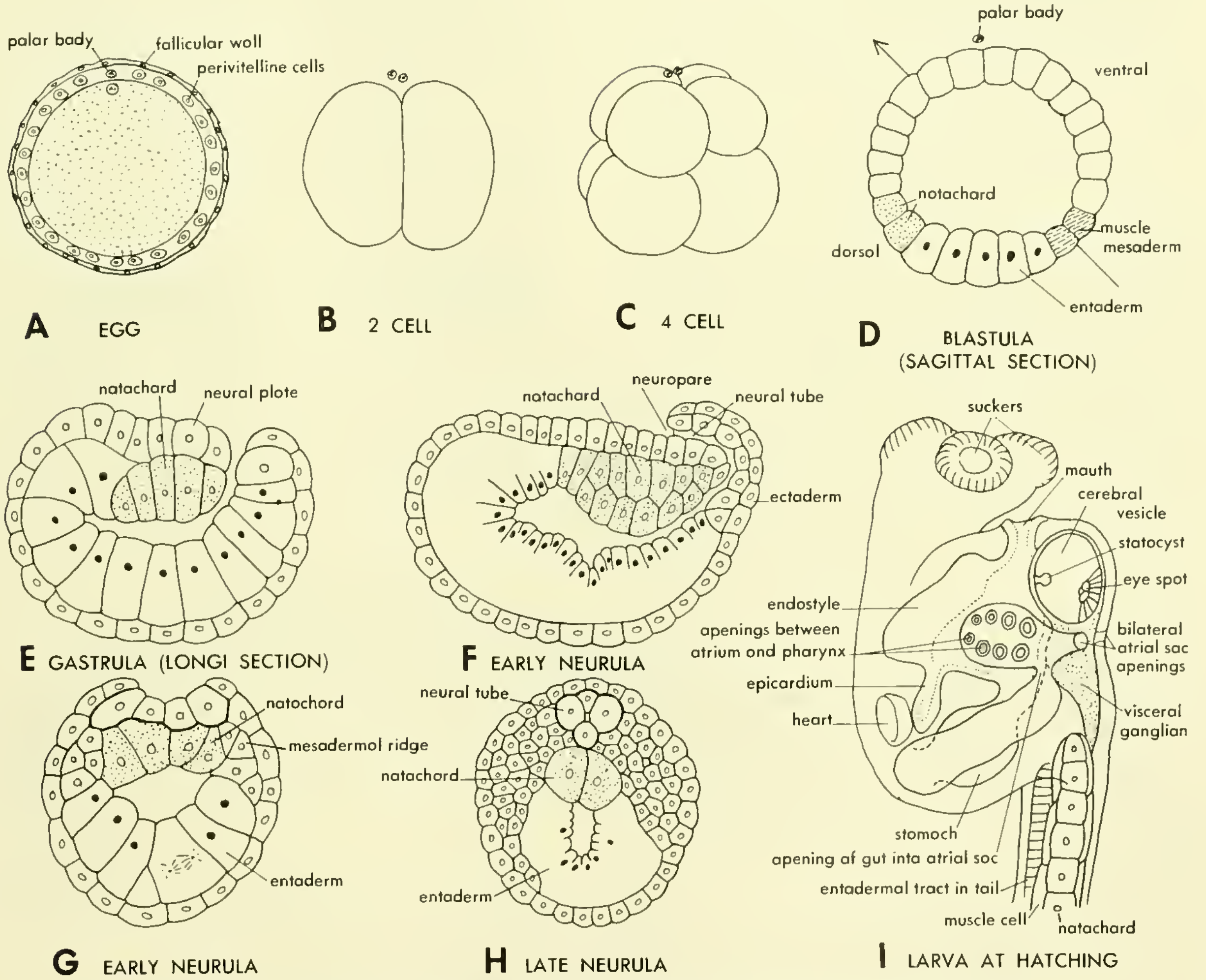


Figure 7-5. Early stages of the tunicate, *Clavelina.* A, egg with follicular wall and envelope of perivitelline cells; B, 2-cell stage; C, 8-cell stage; D, blastula with arrow indicating axis and future dorsal and ventral aspects; E, sagittal section of gastrula with anterior end to left and dorsal side up; F, cross section through E; G, sagittal section of an early neurula; H, cross section of G; I, larva at hatching. (After van Beneden and Julin)

Lamprey The egg of the lamprey (Figure 7-1 B) is ovoid in shape and covered by a **chorion** (shell and microvilli) and a **vitelline membrane.** There is a small opening, the **micropyle,** through the shell at the apex of the egg. The egg is essentially **isolecithal,** although there is an accumulation of larger yolk spheres at the vegetal end. With fertilization, the membranes lift from the egg surface, forming a perivitelline space (Figure 7-6). The cleavages are as in Amphioxus, and the resulting blastomeres are fairly equal in size. A blastula is formed with a large blastocoel. The dorsal wall of the blastula is about two cells thick. Invagination begins with the formation of a blastopore groove at what will be the posterior end of the organism. Involution of cells occurs particularly at the **dorsal blastopore lip;** there is some **epiboly,** overgrowth by the dorsal lip.

With the completion of invagination, a **medullary plate** forms along the dorsal midline. This plate gradually sinks as the outer neural ridges move inward to meet at the midline, thus forming a solid **neural strand** or keel. The **blastopore** remains open throughout the process of neural keel formation.

As this keel is formed, the mesoderm and notochord

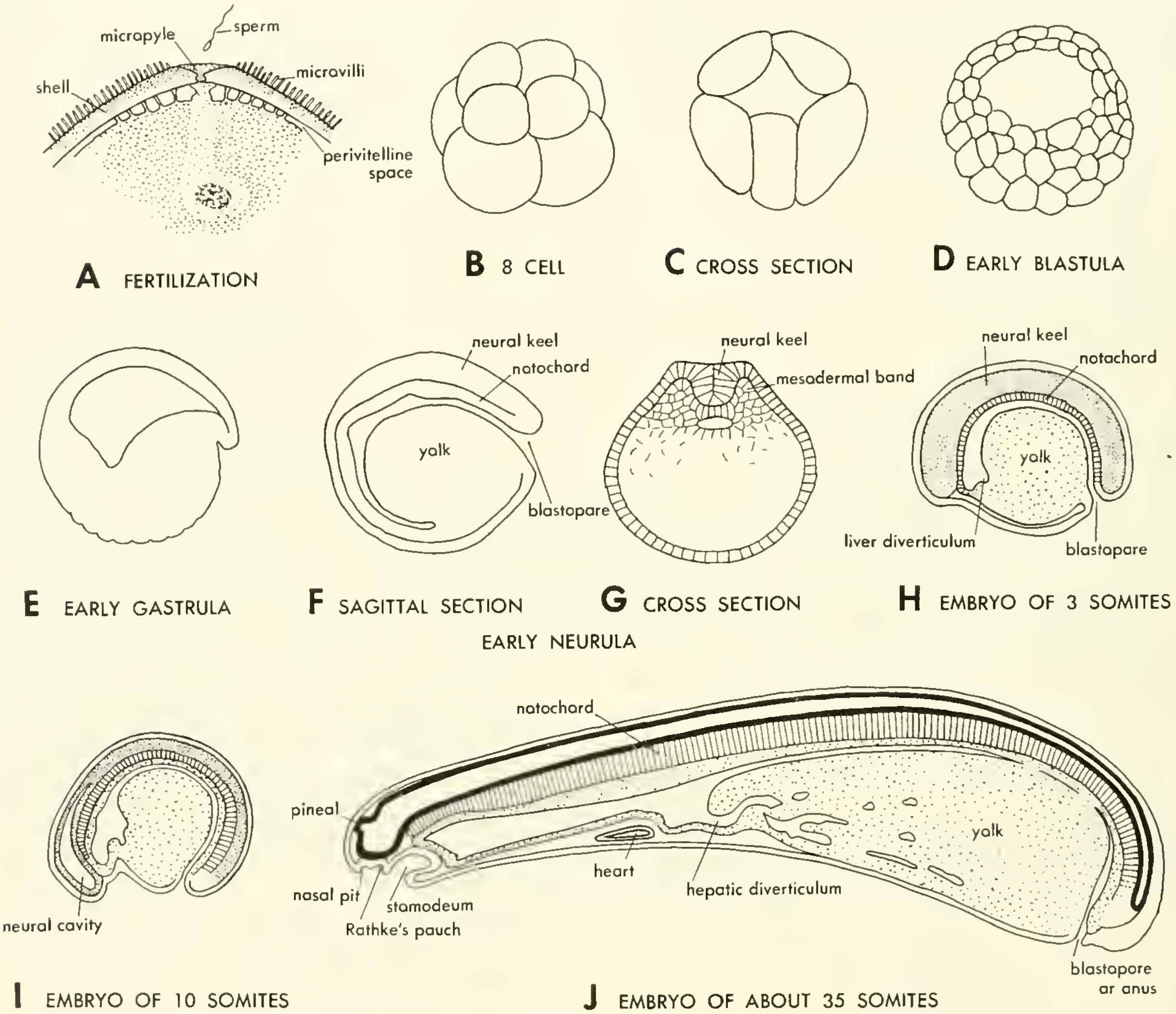


Figure 7-6. Stages of the lamprey (*Lampetra*). A, upper end of egg showing micropyle for entrance of sperm and perivitelline space which forms after fertilization; B, 8-cell stage; C, section of early cleavage stage; D, section of early blastula; E, sagittal section of early gastrula, anterior end to left; F, sagittal section of early neurula; G, cross section of early neurula; H, sagittal section of embryo with three somites; I, sagittal section of embryo of 10 somites; J, sagittal section of embryo with 35 somites. (A, after Nelsen, 1953; B, C, D after Glaesner; E, F after Sélys-Longchamps; H, I, J after Goette)

separate anteriorly. These are formed from materials of the roof of the archenteron. The mesoderm forms solid bands to either side of the medullary plate as it sinks down, and the notochord lies between these mesodermal ridges. In the region of the **prechordal plate** of mesoderm, three pairs of **preotic coelomic pouches,** lying anterior to the **otic capsule,** are indicated. These pouches, and also the notochord, are formed very much as they are in Amphioxus. The lateral walls of the archenteron now move medially below the notochord and pouches to form the entodermal roof of the pharynx. More posteriorly, the mesoderm forms outside of the presumptive gut, without any evident relationship to the lumen of the archenteron (evolution of cells from gut wall).

The floor of the archenteron is thick with cells which are large and contain much yolk. Very early in development, a diverticulum of the archenteron extends downward into the mass of yolk cells, forming the anlage of the **liver.** The cavity of the **neural tube** begins to form anteriorly and to extend posteriorly. Since a neurenteric canal is lacking, the neural cavity is never in connection with that of the gut.

The liver diverticulum branches and liver cells appear in conjunction with these branches. The **heart** lies ventral to the pharynx, anterior to the liver diverticulum. A **stomodeum** appears anteriorly; the blastopore remains open as the **anus.** The membrane between stomodeum and **pharynx** ruptures to form the **mouth,** part of it remaining as the **velum.** The midline invagination for the **olfactory capsule** and the **hypophyseal sac** lie outside the mouth (Figure 12-1). As the buccal funnel develops, the common opening for these pouches is displaced to the top of the head.

Eight pairs of pharyngeal pouches develop, and all open to the exterior except the first, or spiracular, pouch. The hyoid arch has anterior and posterior hemibranchs, but later loses the anterior one. An elaborate "thyroid" gland forms from the **subpharyngeal gland,** or endostyle.

In its development, the lamprey resembles Amphioxus in that several pairs of anterior mesodermal pouches are formed. The mesoderm and notochord have a close relationship to the roof of the archenteron, for the entoderm moves medially below this tissue to form the roof of the pharynx. The lamprey larva is similar to Amphioxus in its way of life and filter feeding mechanism. They differ in the origin of the neural tube and the lack of a neurenteric canal or neuropore.

The development of the lamprey is quite different from that of the myxinid (Figure 7-14). The latter has an extreme telolecithal egg with a germinal disc that cleaves discoidally. It will be considered after the frog and chick types have been examined.

Frog The egg of the frog is **mesolecithal** with a distinct ventral concentration of yolk (Figure 7-1 C). The animal half of the egg is covered by a thin cytoplasmic film in which there is melanin (black) **pigment.** This pigment is assumed to warm the eggs when they are exposed to light and thus increase their rate of development. In contrast to this, there is the idea that in the lamprey light slows down the development of the eggs.

The egg is covered by a thin **chorion** and **vitelline membrane,** although some writers recognize only the presence of a vitelline membrane. When the eggs are shed, they have three unexpanded **jelly coats,** which may be but an extension of the chorion. The eggs are fertilized at the time of shedding; following fertilization, the jelly coats begin to expand and eventually are twice the diameter of the egg itself.

Fertilization occurs in a band 35 to 40 degrees from the central axis of the egg, and the path of the male gamete is marked by its drawing a strand of pigmented cytoplasm along behind it (Figure 7-7). This **penetration path** results in movement of pigment from an area opposite the point of entrance; this area of diminished pigment is identified as the **gray crescent.** The penetration path usually, but not in all amphibians, marks the path of the first cleavage plane. This plane passes along the penetration path through the animal pole and the middle of the gray crescent; it separates the egg into right and left halves.

The second cleavage plane is at right angles to the first and separates the animal into dorsal and ventral halves. The third cleavage is usually an equatorial one dividing the four cells into animal and vegetal quadrants. The division of the four cells are not synchronous or necessarily in one plane. The subsequent cleavages are more asynchronous.

At the eight-cell stage there is already a small **blastocoel,** but this becomes more distinct with further divisions. The **blastula** has several layers of small cells at the animal pole, and many layers of larger cells at the vegetal pole. The **blastopore** begins to form as the ventral margin of the gray crescent.

The process of **gastrulation** involves **invagination, involution,** and **epiboly.** The more actively dividing cells of the animal pole, particularly those at the dorsal lip, are responsible for these movements. Many of the internal structures are traceable to surface areas of the blastula; some of these are indicated in Figure 7-8. The cells move from these areas to the dorsal lip of the blastopore, enter the blastopore, and then move away from that opening, within the gastrula, to their final position. The moving of cells into the gastrula through the blastopore (involution) produces a roof for the archenteron of animal pole cells or **mesentoderm.** The layer of cells next to the **archenteron** is **entodermal;** the layers above are **mesodermal** and give rise to a medial **notochord** and lateral plates of **mesoderm.**

The plates of mesoderm separate from the notochord and entoderm at the anterior end of the embryo first. The notochord begins to separate from the entoderm anteriorly and this process continues in a posterior direction. In the region of the dorsal lip of the blastopore, the ectoderm, mesoderm, and entoderm form a common mass.

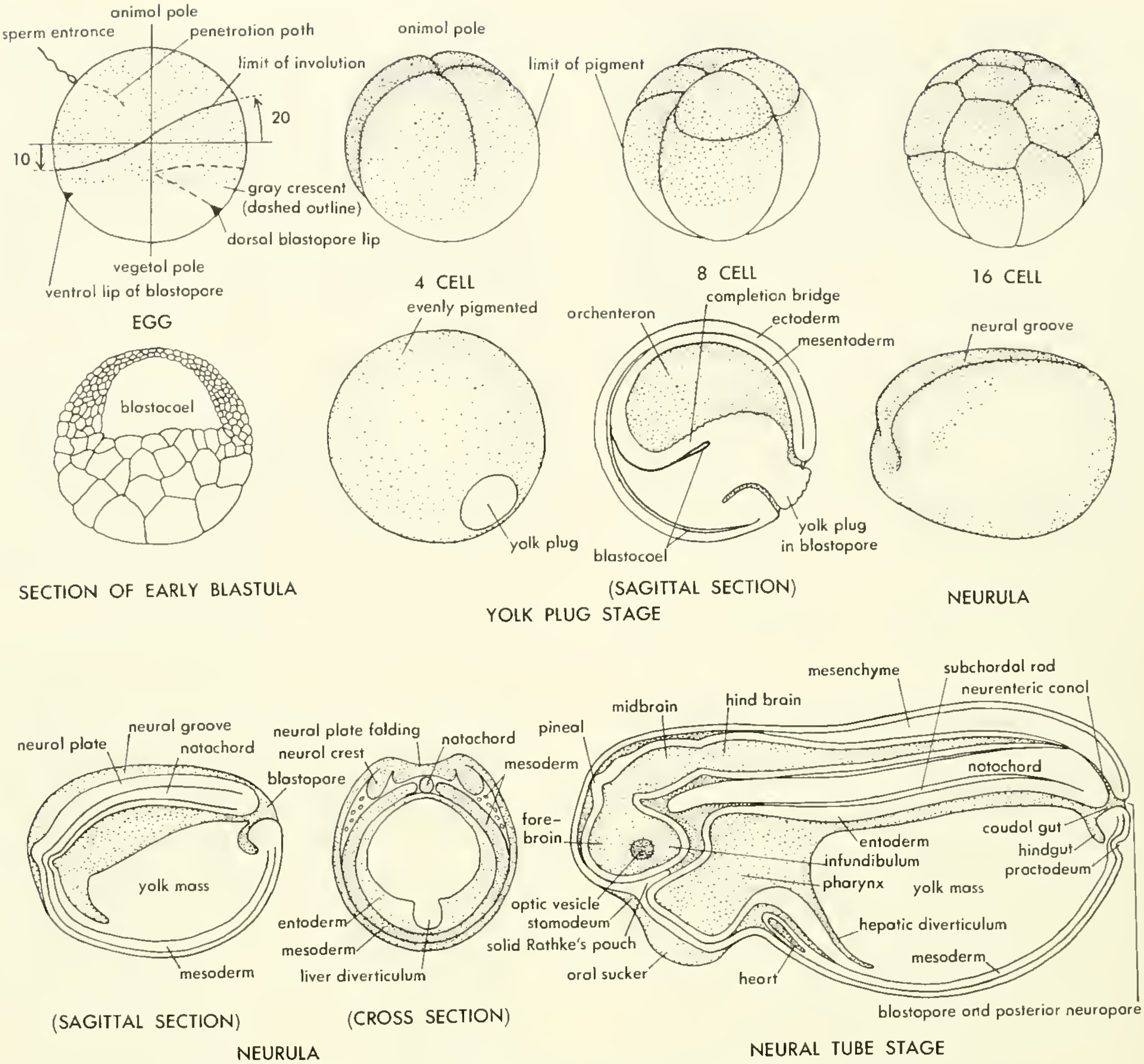


Figure 7-7. Stages of the frog. Outline of egg with a variety of information superimposed; 4-cell stage as seen in dorsolateral view; 8-cell stage (note irregularity of cleavage planes separating animal pole cells from those below); 16-cell stage (note irregular arrangement of animal pole cells); section through the blastula; external appearance of yolk plug stage (late gastrula); yolk plug stage in sagittal section, anterior end to left; external appearance of neurula stage; sagittal section of neurula, anterior end to left; cross section of neurula; sagittal section embryo just before hatching (early tail bud). (Mainly after Rugh, 1951, and Huettner, 1949)

Mesoderm formation involves a sorting of cells at the blastopore. This sorting becomes apparent with the separation of layers some distance from the blastopore. The bilateral plates of mesoderm hollow out to form the **coelom.**

At the completion of gastrulation, the blastopore has been moved nearly half way around the spherical embryo as a result of epiboly by the dorsal lip of the vegetal half of the original blastula—the animal pole now lies ventroanteriorly.

A **neural plate** is formed along the dorsal midline, which sinks down between **neural ridges.** These ridges move up and medially to meet, first near the head end. Closure proceeds anteriorly and posteriorly from this point, producing **anterior** and **posterior neuropores.** The posterior neuropores lie just above the closing blastopore. As these pores close, the **neural canal** is continuous with the **archenteron** by means of the **neurenteric** canal, which soon closes. A hindgut evagination develops from the archenteron growing downward and backward to meet an invagination

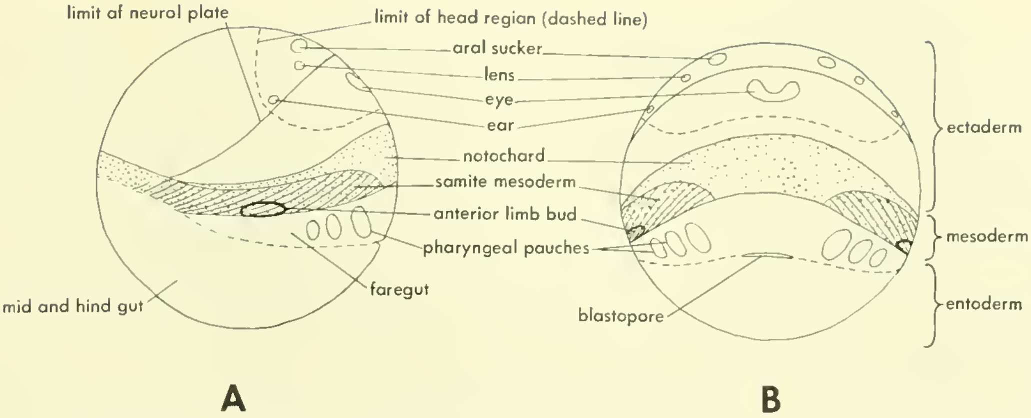


Figure 7-8. Outline of late frog blastula with organ-forming areas of the surface outlined. A, lateral view with future anterior end up; B, anterior view. (After Walter Vogt)

called the **proctodeum.** The fusion and breaking through between these two structures forms the **anus.**

Anteriorly, a **stomodeal groove** has formed and breaks through into the pharynx to form the **mouth.** A **liver** diverticulum has penetrated into the yolk-ladened cells; a **heart** has formed in the region below the **pharynx** and in front of the liver. The neural tube is differentiating into the **brain** at the late neurula stage.

The development of the frog differs from that of the lamprey in that the mesoderm arises not as pouches or ridges from the roof of the archenteron but as mesoderm essentially separated from the entoderm during the process of involution at the dorsal lip. The mesoderm arises as bilateral plates, which secondarily form segmental myotomes and nonsegmental layers of **splanchnic** and **somatic** mesoderm enclosing bilateral coeloms. These layers of mesoderm cover the organs suspended in the coelom and the body wall respectively. The medullary plates of these two types arise in somewhat similar fashion, but that of the frog invaginates to form a tube instead of sinking in as a solid strand. The closure of the neural ridges begins anteriorly in the frog rather than at the posterior end of the neurula. In both Amphioxus and the frog, a proctodeum forms the anus, whereas the lamprey retains the blastopore as this structure. Both Amphioxus and the frog have a neurenteric canal; that of the frog is closed very early, while that of Amphioxus persists for some time. In the lamprey such a canal is never formed.

The development of the lamprey neural tube appears to be specialized. That of the frog is a more primitive type of tube, for it is a neurenteric canal.

Chick The chicken egg is more complex structurally than the previous types (Figure 7-1 D). It has a hard **shell** inside of which is an **outer** and **inner shell membrane;** the two membranes are separated by a small **air space** at the large end of the egg. Inside the inner shell membrane is a layer of albumen and inside this, the ovum consisting of a yolk mass on top of which floats a small **germinal disc** of cytoplasm containing the nucleus. The ovum is enclosed in an albuminous chalaza forming a spiral strand at either end, and the whole floats in the albumen.

The ovum is of an extreme telolecithal type; in fact, it has been described as megalecithal. The egg is fertilized before it is enclosed in the chalaza, albumen, and shell in the oviduct. It is laid at an early gastrula stage, after about 24 hours of development.

The germinal disc is all that undergoes cleavage. The first cleavage plane is simply a groove in its surface (Figure 7-9); the second lies at right angles to this. From this stage, the cells form a rather irregular and expanding pattern on the surface. The free margin of the blastodisc moves out laterally and gradually overgrows the yolk mass. **Periblast** or incompletely separated yolk **cells** unite the blastodisc with the yolk mass, particularly at its anterior end, thus forming a **zone of junction.**

As cleavage continues, the blastodisc becomes several cells in thickness and separates from the yolk centroposteriorly by the **blastocoel.** Below the center of the blastocoel, there are no periblast cells. As the blastodisc expands, it develops a distinct **margin of overgrowth.** It begins to thin in its posterior region, becoming about two cell-layers thick.

The margin of the blastodisc forms a pit-like **blastopore** where the cells begin to involute. Along with involution, there is also a certain amount of ingression of individual cells toward the blastocoel surface. The involution and ingression increases the thickness of the blastodisc in this area, which now delaminates anteriorly into an outer **epiblast** and an inner **hypoblast** (Figure 7-9 G). The area overlying the blastocoel is somewhat transparent and is called the area opaca, while that part of the blastodisc in contact with the yolk, the zone of junction, is called the area pellucida. As the process of gastrulation continues, there is a distinct movement of cells (**concrescence**) toward the blastopore

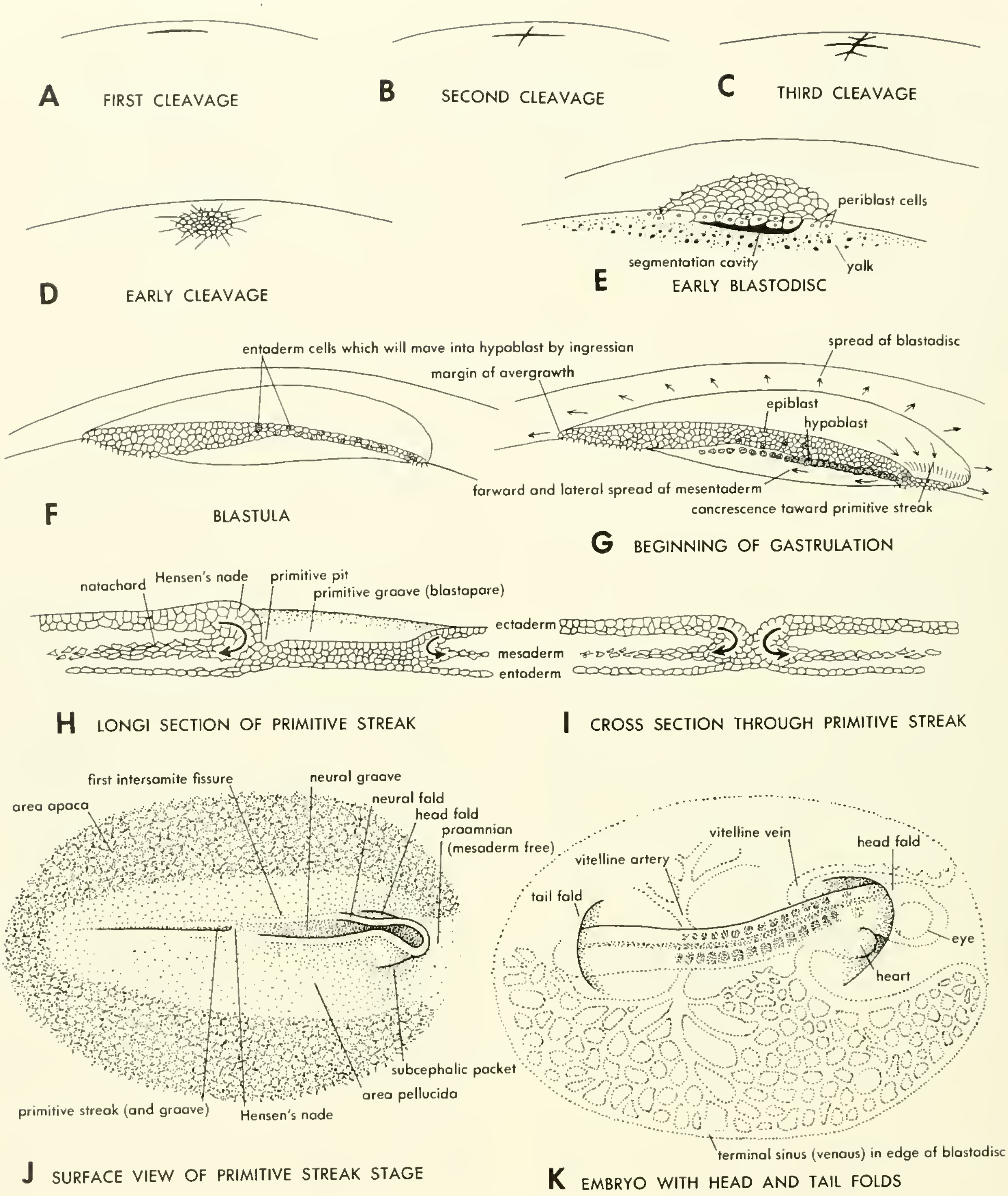


Figure 7-9. Stages of the chick. A, first cleavage groove; B, second cleavage; C, third cleavage grooves; D, early blastodisc; E, blastodisc with underlying segmentation cavity; F, blastula; G, beginning of gastrulation; H, diagrammatic presentation of events along a sagittal section in the region of gastrulation; I, cross section through the primitive groove; J, surface appearance of early embryo (head to right); K, early embryo with head and tail in pockets of the germinal disc. (After Huettner, 1949, and Patten, 1958)

from all directions. The cells move to this depression or notch, then downward, and finally outward on the underside of the blastodisc.

The blastodisc expands in all directions except at the blastopore margin. This overgrowth is a continuing process and results in the blastopore being converted from a transverse line to a V-shape and finally a midline groove, as the margins of overgrowth meet behind it. The blastopore is now identified as the **primitive streak.** Marginal growth continues behind the primitive streak, and the latter also moves posteriorly, laying down the axis of the embryo. The primitive streak has at its anterior end a Hensen's or **primitive node,** behind which is the **primitive pit.** Concrescence continues through all of this period with cells moving back and medially to the primitive streak, down through the streak, and then forward and laterally. Involution and ingression are particularly marked at the primitive pit, which corresponds to the dorsal lip of the blastopore. From this pit, the notochord extends forward along the midline between plates of mesoderm.

Entoderm and mesoderm separate as they move out from the primitive pit and streak. The entoderm forms a complete sheet below the blastodisc, while the mesoderm grows out and around an area in front of the head. The spread of the mesoderm is marked by the appearance of the blood islets and eventually the **sinus terminalis.** Within the body, the mesoderm forms segmental blocks, the somites, while laterally it is a continuous plate which later splits into two layers to form a coelom, both within the embryo and outside the embryo.

As a result of the gastrulation process, the **blastocoel** is converted into the archenteron, a process quite different from that heretofore observed.

The anterior end of the embryo, which is approximately in the position of the original blastopore, is well advanced in its development and differentiation as compared with the posterior part of the blastodisc, which is still expanding marginally, still rolling in along the primitive groove, and differentiating entoderm, mesoderm, and notochord. The anterior end of the embryo with its **neural ridges** and **groove** is gradually raised up from the sheet. As this head fold separates from the blastoderm, it extends forward both by growth and by posterior constriction of the area of attachment to the yolk sac. The underlying entoderm is also effected in the separation of the **head fold** and produces a pocket, the **foregut.** The separation of the embryo from the blastodisc continues from front to back until much of the anterior half of the body is formed. About this time, a **tail fold** appears, rises up, and a part of the entoderm is cut off within it as the hindgut. The head and tail portions constrict from the blastodisc until only a stalk connects the embryo with the yolk sac.

The embryo, as it increases in size and the head flexes to the right, begins to sink down into the surface of the disc. As it sinks, the surface membranes form a fold which moves back over the head region as that grows in size. A similar fold appears over the tail part, and eventually the folds meet above the embryo to enclose it in an **amniotic cavity.** This cavity is lined by a layer of ectoderm called the **amnion.** The amnion is covered on its internal surface by a layer of mesoderm which separates it from the **extraembryonic** (outside the embryo) **coelom.** The outer cover of these extraembryonic tissues is the **chorion** (see Figure 9-6). The chorion, a layer of ectodermal cells, along with its mesoderm is called the **serosa.**

As the embryo lifts from the blastodisc and the yolk-sac stalk constricts, a diverticulum of the hindgut, the **allantois,** appears and grows rapidly. This extends out through the **umbilicus** and expands in the **extraembryonic coelom** as a storage vesicle for waste products from the excretory system. Meanwhile, the blastodisc has been extending around the yolk to enclose it as a yolk sac. There is, between the entoderm and yolk, a layer of periblast cells. The periblast in the chick is never well marked and appears to contribute new cells to the overlying entoderm. At hatching, when the remaining yolk lies free in the gut, it can be assumed that some periblast cells still adhere to it. Thus, in the chick a part of the entoderm is lost and a part of the yolk never becomes intracellular.

Since telolecithal eggs show a wide range of variation in their development, some of these modifications should be examined.

Shark The egg of the shark is strongly telolecithal and undergoes discoidal cleavage much as that of the chick (Figure 7-10). The early cleavages separate a **blastodisc** from a layer of **periblast** cells. These cells form a **syncytium** (cells not separate from each other by membranes) over the yolk below and at the margin of the blastodisc. A segmentation cavity, called the **blastocoel,** forms between the central part of the periblast and the blastodisc. As it gradually expands, the blastodisc becomes many cells thick, and the marginal growth is primarily directed posteriorly. The posterior margin and lateral margins tend to rise up slightly from the yolk mass as the blastoderm spreads, and this edge turns under to form a two-layered **germ ring.** At the posterior margin, the germ ring is raised to form a **blastopore,** and the separation of overlying **epiblast** and involuted **hypoblast** is more marked.

Gastrulation begins with the formation of a **dorsal blastopore lip** which gradually condenses to a **primitive pit.** Gastrulation involves concrescence and involution particularly of mesoderm; the entoderm spreads on the underside of the hypoblast mainly by cellular proliferation. As gastrulation continues, the blastodisc becomes two-layered. The blastocoel now lies between the outer ectoderm and the inner mesoderm.

The earliest invaginated mesoderm produces a **prechordal plate.** This has a notochordal section in the middle of the roof, and bilateral mesodermal plates joining the entoderm

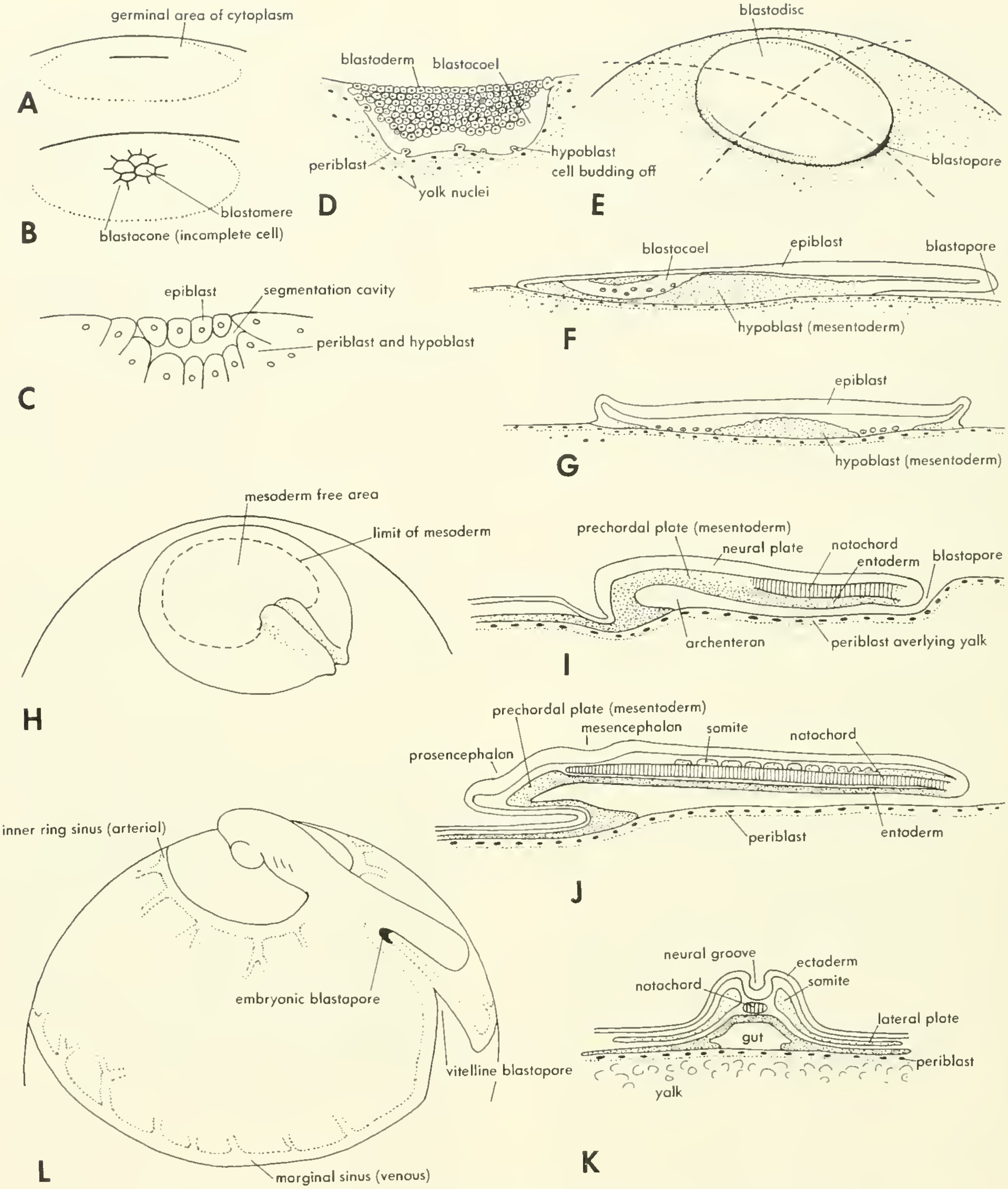


Figure 7-10. Stages of the shark. A, first cleavage groove; B, early cleavage of *Torpedo;* C, early cleavage of *Torpedo* in section; D, blastula of *Torpedo;* E, blastoderm of *Scyllium* undergoing gastrulation; F, sagittal section of blastoderm shown in E (along line a); G, cross section of blastoderm seen in E (along line b); H, early neurula or primitive streak stage of *Squalus* (stage 13); I, sagittal section of primitive streak stage; J, sagittal section of neurula of 10 or 11 somites of *Squalus*); K, cross section of J in region of somites; L, tail bud stage (stage 18). (After Ziegler, Rückert; Witschi, 1956, and Nelsen, 1953)

to either side. As the germinal disc extends posteriorly and involution of mesoderm continues, a **primitive node** is formed above the blastopore at which entoderm and mesoderm are delaminated; the entoderm is now continuous below the notochord and the bilateral plates of mesoderm.

As the embryo lengthens, the blastodisc also extends marginally at a somewhat greater rate, so that the blastopore comes to lie at the apex of a notch. Meantime the **head fold,** bearing with it the anterior ends of the **neural folds** and **neural groove,** is rising up from the blastodisc. The first evidences of the circulatory system, the **blood islets,** appear in the mesoderm involuted (and in part formed by ingression) at the germ ring. The islets join and form the vascular network of the developing yolk sac with **inner** and **outer sinuses.**

The yolk sac expands in all directions as the embryonic body is constricted from the blastoderm and is added to posteriorly; eventually, the **tail fold** is differentiated and extends backward above the blastopore. The neural groove of the tail leads into the blastopore, which becomes separated into an **embryonic** and **vitelline blastopores** by the meeting of the edges of the yolk sac. At this time the caudal vein is supplying blood to a **terminal sinus** around the outer margin of the germ ring, while the **ring sinus,** marking the inner margin of the germ ring or the mesoderm-free area under the head, becomes supplied with arterial blood. The embryonic blastopore gradually closes as the yolk mass is overgrown by the yolk sac. The gut and neurocoel are connected by a **neurenteric canal.** This connection is soon lost. The **mouth** is formed from a stomodeal invagination. The **anus** is a secondary formation involving a proctodeal invagination.

Teleost The development of the telolecithal egg of the teleost follows a pattern similar to that in the shark (Figure 7-11). The **germinal disc** undergoes cleavage producing a cellular mass which is united with the yolk through the **periblast.** The periblast at any particular time appears to be a syncytium, but it can be assumed that cells are differentiated from it and are added to the blastodisc, or, later, the yolk sac. The periblast extends outward more rapidly than the disc and comes to enclose the yolk before the yolk sac.

The central area of the blastodisc of the teleost is raised somewhat above the yolk mass and forms a segmentation cavity. As the blastodisc expands, its margins fold under to form a **germ ring** whose posterior margin is raised as the **blastopore.** The two layers in the germ ring are the **epiblast** and the **hypoblast.** The latter at the blastopore delaminates into entoderm and mesoderm. With concrescence, involution, and ingression, the mesodermal cells of the epiblast produce a **primitive node;** the involuted cells then move forward above the rapidly expanding sheet of entoderm. Entoderm, notochord, and bilateral plates of mesoderm are delaminated at the primitive node. In some fishes the **notochord** appears to separate from the "chordoentodermal" roof of the archenteron some distance from the node.

The **neural plate** develops as a solid strand of involuted cells similar to that observed in the lamprey. As the embryonic body is differentiating anteriorly (**head fold,** brain, and sensory organ development), the process of gastrulation continues at the primitive node. Eventually, gastrulation is completed and the tail fold produced with its contained hindgut. The **blastopore** finally closes beneath the **tail fold** in the position of the **anus**—separate embryonic and vitelline blastopores are lacking.

Like the selachian, the teleost has large **pellucid** areas to either side of the body and a mesoderm-free area in front of and below the head (**proamnion**). The inner **ring sinus** or vitelline veins of the teleost are venous rather than arterial as in the shark.

In the more primitive types of actinopterygian fishes, the eggs do not develop in the extreme meroblastic style (Figure 7-12). A distinct blastodisc is not formed, rather the cleavage planes are superficial and extend gradually down around the egg as the animal end continues to undergo divisions. The first three cleavages are vertical. A horizontal cleavage as such is not distinguishable. Gastrulation resembles that of the frog, but the yolk is enclosed in a syncytial periblast. A part of the yolk is never intracellular.

In vertebrates the liver is a diverticulum from the foregut. It usually lies in front of the yolk stalk, which opens into the midgut. In the case of the sturgeon, however, the yolk mass lies in what might be identified as the stomach, a part of the foregut, as well as in the mid and hind guts. The liver is a diverticulum of the gut wall behind and below the yolk mass (Figure 9-17). This is the one exception observed in the actinopterygian fishes.

Dipnoan The cleavages of the choanate fish, *Lepidosiren,* resemble those of the sturgeon or the holostean (Figure 7-13). The first three planes are vertical and limited to the animal pole. The superficial cleavages gradually extend around to the vegetal end and eventually the entire egg is divided into cells. The relationship between the yolk sac and the gut is not generally described, but the yolk mass appears to lie in the cells of the gut wall just as in the frog. The liver diverticulum extends into the anterior part to this yolk mass. The egg has a limited amount of yolk and the larva is quite small when fully formed.

Myxinid The telolecithal egg of the myxinid is elongate ovate in shape (Figure 7-14). It is shelled and has a series of hooked filaments at either end. With fertilization, discoidal cleavage takes place at the animal-pole end of the egg. The embryo differentiates at the posterior margin of the **blastodisc** as in the teleost or shark. The blastopore closes at the site of the anus. Whether the blastopore forms the anus, as in the case of the lamprey, is not known.

The heart is formed anterior to the head. A proamniotic

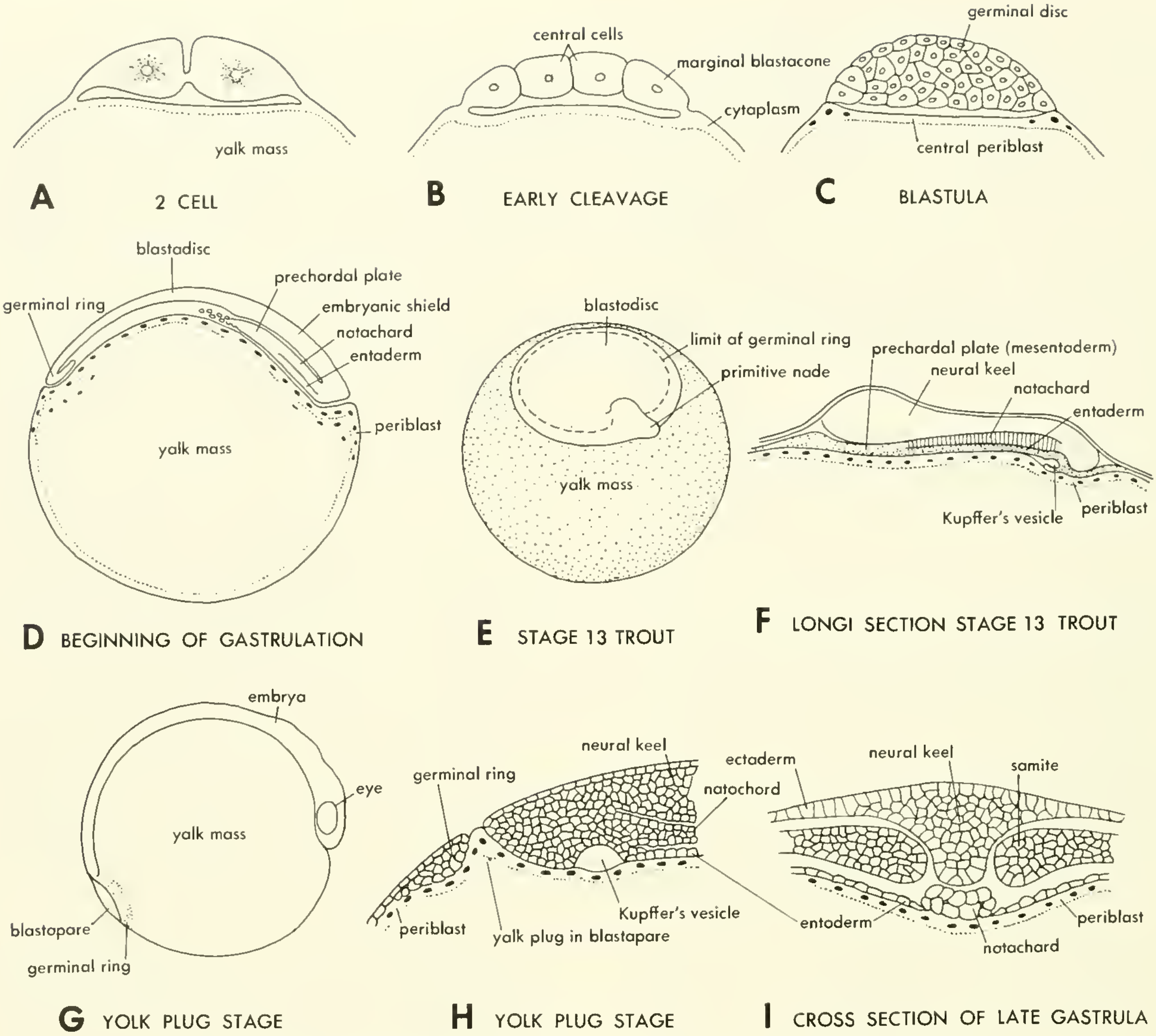


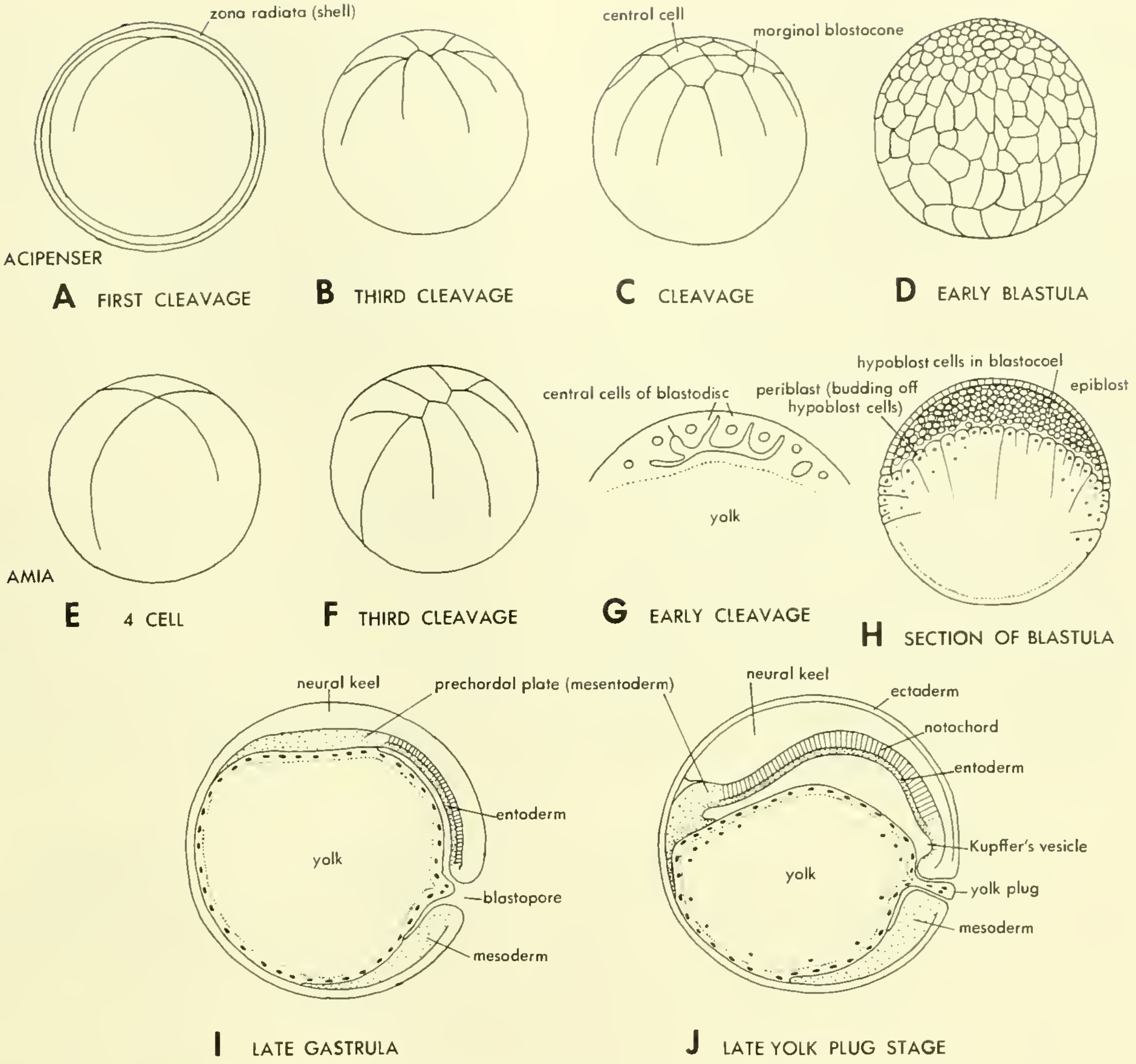
Figure 7-11. Stages of a teleost, mainly the Sea Bass (*Serranus atrarius*). A, section of 2-cell stage; B, section of early cleavage; C, section of blastula; D, sagittal section of gastrula (head to left); E, appearance of blastodisc and early embryo (trout, stage 13); F, sagittal section through early embryo (trout, stage 13); G, yolk plug stage; H, details of posterior end of embryonic body at late yolk plug stage; I, cross section through neurula (late yolk plug stage). (After Wilson, Witschi, 1956, and Nelsen, 1953)

mesoderm-free area is lacking and a midline vitelline vein drains the yolk sac. The paired ventral aortae arch upward into the head and give rise to a number of arches. These shorten as the head rises up from the yolk sac. The yolk sac is probably supplied with venous blood.

The larva resembles the lamprey in that the entire length of the mid and hind guts is occupied by the yolk mass. The head end develops rapidly and extends far out from the yolk mass. The tail end appears much later as the yolk mass shrinks to the general body dimensions.

The relationship of yolk to larva and the general shape of the egg appear to be the same in both the lamprey and the myxinid, but there is a great difference in their styles of cleavage and the details of development. For example, a neural tube is formed directly by invagination in the myxinid. This type of tubulation is observed in most vertebrates and is quite different from that observed in the lamprey or the teleost. The style of the teleost must be considered a modification.

Mammals The eggs of mammals range from a reptile-like form with a leathery shell to a very small isolecithal type



A FIRST CLEAVAGE **B** THIRD CLEAVAGE **C** CLEAVAGE **D** EARLY BLASTULA

E 4 CELL **F** THIRD CLEAVAGE **G** EARLY CLEAVAGE **H** SECTION OF BLASTULA

I LATE GASTRULA **J** LATE YOLK PLUG STAGE

Figure 7-12. Stages of *Acipenser* (A-D) and *Amia* (E-J). A, first cleavage; B, third cleavage furrows; C, fourth cleavage plains cutting off central cells from marginal blastocones; D, early blastula; E, 4-cell stage of *Amia;* F, third cleavage furrows in *Amia;* G, section of early cleavage blastodisc of *Amia;* H, semidiagrammatic blastula of *Amia;* I, sagittal section of yolk plug stage of *Amia* (late gastrula); J, neurula stage of *Amia.* (After Dean, 1895, 1896)

resembling that of some of the simplest animals (Figure 7-1 E).

The egg of the monotreme is shelled; albumin encloses a large yolk mass on which a small germinal vesicle lies. When fertilized this egg cleaves discoidally, producing a mass of cells, the **blastodisc.** This blastodisc is connected by **periblast cells,** forming a **zone of junction,** with the yolk mass.

As the blastodisc expands, it tends to thin to nearly a single layer of cells; from this, by **multipolar** (many points) **ingression,** an **entoderm** layer is formed below what is now the **epiblast.** The entoderm layer expands rapidly in all directions until it underlies the entire blastodisc and encloses a yolk sac. Mesoderm is formed from the epiblast by the usual movements of **concrescence** and **ingression** of cells which form first a **blastopore,** then a **primitive streak.** At the anterior end of the primitive streak is a **pit** and a Hensen's **node.**

A mesodermal **prechordal plate** is formed by thickening of the epiblast and involution of a small portion of the posterior margin of the blastodisc at the "blastopore." This prechordal plate later separates into **head mesoderm** and entoderm. As the body axis is laid down behind this area, the **notochord** is separated at the primitive node from the entoderm; laterally and anteriorly, **mesodermal plates** extend out and later form the **somites** and enclose the coelomic space. The **extraembryonic mesoderm** in the human appears early by egression of cells from the central mass.

In the marsupials there is some variation in eggs. That of the opossum has a distinct albumin layer enclosed by a shell membrane. The egg is isolecithal, the cleavage holoblastic; the resulting cells tend to orient themselves around an internal **blastocoel.**

Among the placentals there may be some albumin outside the zona pellucida, or chorion. The egg is isolecithal, centrolecithal, or alecithal and cleaves holoblastically to form a solid ball of cells, the **morula.** From the morula a blastula is formed by the development of a central hollow (Figure 7-15). The development of this hollow also produces a thick mass of cells at one end. From this central mass the embryo and its overlying membranes develop. In some of the marsupials, a central mass of cells is only poorly developed or even lacking. In the latter case, a central mass is produced by increased mitoses at one end of the **blastula.**

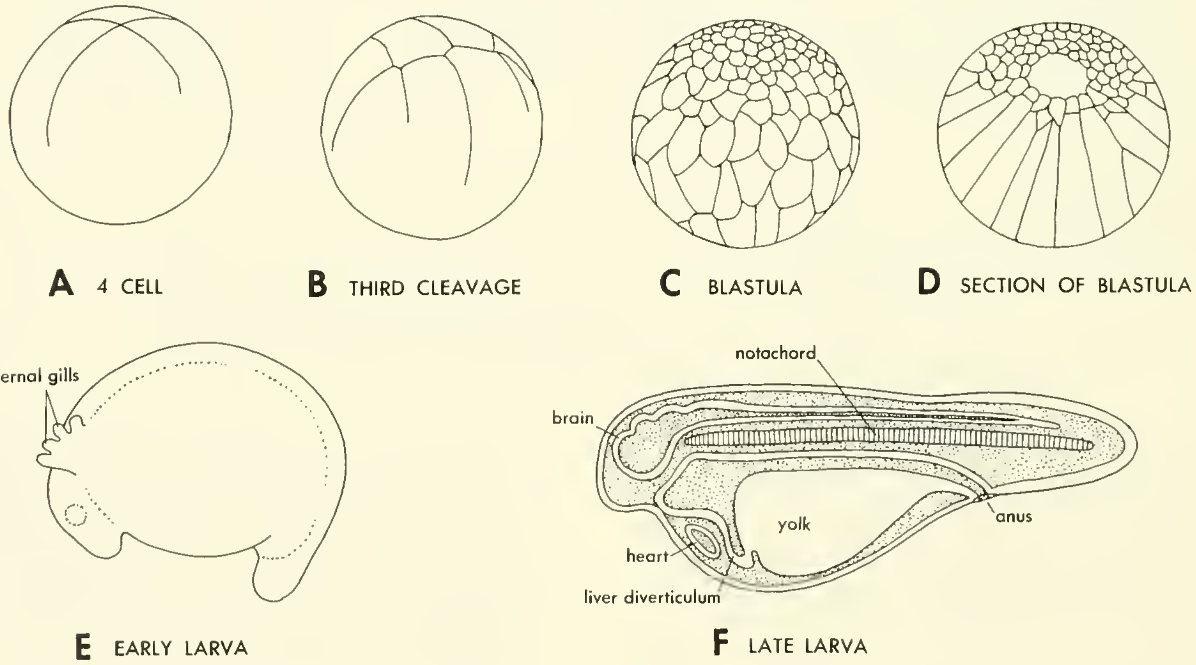
The outer layer of cells of the placental blastula forms a **trophoblast.** The central mass gives rise to entoderm by ingression of cells which spread out as a lining layer, converting a part of the **blastocoel** to an **archenteron.** The central mass, inside the trophoblast, now becomes an **epiblast.** In some placentals the trophoblast overlying the central mass disintegrates, whereas in other mammals, the primates, or rat, the trophoblast remains.

Development from this point follows two lines. In those with the overlying trophoblast, as amniotic cavity, enclosed by epiblast cells, hollows out above the **embryonic disc.** In the other group, this cavity develops by a sinking of the germinal disc and an overgrowth by anterior and posterior folds. In the latter group, the process of **amnion** formation is like that observed in the chick or the reptile (Figure 9-6).

In the mammal the process of mesoderm formation involves the development of a **primitive streak, pit,** and **node** as in the lower forms. It should be noted, however, that this is a mesodermal "gastrulation." In marsupials and more so in the placentals, the trophoblast, which corresponds to the chorion of the reptile, is involved in the placentation of the embryo.

PLACENTA

Possession of a **placenta,** the device by which the foetus receives nourishment from the maternal animal, is not limited to mammals, and it is not always the same. In the shark, for example, the function of the placenta and the relationship between the young and the mother varies. In the case of the Spiny Dogfish, it is one of shelter and protection. In other sharks, the uterine lining secretes a nutritional material necessary, or at least helpful, to the development of the young. The most advanced type involves a yolk-sac



A 4 CELL **B** THIRD CLEAVAGE **C** BLASTULA **D** SECTION OF BLASTULA

E EARLY LARVA **F** LATE LARVA

Figure 7-13. Stages of the lungfish *Lepidosiren.* A, 4-cell stage; B, third cleavage furrows; C, external appearance of early blastula; D, section of early blastula; E, tail-bud larva; F, sagittal section of early larva. (After Kerr)

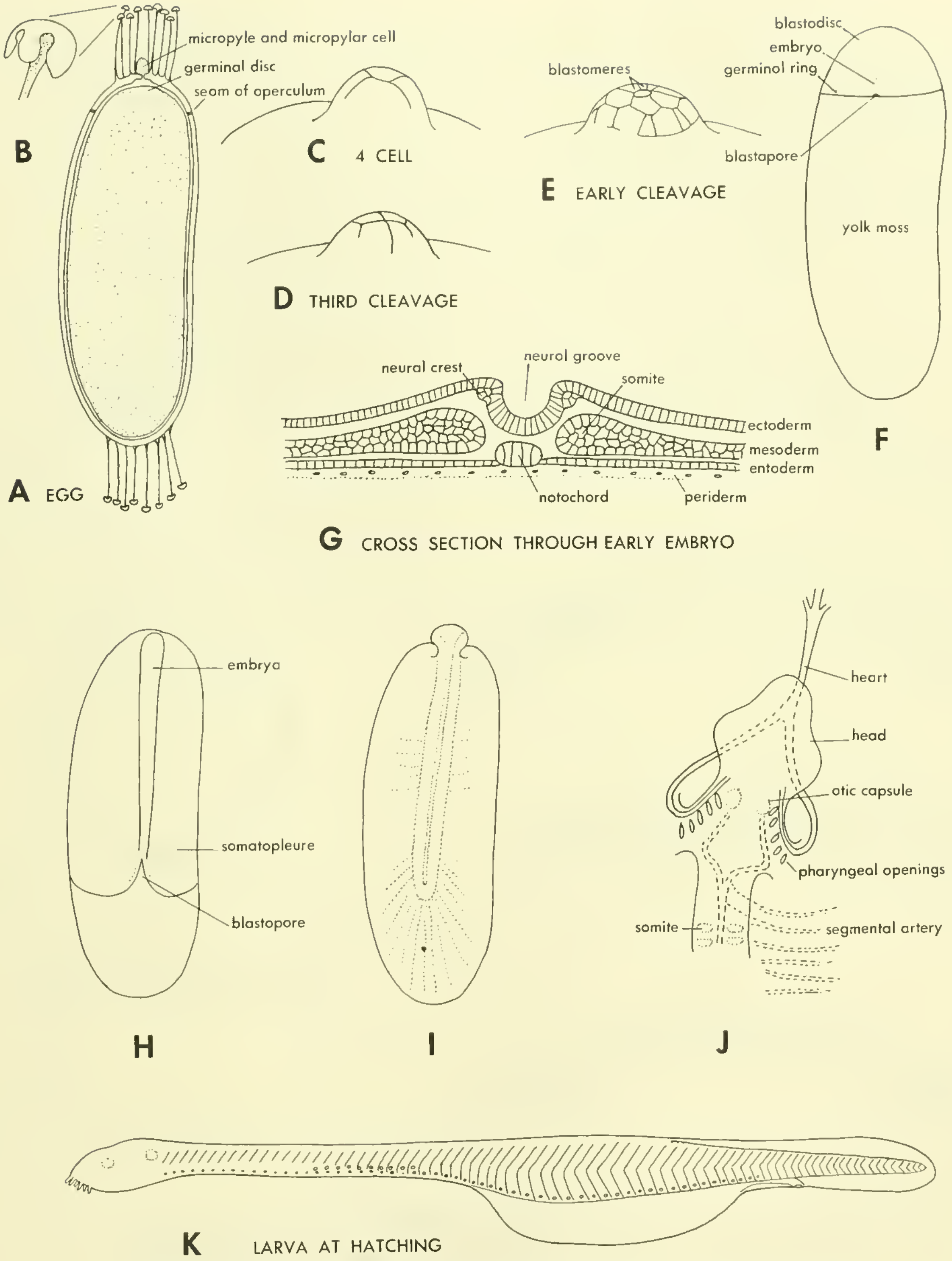


Figure 7-14. Stages of *Eptatretus* A, shelled egg with anchor filaments at either end; B, tip of anchor filament enlarged; C, 4-cell stage; D, third cleavage furrows; E, early cleavage; F, egg with blastodisc cap at animal pole; G, cross section through early embryo; H, blastoderm overgrowing yolk mass; I, later stage with yolk enclosed by blastoderm; J, head of embryo rising off blastodisc; K, larva at hatching. (After Dean)

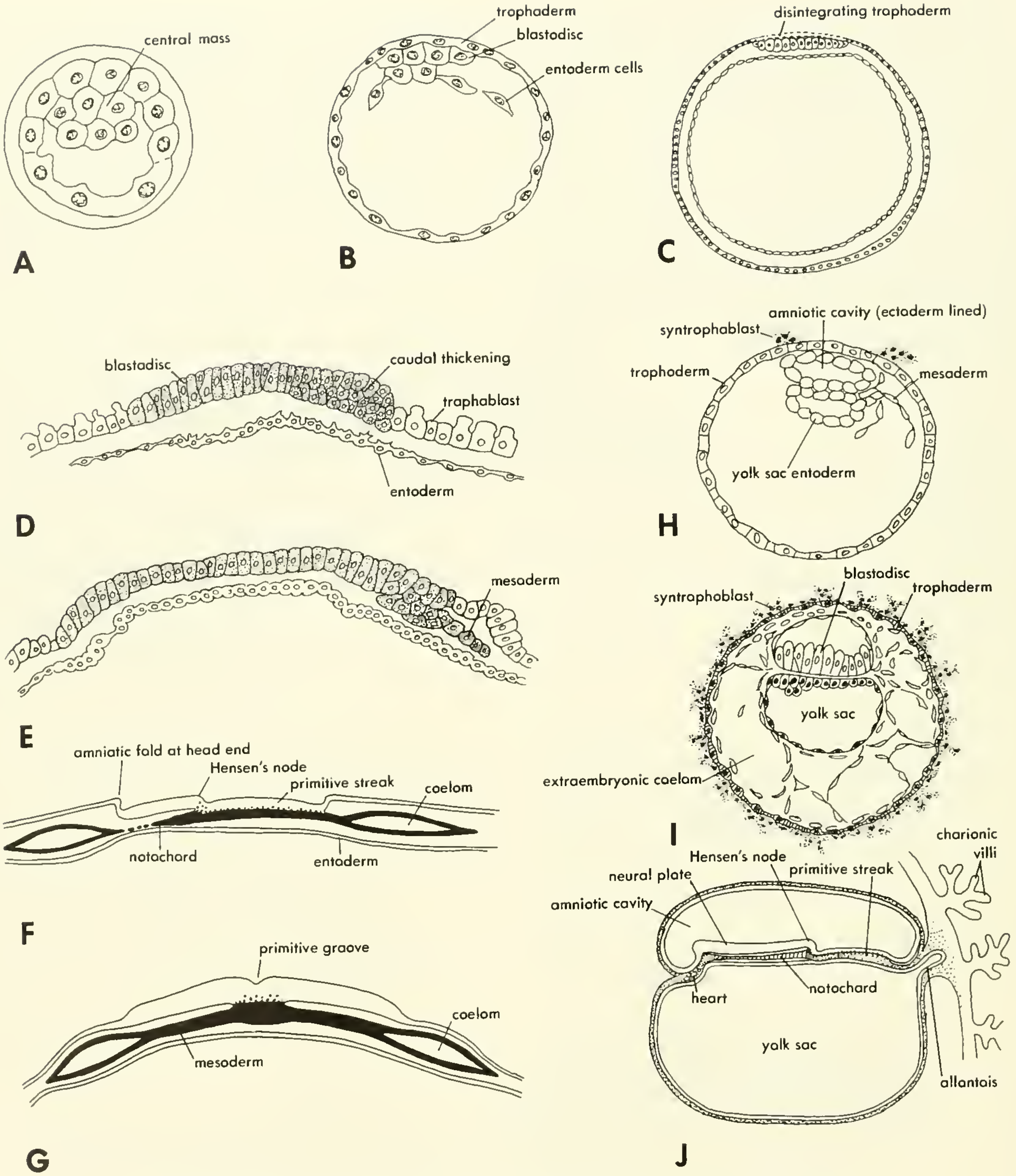


Figure 7-15. Stages of mammals. A, early blastula of pig with central mass; B, central mass cells forming blastodisc and entoderm; C, fully formed blastodisc without overlying trophoderm; D, sagittal section of blastodisc beginning gastrulation; E, early gastrulation; F, primitive streak stage and formation of head and tail fold of amnion; G, cross section of primitive streak of pig; H, formation of amniotic and yolk-sac vesicles and extraembryonic mesoderm from central mass in human; I, blastodisc development in human and differentiation of syntrophoblast and trophoderm; J, primitive streak stage of human (gastrulation of embryonic mesoderm and notochord). (After Patten, 1946)

placenta which is attached by folds to the uterine wall and which absorbs materials from the maternal blood (Figure 7-16). Many teleosts are **viviparous** (live-bearing) and show the same range of adaptations as the sharks.

Some other terms can be introduced here which apply to the conditions described. **Oviparous** describes those animals which lay eggs. **Ovoviviparous** describes the retention of eggs within the reproductive tract, or some specialized area (pits in skin, vocal sacs, or brood pouches), until the young hatch or complete their yolk-sustained development. Ovoviviparity grades into "viviparity." In the latter, the egg is usually yolk-poor, the developing embryo absorbs nutritive materials secreted by the uterine wall or has a very close tissue relationship with the uterine wall so that materials can be absorbed directly from the blood. This type might better be described as **metaviviparous** since viviparous only infers being born alive. From these definitions it follows that some sharks and teleosts are ovoviviparous, while others are metaviviparous.

In amphibians and reptiles viviparity sometimes occurs and a variety of relationships exists between the young and the parent. Among amphibians there is no indication of the absorption of nutritive materials. The opposite extreme is seen in some reptiles. In the lizards *Chalchides* and *Tiliqua,* a kind of placentation similar to that of the mammal is observed (Figure 7-17).

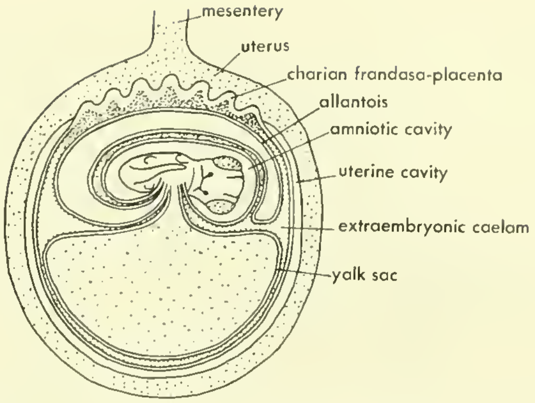


Figure 7-17. Chorioallantoic placenta of the lizard, *Tiligua scincoides.* (After deLange)

Mammals range from the nonplacental monotremes (oviparous to the highly developed placentals. In the marsupials the transition from ovoviviparous to metaviviparous is seen. In the former, the yolk sac is large and its blood supply modified. The embryo sinks down and is nearly enclosed in the yolk mass; the allantois develops as a finger-like projection down into the yolk mass. The vitelline veins on the surface of the yolk pass to either side of the neck of the allantoic sac (Figure 7-18).

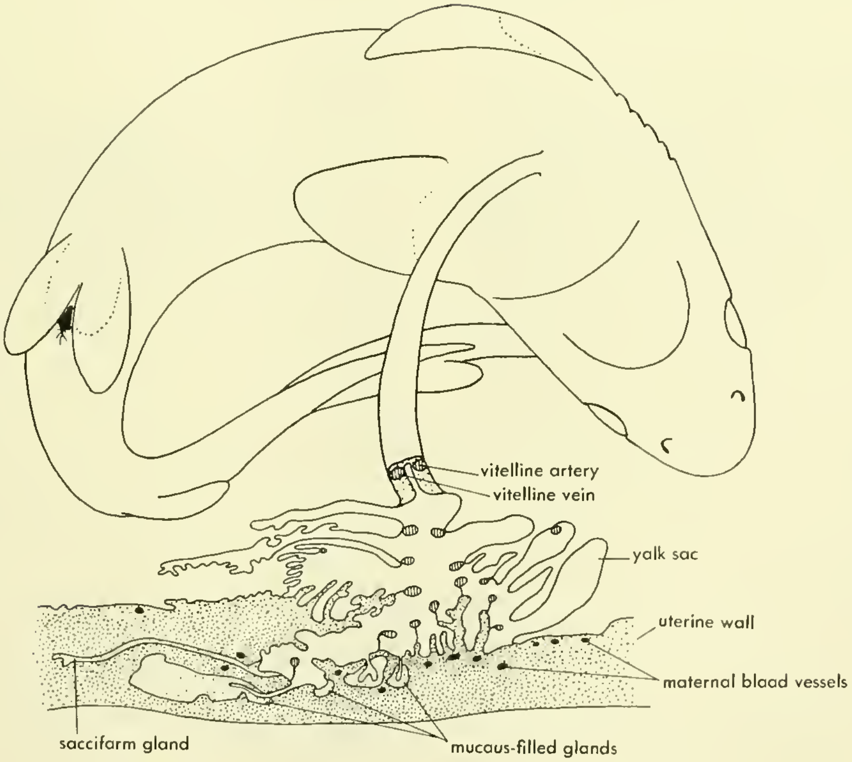


Figure 7-16. Yolk-sac placenta of *Mustelus canis.* (Mainly after Ranzi)

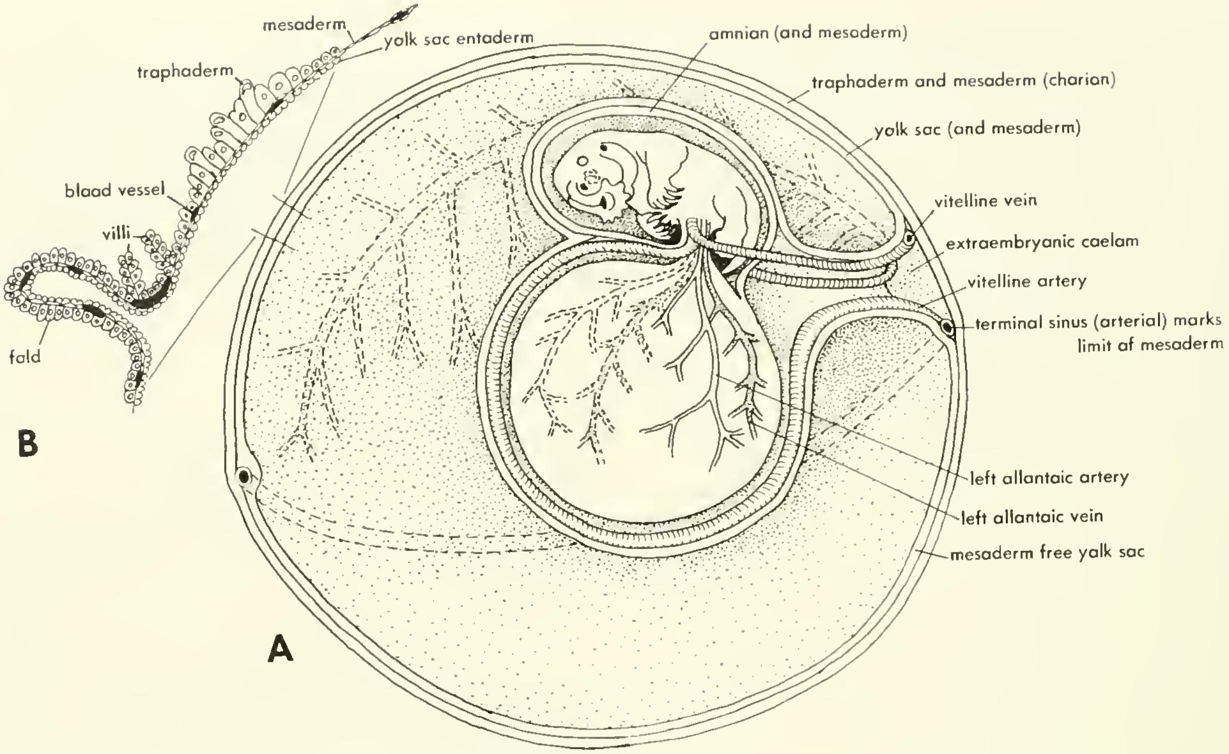


Figure 7-18. Yolk-sac placenta, enclosing allantoic vesicle, of the opossum, A, and details of the membranes of the placenta, B. (After de Lange)

The vitelline arteries unite and the single vessel passes down the posterior surface of the yolk-sac neck, then below the allantoic sac, and up behind that sac and back to the terminal, arterial sinus. The terminal sinus encircles the yolk mass at its middle. From here the blood is distributed to the ventral half of the yolk sac as well as the dorsal part. The yolk sac below the sinus terminalis has placental villi which interdigitate with processes of the lining of the maternal uterus, at least in the opossum.

The amount of nutritive material exchanged is probably slight. The young in the opossum are born about three days after the development of the yolk-sac placenta. In some marsupials the yolk-sac placenta is better developed and the period of its utilization is increased. In at least two genera, *Parameles* and *Phascolarctus*, the allantois reaches the chorion and fuses with its inner surface, so that during the later stages of placentation both vitelline and allantoic (chorio-allantoic) placentas function side by side.

In the placental mammals, one sees the gradual decrease in the importance of the yolk-sac placenta and an increase in the allantoic placenta. In this group, the yolk sac is never very large, nor does it form a part of the placenta (that part of the serosa which develops finger-like extensions or villi and attaches to the uterine wall). The allantois changes as its placenta becomes more effective. It changes from a large vesicle to a rather rudimentary one, but its blood vessels supply the mesoderm of the chorion and thus the placenta.

To increase the effectiveness of the placenta, it is necessary that the amount of tissue between the embryo and the parent be reduced. Various grades of reduction occur. In the **epitheliochorial type,** the embryo and maternal tissue lie in close interdigitating contact (pig—Figure 7-19). In the **syndesmochorial type,** the maternal uterine epithelium is eroded away between the embryonic membranes and the connective tissue of the uterus. The **endotheliochorial type** goes further with the erosion of the connective tissue, so that the embryonic tissues contact the maternal blood vessels (cow, sheep, goat). In the most advanced type, the **hemochorial** type, the embryo's blood vessels, enclosed by connective tissue, are bathed in the maternal blood.

The types of placentation observed in mammals are several (Figure 7-20): **diffuse,** having villi over the whole surface of the extraembryonic membranes (pig); **cotyledonary,** having patches of placental villi over the entire surface of the extraembryonic membranes (cow); **zonory,** having a band of villi encircling the membranous cover (cornivores); and **discoidal,** in which there is a single round area of **villi** (man) or two such areas (monkey). Generally, the embryo within its membranes lies in the uterine cavity, but in man it develops within the tissues of the uterine wall.

It is difficult to say whether there is any comparative

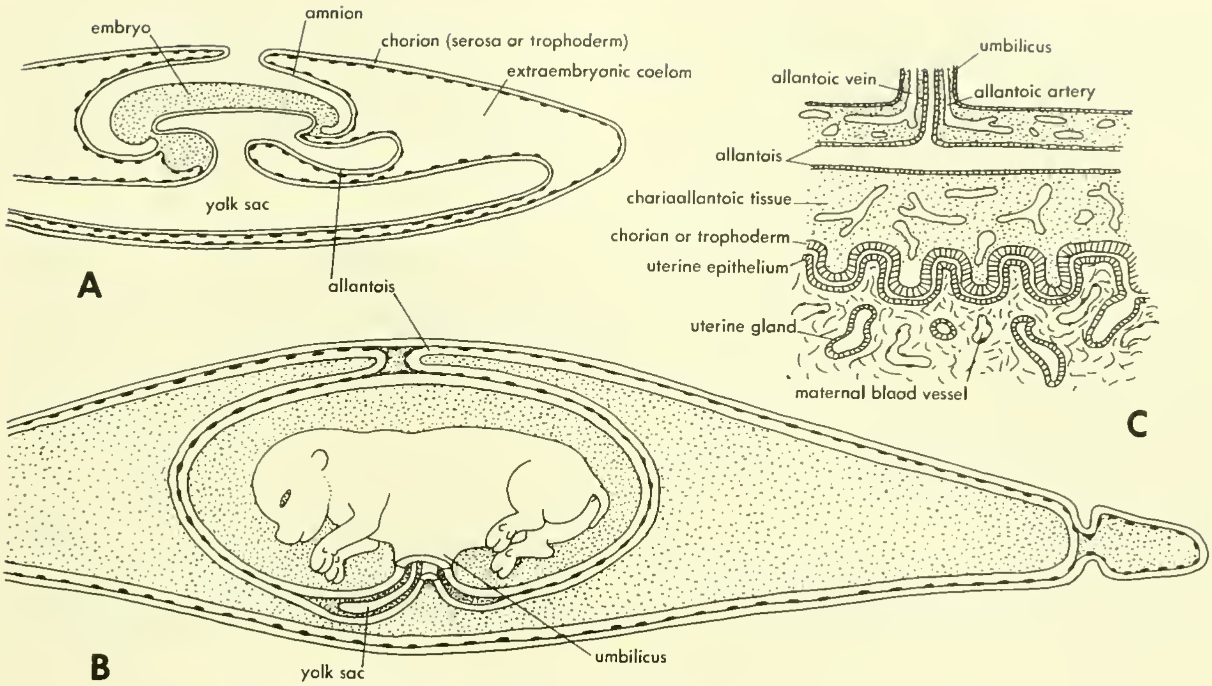


Figure 7-19. Amnion and placental development of the pig. A, 16 to 17-somite embryo and extraembryonic membranes seen in sagittal section; B, 4 to 5-week foetus in its membranes; C, diagrammatic detail of placental relationship to maternal tissues. (After Nelsen, 1953)

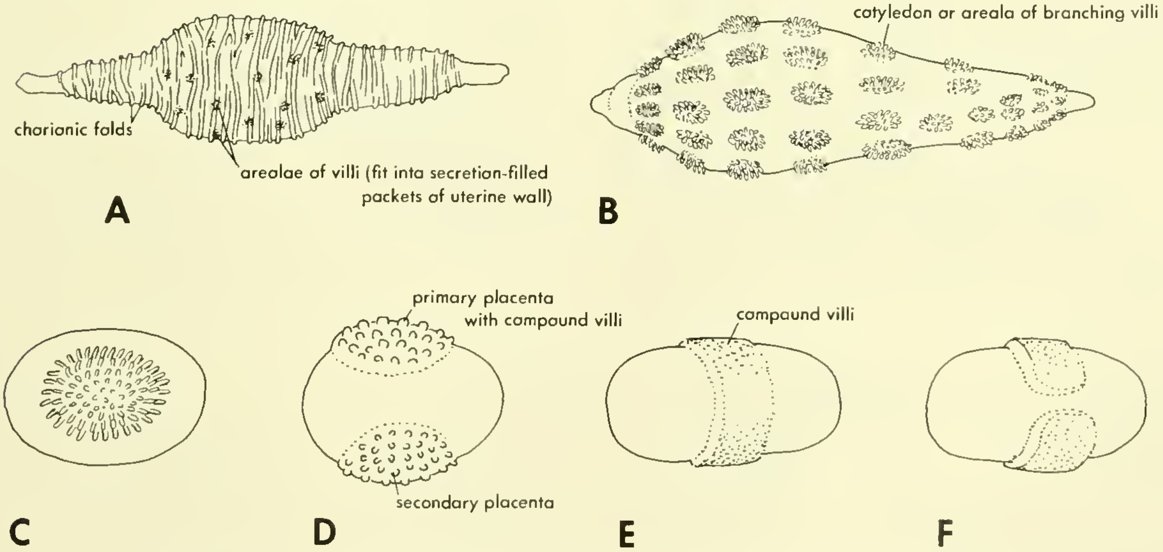


Figure 7-20. Placental types observed in mammals. A, diffuse with chorionic folds as scattered areolae of simple villi (pig); B, cotyledonary with scattered large areolae or cotyledons of branching villi (cow); C, discoidal with a single large arealus of compound villi (human, bear); D, double discoidal (monkey, gorilla); E, zonary formed by a belt of compound villi around the middle of the elongate foetal sac (dog, cat, seal); F, incomplete zonary (raccoon).

value in a study of placentation. This is a kind of specialization that, by its appearance in simpler forms, suggests that it is not particularly, important in revealing basic phylogenetic relationships. It is, however, certainly an interesting topic for functional investigation.

LARVAE

The larvae of vertebrates are of interest since they may indicate the primitive body form of this group (Figures 7-21 to 7-23). They may only indicate a developmental specialization brought about by the increase in size of the vertebrate. There is no evidence that the larval form is like the primitive or original stage on which the new adult form has been superimposed. All evidence seems to suggest that the larva, although it may be simpler in its structure, can be as highly specialized as the adult. The direct development observed in the higher forms is probably also a modification.

The larvae of vertebrates share various features in common. The general body organization includes a head, trunk, and tail, and there are two pairs of limbs. Development of these limbs appears to be direct to the fin or the foot. Larvae often have both external and internal gills. The external are perhaps a specialization for small size and simplicity, and the internal represent the adult type.

The larvae agree in that they undergo some sort of metamorphosis. This is well marked in the amphibian since it involves a conversion from an aquatic adaptation to an air-breathing terrestrial habit. However, a metamorphosis occurs in Amphioxus and the lamprey, which remain aquatic. Metamorphosis thus appears to be a basic part of the developmental sequence. This basic feature involves specialization of the larva in one direction, the adult in another. Metamorphosis may involve transfer from microscopic to macroscopic food.

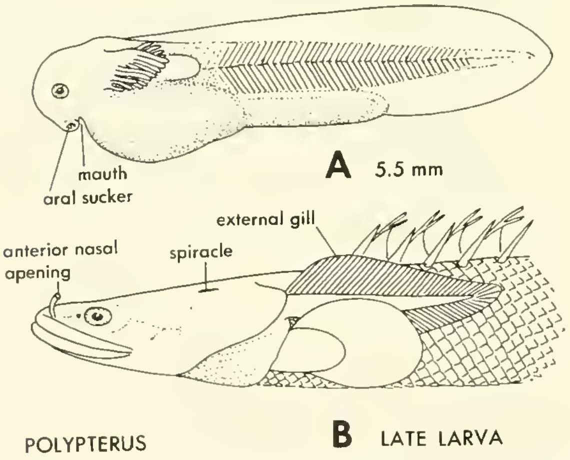


Figure 7-21. External form of early larva of *Polypterus*, A, and the form of the external gill of a later larva. (After Kerr, 1907, and Steindachner, 1869)

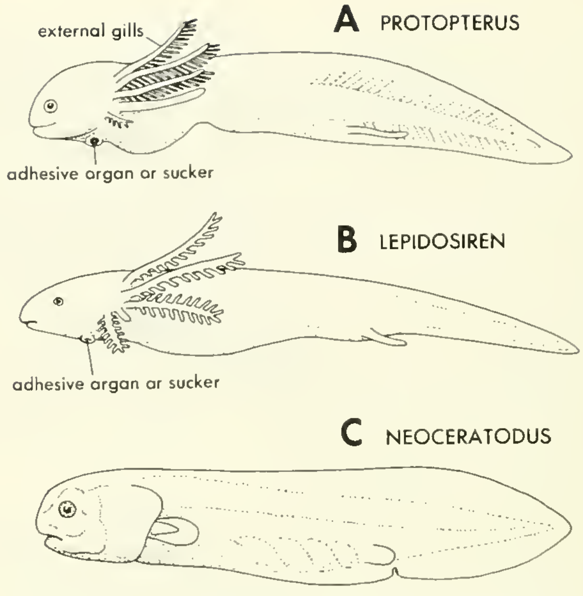


Figure 7-22. External form of early larvae of *Protopterus*, A, *Lepidosiren*, B, and *Neoceratodus*, C. (After Budgett, Kerr, Seman)

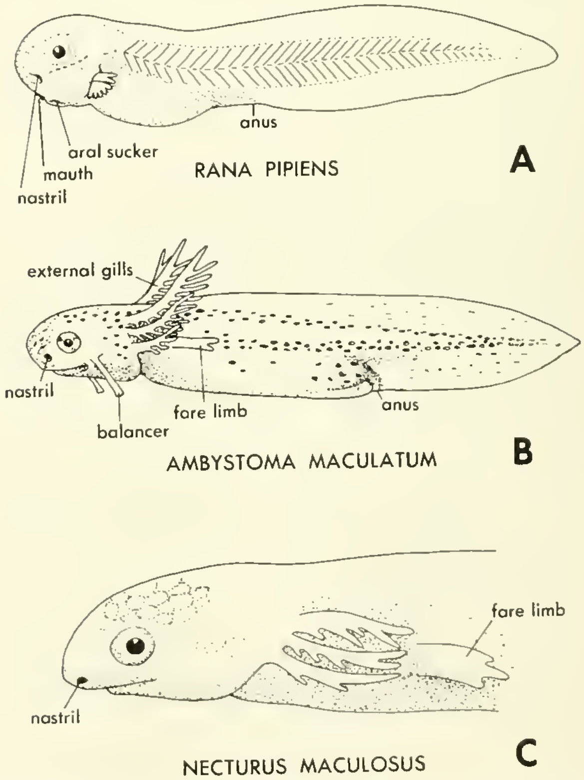


Figure 7-23. External form of larvae of *Rana pipiens*, A, *Ambystoma maculatum*, B, and *Necturus maculosus*, C. (A and B after Witschi, 1956; C after Nelsen, 1953)

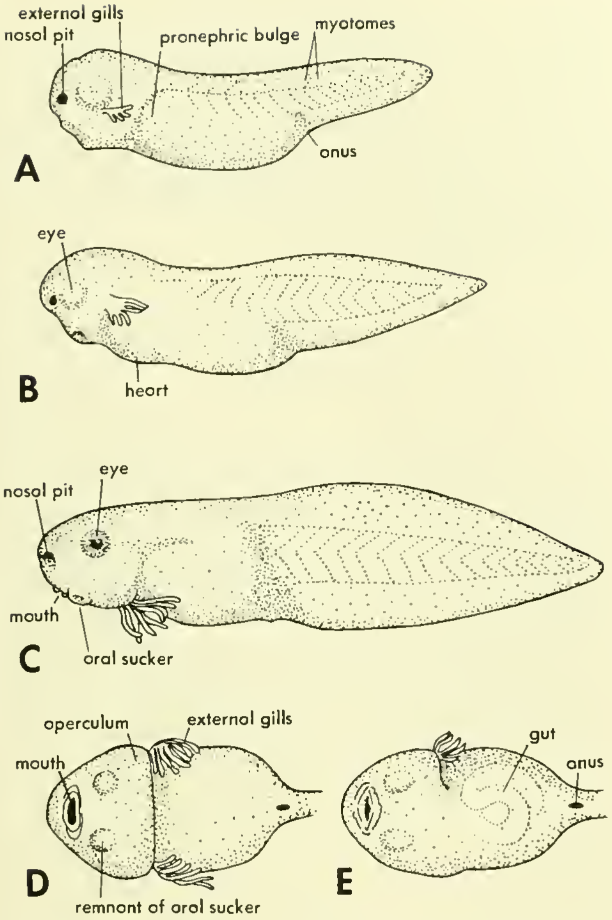


Figure 7-24. Some stages in the development of the frog larva. A, at hatching; B, 8-mm larva; C, 11½-mm larva; D, ventral view of head end of C to show beginning of opercular fold; E, opercular fold covering right branchial chamber with left chamber still opening broadly behind it. (After Huettner, 1949)

TABLE 7-1 A COMPARISON OF SOME OF THE FUNDAMENTAL EMBRYOLOGICAL FEATURES DIFFERENTIATING THE PROTOCHORDATES AND VERTEBRATES

Protochordate	Vertebrate
1. Sperm enters near vegetal pole.	1. Sperm enters near animal pole.
2. Mesoderm mostly from enterocoelous pouches.	2. Only a part of the mesoderm of the anterior head segments from enterocoelous pouches.
3. Notochord directly of archenteron wall origin.	3. Only the tip of the notochord indirectly from archenteron wall.
4. Blastopore converted by ventral blastopore lip growth into anterior neuropere. Gut and neural canal connected.	4. Blastopore closes; neurenteric canal of secondary origin and short lived
5. Neural tube formed by rolling upward of margins from rear to front.	5. Neural tube formed from groove which closes from front to rear.
6. Atrium formed by invagination of bilateral pouches or outgrowth of bilateral folds.	6. Atrium absent.
7. Gastrulation by simple invagination.	7. Gastrulation only partly due to invagination along a crescentric, circular, or straight line blastopore.
8. No neural crest.	8. Extensive sensory placodes and neural crest development in head and segmental pairs of neural crest masses through full length of body.

The larval forms of some tetrapods may be modified for direct development. Fine examples are observed among the frogs. The tail undergoes reduction, the limbs appear at a very early stage, an operculum covering the gills may not develop, and, in fact, the gills may not appear.

The young of the frog is one of the most interesting vertebrate larvae since it shows a certain parallelism to an assumed primitive type. The agnathous mouth is armed with horny teeth used for eating algae. Bony jaws develop later, replacing the original mouthparts. There is an operculum-enclosed branchial chamber which could be considered as a kind of atrium. This atrium opens on the left side of the body by a single opening. The asymmetry of this larva is suggestive of that observed in the protochordates.

The general opinion is that the frog larva is highly specialized rather than primitive. The fact that the anuran as an adult is greatly modified does not necessarily imply that its larva has not retained basic agnathous or even preagnathous features. Surely the algal food, reflected by the highly coiled gut, the mouth parts and other features, could be primitive. These features could just as easily represent a more modified scheme than the relatively straight, simple gut of the salamander larva. The observation that the straight gut precedes the highly coiled gut does not solve this problem, since it is necessary, as a matter of mechanics, that a short tubular gut increase in length to give rise to a coiled one.

Although a study of larvae could certainly be expanded far beyond the above brief account, the resulting contribution to the question of vertebrate phylogeny would be slight.

RESUMÉ OF EMBRYOGENESIS

The vertebrates generally agree in their early stages of development and show a marked similarity to the protochordates in some features. These two groups differ most notably in the ways summarized in Table 7-1. They agree in the general stages of cleavage, blastulation, gastrulation, and organogenesis. They are alike particularly in having the mouth and anus as secondary openings, the latter at the site of the blastopore, in having a large and variable number of segments, and in having a part of the body modified into a tail for swimming.

The general similarity of the early stages of development strengthens the idea that the vertebrates are monophyletic. There are some indications that the agnaths and gnathostomes are independent lines from the common ancestor. In terms of development the lamprey appears to be intermediate between the protochordate and gnathostome, being specialized only in having a solid neural keel. The neural tube of the myxinid tends to cancel this variation. In contrast to the gnathostome, the head somites are retained into the adult stage, suggesting less modification of this region, and thus giving some support to view that the agnaths preceded the gnathostomes.

8

The Skin and its Derivatives

The skin of the vertebrate consists of two layers, an outer epidermis of ectodermal origin and an inner dermis of mesodermal origin. Each of the layers, in contrast to those of the invertebrates, is formed of several kinds of cells and several forms of the same kind of cell (Figures 8-1, 8-2). Both parts may be involved in the skin derivatives, which include teeth, scales, bony plates, keratinized scales, nails, feathers, hair, several types of glands (including the mammary glands), and many sensory structures. The latter, with one exception (prototrichs), will be described as parts of the nervous system.

SKIN

The **epidermis** of the higher forms is stratified into several layers of cells. Essentially one type of cell is envolved in the epidermis, and it undergoes several changes in form as it moves from the base of the epidermis to the surface. This outer layer of the skin is generally without a blood supply and without nerves, although sensory cells, are found here in the lower forms. In a few instances, nerve endings may penetrate the epidermis. Capillaries lie close to the basal layer of the epidermis, the Malpighian layer or **stratum germinativum,** from which the cells of the epidermis are

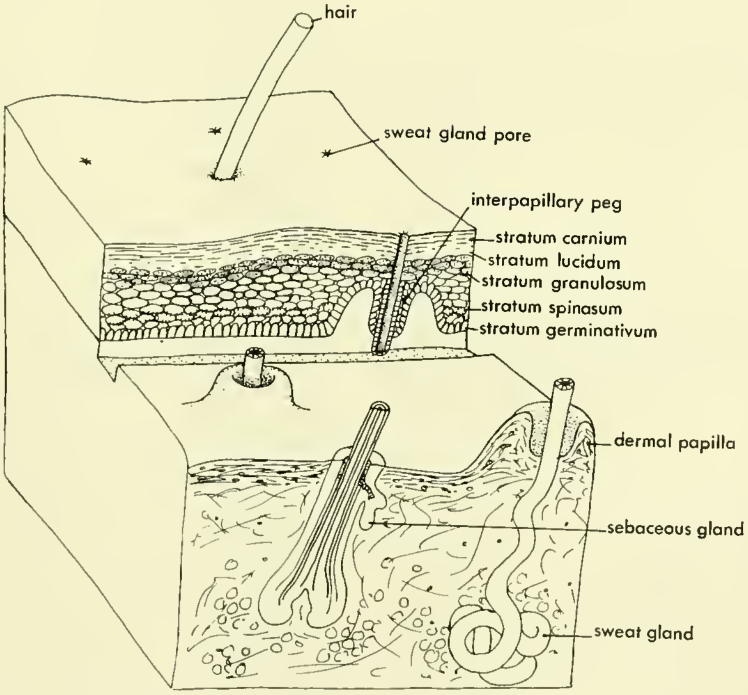


Figure 8-1. A steriadiagram of human skin. The outer layer of epidermis is several times thicker than it should be in order to show its layering. The hair follicle is proportionally reduced in order to keep the follicle within the limits of the diagram; the diameter of the hair is actually somewhat greater than the thickness of the epidermis (see Figure 8-3).

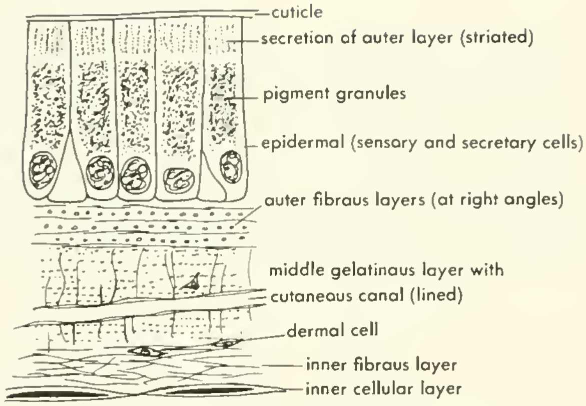


Figure 8-2. Section through the skin of amphioxus.

derived. New generations of cells are **delaminated** from this layer and move outward with each subsequent generation until they reach the surface and are sloughed off.

The **dermis** is a fibroelastic connective tissue in which the multicellular glands of the epidermis are embedded. This layer of the skin is formed around interlaced collagenous and elastic fibers in a gelatinous matrix. The outer layer is usually the more densely fibrous, while deeper parts are more open. This tissue may become bony or filled with fat cells. Its surface capillary net is of importance in the maintenance of the epidermis and, in some animals, for respiration.

The skin functions in a number of ways. It forms an envelope for the body, and a surface of contact with the environment. It protects the body from abrasion, presents a barrier to disease, acts as a barrier to free exchange of material with the environment (mainly water), and becomes involved in body temperature control with the production of feathers and fur.

Mammals

The epidermis of the mammal is covered externally by the **stratum corneum,** a layer of flattened, keratinized, dead cells. The thickness of this cornified layer varies according to the amount of wear to which the skin is exposed. Thick or thin, this layer functions as a protection against drying and is lubricated by **sweat** and by **sebaceous** (oil secreting) **glands.** In the epidermis of man there is a sequence of cell layers. This sequence is as follows: stratum germinativum at the base, **stratum spinosum, stratum granulosum, stratum lucidum,** and **stratum corneum.** The cells of the stratum germinativum are generally pigmented. This pigment is produced by **melanoblasts** (melanin is the name of the black or brown pigment) and passed from these cells to **chromatophores** (literally "I carry color"). The term chromatophore is sometimes used as a synonym for melanoblast.

The dermis, or **corium,** has an outer **papillary layer** in which there is a dense mat of fibers parallel to the surface. Below this is a **reticular layer** with much intercellular material. The two layers grade one into the other. The collagen fibers of the papillary layer are finer than those of the reticular part. The cells of the dermis are mainly **fibroblasts** with a few **macrophages** and **pigment cells** (melanoblasts). **Fat cells** vary in number and are particularly abundant in the deeper part.

Sweat glands are found over most of the body in many mammals; they may be lacking in some rodents and rabbits, or limited to the pads of the feet in other rodents. In man, these glands are particularly numerous in the thick skin of the palms and soles. They are **tubular glands** extending from the surface far down into the dermis through the **interpapillary pegs** of the **papillae.** Sweat glands are of two basic types: the **apocrine,** which secretes a milky fluid, and the **eccrine,** which produces a watery fluid. The eccrine, the smaller of the two, is the typical sweat gland of the body surface.

The apocrine type occurs in the armpit, on the external genitalia, around the nipples of the breasts, and around the anus. Modified sweat glands produce the wax of the **external auditory meatus** (outer ear opening), and give rise to the **Moll's glands** of the eyelid. The sweat is expelled from the secretory basal part by the contraction of the enclosing myoepithelial cells.

The thin skin of the general body surface has irregular dermal papillae; each of these has an interpapillary peg of epidermis penetrated by a sweat gland. The body is covered by **hair.** Each hair is embedded in a **follicle** and each follicle has **sebaceous glands** opening into it. Sebaceous glands are simple, branched, **alveolar** (little sacs) glands (Figure 8-3). Such glands are also found in the lips at the corner of the mouth, on the glans penis and the internal fold of the prepuce, on the labia minora, and on the nipple. In these areas they open directly on the skin surface and are not related to hairs. The **Meibomian glands** of the eyelid edge are similar.

The hair may be short or long and of different textures. It is deciduous and continually replaced. Hairs may be modified into **spines** in the Echidna, the hedgehog, or porcupine. Scales occur on the tails of rodents and over the entire dorsal and lateral aspect of the body of the pangolin (Figure 8-4). Hairs grow from between these scales, and, when scales are lacking, the groups of hairs have the same pattern as when scales are present.

The stratum corneum is modified in the production of horns (Figure 8-5), hoofs, claws, and nails. In these, and in the scales of pangolin, a harder, more homogeneous keratin layer is produced, which grows outward from a basal area of origin.

The horn of the rhinoceros is described as being formed of hair, but it can also be described as formed of cornified fibers or tubes embedded in a keratin matrix. The nature of the follicles of these hairs is generally not described. The horn grows upward from a basal generative area of the skin

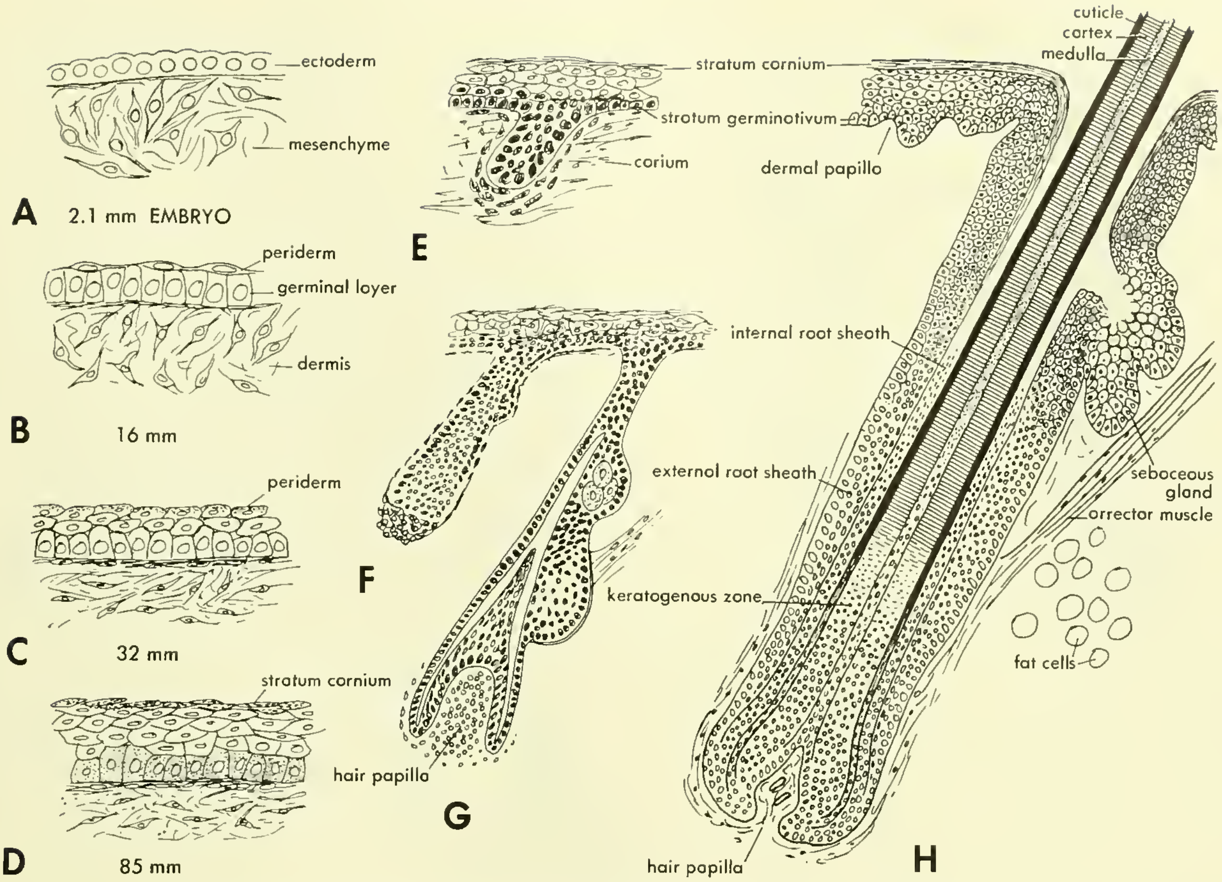


Figure 8-3. Development of the human epidermis and hair follicle. A, epidermis of 2.1-mm embryo; B, epidermis of 16-mm embryo; C, epidermis of 32-mm embryo; D, epidermis of 85-mm embryo; E to H, progressive stages in the development of the follicle and hair. (After Patten, 1946)

of the snout. It is not strengthened by a bony core as in the cow but is seated on a bony knob of the skull. The pointed tip is produced and maintained by wear.

Embryological development The ectoderm is at first a simple cuboidal epithelium which gradually becomes stratified (Figure 8-3). Hair begins its development as thickenings of the epidermis. Each such thickening grows down into the dermis as a strand which carries the stratum germinativum before it. A dermal papilla now forms which projects upward into the strand. The cells overlying the papilla form the matrix from which the hair grows upward through the strand. The strand is thus converted into a follicle. Sebaceous glands form from the wall of the follicle. The sweat glands form as ingrowths from the epidermis.

The soft keratin of the stratum corneum is formed by accumulation of granules within the cells which pass through a number of steps. Being cellular, the stratum corneum desquamates at its surface.

The mammary glands are generally considered to be modified sweat glands, although they might just as easily be viewed as sebaceous glands. Pertinent to this question is the observation that in man the apocrine sweat gland of the arm pit and the nipple undergo cyclic changes which can be correlated with the menstrual cycle. Unlike the sweat glands, the mammary glands are compound and alveolar, and they are related to mammary hairs. In man about eight hair fol-

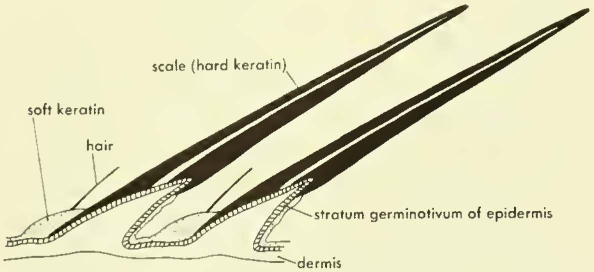


Figure 8-4. Section through two scales of a pangolin, *Manis tricuspis*. (After Weber)

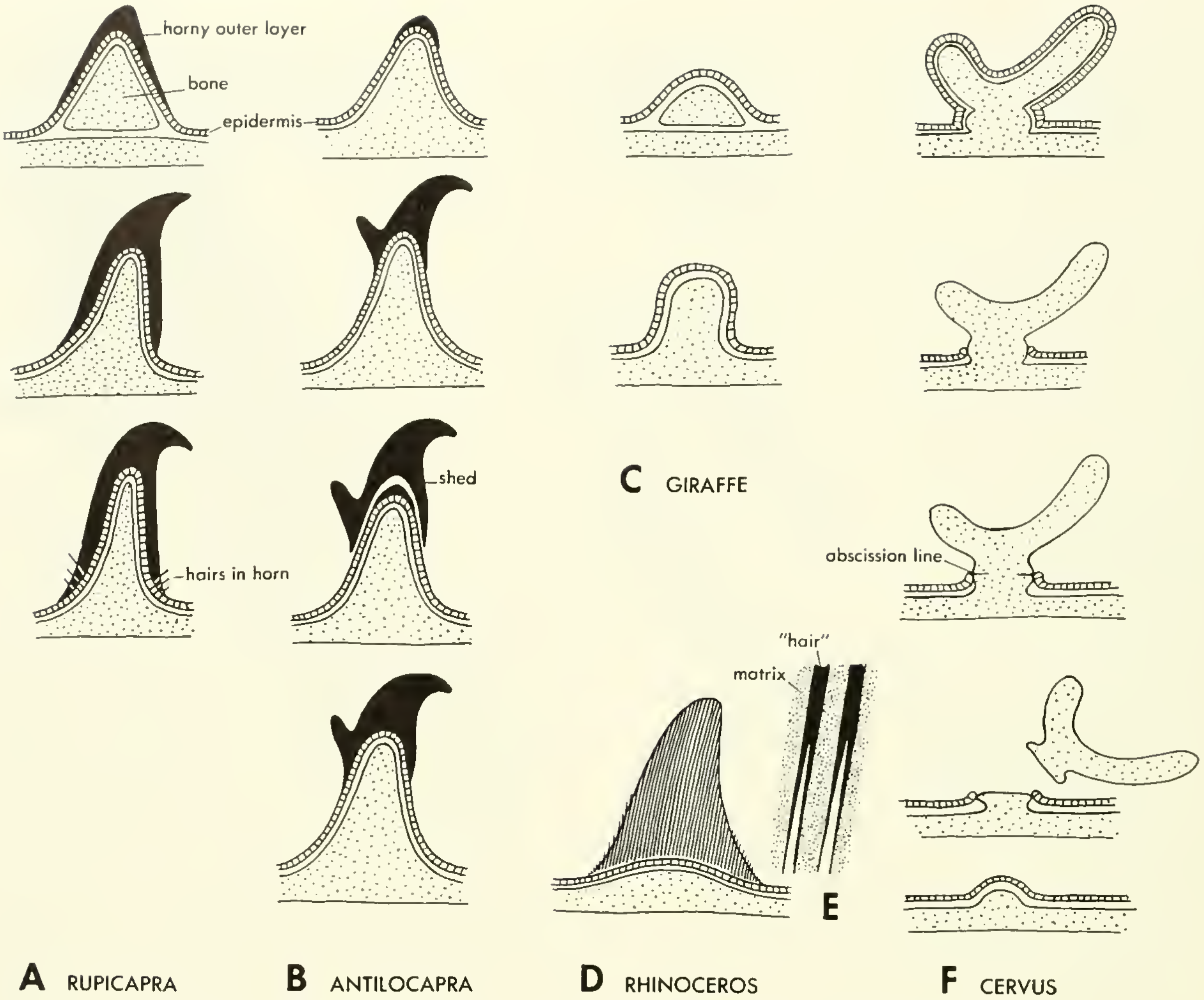


Figure 8-5. Horns of different types; their growth and replacement. A, chamois or cow (continuous growth); B, Prong-horned Antilope (shed annually); C, giraffe with knobs of skull covered by skin (continuous growth); D, fibrous or "hair" horn of rhinoceros (continuous growth); E, detail of hairs embedded in matrix of rhinoceros horn; F, bony horn of the deer (shed annually). (After Erdmann, 1934)

licles are involved in the origin of the mammary glands, which suggests that they are modified sebaceous glands.

The **areolar glands of Montgomery** are about intermediate in form between the apocrine sweat gland and the mammary glands, thus indicating the possibility of transition from sweat to mammary gland. The apocrine sweat glands and sebaceous glands at the edge of the areola of the nipple open together. These glands may have developed from lactation hair follicles. The intergradation of sweat, mammary, and sebaceous glands suggests they are all intimately related.

In monotremes, the mammary glands originate from hair follicles that form two bands along the belly of the embryo; these bands are called the milk lines. Mammary development is limited to bilateral areas of these strips on the lower part of the belly, and nipples are not formed. The glands open on a pair of bare areas in **Ornithorhynchus**, and, in the Echidna, into a pair of invaginated pockets lying in the side walls of the marsupium, or pouch.

In marsupials, several mammary glands arise from paired invaginations of epidermis along the milk lines on the lower belly. From the bottom of these invaginations, hair follicles develop, and from these, mammary and sebaceous glands arise. Later the hair follicles degenerate, leaving the glands opening into the bottom of the nipple primordeum, which then evaginates. The several pairs of nipples are located in the marsupium.

In the mammal, the nipple primordea develop along the milk ridge as in the marsupial. These anlagen are associated with mammary hairs which, if they persisted, would project from the tip of the nipple—through the openings of the mammary gland ducts. Lactation hairs may surround the area of the nipple. The position and number of the mammary glands varies.

Reptiles

The skin of the reptile is covered by **keratin scales,** each of which covers an epidermal and dermal scale elevation. The scale cover is continuous over the entire body but thinner in the grooves between the scales. Periodically it is shed, a process called **ecdesis** (Figure 8-6).

Close examination of the lizard's skin shows at least two types of scales: the large scales usually described and smaller ones lying between these (Figure 8-7). In *Iguana,* the small scales are quite pointed. Histological examination reveals sensory structures, the **prototrichs,** on some large and many small scales (Figures 8-8, 8-9). The **protothrix** (singular of prototrichs) of the reptile has been described as the precursor of the hair of the mammal, as the term itself declares. It is quite possible that the small scales margining the large scales are the forerunners of both hair and feathers. The homology of these scales with the feather is most probable.

Osteoderms sometimes lie in the dermis below the scale. These bony plates may have the same distribution as the keratin scales or be quite independent of them. The bony plates (**osteoderms**) are tied into the dermis by **Sharpey's fibers,** just as the scales of fishes are. Osteoderms are typical of the crocodilian and some lizards. In the turtle, the carapace is formed basically of osteoderm and rib contributions. These are covered externally by horny epidermal scales; the epidermis lies between these scales and the bony base.

The epidermis of the reptile is generally without glands, although special glands occur in different reptiles; the lizard has femoral glands along the posteroventral margin of the thigh (Figure 8-6). The alligator has inframandibular and cloacal scent glands which are functional during the reproductive period.

The development of the skin of the reptile is very much the same as that of the mammal (Figure 8-3). At first there is a simple cuboidal ectoderm which differentiates into an outer periderm and a basal germinal layer. As outer layers are added, the epidermis becomes stratified, and the scales appear.

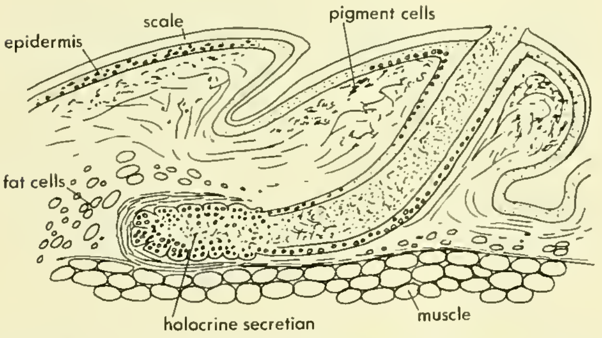


Figure 8-6. Section through skin showing a femoral organ (male) and the scales of the lizard, *Lacerta agilis.* (After Tälg, 1905)

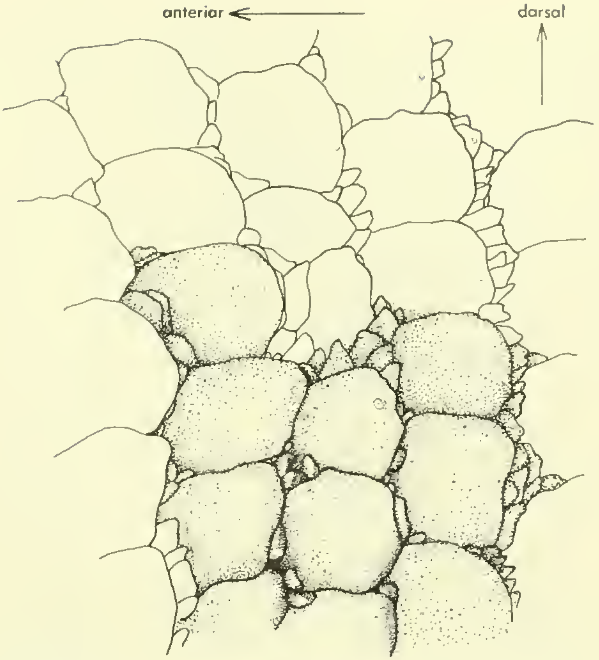


Figure 8-7. View of an area of scales in the shoulder region of *Iguana.*

Bird

The skin of the bird is generally thin since it is overlaid by a thick cover of feathers. The skin is dry with a stratum

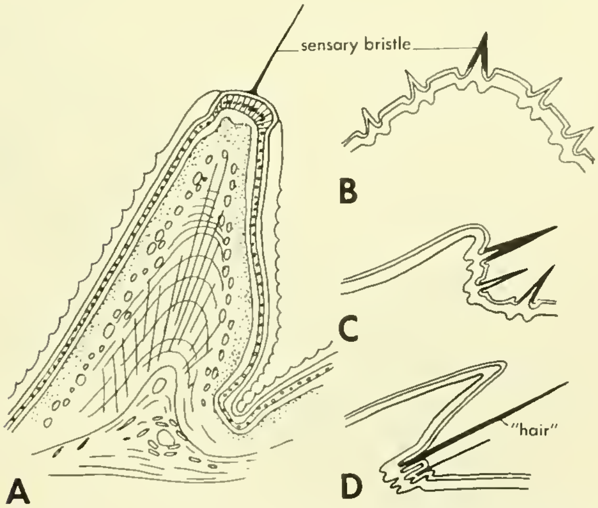


Figure 8-8. A, section through a scale of *Calotes* with a sensory bristle at its tip. B to D, series of sketches showing transition from wart and prototriches of the amphibian to the retrosquamous hairs of the mammal as conceived by Elias and Bortner (1957).

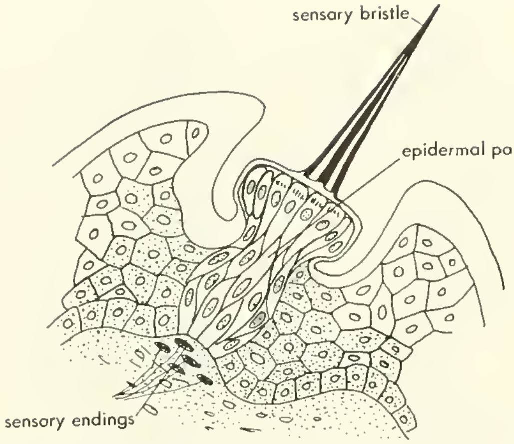


Figure 8-9. Histology of a sensory organ or the scale of a lizard (*Agama*). (After Elias and Bartner, 1957)

corneum of soft keratin and a few layers of transitional cells above the flattened (**squamous**) stratum germinativum (Figure 8-10). The dermis is frequently filled with fat cells. The only glands are the paired multisacculate **uropygial glands** opening on a papilla above the tail. These glands secrete an oily fluid used by the bird to condition the bill sheath and the feathers. The bill sheath (Figure 8-11) is like the nail or claw of the mammal; there are also scales and claws on the feet. Claws frequently occur at the tips of the anterior and middle wing digits, at least in the young.

The feathers are epidermal derivatives usually described as modified scales. This homology is based on the observation that, in the pigeon, feathers appear to arise out of the scales of the lower leg. The scales of the pigeon leg are really scutes formed by the fusion of several scales. Where scales and feathers are both present, as in the Barn Owl, it is observed that the feather is an interscale structure like the hair. This similarity in scale relationship between feather and hair does not indicate an homology, even though these structures are analogous in that they insulate the body surface. The feathers have two functions: they help in maintaining a high body temperature and they are important for flight.

The feathers are of two main types: **plumes** or pinnaceous structures and **plumules** or down, including filoplumes. The plumes are distributed on the body in oblique rows and concentrated into **pterylae** separated by areas free of such feathers, the **apteria.** Down may cover the apteria and occur among the plumes as well. In structure the feather is complex, and in development it stems from a papilla enclosed by a **follicle** not unlike that from which the hair develops.

Amphibians

Although it has a thin cellular **stratum corneum** (Figure 8-12), the skin of the amphibian is moist and fre-

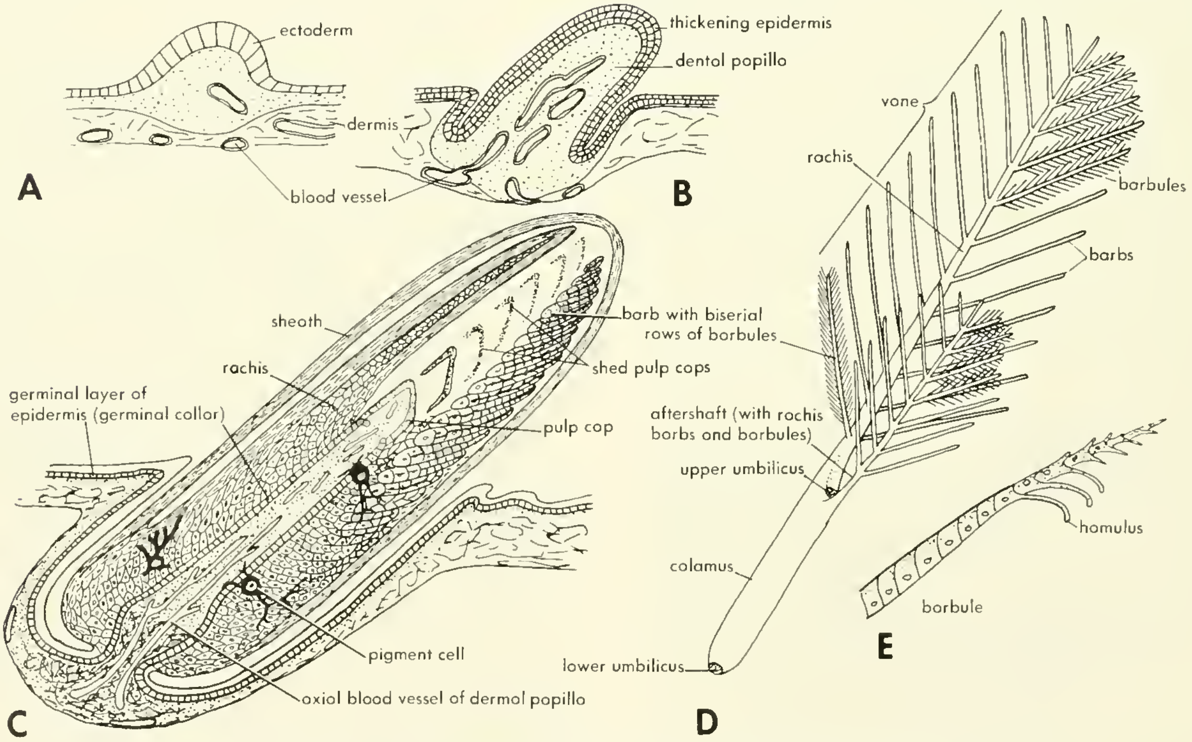


Figure 8-10. Development of the feather. A, initial papilla; B, beginning of follicle formation; C, differentiation of feather parts which are identified in D and E. (After Witschi, 1956)

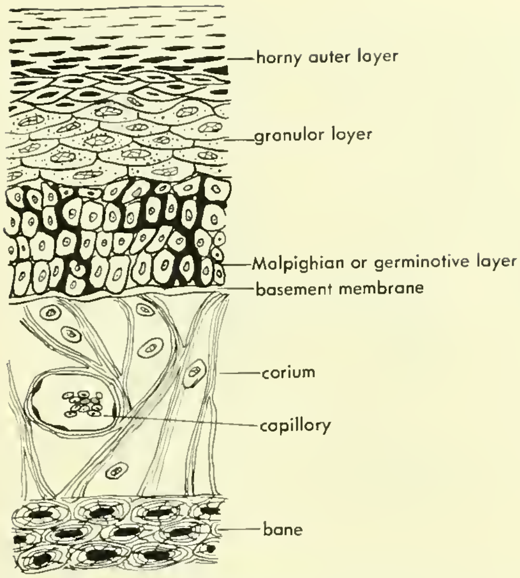


Figure 8-11. Section through the bony sheath of the bill of a young sparrow. (After Witschi and Woods, 1936)

quently slimy. The frog skin, representative of the class, has a low, columnar **stratum germinativum,** several layers of increasingly shorter cells grading into flattened cells, and an outer squamous ("scaly") layer, which is slightly cornified. In toads the stratum corneum is thicker. In most amphibians a periodic **ecdesis** of the stratum corneum occurs. Keratinization is carried further in forming the covers of the tips of the toes and in the digging spade of *Pelobates,* the Spade-foot Toad. Most amphibians have microscopic bumps or warts on the skin which are the sensory papillae and are formed of knots of enlarged cells associated with nerve endings (Figure 8-13). The sensory papilla may have a thickened overlying stratum corneum suggesting the protothrix.

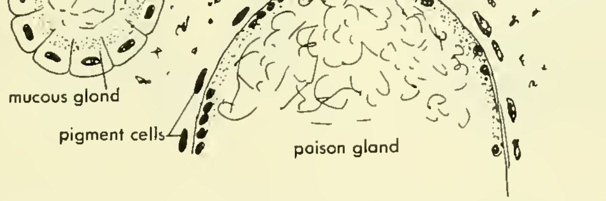


Figure 8-12. Somewhat diagrammatic section of frog skin (*Rana pipiens*).

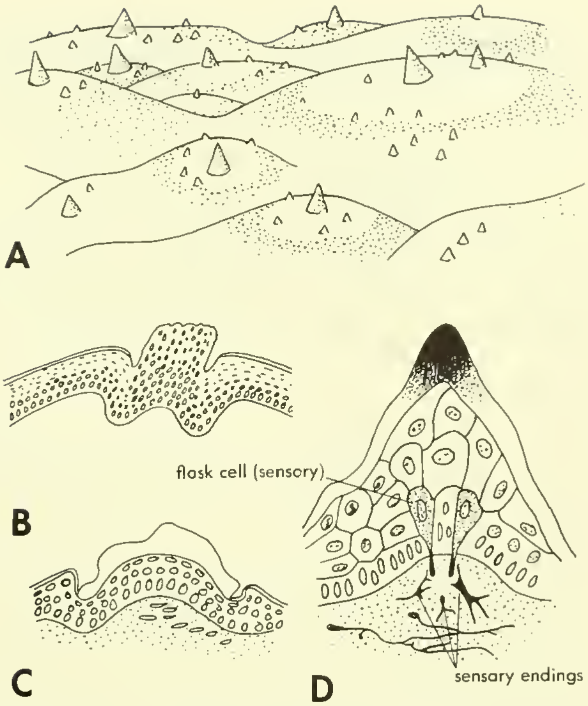


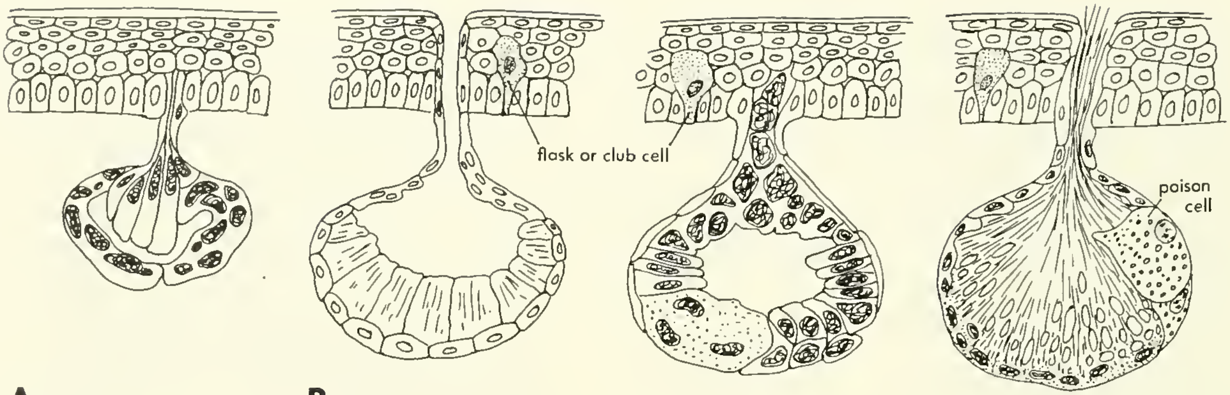
Figure 8-13. Prototriches of the skin of amphibians. A, surface view of skin of toad, *Scaphiopus hammondi;* B, section of sensory bud of *Cryptobranchus;* C, section of circumfossate cone of *Scaphiopus hurteri;* D, section through cone of *Bufo americana.* (After Elias and Bortner, 1957)

The epidermis is separated from the dermis by a **basement membrane** and a fibrous layer containing **pigment cells.** There is a problem here of differentiating between cells which actually produce the pigment, **chromatoblasts,** and cells, the **chromatophores,** which contain pigment acquired from the chromatoblasts. The chromatoblasts are of neural crest origin (Figures 7-7 J and 9-15) and have numerous and irregular processes extending out from the cell body. Cells with such processes will hereafter be referred to as **chromatocytes.** The chromatocytes act in the color changes so characteristic of amphibians and reptiles. Some of the chromatocytes invade the epidermis.

Embedded in the dermis are saccular **poison** and **mucous glands** of epidermal origin. The poison gland, with granular secretory cells, is the larger and more deeply located. The cells of the poison gland wall are irregularly spaced with clumps of nuclei around the periphery. This type of gland has a heavier sheath of connective and muscular tissue. The poison glands occur on the dorsal surface of the body and function as a predation deterrent.

The mucous glands, lying close below the epidermis, have a low cuboidal, or almost squamous, cell lining. Occasionally, mixed mucous and poison glands are observed.

In *Necturus,* there are numerous club or flask-shaped cells in the epidermis (Figure 8-14). These cells appear to be



A YOUNG MUCOUS GLAND **B** SPENT MUCOUS GLAND **C** POISON GLAND **D** MIXED GLAND

Figure 8-14. Sections through various epidermal glands of *Necturus*. A, young mucous gland; B, spent mucous gland; C, poison gland; D, mixed mucous and poison gland.

glandular and function along with the saccular mucous glands. In the salamander, the poison glands are nearly the same size as the mucous glands, but the lining of secretory cells is of a more irregular thickness and has clumps of nuclei. The granular contents of the gland is somewhat different in appearance from that of the mucous gland. The epidermis of *Cryptobranchus* is invaded by blood capillaries as a part of the respiratory function of the skin.

The skin of the Gymnophiona is thick and contains groups of dermal scales and large multicellular posion glands of a **holocrine** (entire cell breaks down) type (Figure 8-15).

The epidermis of the early embryo is composed of an outer ciliated **periderm** and a deeper **stratum germinativum.** This condition persists up to a size of about 10 mm. when the epidermis, now somewhat thicker, loses the cilia and becomes covered by a thin hyaline (clear) cuticula of secreted material similar to the basement membrane and the intercellular substance.

Choanate fishes

The skin of *Latimeria* is described as simple in structure. The epidermis is stratified and has a thick basement membrane. There are mucous cells and chromatocytes in the epidermis. The dermis is thick, fibrous and has many fat cells.

In *Protopterus*, a dipnoan, the epidermis is stratified with a basal, low columnar stratum germinativum and four or

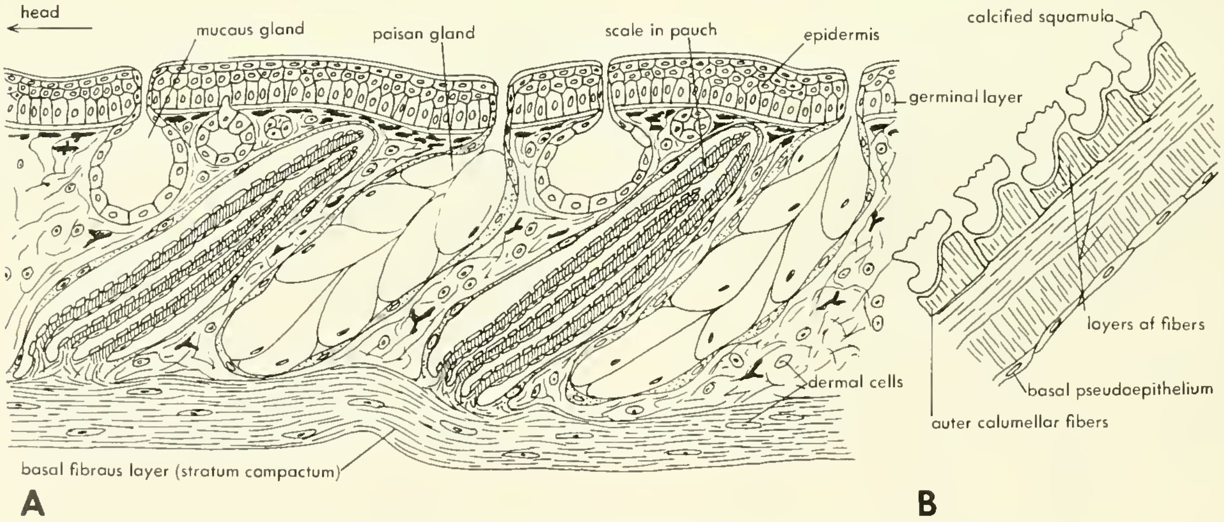


Figure 8-15. A, section through the skin of *Ichthyophis glutinosus* showing glands and groups of scales enclosed in sacs. B, enlarged section of a scale showing the various layers. (After P. and F. Sarasin, 1887)

five layers of cells. There is a well-marked external squamous layer (Figure 8-16) and a thick basement membrane. In the epidermis there are large **mucous cells** (Becker's cells) which move outward as they develop. They shed their contents from a narrow surface tip, and then are moved out of the epidermis. Multicellular glands like those of the amphibian, but smaller, have been described but are not observed in most preparations. Sensory organs, much like those of *Squalus* (Figure 8-19 C), are scattered over the body. Pigment cells are found in the epidermis and throughout the dermis.

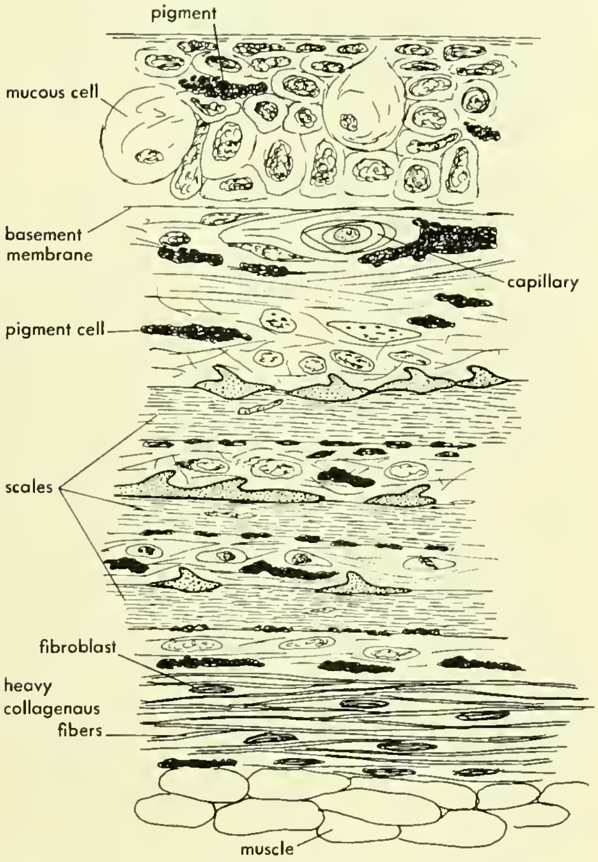


Figure 8-16. Section through the skin of the lungfish *Protopterus* showing the overlapping scales deep in the dermis.

The dermis has many fibroblasts in it and is permeated superficially by a network of capillaries. The outer layer of the dermis, which contains the scales, is a loose **areolar** (referring to the scattered spots or nuclei) **tissue** which may have fat cells scattered through it. A dense layer of collagenous fibers lies next to the body muscles. In cross sections of the dermis, one sees parts of several scales, which lie in dermal pockets.

Actinopterygian fishes

The skin of the actinopterygian fish is like that of the choanate (Figure 8-17). The epidermis is dotted by **pearl** (or sensory) organs and overlies the scales (Figure 8-18). The pearl organs are perhaps related to the prototrichs of higher forms. In addition to the mucous cells of the surface, two types of secretory cells are observed. These are the **granular secretory cells,** or serous bladders, and the **club cells.** The former begins as a large **Leydig's cell,** then becomes filled with a granular secretion which is expelled to the surface by a tubular extension of the cell. The club cells produce the **intercellular matrix** of the epidermis. Tubular, multicellular glands are observed on the snout and with decreasing frequency further back on the body. **Poison glands,** formed by clumps of holocrine cells, are associated with opercular or dorsal spines in some fishes. The epidermis is occasionally invaded by blood capillaries as in the upper lip of *Periophthalmus.*

As in the choanates, the dermis encloses the scales lying in sacs. **Sharpey's fibers** penetrate the ganoid type of scales, tying them together as well as into the fibrous network of the dermis (Figure 8-36). Sharpey's fibers are evident only in teleosts with thick bony scales (siluroids, Figure 8-39 C). The dermis contains several colors of **chromatocytes** and

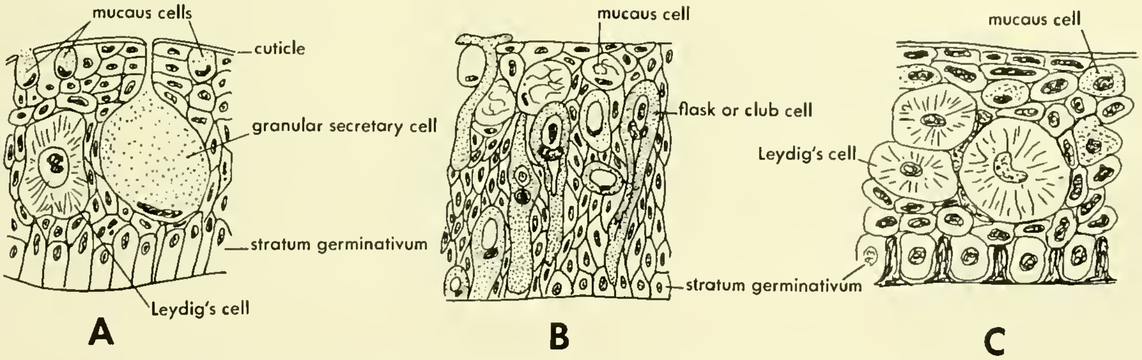


Figure 8-17. Sections through the epidermis of three teleosts, A. *Callichthys punctatus,* an armored catfish; *Anguilla vulgaris,* the common eel; C, *Perca flavescens,* the yellow perch.

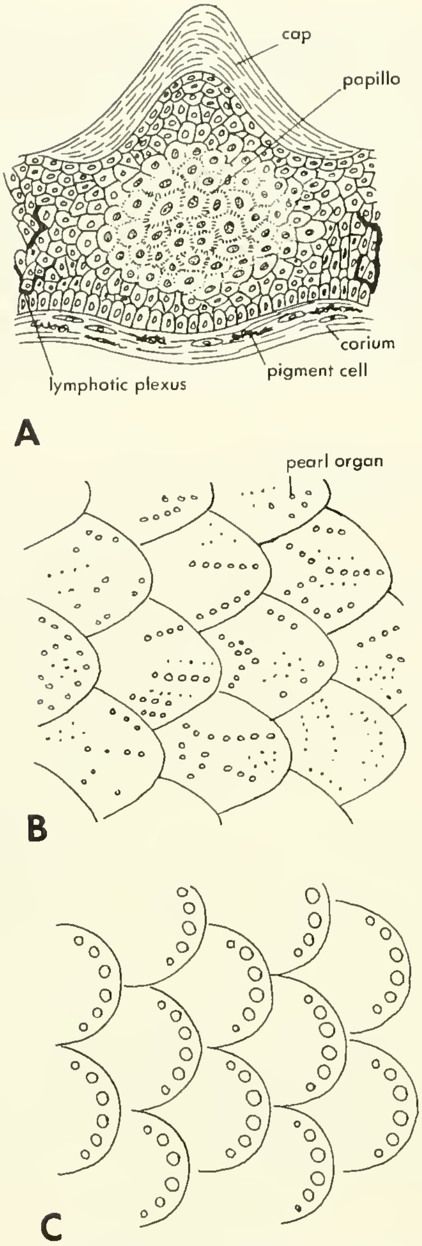


Figure 8-18. Prototriches or "pearl organs" of teleosts. A, section through one on the forehead of *Idus melanotus;* B, on body scales of *Barbus vulgaris* and, C, *Phoxinus phoxinus.* (After Rabl, 1931)

also guanin containing **iridocytes,** which are responsible for the silver color of many fishes. The innermost layer of the dermis is densely fibrous.

Chondrichthyes

In the sharks, the points of the placoid scales extend out through the epidermis (Figure 8-19). The dermis has three layers: an outer layer around the necks of the scales, which is nearly free of fiber; the **stratum laxum,** a laminated fibrous layer to which the base of the scale is tied by Sharpey's fibers; the **stratum compactum;** and a **subcutaneous layer** of variable thickness, in which a reticulum of fine fibers is observed. There is a fairly sharp line of demarcation between the last two.

The young shark has ciliated cells intermixed with large mucoid cells in the epidermis. As the animal increases in size the cilia are lost and the stratified condition is achieved. Sensory organs (Figure 8-19 C), presumed to be related to prototrichs, are scattered over the body. The scales do not appear till quite late.

Cyclostomes

In the lamprey, the epidermis is many cells thick (Figure 8-20). The main **epidermal cells** are very small, and among them are **granular** and **club-shaped** secretory **cells.** The outer layer of this epithelium is modified into "calcareous cells," which have a modified, impregnated, outer surface. These cells are overlaid by a thin **cuticle** and the entire epidermis is supported by **perpendicular fibers** from the thin **basement membrane.**

The **dermis** is stratified into an outer, thick, laminated, **fibrous layer** below the epidermis; next is a thin **pigment layer,** and below this a reticular **subcutaneous layer.** There are no scales.

Myxine is similar in having a thick epidermis covered by mucous (Figure 8-21). The outer cell layer is made up of columnar **mucous cells,** while deeper in the epidermis are large **bladder cells** and somewhat smaller **thread** or filament **cells.** Along the ventrolateral margins of the body, the epidermis forms saccular **slime glands,** which utilize the same kinds of secretory cells as the general epidermis.

The dermis is stratified into an outer layer of **fibrous laminae** enclosing **pigment cells** and **fibroblasts** and a deeper **subcutaneous layer** of fatty areolar tissue.

SCALES

One of the most informative products of the skin, in terms of phylogeny, is the scale. The fish scale is not the homolog of the mammal or reptilian scale that has already been described. The mammalian and reptilian scales are imbricated, keratinized thickenings of the stratum corneum, while the fish scale is a bony product, primarily of the dermis. The osteoderm of the reptile may be the homolog of the fish scale, or at least the closest approach to it. Teeth are related to, or derived from, true scales. Scales and teeth are easily preserved and present the first fossil evidence of the vertebrates.

Structural materials of the scales

By way of introduction, the placoid scale of the shark, which is also presumed to be like the forerunner of the tooth,

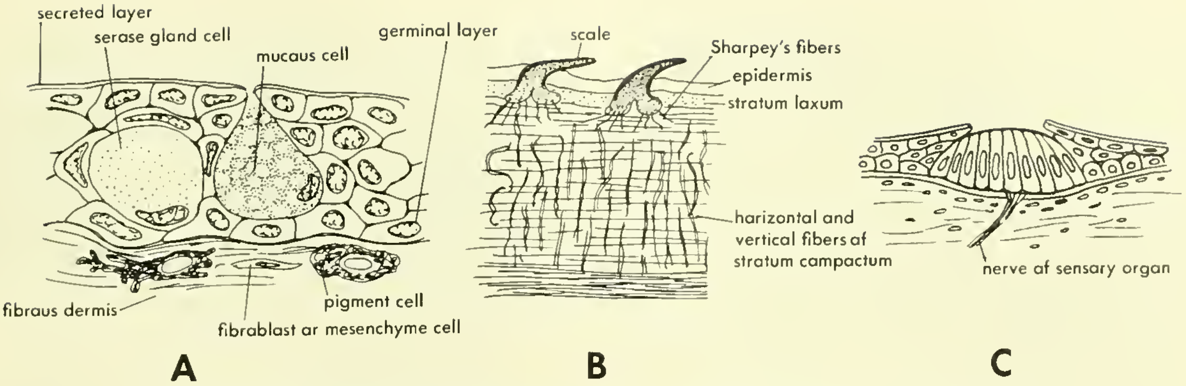


Figure 8-19. The skin of elasmobranchs. A, section of epidermis of the ray, *Raja punctata;* B, section of skin of *Squalus* showing fibrous divisions of the dermis; C, sensory organ of epidermis of *Squalus acanthias.* (After Rabl, 1931)

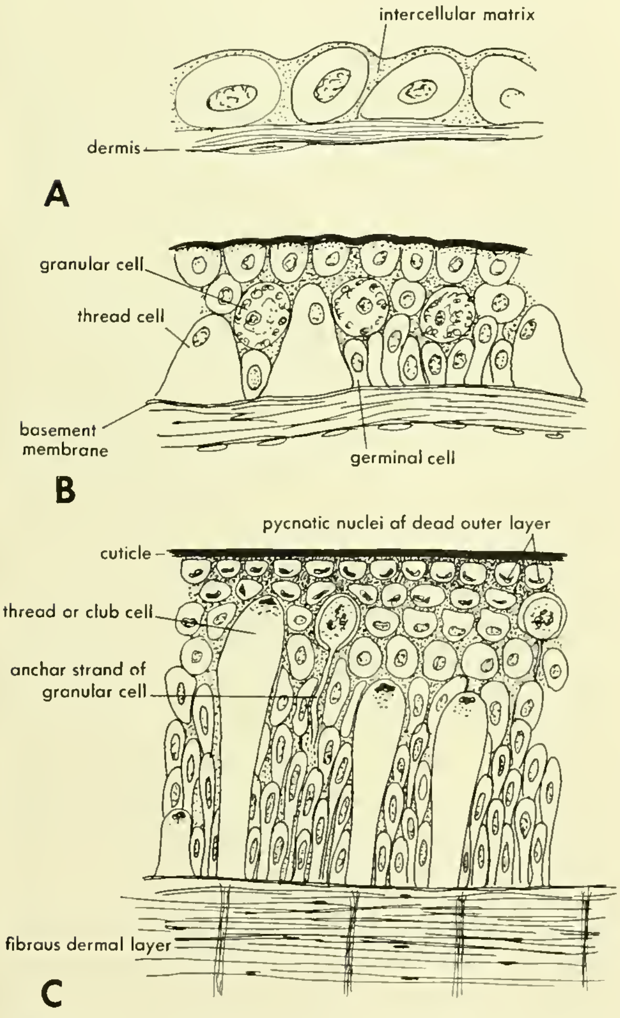


Figure 8-20. Development of the skin of the lamprey. A, skin of 10-mm larva; B, skin of 90-mm lamprey; C, epidermis and part of dermis of adult.

can be described. The denticle (Figure 8-22) consists of an enamel cover over a dentine tubercle containing a pulp cavity. This tubercle is attached to a dentine or bony basal plate set in the dermis. The terms enamel, dentine, and even bone refer to human materials; the first two to parts of the tooth.

Enamel Enamel can be described in terms of its crystalline structure and low organic content; it does not contain cell spaces. It is also described in terms of its embryological origin, being a product of an ectodermal enamel organ. In discussing the scales of various fishes, there is considerable doubt as to whether the smooth, glassy material on the outer surface of the tubercles is enamel and the interior substance dentine. These hard materials may be only analogous products to those of the human tooth.

The question whether or not the selachians possess enamel has been much discussed with divergent conclusions. The enamel-like materials of lower vertebrates agree with dentine in terms of the orientation of their hydroxyapatite crystals, but the birefringence of these materials is as a rule

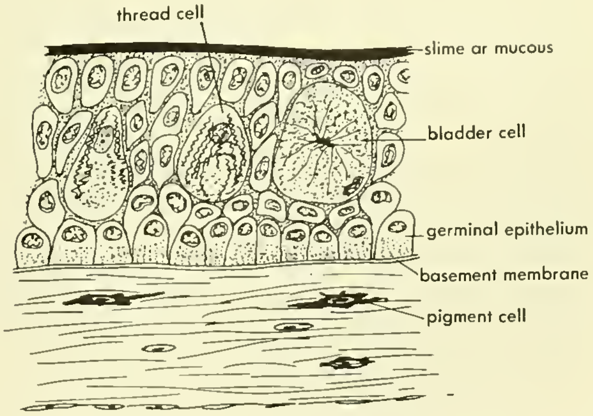


Figure 8-21. Skin of *Myxine* (After Schreiner).

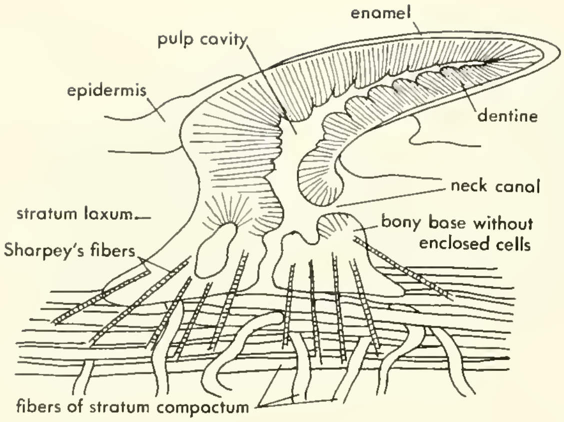


Figure 8-22. Section of placoid scale of *Squalus*.

stronger than that of the normal dentine, the collagen has almost disappeared, and the lime-impregnation has increased. These hard substances do not differ much from true enamel and may represent enamel at an early phylogenetic stage.

One of the most controversial enamels is ganoin, which occurs in many of the actinopterygian fishes. It has been considered as bone, as dentine, and as enamel. Many have regarded ganoin as a special type of hard tissue not because of its structure, which has been fairly little known in recent forms, but because of its development—its mesodermal origin. The growth of ganoin takes place as the result of periodic overgrowth of the external face of the scale by mesodermal tissue. A salt-impregnated layer is laid down in this tissue under the influence of the overlying ectoderm. This periodic growth in thickness by apposition of new layers is quite different from the development of mammalian enamel. The position of the ganoin films between layers of bone or dentine in the fully developed spines and dermal bones of *Polypterus* does not prove anything with regard to the original place of formation and the nature of ganoin.

Dentine Definition of dentine presents similar problems. There are three principle types: **osteodentine, tubulodentine,** and **orthodentine.** Orthodentine consists of an outer layer of **pallial dentine** and inner layers of **circumpular dentine** (Figure 8-23). In these the dentinal tubules radiate out from a central pulp canal. **Vasodentine** is a modification lacking the dentinal tubules but with radiating capillary channels which anastomose (join) through numerous cross channels. **Plicidentine,** as observed in the labyrinthodont tooth (Figure 8-61), is a variety of orthodentine.

Tubulodentine is made up of parallel orthodentine tubules joined by an interstitial material: an enamel-like petrodentine or bone (Figure 8-55). This type appears to have originated by the fusion of a large number of teeth into a plate, as in the lungfishes, and some rays (Figure 8-55).

Osteodentine (Figure 8-23) is composed of a reticulum (net) of dentinal osteons, similar to the Haversian systems of bone, and an interstitial bony substance which contains or is devoid of cell spaces. This bony substance arises first as trabecles, in the pulp tissue. The dentinal osteons are then deposited within the trabecles without any prior resorption of hard tissue. The periodic deposition of the osteodentine produces the increasingly smaller tubular laminae making up the osteon.

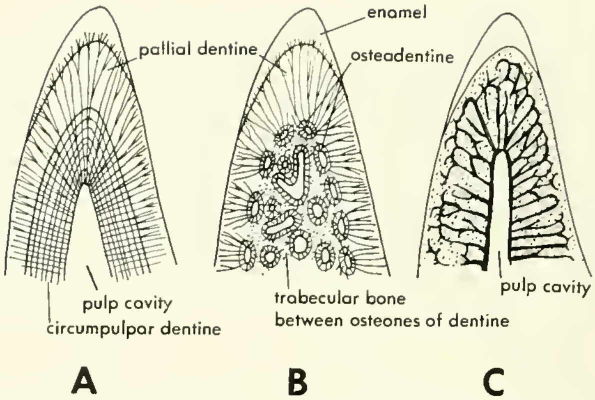


Figure 8-23. Types of dentine observed in fish teeth. A, orthodentine outer layer of pallial dentine enclosing circumpulpar laminae; B, osteodentine inside pallial orthodentine; C, vasodentine. (After Ørvig, 1951)

Typical dentine has very fine, sometimes branching, nearly parallel tubules extending outward from the pulp cavity. In **semidentine** (Figure 8-27) the tubules are still quite parallel one to another, but they have fine side branches extending out almost at right angles. The **unipolar odontoblasts,** the cells producing dentine, are embedded in the dentine next to the pulp or vascular cavity and the single large protoplasmic extension (which may branch) of each extends into the dentinal tubule for some distance. The term unipolar refers to this process. In **mesodentine,** a variant of semidentine (Figure 8-26), the embedded cells are of the unipolar type; there are more of them, and their lacunae (the spaces in which the cell bodies lie) are interconnected.

Summarizing, enamel is produced by the epidermis or in the most superficial part of the dermis under the influence of the epidermis; it may consist of modified dentine, calcified basement membrane of the epidermis, a modified layer of mesodermal tissue, or a secreted layer of epidermal origin. Dentine is presumed to be a product of the outer region of the dermis. The deeper this material is formed in the corium, the more bone-like it is. Dentine may enclose the cells forming it or be acellular.

Bone Thin sections of mammalian bone show **Haversian systems** of cell lacunae around **vascular canals** (Figure 8-24). These systems, or **osteons,** can be laid down or resorbed by the cells of the bone. In a typical bone, primary osteon systems are sometimes partly resorbed and the

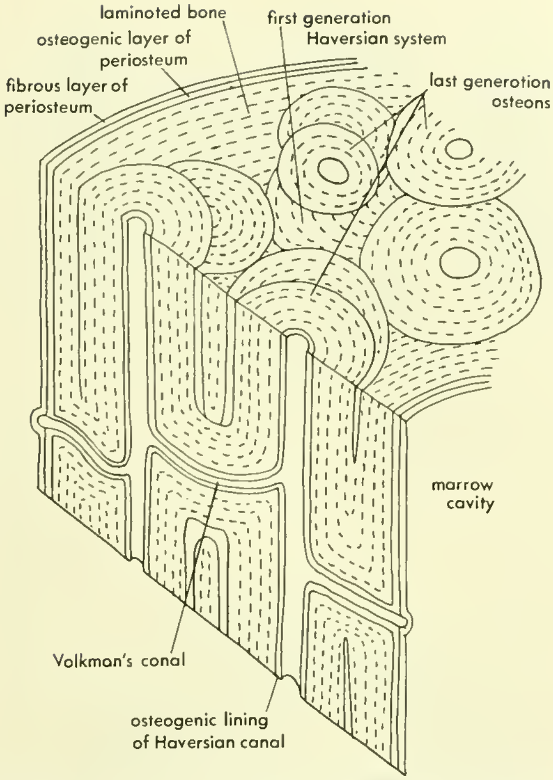


Figure 8-24. Stereodiagrammatic piece of mammalian bone showing the outer and inner laminate layers between which are several generations of Haversian systems.

spaces filled in with new osteon systems. In contrast to dentine, the cells are **multipolar** with arborizing (branching) processes extending out in every direction. Acellular bone is without lacunae or channels for cell processes.

Among primitive vertebrates Haversian or osteon systems were not generally employed in bone structure; the bone was of a simple laminar type, being added to at its surfaces. This laminar bone was penetrated by blood vessels, the focal point for tubular arrangements of cell systems. The interior of thick bones was generally spongy, and the marrow spaces were irregularly crossed by thin splints (trabecles) or plates of bone. In development, an animal may start with laminar bone, erode parts of this away around blood channels (through the action of **osteoclasts**), and replace these regions with osteon systems. The marrow spaces may also be filled with osteons. In this way, an adult bone may be a complex of structural types.

In some groups, bone has been modified by the removal of cells. In the teleost fishes, the bones generally are thin and formed of laminae between which there are no cell lacunae.

In considering the scale structure of the various kinds of vertebrates, it seems best, in order to retain the sequence of simple to complex, to begin with the agnaths.

Agnaths

The earliest scales and plates (Middle Ordovician) are assumed to be those of heterostracan agnaths, *Astraspis, Pycnaspis,* and *Eriptychius.* These identities are based on the histological differences observed in sections cut from the fossil scales and plates.

The plates of these genera have scattered superficial **tubercles** formed of dentine (Figure 8-25). The plate is formed of **aspiden,** an acellular bone. The aspiden is permeated with irregular and anastomosing channels which extend up into the bases of the tubercles as **pulp cavities** and open through the dorsal and ventral surfaces of the plate. These channels were occupied in life by blood vessels and the cells producing the aspiden. The aspiden between channels is permeated by tubules for collagenous **Sharpey's fibers.**

In some of the heterostracans, the pteraspids, the plates have a thin **enamel** cover for the tubercles or ridges. The outer and basal plates of aspiden laminae are separated by thin verticle **septa.** These septa form a polygonal pattern when seen in frontal section. The large chambers enclosed by these septa were probably filled with marrow.

The osteostracan plate is like that of the heterostracan, except that it is formed of cellular bone (Figure 8-26). The dentine is cellular, that is, **semidentine** or **mesodentine.** A thin layer of **enamel** covers the tubercles or the general surface of the plates. The plate may have large chambers or a spongy interior.

The development of the plates of *Tremataspis,* an early Upper Silurian form, has been described. It is of interest that all of the specimens (2000 or more) are of adult size and that all but a few are fully armored. The conclusion is that armor did not develop until the animal was fully grown and once present, the animal's size was fixed. The outer layers of mesodentine appeared first; then bone enclosed the mucous canals of the sensory system (Chapter 13) and the underlying and parallel vascular channels. The laminated basal part began to form. The space between the superficial mesodentine layer and this base was filled in gradually with spongy bone, while new laminae were added to the inner surface of the base.

It has been assumed that at least some immature osteostracans were covered by a **shagreen** (referring to the rough surface) of small denticles. These denticles consist of **dentine** and semidentine (or mesodentine) with an interior **pulp cavity,** covered externally by a layer of **enamel**—that is, they are placoid scales. If the young were covered by such scales, growth of the armor would involve connecting these and adding deeper layers just as in *Tremataspis.* Sometimes the first placoid scales are retained on the surface of the armor or they may be replaced with secondary and larger denticles. In the armor of some cephalaspids, new generations of denticles are superimposed on earlier ones. As a generality, later growth of the armor involved only additions to the

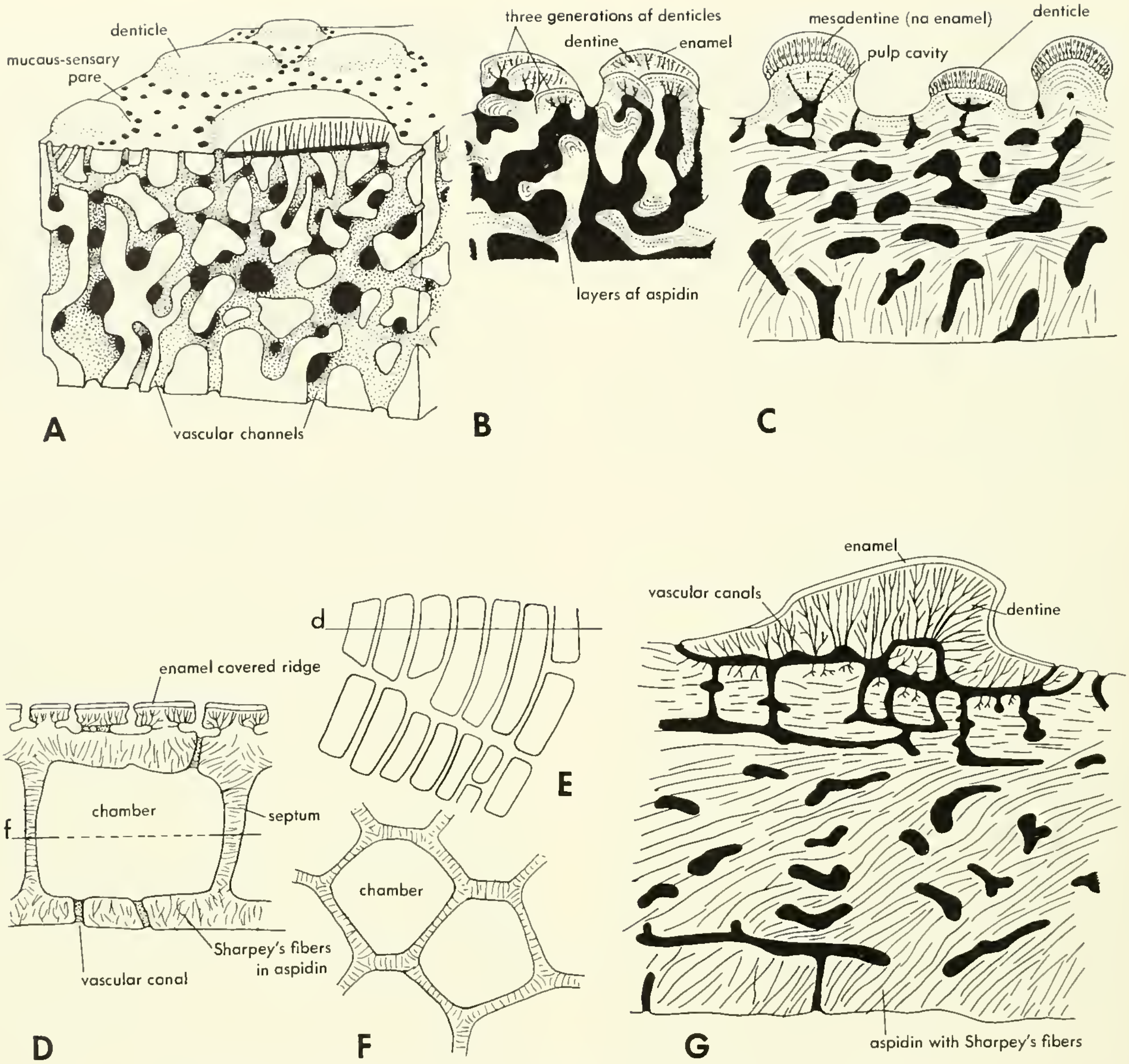


Figure 8-25. Armor and scale structure of heterostracans. A, stereodiagram of piece of plate of *Eryptychius* sp? from the Upper Ordovician; B, *Eryptychius* sp?, section of scale with three generations of denticles; C, *Pycnaspis splendens,* section of plate; D, section of armor of *Sanidaspis siberica* cut along line d shown in E; E, surface pattern of enameled ridges in *Sanidaspis;* F, horizontal section of armor in *Sanidaspis* cut along line f shown in D; G, section of armor of *Drepanaspis* sp?. (A to C after Ørvig, 1958 and 1959 (Ms); D to G after Bystrow, 1959)

basal layer and filling in of the cavernous interior. The fully developed armor fused with underlying endoskeletal elements.

Arthrodires

Euarthrodire The armor of some species of arthrodires has been described, and, in some of these, enamel-covered denticles are exposed on the surface (Figure 8-27). These denticles are partly embedded in bone, and, in some species, several layers of denticles are embedded, one above the other. The embedded denticles are usually without enamel but some may retain traces of it.

The denticles have restricted, vertical pulp cavities enclosed by thin osteons of bone. This bone is peculiar in having unipolar osteoblasts and as such it might be described as **prodentine.** The **semidentine** is restricted to a narrow zone near the surface of the denticle, just below the enamel.

The armor has three layers of material; the outer tuber-

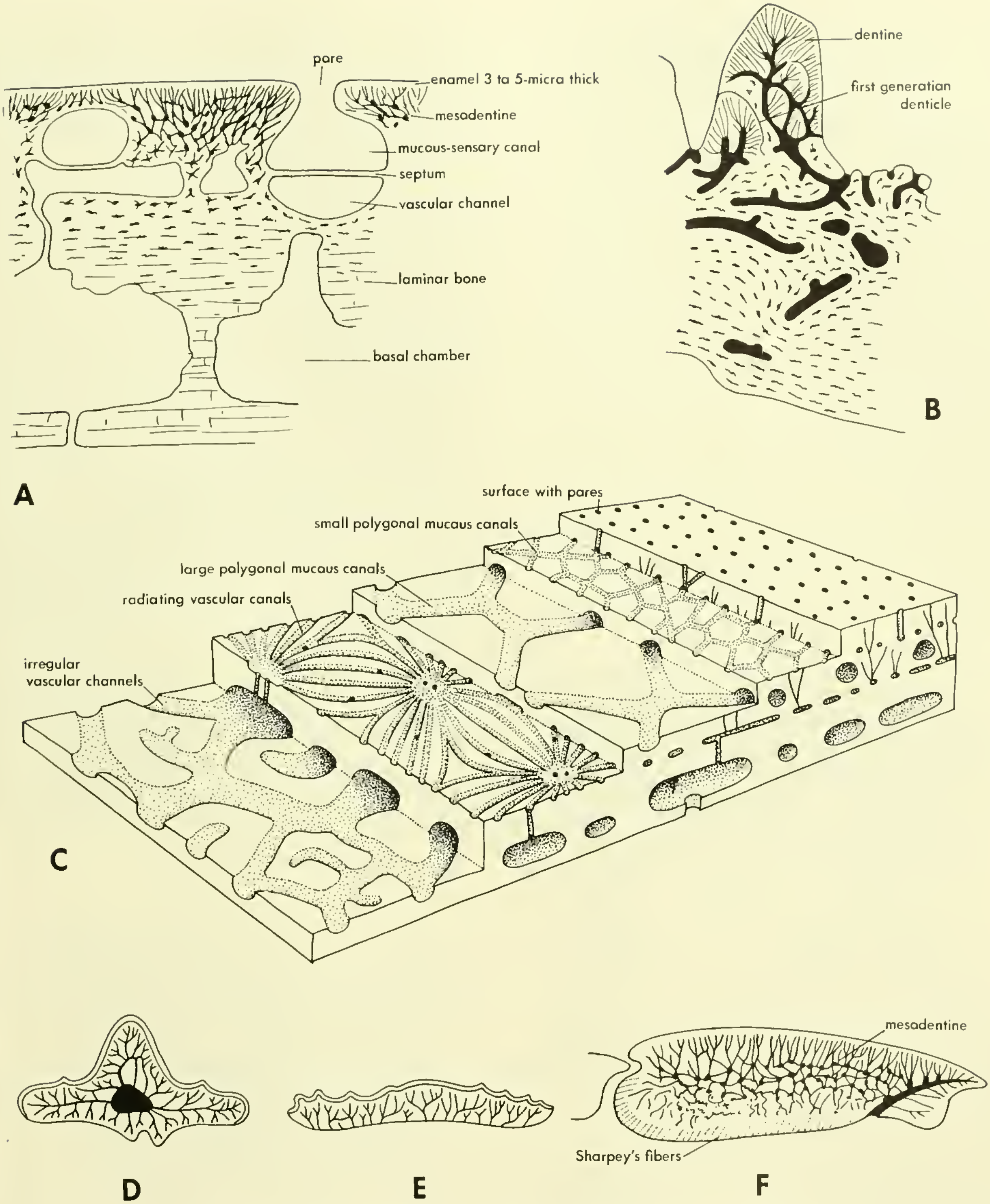


Figure 8-26. Armor and scale structure of asteostracans and thelodonts; A, section of armor of *Tremataspis mammillata;* B, section of shield margin of *Cephalaspis* sp?; C, stereodiagram of armor structure of a cephalaspid; D, E, placoid scales of *Phlebolepis* a thelodont; F, semidentine scales of *Theladus* (upper Silurian), a thelodont. (A after Denison, 1947; B, D, E, F after Ørvig, 1951; C, after Wängsjö, 1946)

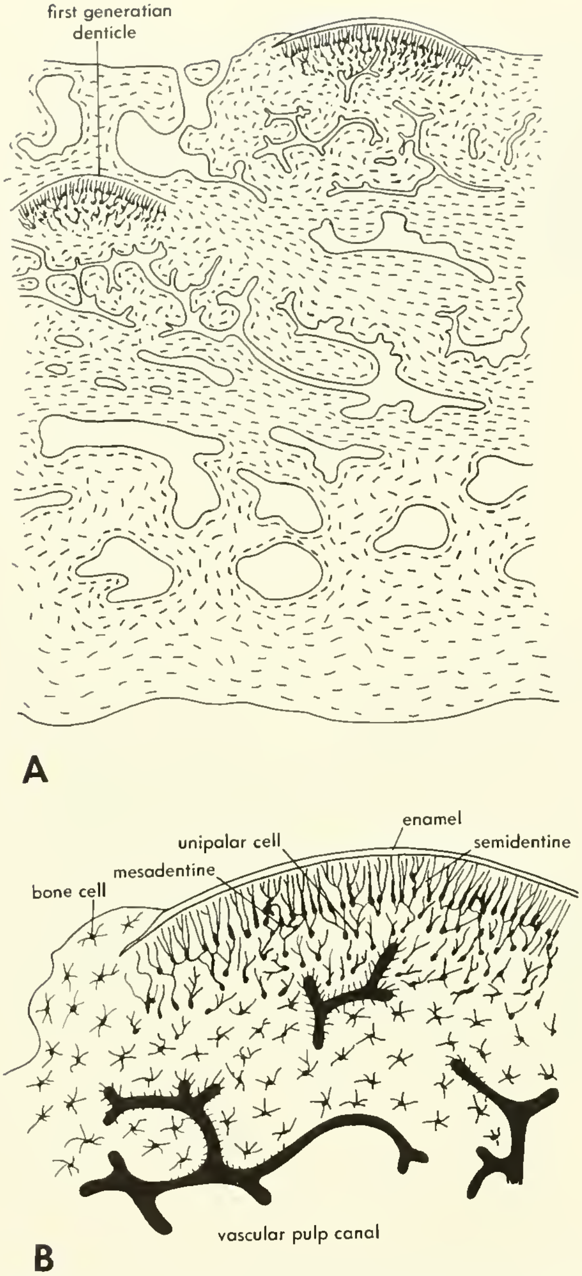


Figure 8-27. A, section of the armor of a Middle Devonian arthrodire, *Tollichthys polaris,* which lacks the basal laminated component; B, enlargement of section through a denticle to show the semidentine and unipolar cell lacunae. (After Bystrow, 1957)

cled part, a spongy middle zone, and a laminated base. There are numerous canals for **Sharpey's fibers.** In forms without enamel and with several generations of semidentine tubercles, Sharpey's fibers penetrate the upper layers of the armor as well.

The ontogeny and phylogeny of the scales of arthrodires has been described as follows. The earliest form had relatively thin armor consisting of a spongy bone, covered with numerous denticles. The denticles had sharp tops and ridges directed anteroposteriorly. It is quite possible that the pulp cavities of these denticles were rather large. In the later forms the armor was thicker but still without the basal laminar portion, and the pulp cavities of the denticles had become largely filled with prodentine osteons.

In the next stage, the dentine of the denticles was replaced by semidentine and new layers of denticles were formed over the old. In the late forms the laminar basal part of the armor had been added, the denticles were reduced in size, the amount of enamel covering them was decreased. Several generations of tubercles were formed and overgrown by bone. The spongy layer of bone underwent extensive reorganization and increased in thickness as the plate was added to both to its outer and inner surface. In the most advanced forms only the semidentine remnants of the tubercles remained, associated with prodentine, and several generations of these were deeply embedded in the bony outer surface of the plate. The bony plate was now thick and had a well-developed laminar base (isopedine).

Antiarch The plates of *Bothriolepis* (Figure 8-28) are quite like those of the euarthrodire; the outer surface has knobs or tubercles covered with a more or less laminar bone. Embedded in this laminar bone are areas of semidentine suggesting interred denticles. Below this is an outer spongy layer separated from an inner spongy layer by a thin zone of laminar bone. The thick base of the plate is laminated.

The structure of the antiarch plate exceeds the most advanced state of the euarthrodire. It appears that the armor of the antiarch has been increased in thickness by the separation of the original spongy bone into an outer region of small irregular channels and an inner region of large chambers. These two regions are separated by a zone of laminar bone which is indicated in at least one species of euarthrodire.

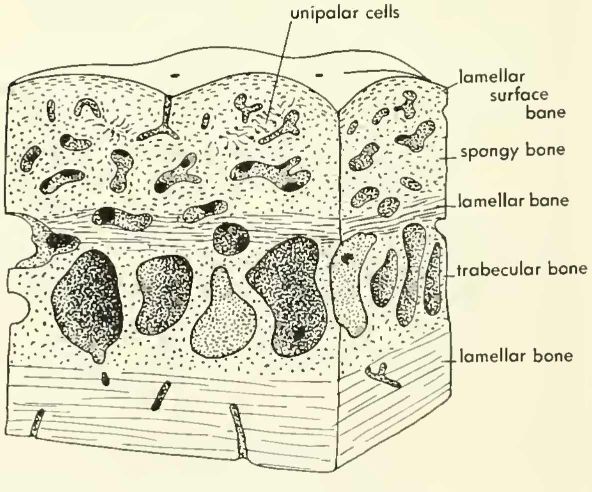


Figure 8-28. Stereosection of armor of *Bothriolepis canadensis.* (After Goodrich, 1907 and Enlow and Brown, 1956)

Acanthodian

The small scales of the acanthodian show a wide range of structure (Figure 8-29). In *Nostolepis* (Upper Silurian) the scale begins as a small mesodentine tooth without an enamel cover. At this stage it qualifies as a placoid scale. Growth involves the addition of material completely enclosing the old. In this way successive layers of mesodentine were added to the crown. These are thin above and thick at the margins; new layers are also added to the bony base. Other scales, resembling those of *Nostolepis,* have mesodentine tubercles set on a bone base. Second generation denticles may overlie the original denticles.

In *Acanthodes* the scale is formed of numerous shells of dentine applied successively over an original denticle, and the whole is attached to a laminated, acellular bony base. The vascular supply for the dentine comes in at the neck of the scale; the base of the scale is penetrated by radiating **Williamson's** and **Sharpey's canals.** The former were occupied by processes of the osteoblasts of the bony base.

The acellular material of the *Acanthodes* scale contrasts with the cellular nature of the *Nostolepis* type. In terms of their scales the acanthodians are thus of two types.

Chondrichthyes

The placoid scale of the shark has already been described (Figure 8-22). A point of special interest is the nature of the **enamel.** This has been called **"fibrodentine"** since it is formed by calcification of the fibrous material formed between the epidermal enamel organ and the dentine (Figure 8-30). This material occasionally encloses odontoblasts and is penetrated by the terminal tips of the dentinal tubules.

Among sharks there is a great variation in scale structure. By way of contrast, the scale of a ray, *Dasybatus,* is broad and flat with an acellular bony base (Figure 8-31). The dentinal layer is supplied by branching vascular canals which penetrate the base and the neck of the scale. The **bony base** shows concentric laminae and is perforated by **canals of Williamson.** These vascular canals also contain the bone cells of the base. **Sharpey's fibers** penetrate the base and anchor the bone to the fibrous dermis. Cellular bone is lacking in living chondrichthyes but was present perhaps in early fossils (edestids of Permian).

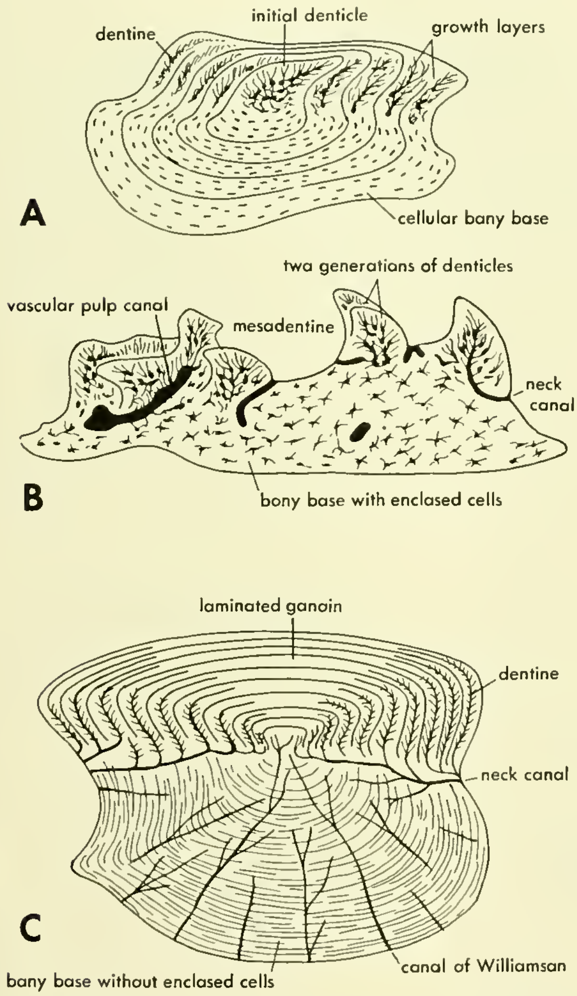


Figure 8-29. A and B, sections of scales of *Nostolepis* from the Upper Silurian (after Ørvig, 1957). C, section of scale of *Acanthodes*, Pennsylvanian, (after Goodrich, 1907).

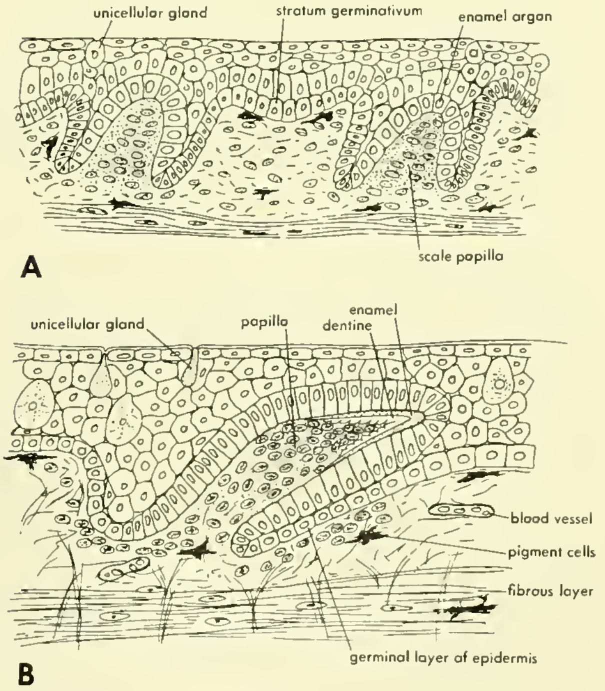


Figure 8-30. Development of placoid scale of the shark. A, early stage in *Squalus* (after Klaatsch, 1894); B, later stage in *Heptanchus* (after O. Hertwig, 1874).

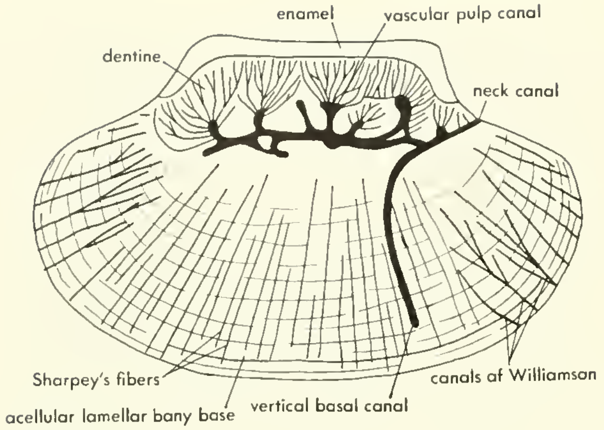


Figure 8-31. Section through the scale of a ray, *Dasybatus* sp?. (After Ørvig, 1951)

In the holocephalans, denticles occur only on the claspers, and in the young there may be a double row of small denticles along the back. The denticles and spine structure are like those of the shark.

General observations The placoid scale of the shark has been described as a basic skeletal unit, and it is apparent that denticles of one shape or another are characteristic of the bone and scales of vertebrates. In very primitive sharks, small units, called **lepidomoria**, are found (Figure 8-32). In more advanced sharks, the simple tooth-like lepidomoria tend to fuse together to form larger compound units. It has been assumed that the history of vertebrate scales and plates has been one of marginal aggregation of these lepidomorial units around a central element—this growth was accompanied by acquisition and thickening of the base. The shark placoid scale is peculiar in its irregular shape as contrasted with the regular-shaped scales of other groups.

Actinopterygian fishes

Ganoid scale The scales and the dermal bone of primitive actinopterygian fishes are described as **ganoid** because of the "shiny," enamel-like material covering their surface. As already pointed out, the fact that ganoin may be produced by the dermis, and not by the overlying epidermis does not mean that, in essence, it is not phylogenetically the same material. If the material occurs on the tooth of the fish, it is described as enamel; if it occurs on the scale, it is described as ganoin. This distinction does not seem quite proper.

In the primitive ganoid scale, the layers of enamel overlie a zone of **dentine.** The dentine has a network of vascular canals below it; these open at the neck of the scale as well as through the base and the outer surface by one or a few channels. The base of the scale is made of laminae of bone (**isopedine**) which continue up around the margins of the scale to meet the layers of "ganoin."

One of the earliest paleoniscoid fishes, *Cheirolepis,* has a small scale with only a single **basal vascular canal** and a posterior **neck opening** (Figure 8-33). In other, later paleoniscoid fishes the vascular system is somewhat more complex, opening both dorsally through the ganoin and ventrally through the bony plate.

The manner of growth of this type of scale is indicated by its structure. It starts with a small central unit (lepidomorium) and grows marginally by distinct increments, each of which is accompanied by a fresh deposition of enamel over the outer surface of the scale and the addition of a basal lamina of bone. In some paleoniscoids, the early denticles may be covered by second-generation denticles; zones of dentine may lie between layers of enamel. With concentric growth, new vertical vascular channels may be enclosed in the hard substance. These **Williamson's canals** extend vertically through the base to the pulp cavities of the dentine.

In the paleoniscoids, two types of scale development are observed: one retains the vertical vascular channels, the basal canals, of the component lepidomoria; the other has only one or a few large vertical vascular channels (Figure 8-34). In the latter the pulp canals are served by neck and dorsal vascular channels. The basal canals are called Williamson's canals. These were thus primarily vascular channels (Figure 8-35), but, as the scale evolved, contact with the vascular plexus of the dentine was lost. The canals now became narrower and served only as areas for the retreat of the osteoblasts from the osteons of the basal part.

Scales without Williamson's canals are the more common

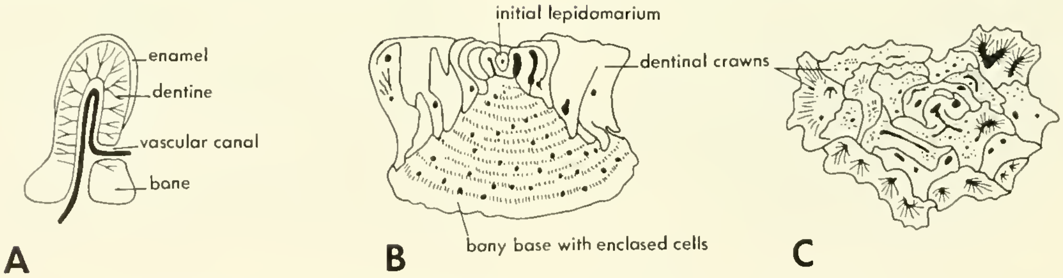


Figure 8-32. Scale structure in primitive sharks. A, a lepidomorium, B, section through scale of an edestid shark from the Permian of Greenland; C, horizontal section through crown of scale in B. (After Ørvig, 1951)

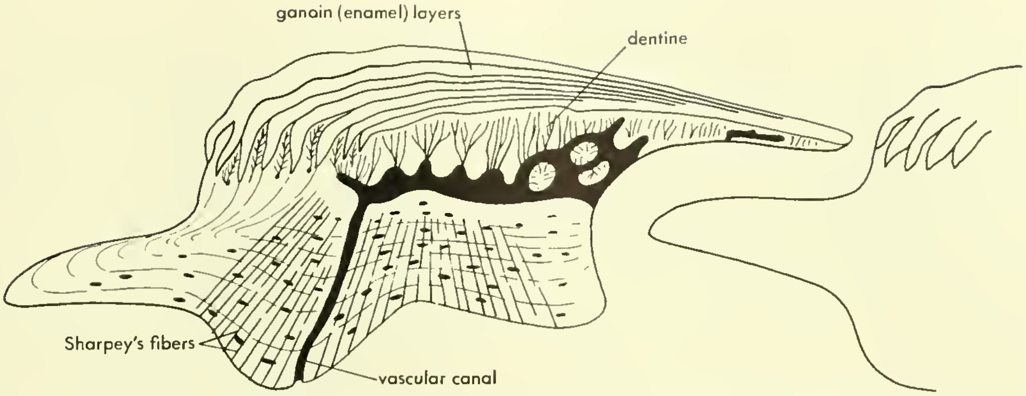


Figure 8-33. Section through a scale of *Cheiralepis* an early palaeoniscoid. (After Aldinger, 1937)

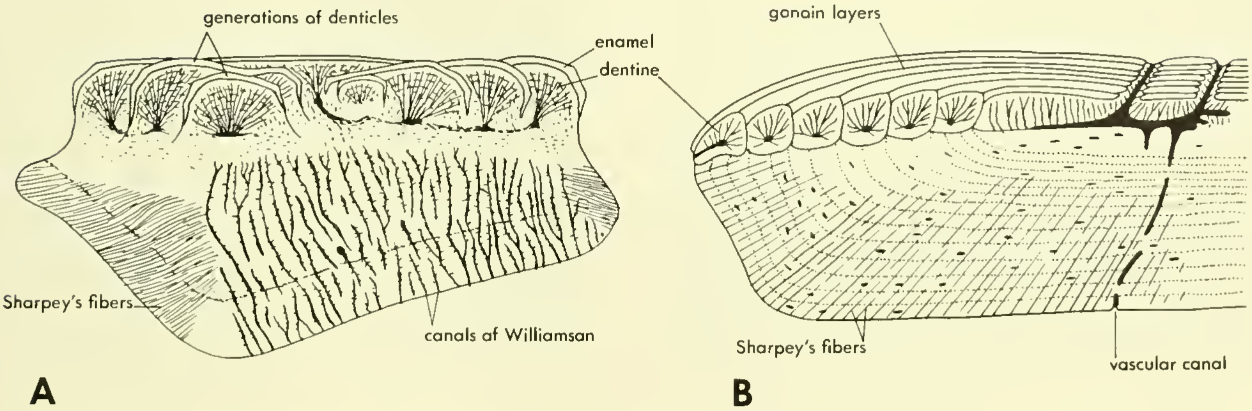


Figure 8-34. Sections through the scales of palaeoniscoids. A, *Orvikuina vardiaensis* (Upper Middle Devonian) in which the acellular base has many branching canals of Williamson; B, *Elanichthys punctatus* with a cellular base and a laminated ganoin cover. (A, after Ørvig, 1957; B, after Aldinger, 1937)

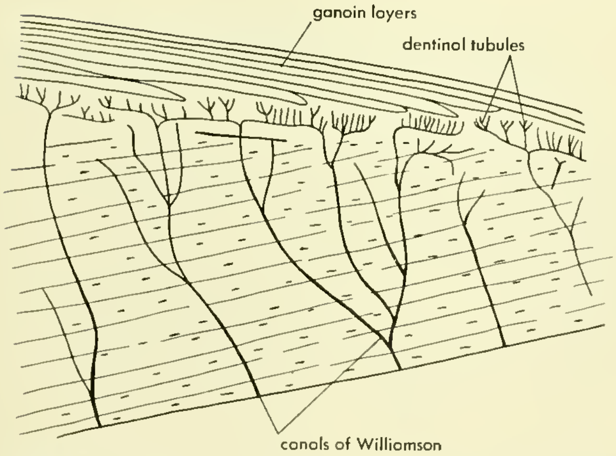


Figure 8-35. Scale of a perleidid, the lepisosteid type having Williamson's canals.

type, occurring already in the Lower Devonian genus *Cheirolepis,* and it is generally assumed that those with the canals (the lepidosteid type) were derived from those without. However, *Orvikuina* (Figure 8-34) of the Middle Devonian already had a scale suggesting the lepidosteid type (Figure 8-37). The base of the scale has numerous ascending canals which show many side branches. These canals do not reach the pulp cavities of the dentine and appear to house only the osteoblasts of the acellular bony base. The early appearance of such a modified scale suggests an early radiation of scale types among the palaeoniscoid fishes.

It is unlikely that the scale of *Orvikuina* is related to that of *Lepisosteus.* The lepidosteid type may have been achieved independently by many kinds of fishes at different times (i.e. a case of parallel or convergent evolution). It is also possible that both types of scales (with and without Williamson's canals) arose at the same time and have continued down to the present, each radiating into a number of subtypes.

Polypterus The scales of *Polypterus* are of the primitive ganoid type, without Williamson's canals (Figure 8-36). There is a thin but stratified layer of **enamel** over the outer surface, a layer of **dentine** above a vascular plexus enclosed in **spongy bone,** and a laminated bony base; the scale is penetrated from top to bottom by a few vascular channels. These scales have many canals for the **Sharpey's fibers** binding them together. Small spines or **denticles** may overlie the margins of the scales but are not attached to them. The dermal bones and fin spines differ only in that areas of dentine are intermixed with the enamel. The denticles may fuse to form separate (from the bony rays) plates on the fins or the denticles may fuse with and become embedded in the bony segments of the rays.

Chondrostean *Acipenser* and *Polyodon* have scales shaped like those of primitive ganoids (rhomboid). *Acipenser* has large scutes along the dorsal midline and along the lateral-line canal. The scales and plates have a glassy surface layer of acellular bone (hyodentine) raised into small tubercles, and irregular ridges.

Holostean *Lepisosteus* has thick heavy scales of a rhomboid shape. The **Williamson's canals,** or the lepidosteid tubules, are reduced to channels for protoplasmic processes (Figure 8-37). Cells still remain, however, in the basal bony laminae. The dentinal layer is lacking and several layers of enamel cover the outer surface. At the posterior and ventral margins of the scale, secondary enamel-clad denticles are formed which attach to the posterior and ventral bony margins of the scale and become embedded in the enamel as the scale grows peripherally.

The scales of *Amia* are greatly modified (Figure 8-38). The outer surface is ornamented and formed of a bony material containing cells only in its anterior (overlapped) part. Below this calcified layer is a series of fibrous laminae with embedded cells. These fibrous laminae correspond to the laminar bone of other scales.

The histological dissimilarity of these holostean scales can be inferred from their difference in shape. Those of *Lepisosteus* overlap only slightly and employ a peg and socket in the imbrication of a vertical series. The dorsoanterior peg, which lies above and behind the extended corner of the scale, and the ventromedial socket are characteristic of the ganoid scale.

The cycloid scale of *Amia* has lost the peg and socket and the Sharpey's fiber bindings. Expansion of the scale margins has also been accompanied by histological changes such as the loss of the enamel and dentine layers, and reduction in thickness and calcification of the laminar base. An acellular bone has been substituted for the enamel and dentine. This transition from rhomboid to cycloid scales, along with corresponding histological changes, is observed also in the choanate fishes.

The dermal bones of *Amia* (Figure 8-38) resemble those of *Lepisosteus* in that they have Williamson's canals penetrating both outer and inner surfaces. These canals allow penetration by cell processes into the depth of the laminate bone—which also contains osteoblasts. These canals indicate growth occurring at both outer and inner surfaces and

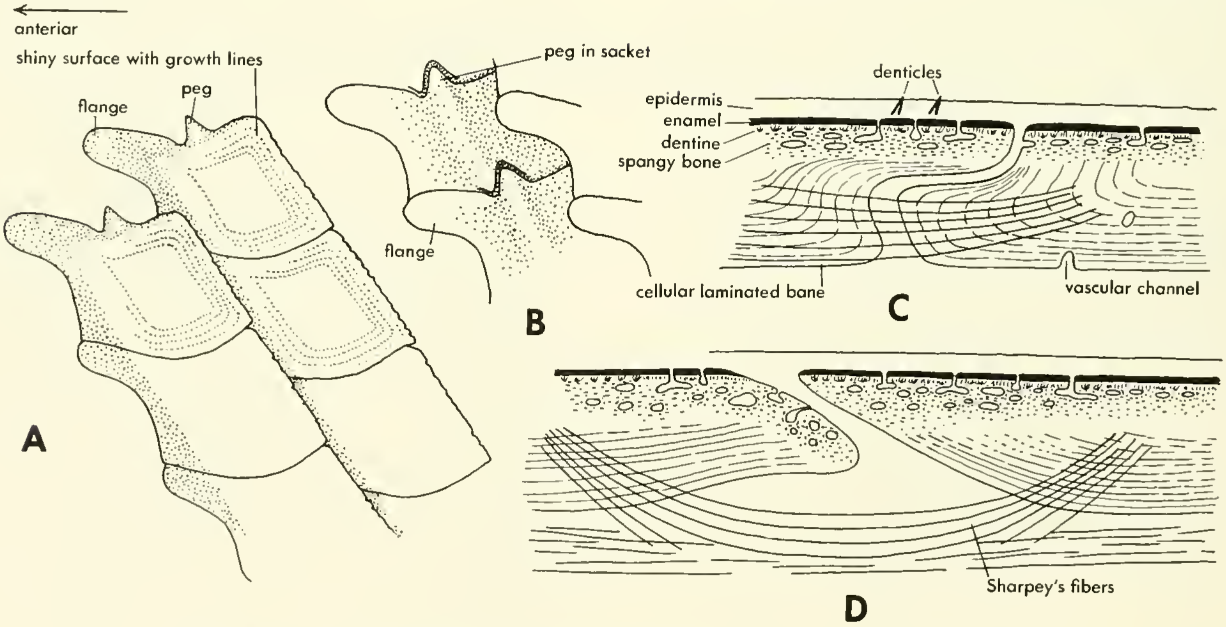


Figure 8-36. Rhomboid ganoid scales of *Polypterus*. A, outer surface of several articulated scales; B, inner surface of several articulated scales; C, longitudinal section of joint between two scales; D, vertical section of joint between two scales. (After Kerr, 1952)

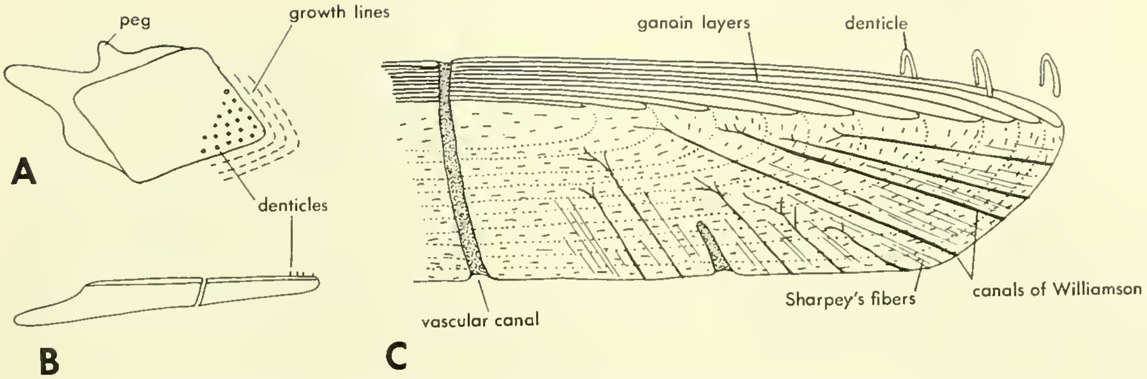


Figure 8-37. Rhomboid ganoid scales of *Lepisosteus*. A, outer view of scale with growth increments indicated by dashed lines; B, longitudinal section through a scale; C, histology of posterior margin of a scale. (After Nickerson, 1893; Kerr, 1952; Rauther, 1927–1940)

probably nothing more. The processes of the flattened osteoblast of *Lepisosteus* extend out in a single interlamellar plane, while those of *Amia* radiate in all directions.

Teleost The teleost may have laminated scales covered with a generally noncellular bony material called hyodentine (Figure 8-39). In *Callichthys* the hyodentine contains canals for protoplasmic extensions of cells lying in the large vascular channels. The hyodentine is also penetrated by Sharpey's fibers. The scales may be associated with spine-like denticles like those observed in *Lepisosteus* or *Polypterus*. These have an enamel cover and a dentine interior surrounding a pulp cavity. The denticles are attached to the scale by ligaments or embedded in the hyodentine. Below the hyodentine is laminated bone or cell-containing, fibrous connective tissue which may be partly calcified.

The scale of the teleost is of a cycloid type with circumferential growth rings (Figure 8-40). In many species, there are tooth-like extensions from the posterior margin; this modification identifies the ctenoid scale.

EMBRYOLOGICAL DEVELOPMENT The scales of *Polypterus* develop in the outer parts of the dermis, where knots of fibroblasts gather to form buds (Figure 8-41). The outer part of this cell aggregation forms the scale sac in which two layers of osteoblasts appear. The two layers become separated by an imperforate lamina of bone. To this initial lamina, which disappears, spongy bone is added above and below. The outer layer of enamel and dentine is now applied along with a lamina of bone to the under surface.

The outer face of the scale lies next to the epidermis or is separated from the epidermis by a mixed layer of mesodermal and epidermal cells. The first layer of ganoin when completed lies in contact with the epidermis. It is then separated from the epidermis by a mesodermal overgrowth which, under the influence of the epidermis, gives rise to a second layer. A third layer of ganoin forms in the same way after the external face of the scale has become overgrown by a new layer of mesodermal tissue. Eventually, the ganoin or enamel consists of several superimposed layers.

In the teleost, the process is much the same. Scale buds are formed by fibroblast masses in the upper layer of the dermis along the lateral-line canal. From these masses, fibroblasts migrate out along lines extending upward and forward and downward and forward. Successive scale buds are formed along these lines by clumps of fibroblasts. Each scale bud becomes organized into a sac enclosing two layers of osteoblasts. The hyodentine layer is formed between the layers of osteoblasts. As the layer grows in thickness, the lower layer of osteoblasts begins to form laminar bone or fibrous laminae. As the initial scale grows, the posterior margin extends back and outward over the next posterior

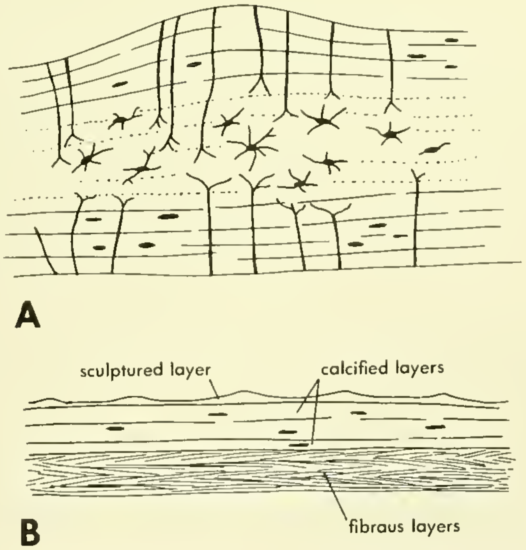


Figure 8-38. Section of a skull bone of *Amia* (A) showing lepisosteid canals; B, section of a scale showing fine structure. (A after Goodrich, 1907; B after Kerr, 1952).

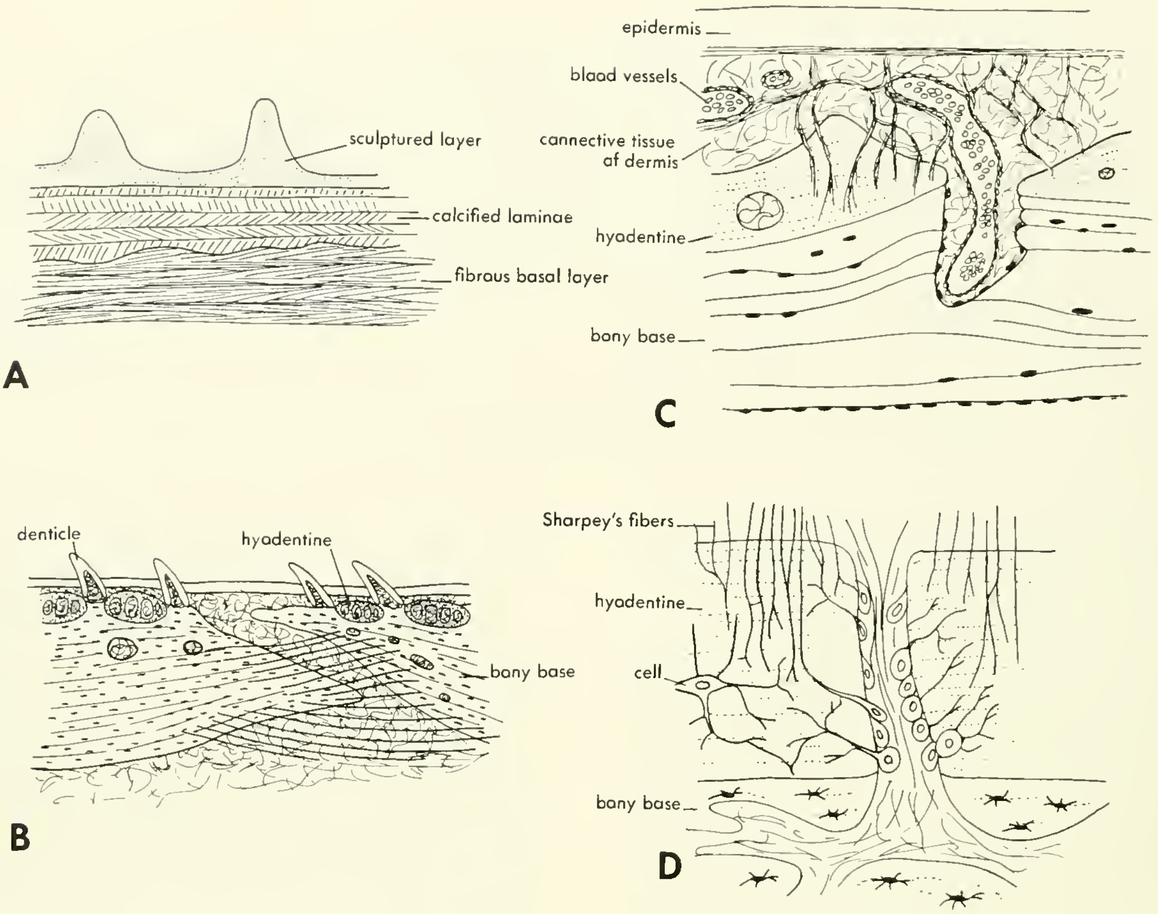


Figure 8-39. Structure of teleost scales. A, section of scale of *Leuciscus rutilus*; B, joint between two armor plates of a catfish *Hypostoma*; C, section of scale and skin of *Arapaima gigas*; D, surface layers of a scale of the catfish, *Callichthyes longifillis*. (A after Hase; B after Rauther; C and D after O. Hertwig)

scale (this is an ontogenic progression from the rhombid interrelationship to the cycloid). The anterior margin is extended forward below the next anterior scale. Growth is largely marginal, and continues throughout life. The surface of the scale is decorated with small circular ridges marking the growth periods.

In *Lepisosteus*, the lateral-line scales ossify first in the tail, then in an anterior progression (Figure 8-42). From this line, scale rows extend up and forward and down and back (or down and forward). The caudal peduncle is fully covered by scales before they appear above, or below, the lateral line anteriorly. The development of the scales parallels that of *Polypterus*.

In most teleosts, the first scale papillae or buds appear along the lateral line on the caudal peduncle and later extend forward along that line. In centrarchids, the row of scale primordia extends forward below the lateral line; this appears to be a deviation from the primitive style.

Choanate fishes

The crossopterygian fishes have a scale identified by the term **cosmoid** (Williamson, 1849) referring to the "decorative" nature of the bunches of dentinal tubules in these scales. In this type, the surface is covered with enamel-clad tubercles joined one with another to form a surface broken only by pores (Figure 8-43). Below the enamel is a layer of dentine, the cosmine, in which the dentinal tubules radiate outward and upward from the central pulp cavity of each tubercle. Below the dentine is spongy bone permeated by many anastomosing channels, and below this is lamellar bone. On the anterior overlapped margins of the scale, one observes typical denticles, and several generations of these, one over another.

Irregular concentric rings mark the surface of these scales and represent resorption and surface replacement areas involved with growth. On the outer surface, new layers of

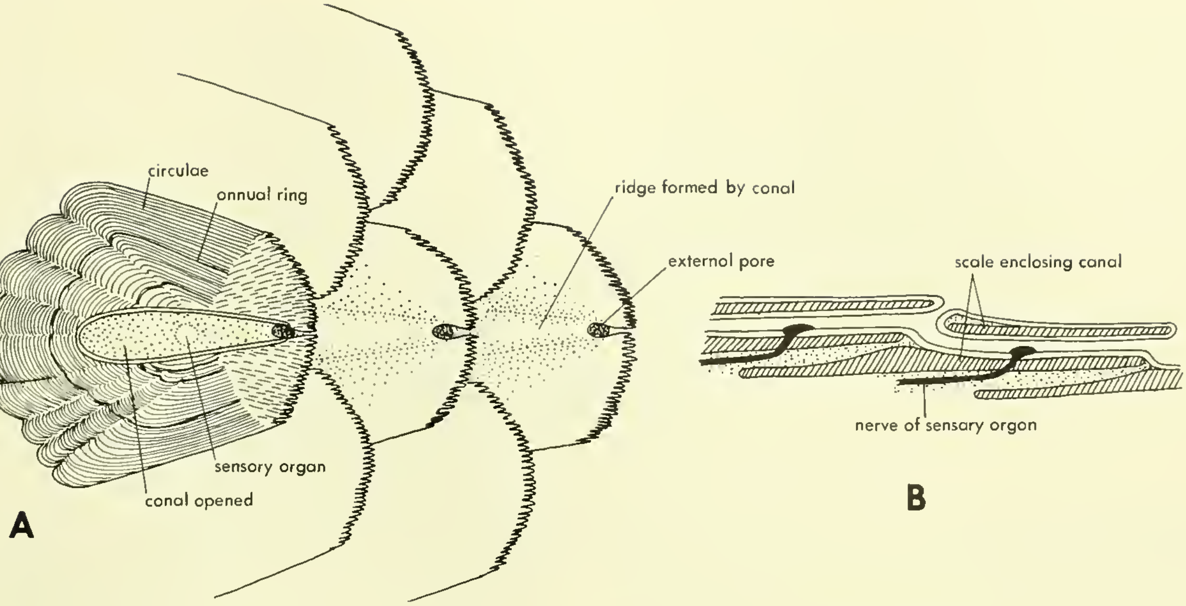


Figure 8-40. Loteral-line scales of o perch as seen in surface view, A, and in longitudinal section, B.

enamel and dentine do not overlay the old; rather, the old surface is first removed (resorbed) then a new surface applied. This type of replacement is a continual process and scales frequently are in a transitional condition with a part of their surface removed.

The primitive cosmoid scale was rhomboidal in shape but without peg and socket. There was some overlapping with adjacent scales. In the several choanate lines—Rhipidistia, Actinistia, and Dipnoi, the rhomboid shape has been replaced by the cycloid. Concurrently, there was a reduction in thickness and an histological simplification. In *Eusthenopteron,* the surface tubercles are bony; below these is a layer of spongy bone and below this a layer of laminar bone. A cosmoid scale of cycloid form, still retaining some of the enamel-covered dentine tubercles, is observed in the coelacanth *Latimeria.*

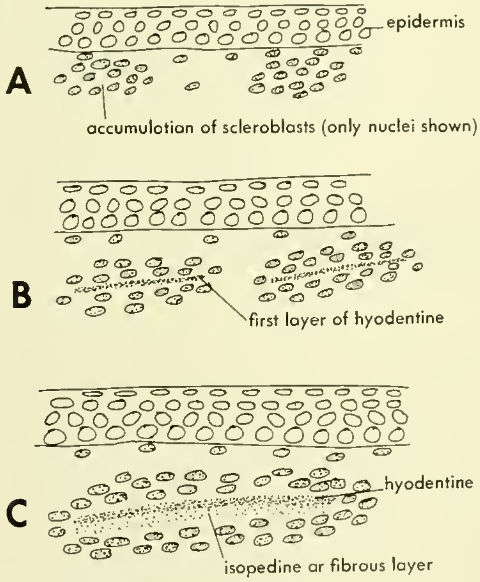


Figure 8-41. Three semidiagrammatic stages in the development of a scale in the teleost.

Among the dipnoans, the scales originally were of the cosmoid type with enamel, dentine, and bony layers. In *Dipterus,* the earliest known of the dipnoans (Middle Devonian), the scales are already cycloid in form but are otherwise comparable to the osteolepid. With time, the outer enamel and dentine layers have been lost, and, in forms such as *Neoceratodus,* only spongy and laminar bone layers remain. *Protopterus* has the scales covered by many small denticles, whose bases flare out as small plates which attach to a laminar but largely acellular bony plate much like that of the teleost.

The exact agreement in scale and dermal bone construction between *Dipterus* and the Crossopterygii suggests a common origin. The cosmoid scale contrasts sharply with the ganoid scale of the actinopterygian or other fishes.

Amphibians

The scale structure of early amphibians is not well known. It appears from the dermal bones of the skeleton that they were entirely bony. There was a tuberculate outer laminated part, a middle spongy zone, and laminated base.

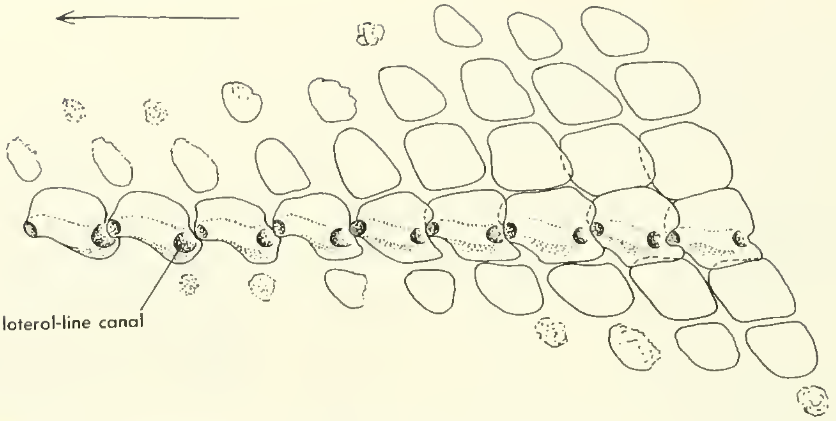


Figure 8-42. Anterior end of the developing scole rows of a 70-mm specimen of *Lepisosteus.*

General observations Practically all the types of hard tissues are found developed already in the Ordovician agnaths. There was an enamel-like tissue (*Astraspis*) and a dentine of two types: ordinary coarse-tubed dentine in *Eriptychius,* agreeing with that in ostracoderms and elasmobranchs, and a more fine-tubed dentine in *Astraspis,* similar to that in many higher fishes. Bone tissue without enclosed cells, similar to the aspiden of the later heterostracans, was present in *Astraspis* and, of a somewhat different type, in *Eriptychius.* That of *Astraspis* was coarsely fibrous with well-developed osteons. In *Eriptychius,* several generations of denticles, one superimposed over the other, occurred on some surfaces.

In contrast to the heterostracans, the osteostracans, as the name implies, had true cellular bone. This same variation is observed in acanthodians and sharks—with cellular or acellular bone forming the bases of the scales. In the actinopterygians, an acellular bone is developed in the teleost and in the early palaeoniscoids, *Orvikuina.* The latter is thus a suspect palaeoniscoid, but other palaeoniscoids (*Scanilepis*) show tendencies in the direction of acellularity.

A possible conclusion is that there are several closely interrelated scale types: placoid, agnath, arthrodire, ganoid, and cosmoid. The primitive condition of the last four involved the early appearance of denticles (placoid scales) followed by the progressive development of a bony base for these. Differences in the ontogeny (developmental stages) and histology can be used to identify the several types.

The various hard materials observed, enamel, dentine, and bone, or the intergrading substances, all appear to be related and to intergrade.

FIN RAYS

The fins of many fishes are supported by fin rays, formed of bilateral components (Figure 8-46). Some rays are jointed and appear to be formed of modified scales (Figure 8-44). In the cyclostomes, there are no scales and also no fin rays, but in fossil agnaths scales were present. Both living and fossil agnaths had **radials,** extensions from the neural and hemal arches into the caudal fin lobes. In *Birkenia,* an anaspid, there were rows of scales forming **lepidotrichia** on either side of each radial (Figure 5-28). In the cephalaspids, rows of rectangular scales paralleled the radials.

The primitive sharks were like the anaspids in having the radials extending nearly, or quite, to the margin of the fin—this is the **plesodic** type of fin characteristic of the rays (Figure 8-44). In the selachian fin, the radials are limited to the basal half and several layers of horny rods or **ceratotrichia** overlap the radials and extend out to the fin margin—this is an **aplesodic** fin. The ceratotrichia lie in the dermis; the overlying skin is studded with placoid scales.

Acanthodians had an aplesodic fin with the radials scarcely extending into the fin. The membrane was supported by ceratotrichia and the skin studded with small scales (Figure 6-68). The ceratotrichia are described as generally unjointed cylindrical rods of uniform diameter, ossified in the proximal part.

The pectoral fins of the arthrodires are **plesodic** with a broad base. The caudal fin of *Bothriolepis* was supported by pairs of calcified rods, which seem to be intermediate in nature between the ceratotrichia of the shark and the radials of the agnath (Figure 8-45). These rods have been identified as **radials.**

Among the choanate fishes, the fins of the dipnoans are the most primitive in that they are covered by scales (Figure 8-45). Within the fin of *Dipterus,* there are **radials** and bony **lepidotrichia.** The lepidotrichia are jointed and branched; basally they overlap the radials and distally extend to the margin of the fin. They are grooved on their inner aspect. The basal half of the fin is covered externally by cycloid scales, which grade into rows of rectangular scales paralleling the lepidotrichia. In *Neoceratodus* or *Scaumenacia* (Devonian), the scales covering the fins do not form distinct rows.

The ceratotrichia of *Neoceratodus* and *Protopterus* are slender pliable rods, irregularly jointed, and generally

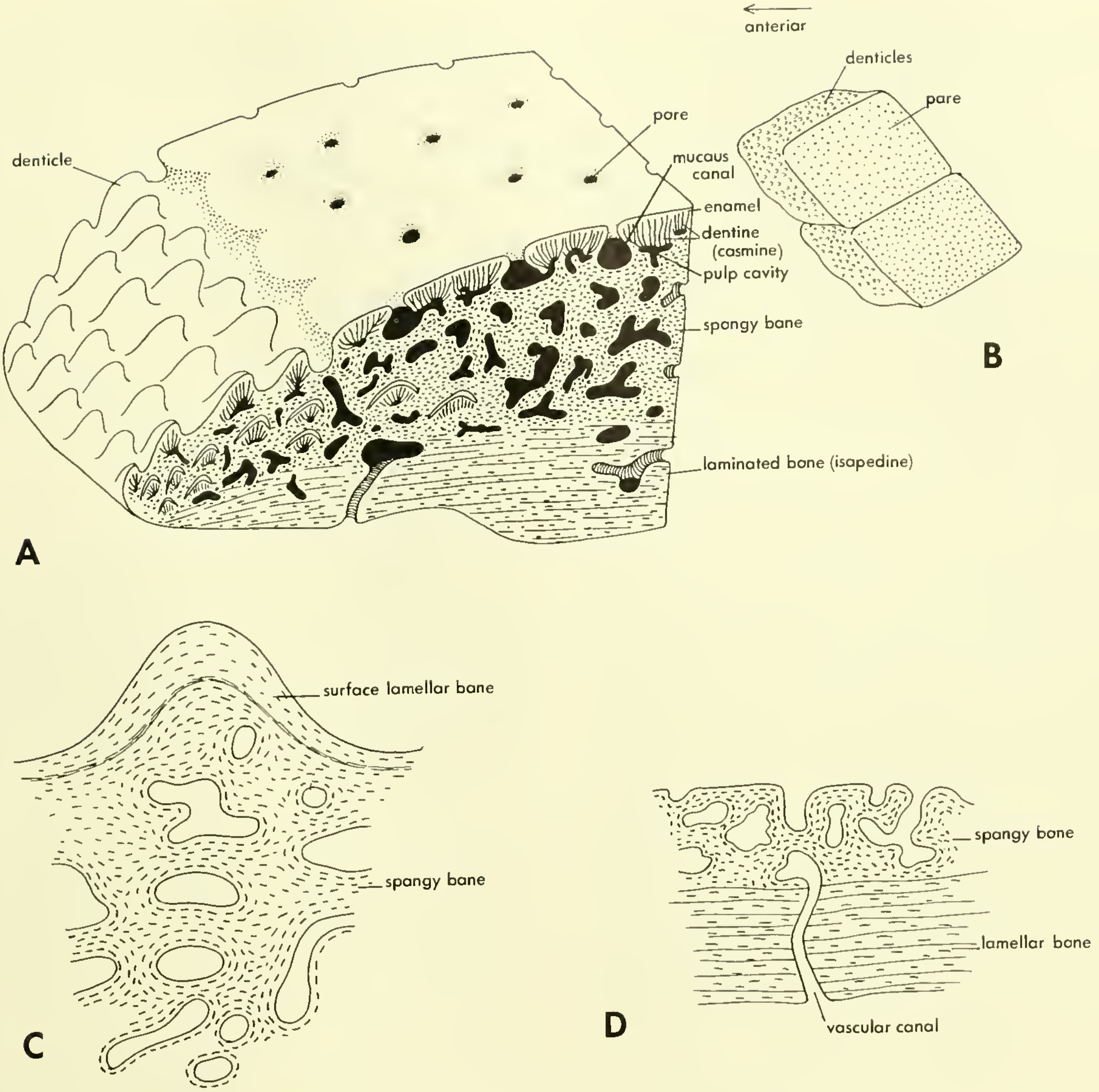


Figure 8-43. Scale structure in choanate fishes, the cosmoid scale. A, stereodiagram of the anterior margin and section of a scale of *Porolepis uralensis;* B, surface appearance and articulation of scales of *Porolepis uralensis;* C, section of dermal bone of *Eusthenopteron;* D, section of scale of *Neoceratodus.* (A, B, C after Bystrow, 1939 and 1959)

branched. They are composed of a fibrous horny material with bone cells in their proximal part, and with an outer calcified layer which extends some distance distally (Figure 8-46). The ceratotrichia of *Lepidosiren* are soft, have few joints, and are unbranched, more like those of the shark.

In the Rhipidistia, the lepidotrichia are like those of *Dipterus:* bony, jointed, branched, and hollowed on their inner aspect, but they are also covered with enamel and dentine in the more primitive types (*Porolepis, Gyroptychius*) where there is a gradual transition from the body scales to those of the lepidotrichia.

This transition is misleading since it involves two distinct entities: the lepidotrichium which continues into the fleshy base of the fin to overlap the radial and the outer body cover of the scales. The transition suggests that the outer cover of scales has been fused with or continued by the scales of the lepidotrichium. In the advanced forms, this break becomes well marked (*Eusthenopteron*). The nature of this break suggests that in the thinning of the fleshy fin, the lepidotrichia have become exposed by the loss of an outer layer of scales and have taken the place of that layer. This event is better explained ontogenetically, in terms of a thin fin extending

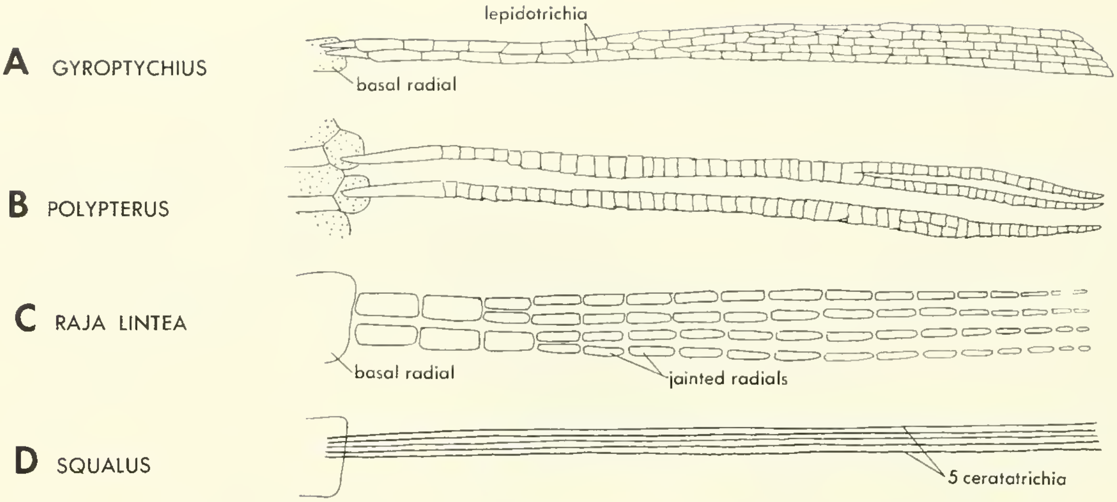


Figure 8-44. Fin rays and radials as observed in a chaanate, an actinopterygian, and two chandrichthians. (After Jarvik, 1959)

outward through the body cover, thus exposing the lepidotrichia as the outermost layer of scales.

In the primitive actinopterygian fish, there is sometimes a gradual transition from body scale to lepidotrichium just as in the primitive choanate. The lepidotrichium is bony, jointed, branched, and guttered on its inner surface. Its basal part extends into the body to overlap the radial. The number of fin rays, or lepidotrichia, was usually greater than the number of radials, but in advanced forms these were generally equal. In advanced forms, such as the teleost, the base of the fin may be scaled and scales may even cover all or most of the fin. Where such scales exist they have no relationship with the underlying lepidotrichium.

The lepidotrichia of *Polypterus* are of interest, because they have denticles and an ornamentation of ridges of dentine and enamel. Separate tooth-bearing plates may occur on the underside of the pectoral fins between the fin rays. The spines of the dorsal finlets of *Polypterus* are formed from modified lepidotrichia as are the spines of teleosts.

The margins of the fins of teleosts and the adipose fin, where such occurs, are supported by unjointed horny rods which resemble ceratotrichia. These rods have been called **actinotrichia** because of their finer structure. In the growing fin, one observes the margin supported by these rods which are replaced by the more superficial lepidotrichia with further growth.

Embryological development Ontogenetically, the various types of fin rays arise in the same way. They appear as thickenings of the basement membrane of the epidermis which are cut away by the movement of mesenchyme cells between this thickening and the membrane (Figures 8-47, 8-48). They tend to sink from here into the dermis. With the first generation of rays sinking into the dermis, a second may form, as is seen in the shark.

This condition demonstrates that actinotrichia or ceratotrichia, which shall be considered as homologs, represent only one expression of a dermal support response which also produces the lepidotrichia. Whether these represent generations of scales, as has been suggested by Jarvik, is another thing, but certainly they involve some of the factors and interactions which produce scales—this is evident in the case of the lepidotrichia.

General observations The relationship between fin rays and the agnath type of "radials" is not understood but the two never occur together. This suggests that they may represent essentially the same thing. Ceratotrichia fused at the midline could form the agnath radial; stated another way, the agnath radial split into bilateral components could give rise to the ceratotrichia. This ceratotrichial-radial relationship is suggested in *Bothriolepis,* and the jointed radials of the ray may be only incipient ceratotrichia.

Only in the teleost fin are there two clearly differentiated generations of elements: the actinotrichia supporting the margin and the lepidotrichia the rest of the fin. The interrelationships of these might suggest the view that there is an outer and inner component—only the inner appears in the shark (but several generations of these!), while both are present and joined in *Neoceratodus.* The grooved inner surfaces of lepidotrichia in general suggests the presence of a "ghost" part.

A simple explanation of all the observed facts does not appear to be possible, for we seem to be dealing with a response system capable of many products.

TEETH

Teeth are presumed to be homologs of scales and are so considered here. The teeth cover the margins of the jaws, and some lie far inside the mouth where they arise from pharyngeal tissues. The fine anatomy of the tooth is best observed in the mammal, which is the source of the various terms applied to teeth (Figure 8-49).

Structure and origin of mammalian teeth

The tooth is capped with a thick layer of **enamel** superimposed over a layer of **dentine** enclosing a **pulp cavity.** The root of the tooth is embedded in a bony **socket** to which it is connected by **cementum** and **Sharpey's fibers** (**periodontal membrane**). Both the enamel and the dentine show growth lines and the enamel also shows refractive lines.

The growth lines of the enamel are called stripes or **lines of Retzius;** these indicate periodic depositions. The enamel is formed of thin prismatic rods standing nearly perpendicular to the interface membrane between the enamel and the dentine. These thin rods are cemented together by a calcified substance of different density. The rods of enamel have the same shape as the base of the cell which produces them. The spiraling of the rods as they are laid down produces the refractive **lines of Schreger.** In addition to the spirals, the rods show very short kinks. The outer surface of the enamel cap when completed is covered by two membranes which wear away as soon as the tooth is used.

The interface between enamel and dentine is richer in organic material than either, and the two substances are interconnected by fine fibers. Some of the dentinal tubules extend a short distance into the enamel. A short distance inside this interface are some irregular spaces, the **interglobular spaces,** the product of incomplete calcification. The dentine has rather coarse tubules extending from the

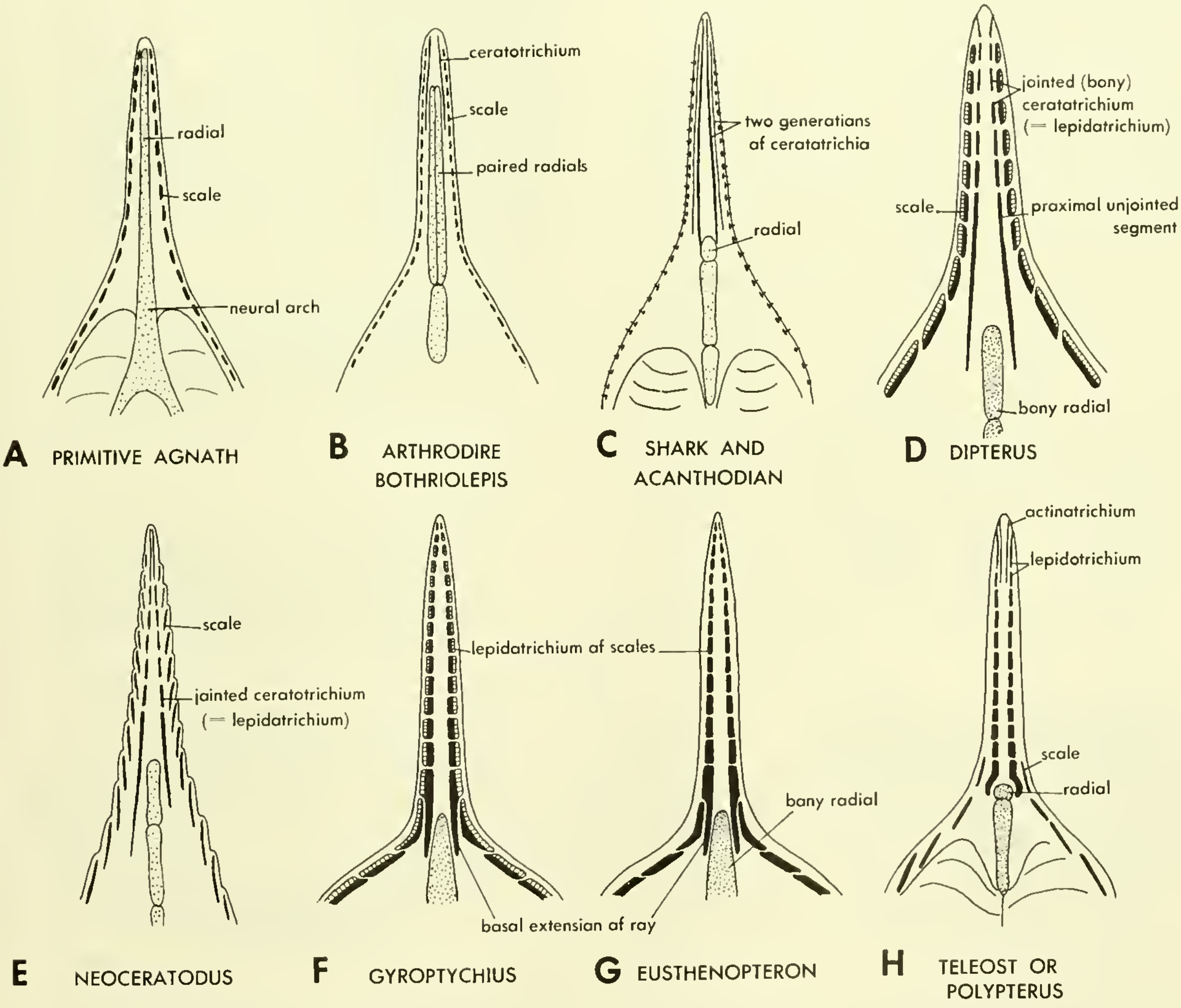


Figure 8-45. Semidiagrammatic cross sections of dorsal fins to show interrelationship of parts. (After Jarvik, 1959)

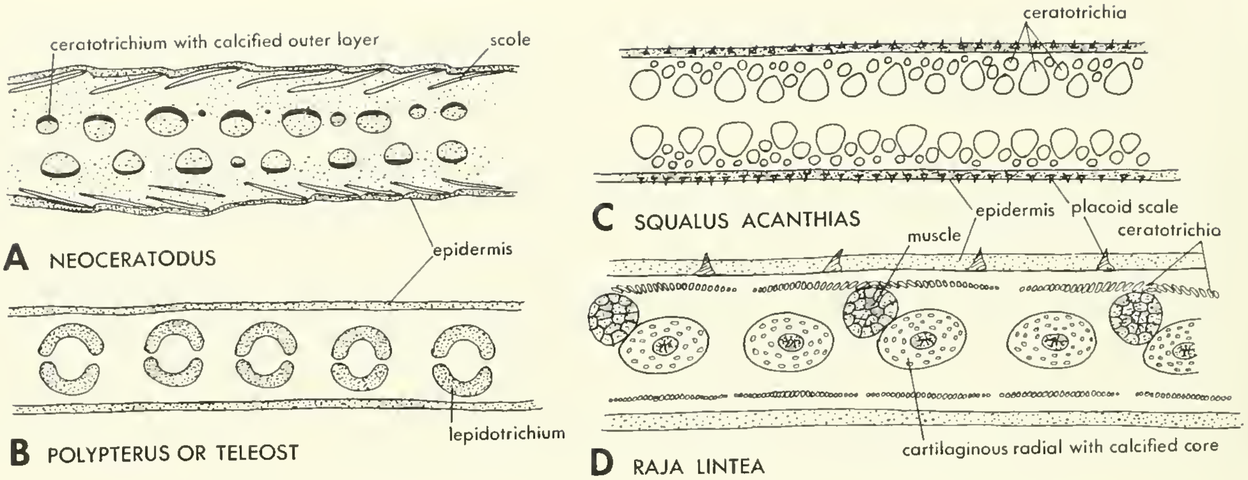


Figure 8-46. Frontal section through fins showing interrelationships of parts. (After Jarvik, 1959)

interface toward the pulp cavity. These lie more or less parallel to each other and act as canals for the protoplasmic fibers of the odontoblasts. The odontoblasts producing the dentine lie on its inner surface, between the dentine and the pulp. The pulp cavity is filled with a gelatinous material in which blood vessels and nerves are found; these extend out through the root of the tooth.

Embryological development Tooth development begins with an epidermal invagination along the margin of the jaw. This band, called the **dental lamina** (Figure 8-50), retains its connection with the outer epidermis. The dental lamina has bud-like extensions at intervals called the **tooth germs.** Each tooth germ produces a cup-shaped **enamel organ** having an inner and outer epithelium and a pulp-filled interior. The enamel organ is attached by a strand to the dental lamina. A mesodermal plug extends up into the ventral

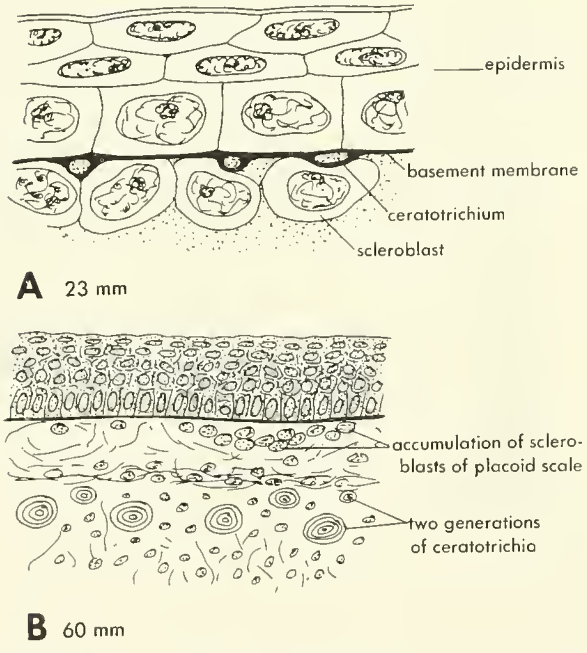


Figure 8-47. Development of ceratotrichia in *Scyllium canicula.* (After Jarvik, 1958, and Goodrich, 1904)

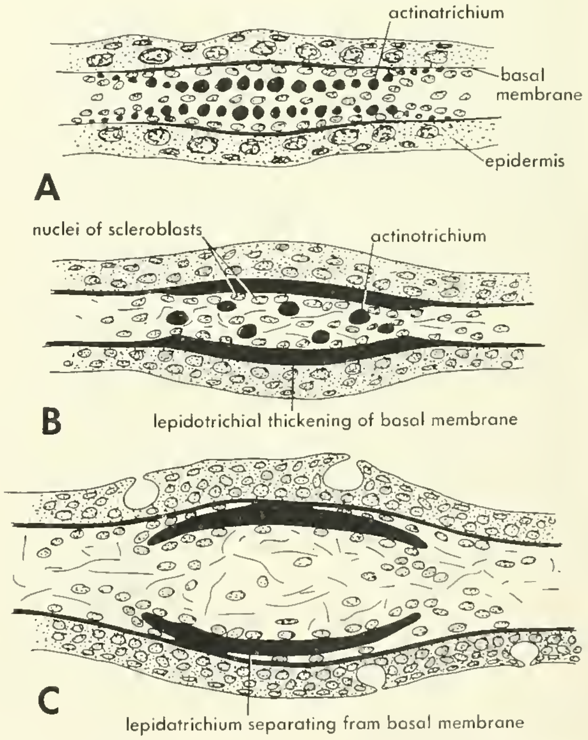


Figure 8-48. Progressively more proximal (toward base) sections through a fin of a *Salmo salar* of 21 mm in length. (After Jarvik, 1959, and Goodrich, 1904)

opening of the cup. The dental lamina at this stage has a second generation of tooth germs extending down from it medial to the initial tooth germs.

The enamel-producing epithelium is bell-shaped and formed of columnar **ameloblasts** or ganoblasts. The ameloblasts induce the formation of **odontoblasts** in the adjacent dermal papilla, and these then produce the first layer of dentinal material, a soft fibrous material called **predentine.** The fibers of the odontoblasts extend between columns of the predentine. The appearance of the predentine next to the basal membrane of the ameloblasts induces the formation of **enamel.** The soft pre-enamel material accumulates at the base of each ameloblast as a **Tome's process;** either this material is secreted through the basement membrane or that part of the cell containing it breaks down (merocrine secretion). As the ameloblasts move away from the secreted pre-enamel, new layers of Tome's processes appear and the long wavy and spiraled column is produced. The production of the soft material is periodic as is its calcification; this periodism produces the cross **lines of Retzius** seen in the rods.

Inside of the enamel-dentine interface, the dentine is laid down in layers toward the pulp cavity, first as a soft predentine and later as a calcified, hard dentine. Dentinal tubules containing the processes of the odontoblast are left behind as this process continues, and the processes elongate as the cells move further and further from the interface.

The tooth structure of vertebrates can now be reviewed beginning with the fishes.

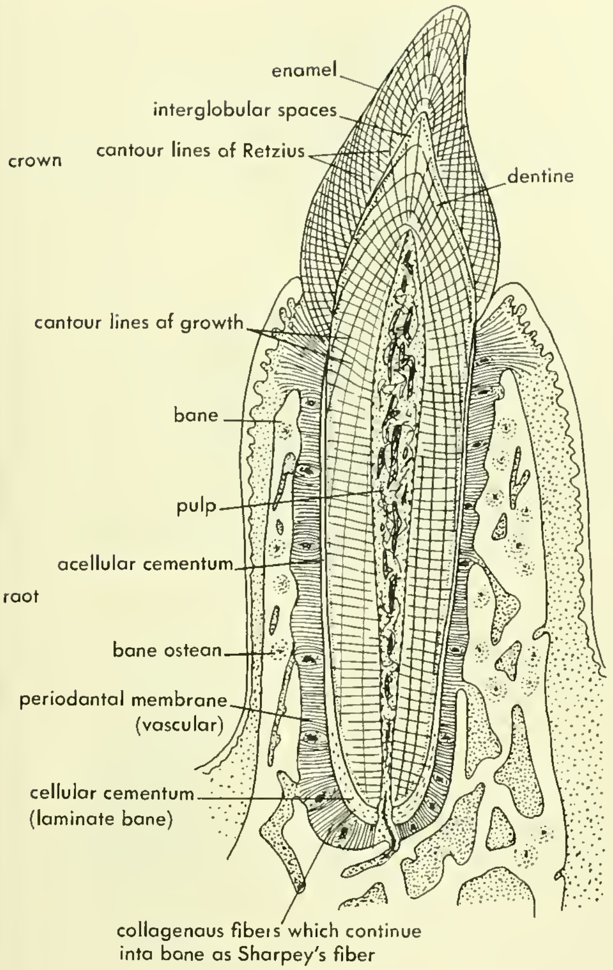


Figure 8-49. Section of a mammalian tooth set in the jaw. (After Ham, 1957)

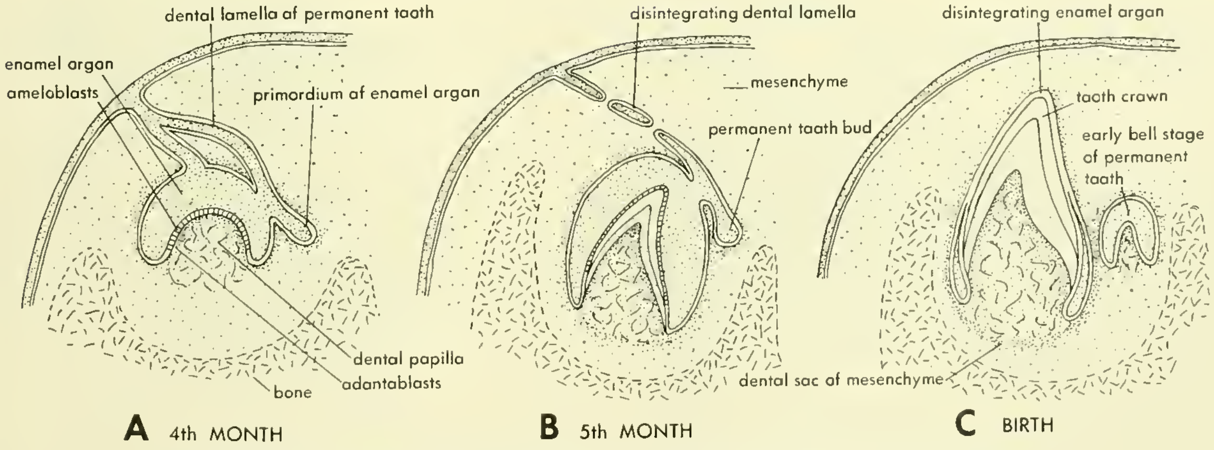


Figure 8-50. Three stages in the development of human (mammalian) tooth. A, cap stage of tooth bud, fourth month; B, bell stage, fifth month; C, milk and permanent teeth at birth. (After Ham, 1957)

Agnath fishes

The agnath fishes are unique in that they do not have teeth of the gnathostome type. Some of the anaspids perhaps had small denticles similar to those of the body armor on the tooth plate in the floor of the mouth. In the

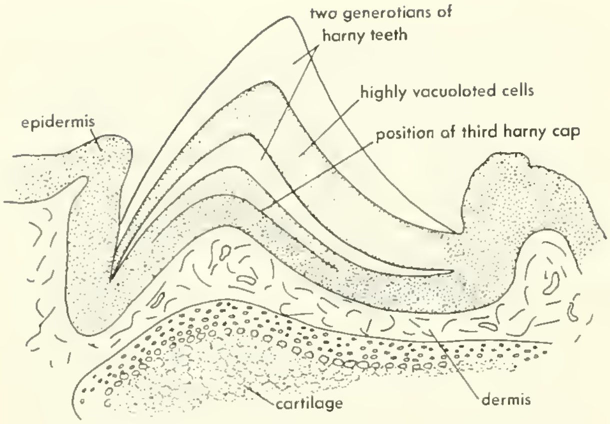


Figure 8-51. Section through a lamprey tooth.

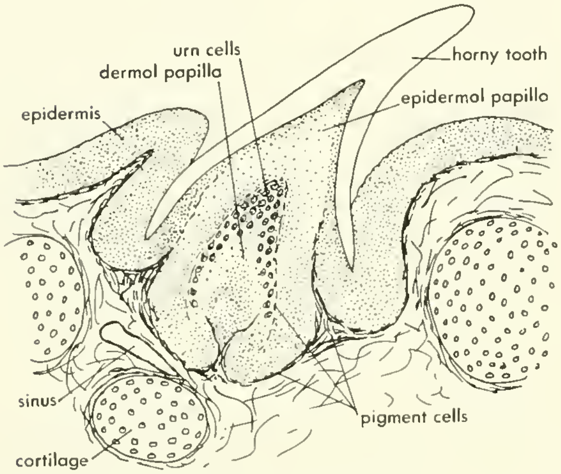


Figure 8-52. Section through a dental plate tooth of Myxine. (After Marinelli and Strenger, 1956, and Lison, 1954)

living cyclostomes, horny teeth are present in the mouth funnel and on the rasping organ. These are formed of keratinized epithelial cells (Figure 8-51, 8-52).

Early gnathostome fishes

In the gnathostomes the teeth are typically conical in shape and formed of the same materials as the skin denticles. The earliest vertebrate remains, from the Lower Ordovician of Esthonia, are described as dermal denticles of two genera, *Palaeodus* and *Archodus*. The structure seen in the case of *Palaeodus* (Figure 8-53) is that of a tooth. The dermal denticles of fossil agnaths are low, rounded tubercles, ridges, or hooked points like the tip of a placoid scale. Identification of the *Palaeodus* denticles as belonging to the dermal armor is based on the supposition that agnaths precede gnathostomes in time and that gnathostomes are unknown from deposits older than Silurian. Since these denticles do not resemble those on the plates of known agnaths, the possibility of their being gnathostome teeth should be recognized.

The arthrodires generally lack teeth on the jaw margins, but some of the smaller forms have them (Figure 8-54). In *Atopacanthus*, the teeth are fused to the acellular jaw bones and have an outer enamel, or modified dentine layer, and an orthodentine core.

Chondrichthyes

The teeth of sharks vary from simple conical points to multituberculate elements or broad, flat crushing plates. The general structure is that of the placoid scale. In the shark *Lamna*, the pulp cavity of the tooth is largely filled with an osteodentine that also forms the basal plate (see Figure 8-23 B). In *Myliobatis*, the flattened, crushing teeth have a tubular dentine in their interior (Figure 8-55).

The development of the teeth in sharks is much like that

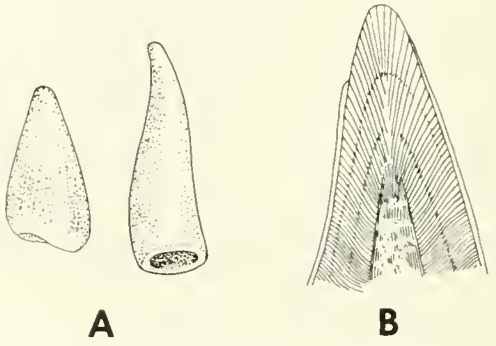


Figure 8-53. Lower Ordovician denticles identified as *Palaeodus* sp?, A, and *Palaeodus brevis*, B. (A after Jarvik, 1960; B after Peyer, 1937)

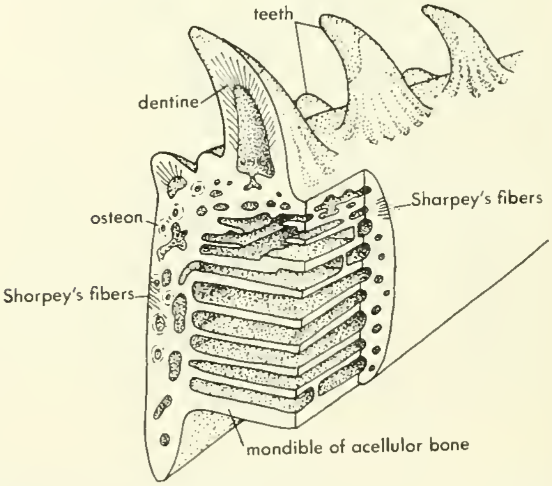


Figure 8-54. Stereodiagram of part of lower jaw of an acanthodian, *Atopacanthus* sp. (After Ørvig, 1957)

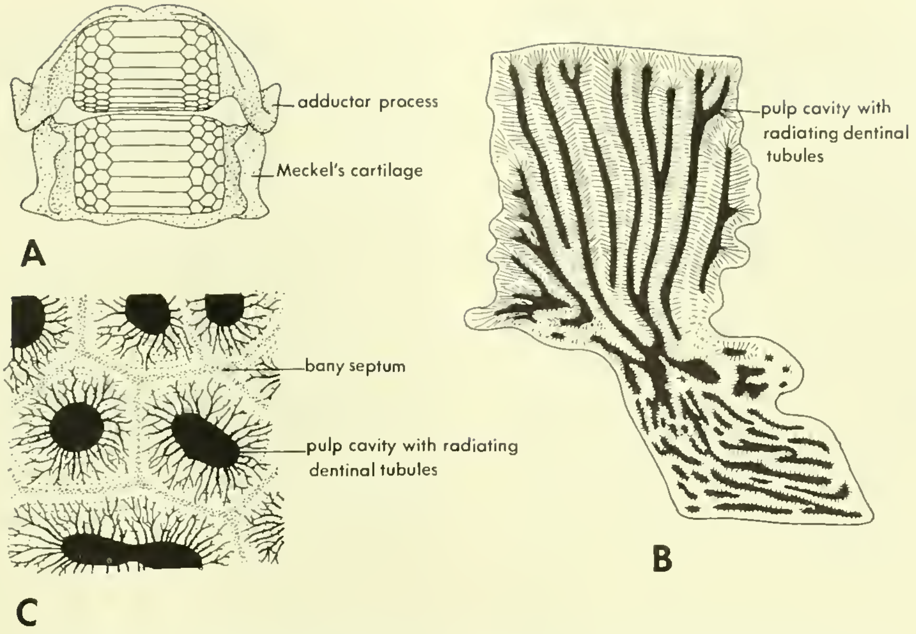


Figure 8-55. Teeth of the ray, *Myliobatis*. A, posterior or inner view of articulated jaws showing plate-like teeth in position; B, vertical section through a tooth plate; C, cross section through the crown of a tooth plate. (A after Owen, 1866, and Arambourg and Bertin, 1958; B after Röse, 1898; C, after Ørvig (1951)

of the other fish described (Figure 8-56). A dental lamina extends into the margin of the jaw and gives off a succession of tooth buds. Each bud forms a cup-shaped enamel organ overlying a papilla in which the crown of the tooth forms. The enamel that covers the crown is relatively thin and formed by calcification of the thickened and fibrous basement membrane of the enamel organ. It is invaded by the peripheral canals of the dentinal tubules and may even enclose cell spaces.

As the tooth develops it becomes larger. The pallial dentine may have circumpulpar dentine laid down inside it, and the pulp cavity may be filled with osteodentine. A small base of osteodentine or acellular bone completes the tooth. As the tooth grows, it moves outward toward the margin of the jaw and its point becomes free of the overlying tissues. The tooth is used for a period of time as it continues to move outward. When it reaches the outer margin of the jaw, it is shed. There is usually a continual process of tooth replace-

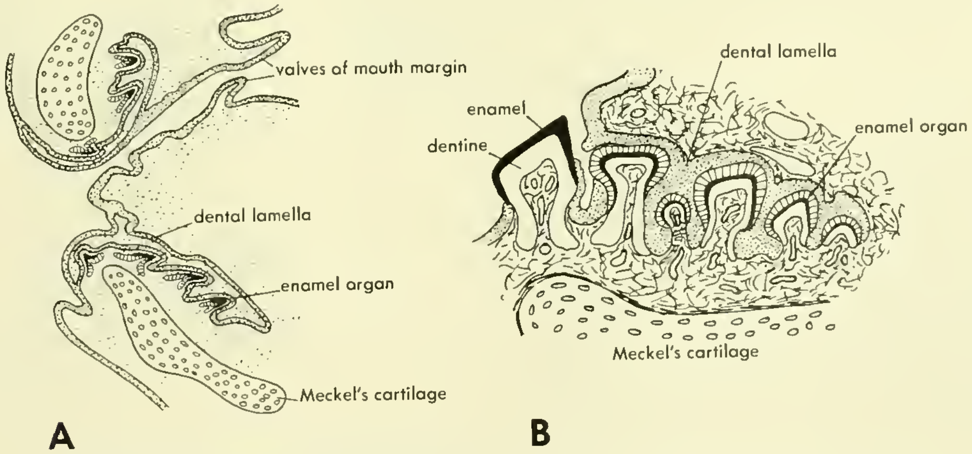


Figure 8-56. Development of teeth in sharks, *Spinax niger*, A, and *Squalus acanthias*, B. (A after Peyer, 1937; B after Kendall, 1947)

ment in this group, a phenomenon referred to as **lyodonti.**

The holocephalan is unlike the shark in that it has tooth plates associated with the jaws, two pairs above and one below. Because of their holostylic jaw suspension, the chimaerids have been related to the late Palaeozoic bradyodont sharks. The latter have simple, pluriserial (many rows) teeth with broad, flat crowns. The rows of teeth form a broad, solid band along the jaw margin. There is some **heterodonti,** i.e. difference in size and shape, from front to rear in the band. The teeth are not replaced, a condition described by the term **statodonti.** They have an outer pallial dentine cover, and the crown is supported by tubular dentine on an osteodentine base, as in the living ray, *Myliobatis* (Figure 8-55).

The teeth of *Hydrolagus* are quite unlike those of the bradyodont, since they are fused into plates with a narrow cutting edge. These plates grow continually but are not shed. Examination of a mandibular plate reveals the outer and inner surfaces covered by pallial dentine. Inside the outer shell is a layer of spongy dentine whose channels tend to be vertically disposed, and in this osteodentine there are columns of ovoid spaces filled with calcified material. These outer layers, along with the supporting columns of calcified balls, form the outer beveled edge of the plate. This margin has an anterior and a middle cusp. Inside this is a layer of spongy dentine in which the cavities tend to run anterior-posteriorly. Vertical ridges of spongy osteodentine lie medial to this and to the anterior and middle cusps. These ridges are strengthened by columns of calcified balls.

In this tooth plate there is a developmental sequence from root to crown. The root is quite spongy and fibrous with wide anastomosing channels. The sacs of the columns are filled with a soft material, predentine. Near the crown, the spaces are largely filled with osteodentine and all parts are well calcified. The middle spongy layer is the softest part of the plate and forms a vale between the outer and inner layers. This middle layer is lacking in the anterior cusp where the columns of calcified balls lies about midway between the outer and inner shells.

Actinopterygians

The teeth of actinopterygians are usually cones. In the palaeoniscoids these have a hard, shiny, outer cover of enamel over pallial dentine and a large pulp cavity. Generally, they are fused to the jaw margin. Again there is the question whether the outer cover is enamel. In some fishes a prismatic structure comparable to enamel is achieved. The outer cover has been identified as vitrodentine or **hyodentine** and is presumed to represent a modification of the surface of the dentine through the agency of the ameloblasts of the epidermal enamel organ. The dentine of some fishes is peculiar and is identified as **vasodentine.** Capillary loops permeate this tissue which lacks dentinal canals (Figure 8-57).

Tooth form is variable in these fishes, as in other groups. There are large fangs or flat-surfaced crushing teeth. The bases of the teeth in *Lepisosteus* (Figure 8-58) show vertical ridges and in section are observed to be of a simple, **labyrinthine** type. The teeth in this group are continually replaced by new teeth forming medially to the old.

Choanate fishes

The crossopterygian fishes have rather large conical teeth, whose bases are strengthened by folding of the dentinal walls (plicidentine) (Figure 8-59, 8-60). This labyrinthodont condition is observed in the garfish, an actinopterygian, in the early amphibians, and in some reptiles.

The labyrinthodont condition is not observed in the primitive dipnoan *Dipterus;* however, in this genus, marginal teeth are lacking and tooth plates are formed on the pterygoids and prearticular. The tooth in this genus is strengthened by filling the pulp cavity with osteodentine (Figure 8-23 B).

In the living lungfishes, the tooth plates are formed by the basal fusion of many teeth. The teeth are joined together by an enamel-like material and are filled interiorly with tubulodentine.

Amphibians

In the primitive amphibians, the labyrinthodont type of tooth is well developed (Figure 8-61): the teeth are often large and set either in shallow pits or in an alveolar groove. The point of the tooth is simple, but toward the base the dentine becomes infolded to form a very complicated pattern as seen in cross section. The pulp cavity is constricted by this infolding process.

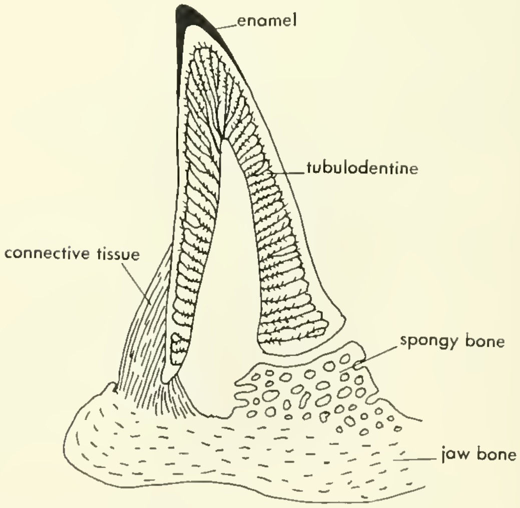


Figure 8-57. Section through tooth and jaw of *Merlucius vulgaris* a teleost. (After Peyer, 1937)

In the modern amphibians, the teeth are simple cones set in a broad alveolar groove and attached in the pleurodont style to the outer wall of that groove. In *Necturus, Cryptobranchus,* or the frog, the crown of the tooth is easily broken off the root portion (Figure 8-62). The abscission line marks the division between the enamel crown and the base. In *Necturus* the crowns are longer and straighter than in the frog or *Cryptobranchus.* The larval anuran is of interest in that it develops keratinized teeth (Figure 8-63). These are not comparable to those of the agnath and can be viewed as a larval specialization.

Reptiles

Reptile teeth are usually simple cones (**haplodont**) with an enamel cap and an orthodentine interior enclosing a large pulp cavity. The teeth are set in a deep alveolar groove, and their attachment to the jaw varies. The usual style is identified as **pleurodont** (Figure 8-64); that is, the teeth are attached to the outer wall of the alveolar groove. This style is observed also in the living amphibians. In the **thecodont** style, the tooth is set in a socket, as in the alligator (Figure 8-65). *Tupinambis,* a lizard, has a **subthecodont** style in which the tooth is fused all around to a bony sheath covering the alveolar groove. The last style is the **acrodont;** in this the teeth are fused all around to basal material filling the alveolar groove.

Tooth replacement in the reptiles is of interest. In the alligator one sees several generations (**polyphyodont**): the old tooth which is fused to the upper margin of the tooth socket, the alveolus; the replacement tooth which lies in a cavity at the base of this large tooth; and a third generation lying

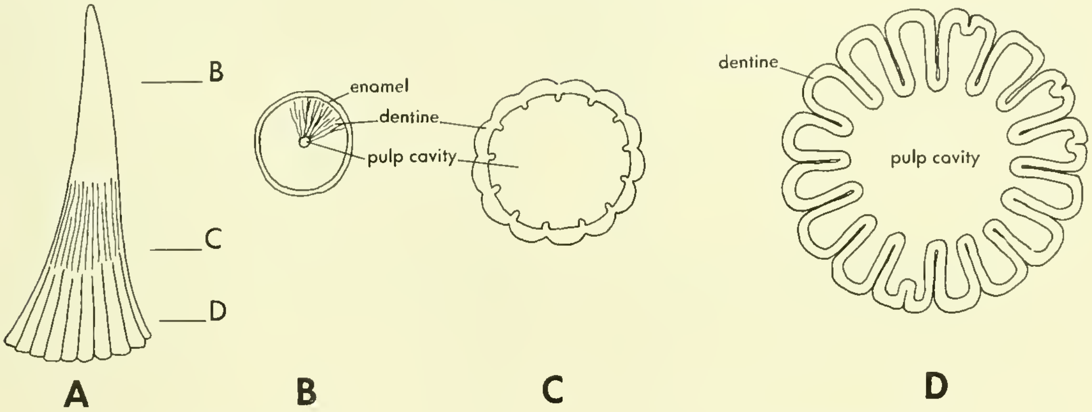


Figure 8-58. External view, A, of a tooth of *Lepisosteus* with sections showing structure near tip, B, middle, C, and base D.

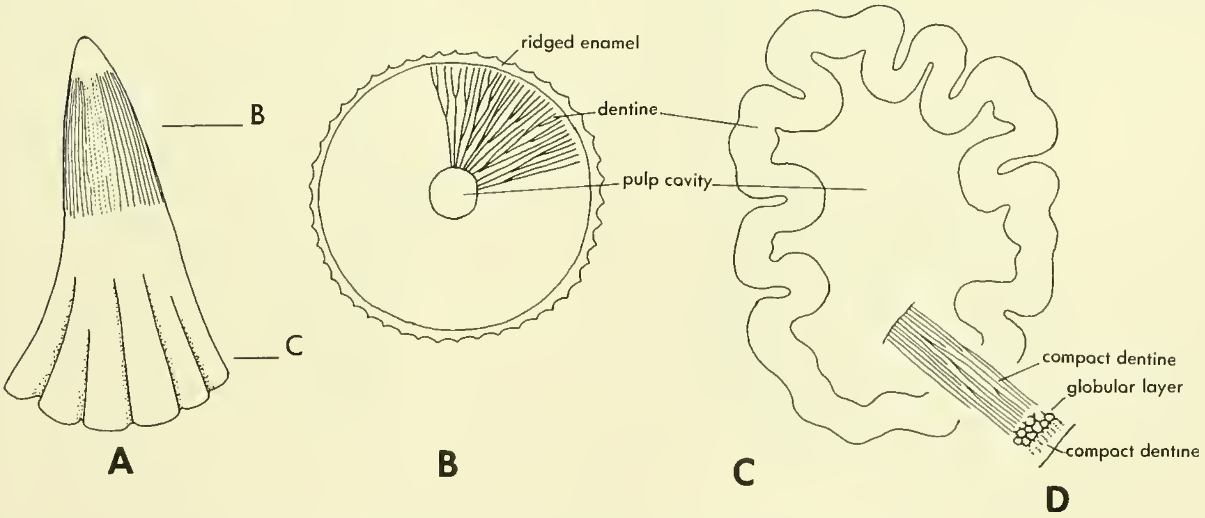


Figure 8-59. External appearance of tooth of *Osteolepis,* A, with sections near tip, B, and at base, C. A part of the wall of C is enlarged in D to show histological detail. (After Bystrow)

medial to the replacement tooth. The usual sequence in reptiles is for new teeth to be formed medial to the old teeth. The new teeth move outward as they form, and the base of the old tooth is resorbed until the crown drops free. A new tooth may move outward below the tooth it is going to replace or it may grow next to the old tooth and then crowd it out. Replacement also involves a sequence along the jaw margin—every other tooth or every third tooth being replaced at any one time.

In the lizard *Tupinambis*, one sees the beginnings of

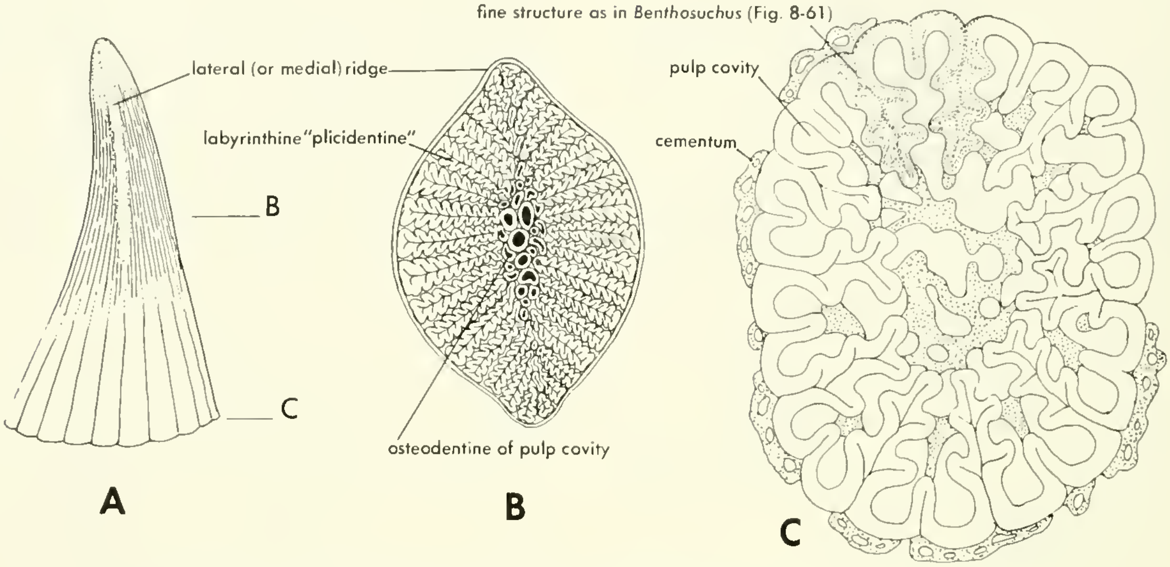


Figure 8-60. External appearance of a tooth of *Holoptychius*, A, with a section near the middle, B, and at the base, C, to show details of structure. The fine structure of the wall is like that of *Benthosuchus* shown in Figure 8-61. (After Pander and Bystrow, 1936)

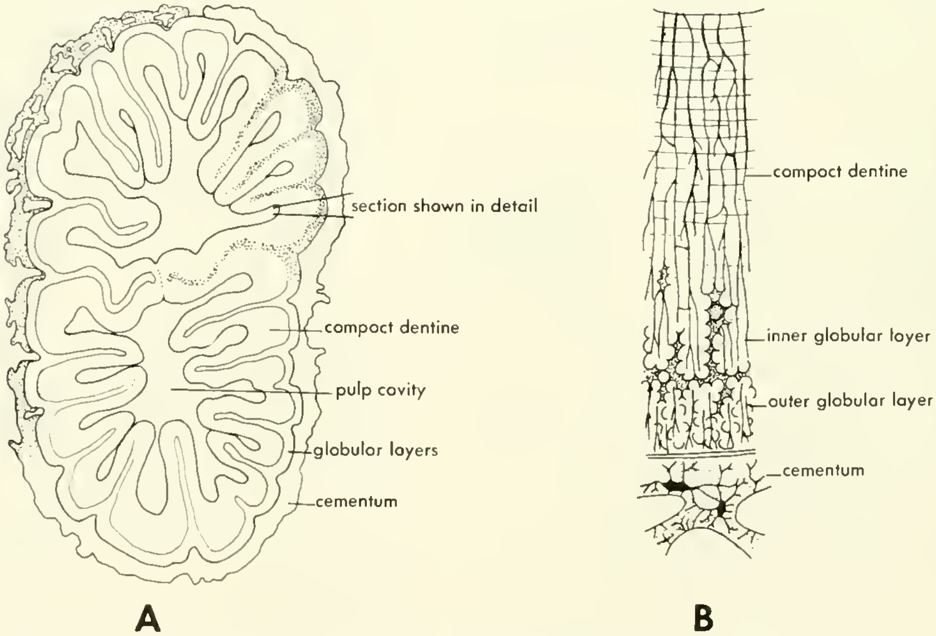


Figure 8-61. Tooth structure of a labyrinthodont amphibian, *Benthosuchus*. A, cross section near base; B, histological detail of wall. (After Bystrow, 1938)

heterodonti, that is, structured specialization of different teeth. The front teeth are incisor-like, with three cusps in a line; behind these are pointed conical teeth, and behind these, large, rounded, crushing teeth. The presence of several cusps may be explained as due to the fusion of several tooth buds or subdivision of the original bud. Although many reptiles are described as **homodontous,** the conical teeth may differ markedly in size in different parts of the jaw margin.

In the reptile, teeth are borne on a large number of bones, just as in the amphibian or fish: the premaxilla, the maxilla, the vomer, and occasionally the pterygoid and palatine. Among lizards and reptiles in general, there is a wide range of tooth modification for various functions, for example, the sharp conical tooth as opposed to the broad, flat crushing plate. In the living turtles, teeth are lacking, but, in the most primitive turtle known, *Triassochelys,* small conical teeth covered the palate and jaw margins. Like the turtle, the bird lacks teeth, although the Cretaceous genus *Hesperornis* had them.

Mammals

The general structure of the mammalian tooth has already been described; it is peculiar in the thickness of its enamel cover and in usually having a tapered root, or roots. The main items of interest in comparing mammals are the variations in the shape of the teeth (**heterodonti**) and the occurrence of two sets (**diphyodonti**), **milk** and **permanent.** The teeth are specialized as **incisors, canines,** and as cheek teeth which grade from simple cones to molariform. Some cheek teeth, the **premolars,** are preceded by milk teeth, but the **molars** are not. The fact that the molars are not replaced is probably related to their late appearance.

In terms of their growth, mammalian teeth vary; diphyodonti for some of the teeth has already been mentioned.

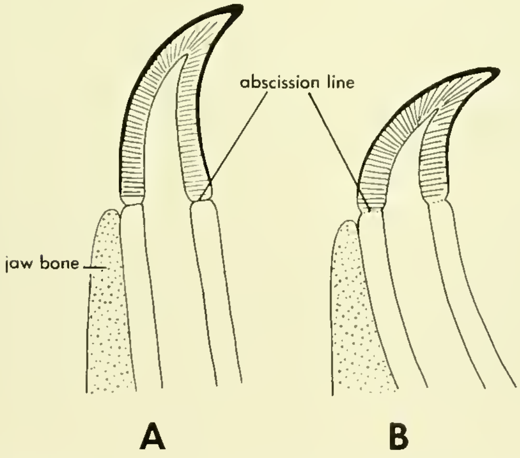


Figure 8-62. Vertical section of tooth and jaw in *Cryptobranchus,* A, and the frog, B.

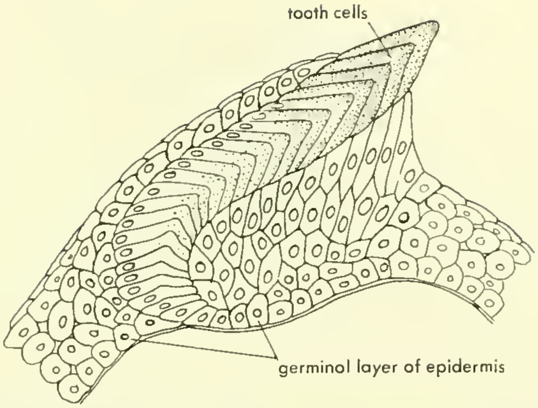


Figure 8-63. Horny tooth of mouth margin of 20-mm larval frog. (After Peyer, 1937)

The **brachydont** type, such as in man, has a limited period of growth during which the tooth is completely formed and the root or roots close. A second type, the **hypsodont** or high-crowned tooth, is observed in the molars of the horse. This type has a long growth period and both root and crown are covered by cement, a bony material. The root does not close till late in life. The last type is seen in the incisors of rodents or rabbits and in many other mammals; growth continues through life, and the root remains open.

There are several theories as to the origin of mammalian teeth. The simplest is that the several tooth types gradually evolved from the ancestral conical tooth. According to the **dimere** (*di,* meaning two; *meros,* parts) theory of Bolk, the primitive reptilian tooth, as well as that of some primitive mammals, the triconodonts, had three cusps (see the front teeth of *Tupinambis*). Two such teeth fused together would produce a typical molariform tooth. One such tooth minus front and back cusps would form a canine tooth. According to this view, some teeth are trimerous or even polymerous, such as the molars of elephants. Another theory, supported

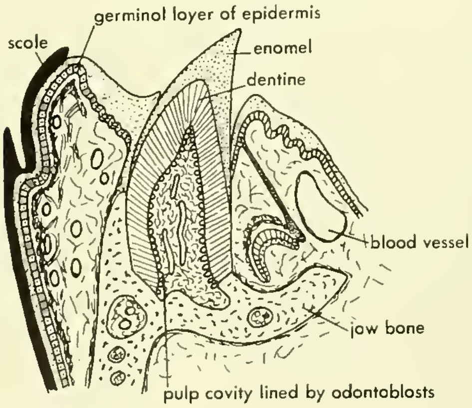


Figure 8-64. Section through tooth and jaw of lizard. (After Kendall, 1947)

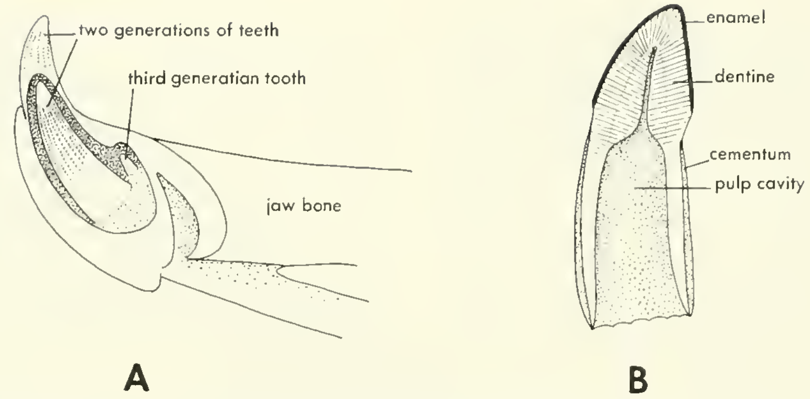


Figure 8-65. Section through tooth and jaw of alligator, A, showing second and third generation teeth in relation to functional tooth. B, vertical section through fully formed tooth.

by Kükenthal, Röse, and others, supposes that even the triconid tooth is a product of fusion of three simple teeth. In view of the compound nature of the placoid scale of *Squalus*, this seems most probable and would mean that all mammalian and most tetrapod teeth are in fact polymers.

The teeth of mammals, at least the molariform teeth, have an intricate pattern of cusps on them. This pattern, which involves a complex terminology, is useful in the taxonomy of the group. The heterodonti of the mammal makes possible the use of a dental formula (Chapter 3). This device indicates the numbers of the various types of teeth in the upper and lower jaws. Such a formula can have a taxonomic value since it reflects an aspect of adaptive modification.

RESUMÉ

In terms of the skin and its derivatives, there are a few salient points. The stratified epidermis of the vertebrate separates this group from the protochordates and invertebrates in general. The histology of the skin has not been used in subdividing the vertebrates. It can be noted that the epidermis of the cyclostomes is thicker in terms of the number of cell layers than that of gnathostome and that the dermis is perhaps less complex in its structure. These differences cannot be sharply defined, however, since most of the agnaths are extinct and the structure of their skin is unknown.

Among the gnathostomes, the amphibians are distinct in terms of their saccular or simple, alveolar, mucous and poison glands. The mammals in contrast have tubular, very coiled sweat glands. The general picture is much as before with three lines of tetrapods (amphibian, reptile, and mammal) stemming from some unknown ancestor. Neither the amphibian, with its specialized glands, nor the reptile, with its stratum corneum modified into scales, can be considered the more primitive.

In fishes multicellular epithelial glands are either lacking or are few in number and highly specialized. The exception is the line of large mucoid glands in the myxinoid. In place of the multicellular glands, fishes have large numbers of mucoid cells which pour their secretion on to the surface of the skin and then are replaced from below. Other kinds of secretory cells are usually present. These may be very large and sunk deep in the epidermis. The nature of their secretions is not known, but in some cases they appear to produce the cementing matrix of the epidermis itself. Usually they contribute to the surface slime layer along with the mucous cells.

Although much is known about the fine structure of the scales of vertebrates and although scales form an important part of the fossil record, there is as yet no clear cut picture of the evolution of these structures. The histology of agnath plates is in some cases like that of gnathostomes or quite different as in the case of the aspidin. The basic differences in scale and armor structure appear to lie in their development; however, such information is still lacking for many types.

For teeth, the same situation exists as for scales. The agnaths are defined as lacking marginal teeth on the jaws although they possessed the dermal denticles from which such teeth are presumed to have evolved. Within the vertebrates, teeth are fairly uniform in structure with highly modified types cropping up in several groups: sharks, dipnoans, and the various tetrapods. A careful histological study of the teeth involved may confirm the proposed relationship between the holocephalans and the bradyodont sharks. Other, and similar, problems may also be solved through such comparative studies.

9

The Viscera

Use of the terms "digestive" and "respiratory" systems has been avoided in the title of this chapter since parts of other "systems" are also discussed. In a dissection the parts and organs of various systems are observed together and are best described together, leaving their separation into "functional units" to a physiological approach. Viscera are defined as the soft contents of the principle body cavities: the entrails together with the heart, liver, lungs, etc. The kidneys and gonads are described separately in Chapter 10, and a description of the heart will be deferred to Chapter 11. A discussion of gills is included here as a part of the "respiratory system."

THE DIGESTIVE TRACT AND ASSOCIATED STRUCTURES

The digestive tract of the vertebrate appears to have remained largely unchanged through the evolution of the several major groups but has shown extreme adaptive plasticity in some species of each of these. This seemingly erratic variation has probably discouraged comparative study.

In studying the digestive tract, most of the observations are made in ventral view, but it seems best to use orientation terms referable to the specimen itself. In other words, structures which lie to the observer's left are a part of the right side of the specimen. Those things which are most superficial in the ventral view lie ventral to the structures they conceal.

Mammals

As represented by the cat, rat, or rabbit, the digestive tract of the mammal begins with the **mouth,** which has **lips, teeth,** a mobile **tongue,** and **salivary glands.** Behind the **oral cavity** is a short **pharynx,** into which opens the **nasal passage** above, and the **glottis** below. The glottis is the opening into the **trachea** and **lungs.** The **esophagus** is tubular and leads to the expanded hook-shaped **stomach.** The esophagus passes above the mass of lungs and through the muscular **diaphragm** separating the **pleural cavities** from the **abdominal cavity.** The esophagus enters the stomach above the large lobed **liver.** Between the liver lobes on the right side (student's left) is seen the **gall bladder.** In the dorsal mesentery of the stomach lies a dark-colored body, the **spleen** (Figure 9-1). Behind the spleen the mesentery bags out as a thin membranous sac studded with fat masses. This bag, the **greater omentum** or omental bursa, underlies much of the intestinal mass (cat). The stomach ends at a constriction, the **pyloric valve,** and the small intestine begins.

A short distance along the small intestine from the pyloric valve, the **common bile duct** and the main duct of the **pancreas,** the **duct of Wirsung,** join and enter the intestine dorsally. At the point of entry is a small lump, the **ampulla of Vater.** Internally, the common duct opens through a papilla (of Vater). Somewhat posterior to the ampulla, an accessory duct of the pancreas (**duct of Santorini**) may enter the small intestine.

The first part of the small intestine, the **duodenum,** forms an arc or open loop. In the mesentery within the arc, and next to the gut, is a flattened irregular **pancreas.** In man, only a part of the pancreas lies in this arc, the larger part lies **retroperitoneally,** that is, outside of the somatic peritoneum, in the region above the stomach. In the rabbit the bile duct enters the first part of the duodenum near the stomach, while the pancreatic duct enters the far end of the duodenal arc. The terminal part of the duodenum is closely bound to the dorsal body wall by the **cavo-duodenal ligament.** The extreme is man where this part of the duodenum has become retroperitoneal. The remainder of the small intestine, the **jejunum** and **ileum,** is long and quite looped; this part of the intestine has been called **Meckel's tract.**

The posterior end of the small intestine enters the large intestine about in the posterior ventral midline. At this junction, there is an **ileocolic valve.** The large intestine extends as a pouch or **caecum,** a short distance back along the course of the small intestine. The caecum is large and coiled in the rabbit, relatively short in the rat, cat, or man. In man the caecum has an **appendix.** The functional significance of the vermiform appendix is obscure, but there is no reason for supposing that it is a primitive or degenerate structure. It is evidently a specialized formation, peculiar to anthropoid apes and man. There are paired caeca in

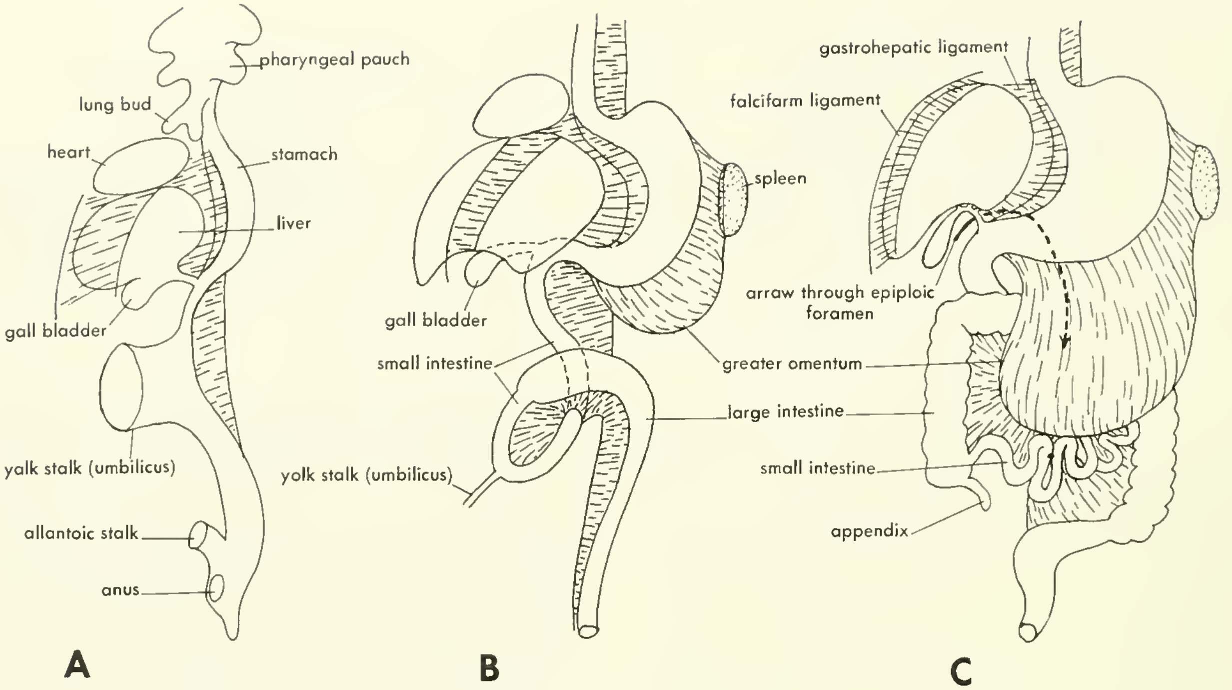


Figure 9-1. Three stages in the development of the digestive tract of a mammal as seen in ventral view. (After Patten, 1946)

armadillos, while *Hyrax* has several caecal pouches along the large intestine, including a pair of lateral diverticula. A caecum is lacking in some mammals—hippopotamus, the shrew *Talpa,* some bats, and bears.

The large intestine curves forward on the right side of the body, as the **ascending colon;** turns across to the opposite side anterior to the general mass of the small intestine as the **transverse colon;** and extends posteriorly as the **descending colon.** From here it extends as the **sigmoid colon** (man) to the midline **rectum,** which reaches to the anus. Either the small intestine (cat, rat, man) or the large intestine (pig) can be quite lengthened and spirally coiled. In some bats and a few primates (Pin-Tailed Tree Shrew—Figure 9-2), the colon is short and straight.

The monotremes agree with this general picture (Figure 9-3). The liver has several lobules that belong to the basic right and left lobes. The **gall bladder** lies to the right of the ventral midline. In *Ornithorhynchus* the stomach is sac-like and has no gastric glands. Its lining is like that of the esophagus (Figure 9-5). The pyloric opening is to the right of the esophageal entrance and there is no pyloric valve. The spleen is very large, extending from the mesentery above the stomach posteroventrally and medially through bifurcate lobes to the posterior end of the body cavity. There is a frilled greater omentum extending back from the stomach between the coils of the gut and the spleen.

The first part of the duodenum, perhaps the pyloric section of the stomach, is thick-walled, with a horny papillate lining and **Brunner's glands** in the submucosa. Since Brun-

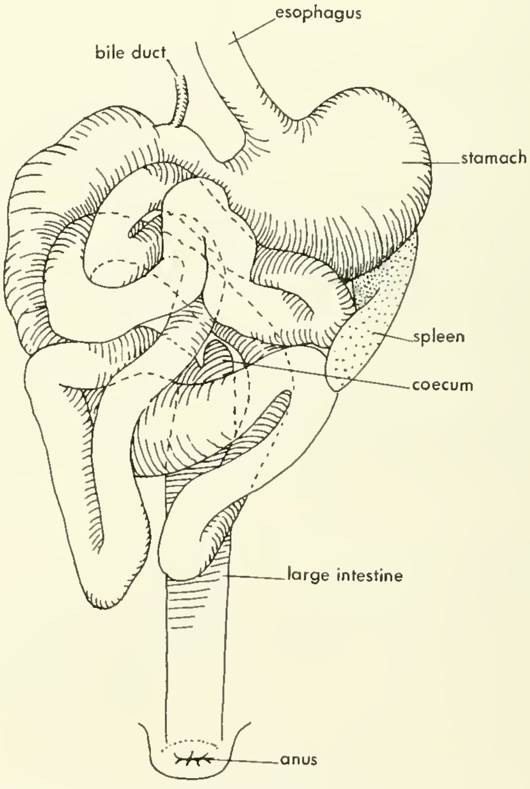


Figure 9-2. Ventral view of the digestive tract of a Pen-tailed Tree Shrew, *Ptilocercus.* (After LeGras Clark, 1926)

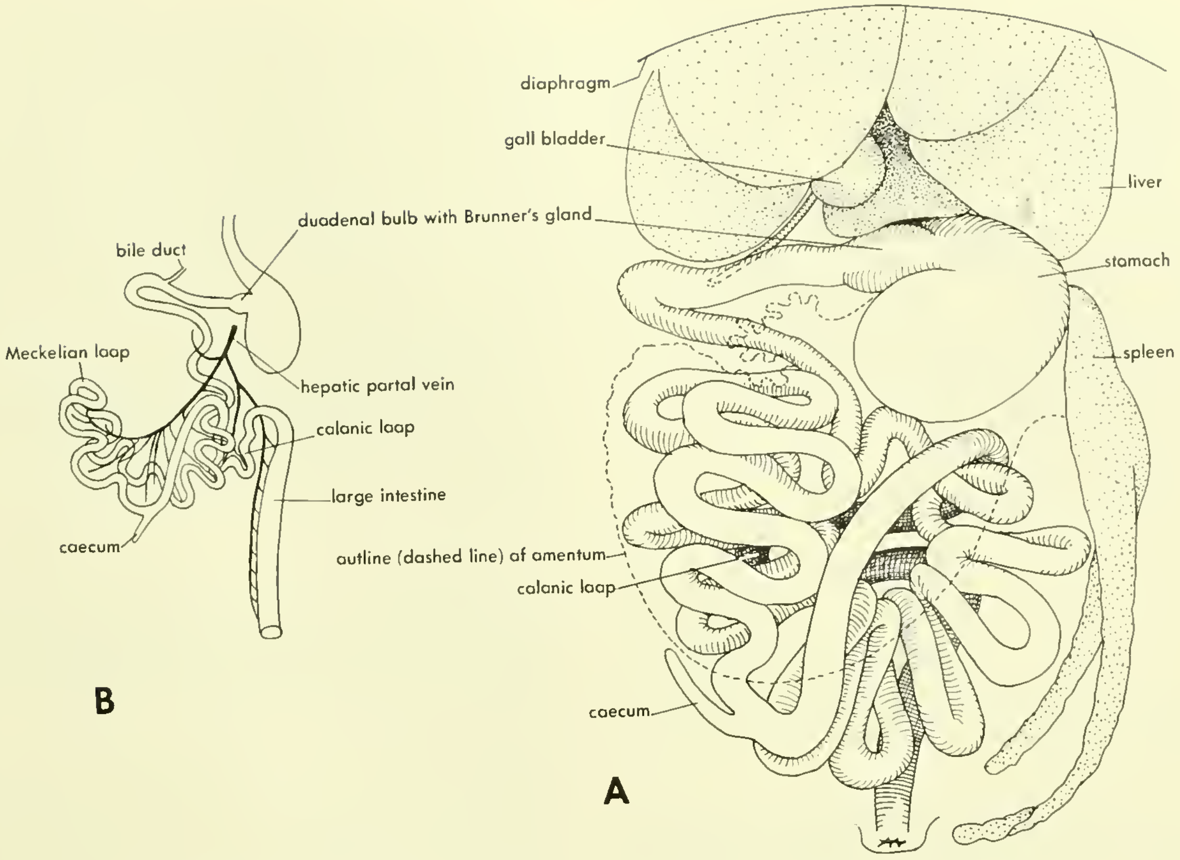


Figure 9-3. Ventral views of the digestive tract of the Platypus. (A, after Owen 1866; B, after Mitchell, 1905)

ner's glands characterize the duodenum of higher forms, this has been called the **duodenal bulb.** From here the gut continues a short distance to the common entrance of the bile and pancreatic ducts. The pancreas lies entirely in the mesentery of the duodenal arc.

The duodenal arc extends first to the right, then back to the left above the hepatic portal vein (Figure 9-3) and next to the dorsal body wall, where it is attached by the cavoduodenal ligament. The remainder of the small intestine, Meckel's tract, is very looped and folded; it joins the large intestine at the ventroposterior margin of the gut mass without an ileocolic valve. The large intestine has a slim caecum projecting back along the small intestine; it extends anteriorly below the coils of the small intestine, forms a **colonic loop,** then passes dorsally anterior and joins with the terminal part of the duodenum; from here it turns posteriorly to the **cloaca** above the loops of the small intestine.

The marsupial, as represented by the opossum, is much like the monotreme (Figure 9-4). The stomach of members of this group shows much variation and specialization, but in the opossum it is a simple large sac (Figure 9-5). It opens to the right of the esophagus into a sacculate duodenum. The bile duct is a short, thick tube which opens into the gut a short distance from the stomach. The duodenal loop passes dorsally across the body cavity to the looped Meckel's tract.

The small intestine enters the large intestine ventrally and just behind the stomach. The large intestine has a large but simple caecum. In *Thalacinus* or *Notoryctes,* a caecum and ileocolic valve are lacking. The large intestine extends dorsally, anterior to the duodenum, then curves posteriorly, to the left of that part of the gut; from here there is a loop to the right, an ansa **coli,** and then a straight transit to the anus.

The liver has a large right lobe with two small dorsal lobules and a smaller left lobe with a digitate margin. The spleen is attached to the dorsal mesentery of the stomach, anterior to the omental bursa (greater omentum). The spleen is intermediate in size between that of the monotreme and the placental.

The digestive system of the mammal can be characterized by several features. There is a greater omentum; the spleen lies to the left of the stomach and can be seen from below. The terminal part of the duodenum is bound to the

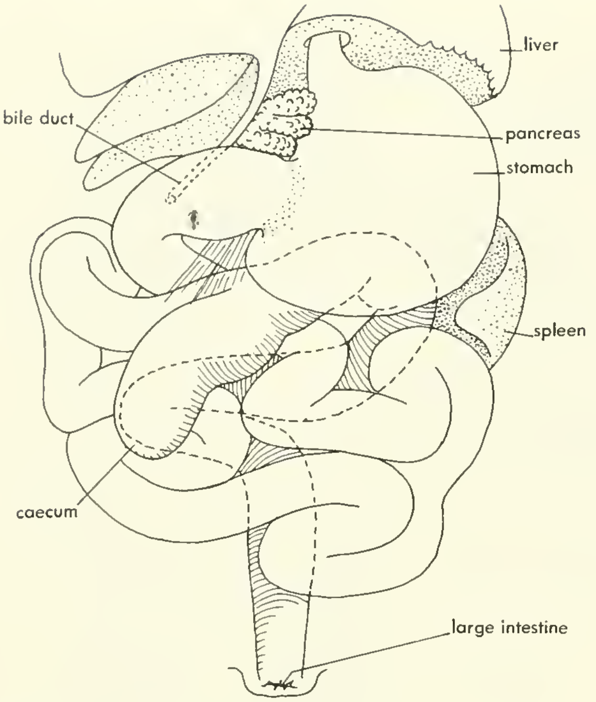


Figure 9-4. Ventral view of the digestive tract of the opossum (*Didelphys*).

dorsal body wall, or lies retroperitoneally; it is attached to the large intestine in this area as a result of the rotation of Meckel's tract. A good part of the large intestine is usually involved in a rotated loop, except in the bat and the tree shrew.

Embryological development In mammals the lining of the digestive tract and its glands is formed of entoderm. The bulk of the wall and a part of the glands are formed from mesoderm. In the early embryo the formation of the head fold produces a forward-projecting pocket of entoderm, the foregut; the similarly produced tail fold gives rise to the hindgut (Figure 9-6). The embryo is gradually separated from the yolk sac by constriction of the yolk stalk. The foregut gives rise to **pharynx, lung buds, esophagus, stomach, duodenum,** and the liver and pancreatic diverticula. The midgut forms much of the **small intestine,** while the hindgut forms the **large intestine.** These are arbitrary assignments for rather vague regions.

The liver and pancreas arise behind the stomach region, which has expanded and arched to the left (Figure 9-7). The **liver** appears first; it arises as a ventral diverticulum. This diverticulum branches many times giving rise to a mass of cell cords embedded in mesoderm. These cell cords produce the secretory cords of the definitive gland. Another diverticulum appears from the main duct of this gland which grows out posteriorly and gives rise to the **gall bladder.**

The **pancreas** arises from dorsal and ventral diverticula. The first opposite the duct of the liver and the second just to the left of the liver duct or from that duct to the left of the gall bladder evagination. In the process of development the ducts of the dorsal and ventral pancreatic outgrowths cross. Frequently the dorsal pancreas comes to drain through the ventral duct, but sometimes the dorsal duct is preserved as the **duct of Santorini.** The two pancreatic diverticula and the early gut relationship can be observed in the 10-mm pig. At this stage a loop of the gut attached to the yolk stalk extends out from the body into the umbilicus. This loop is rotated in the course of development.

The **allantois** (Figure 9-6) grows out from the hindgut. As the embryo is separated from the yolk mass, its stalk extends forward and then out through the umbilicus into the extra-embryonic coelom. The base of the allantois forms the **bladder.**

Reptiles

Up to this point the various visceral structures have been described in an anterior to posterior sequence. A more systematic approach is now feasible. The pattern will be as follows: the intestinal tract from anterior to posterior, then the liver, pancreas, and spleen.

Lizard and Sphenodon The **stomach** is of a simple tubular form tapering posteriorly and curving to the right (to the left as seen in ventral view) to end at the **pyloric valve** (Figure 9-8). The **duodenal loop** of *Iguana* is open except for its mid section. A closed loop is one in which the two limbs lie in contact, or nearly in contact. *Tupinambis* has a completely open, arc-like duodenal loop. The bile duct enters the gut anterior to the mid part of the duodenal loop. Frequently two bile ducts are evident. In a large lizard such as *Iguana,* which is like *Tupinambis,* the limbs of the stomach loop are joined by the ventral mesentery; the gastrohepatic ligament and the coils of the **small intestine** lie above this membrane. In most lizards, and Sphenodon, the small intestine lies posterior to the stomach. The small intestine loops irregularly and opens into the large intestine.

A small dorsal caecum of the **large intestine** is usually present at the **ileocolic junction.** This part of the intestine makes a loop or two and extends back to the cloaca. The large **urinary bladder** lies below, and extends forward from, the **cloaca.** The bladder is attached to the ventral body wall. There is no ventral mesentery for the gut, but the dorsal mesentery is retained and fans out to the various loops and coils of the intestine. The vessels of the hepatic portal system as well as the arterial supply of the gut are seen in this mesentery.

In *Iguana* the large intestine is lengthened. Its anterior end is much expanded and sacculate, and there is a caecum extending back along the course of the small intestine. Following the caecum there is a tightly closed colonic loop

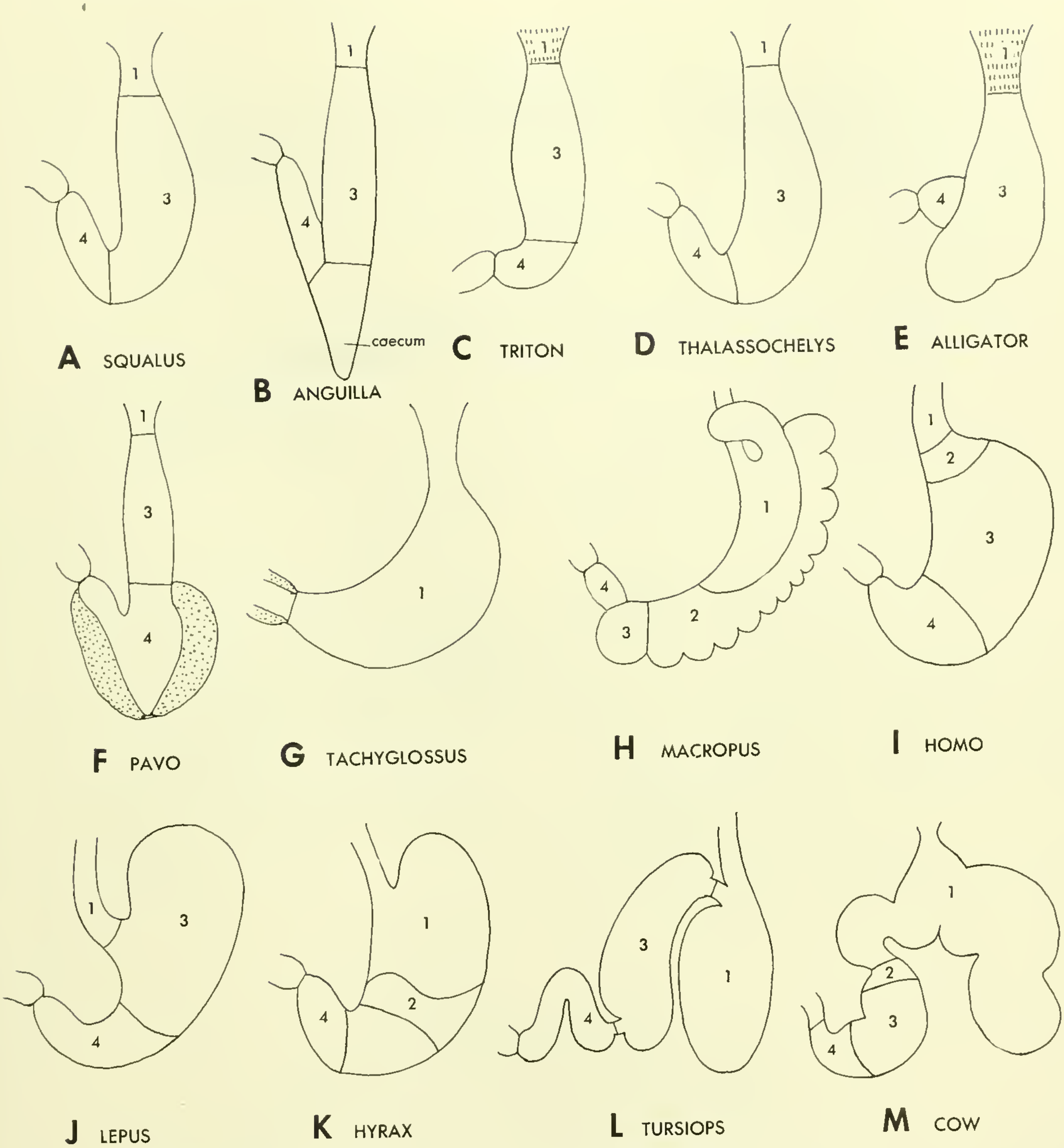
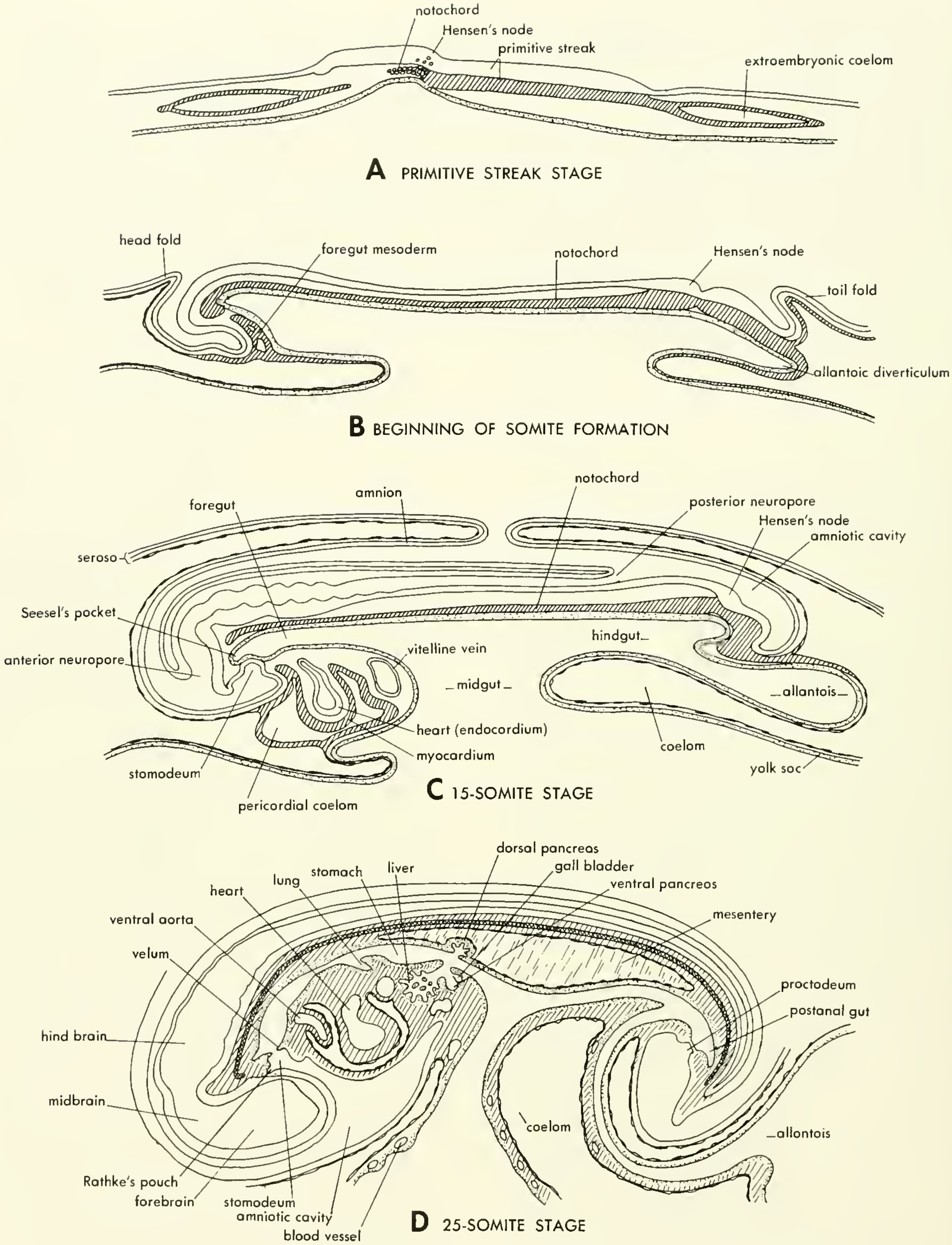


Figure 9-5. Modifications observed in the shape of the stomach and in its lining in vertebrates. 1, cutaneous lining of esophagus; 2, cardiac glands present; 3, gastric glands present; 4, pyloric glands present. (After Pernkopf, 1937)

from which a fairly direct course is taken to the **cloaca.** The cloaca has an anterior chamber (**coprodeum**) into which the gut opens, and a posterior chamber (**urodeum**) for the ureters and sex ducts. Between these on the ventral aspect opens the urinary bladder. The region just inside the **cloacal sphincter,** from which the hemipenes of the male project, is identified as the **proctodeum.**

The **liver** is bilobed; the lobes may be fused ventrally along the ventral septum, the **falciform ligament.** The **gall bladder** is large and to the right of the ventral septum. The pancreas is easily observed in the loop formed by the pyloric section of the stomach and the beginning of the small intestine. In *Iguana* this gland lies along both the pyloris of the stomach and the duodenum; it ends medially at the duo-



A PRIMITIVE STREAK STAGE

B BEGINNING OF SOMITE FORMATION

C 15-SOMITE STAGE

D 25-SOMITE STAGE

Figure 9-6. Development of the gut (and amnion) in the early stages of the pig. (After Patten, 1958)

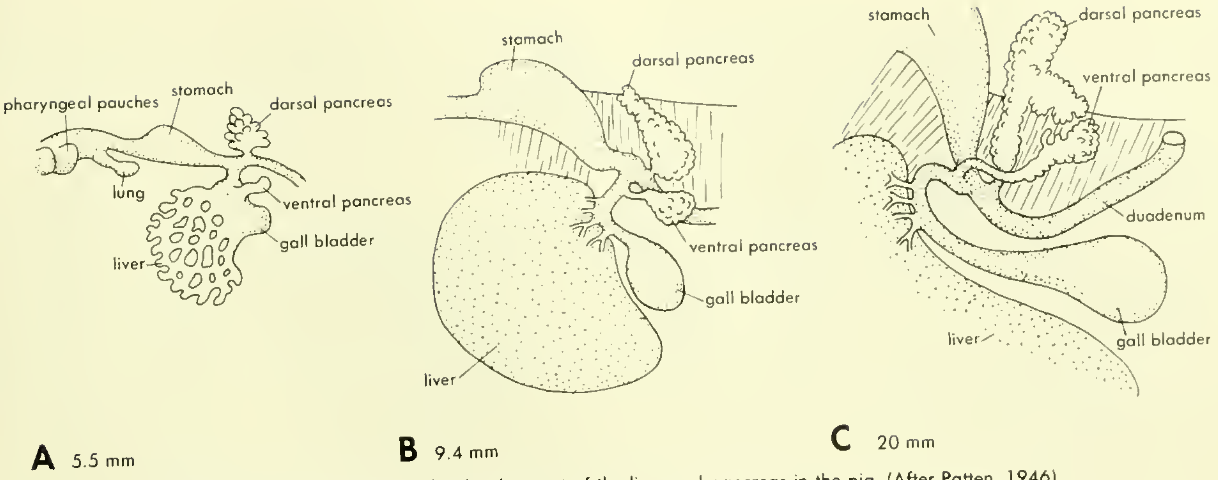


Figure 9-7. Three stages in the development of the liver and pancreas in the pig. (After Patten, 1946)

denal loop where it extends forward along the bile duct and hepatic portal stem. The relatively small, elongate-ovoid spleen lies above the stomach in the dorsal mesentery near the posterior end of the body of that structure.

Alligator The viscera of the alligator are peculiar in that they are enclosed in the muscular peritoneum which is free from the muscular body wall. Muscle fibers radiate, from an origin along the pubis near the acetabulum, over the outer surface of the peritoneal sac to the posterior margin of the liver. These muscles act in drawing the liver mass posteriorly. In this way the volume of the pleural space is increased and the lungs inflated. In *Tupinambis* a similar peritoneal sheet of musculature from the liver margin attaches to the body wall a short distance behind.

The body of the stomach is thick-walled and muscular; to this is appended a thin-walled pyloric sac (Figure 9-9). The esophagus is a simple tube entering the body of the stomach anteriorly, and the pyloris opens through a narrow passage just posteromedial to this entrance. The small intestine opens into the middle of the dorsal surface of the pyloric sac. There is a well-developed, closed duodenal loop between the limbs of which lie the pancreas and the bile duct. The small intestine makes several loops posterior to the stomach before opening into the expanded large intestine. There is no caecum and the large intestine extends nearly straight back to the elongate cloaca. The cloaca has three chambers: a posterior coprodeum into which the gut opens, a middle urodeum for the ureters, and a posterior proctodeum for the sex ducts. In the male the penis lies in the floor of the proctodeum. There is no urinary bladder (Figure 10-38).

The liver is bilobed with the gall bladder to the right of the ventral midline. A process of the liver projects back along the postcaval vein, as it also does in the lizard and the turtle. The pancreas is relatively small and inconspicuous; it lies largely on the dorsal aspect of the duodenal loop. The spleen is a round mass at the dorsal midline above the stomach. It does not appear to lie in the mesogaster, but veins extend from it to the stomach.

The ventral septum is not evident even below the liver. The cloaca is attached to the ventral body wall.

Turtle Although many turtles show some specialization of this tract, *Pseudemys* appears to have remained relatively unmodified (Figure 9-10). The stomach first curves strongly to the left, where it is partly embedded in the liver, then back and to the right to reach the pyloric valve at the ventral midline. The valve is not conspicuous, but the lining of the stomach differs from that of the duodenum in that it is coarsely folded.

The duodenum extends to the right side, where it arches dorsally and receives the bile duct from the gall bladder. From here the duodenum passes posteromedially above the transverse limb of the large intestine, then below the descending section of the large intestine, to which it is attached by a supporting mesentery. From here the small intestine loops back to the right side where it enters the large intestine. The large intestine has a small saccular caecum, a long transverse limb, a loop to the left, then a straight terminal portion which extends to the cloaca.

The liver is massive with several lobules or incisions in its margin. The gall bladder lies far to the right and the bile duct drains almost directly into the mid part of the duodenum. The pancreas lies along the limb of the duodenum which leads from the stomach. The ovoid spleen lies in the mesentery just above the caecal end of the large intestine.

General observations on tetrapods

The reptile digestive tract is distinctive as compared with the mammal. An omental bursa is lacking, the spleen is smaller and rounder, and it lies in the mesentery dorsal to the stomach or gut and does not show on the left side of

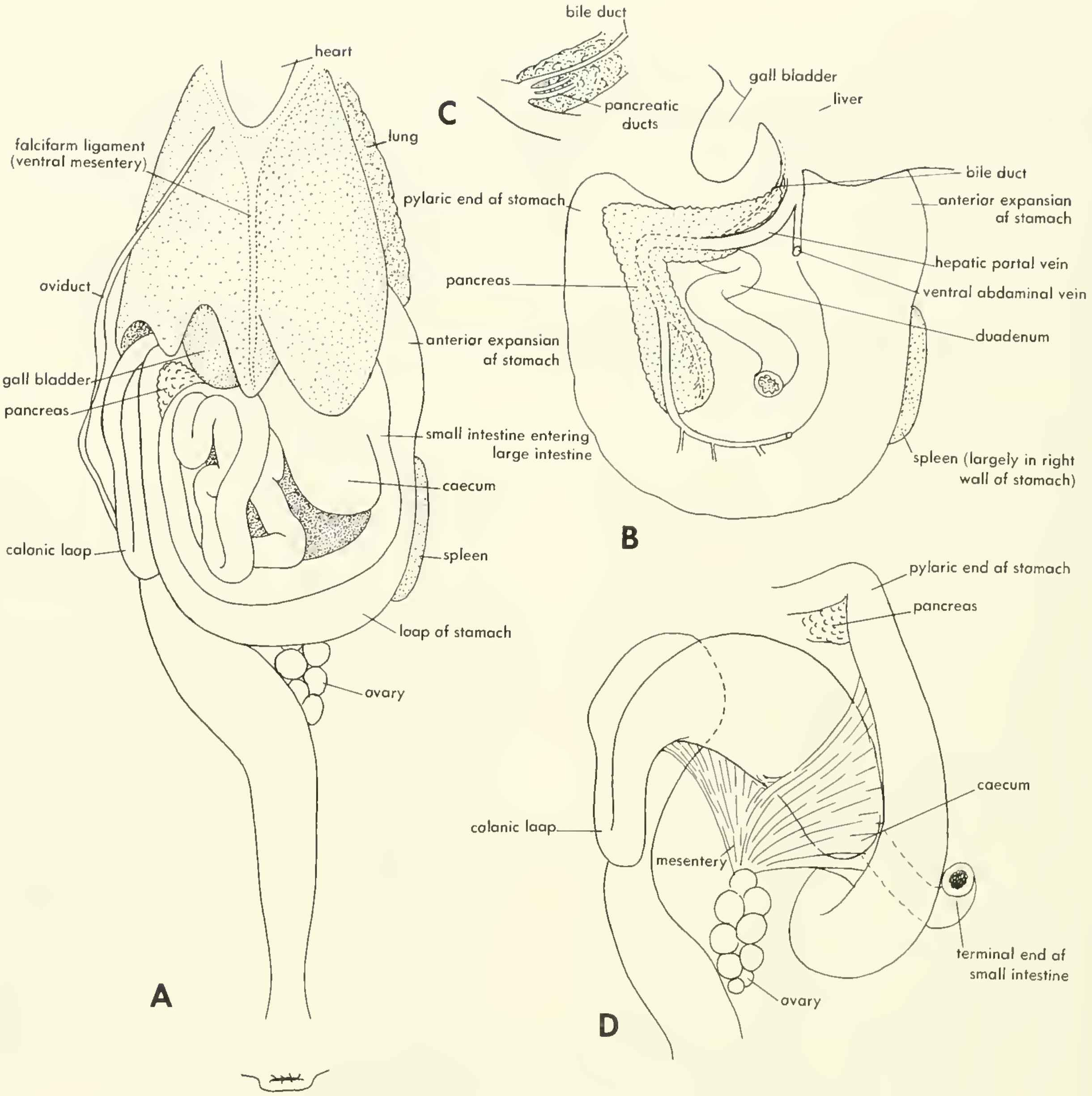


Figure 9-8. Ventral views of the viscera of *Iguana*. A, ventral view of contents of body cavity; B, loop of the stomach and relationships of the pancreas; C, bile and pancreatic ducts entering gut; D, large intestine with its colonic loop and mesentery—stomach rotated to observor's right.

the stomach. The Meckel's tract and first part of the large intestine are not rotated, with the result that the latter comes to lie below and in front of the former—rather it lies above it suspended from a relatively unmodified dorsal mesentery. The duodenal loop of the bird and reptile is usually at least partly closed, while that of the mammal is an open arc.

In *Iguana* or *Tupinambis* a unique situation is observed: the stomach encircles the mass of the small intestine. In most tetrapods the small intestine coils behind the stomach. The turtle agrees with the mammal in most features including rotation of the middle part of the gut; however, it lacks the greater omentum (omental bursa) and the spleen lies above the caecal end of the large intestine. It is possible that the primitive mammal, or the mammal-like reptile, had the midgut rotated, and that this condition is shared as a common heritage with the turtle. It is just as possible that the turtle acquired this rotation independently, starting from the simpler gut condition observed in the other reptiles. The simpler gut pattern of the lizard or alligator could be a retrogressive modification of the rotated type of turtle and mammal.

Bird

The gut of the bird shows much modification and can only be described in the most general terms. The stomach usually has an anterior glandular expansion which opens into a thick-walled grinding stomach. The grinding stomach is lacking in birds of prey. From the anterior end of the muscular stomach, a small pyloric section extends to the left to the pyloric sphincter.

The gut has several closed loops. It is folded or coiled within or between these looped sections. The first loop is the duodenal, which involves the entire length of the duodenum. There is only a short, closed medial portion in many lizards; in this respect the alligator is like the bird. The remainder of the small intestine, the Meckelian section, may have a median closed loop, a supraduodenal loop dorsal to and attached to the posterior end of the stomach, and a small precolonic loop just before it joins the large intestine.

The large intestine usually has bilateral caeca at its anterior end. These are right and left caeca and are not comparable to the usual dorsal caecum of the reptile. The caeca may be quite long and expanded or quite rudimentary. The large intestine extends straight back to the cloaca, which is divided into an anterior coprodeum, middle urodeum, and posterior proctodeum. There is no urinary bladder, but there is a dorsal diverticulum from the proctodeum, the bursa of Fabricius. This structure is large in young and small in adults. Some birds have a penis in the floor of the proctodeum.

The coiling of the gut suggests the mammal in that the posterior part of the small intestine loops up and over the first part, as viewed ventrally, attaching to the stomach. This appears to be a parallelism since, in the mammal, it is

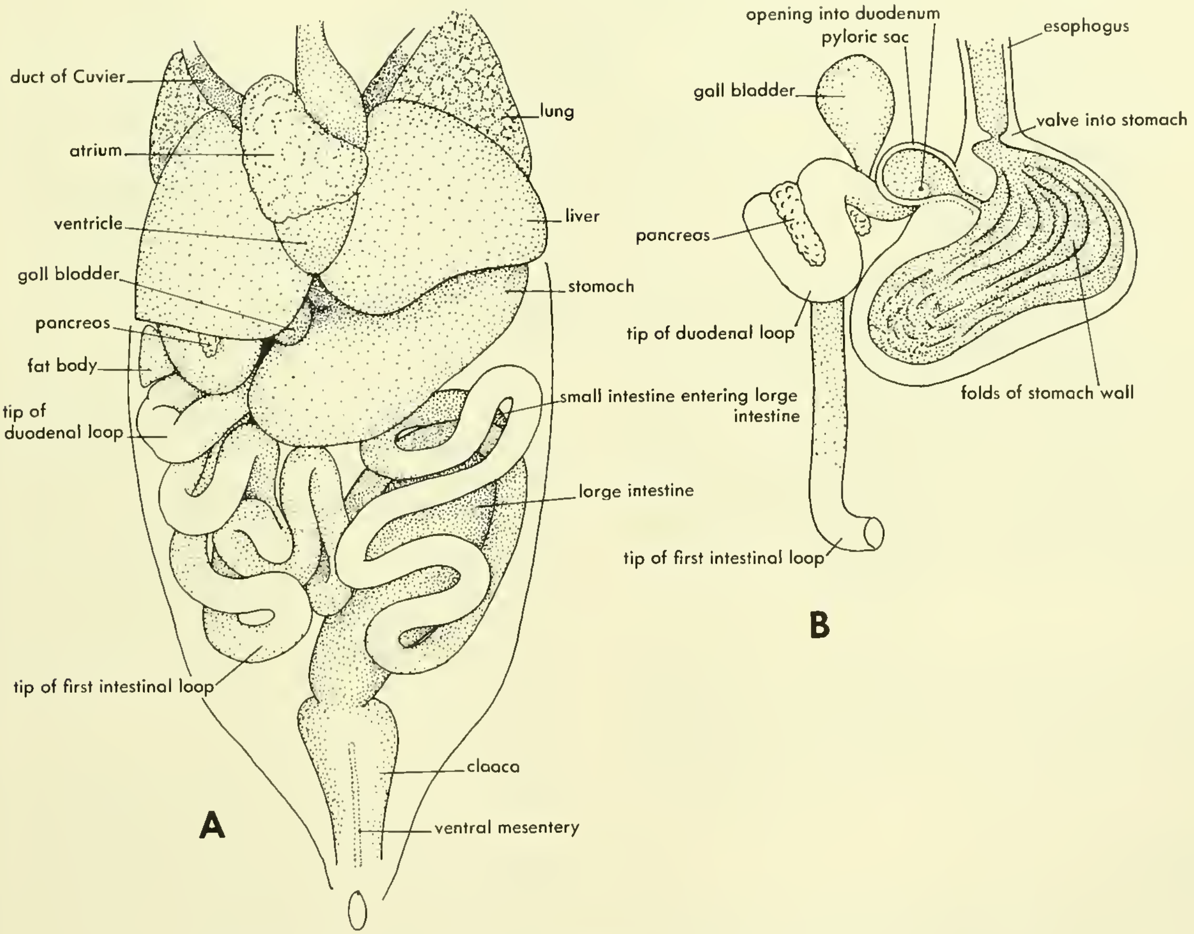


Figure 9-9. Ventral view of viscera of the alligator. A, contents of body cavity; B, ventral wall of stomach and pyloric sac cut away to show thickness of walls and internal surface contours as well as relationships of other organs to stomach.

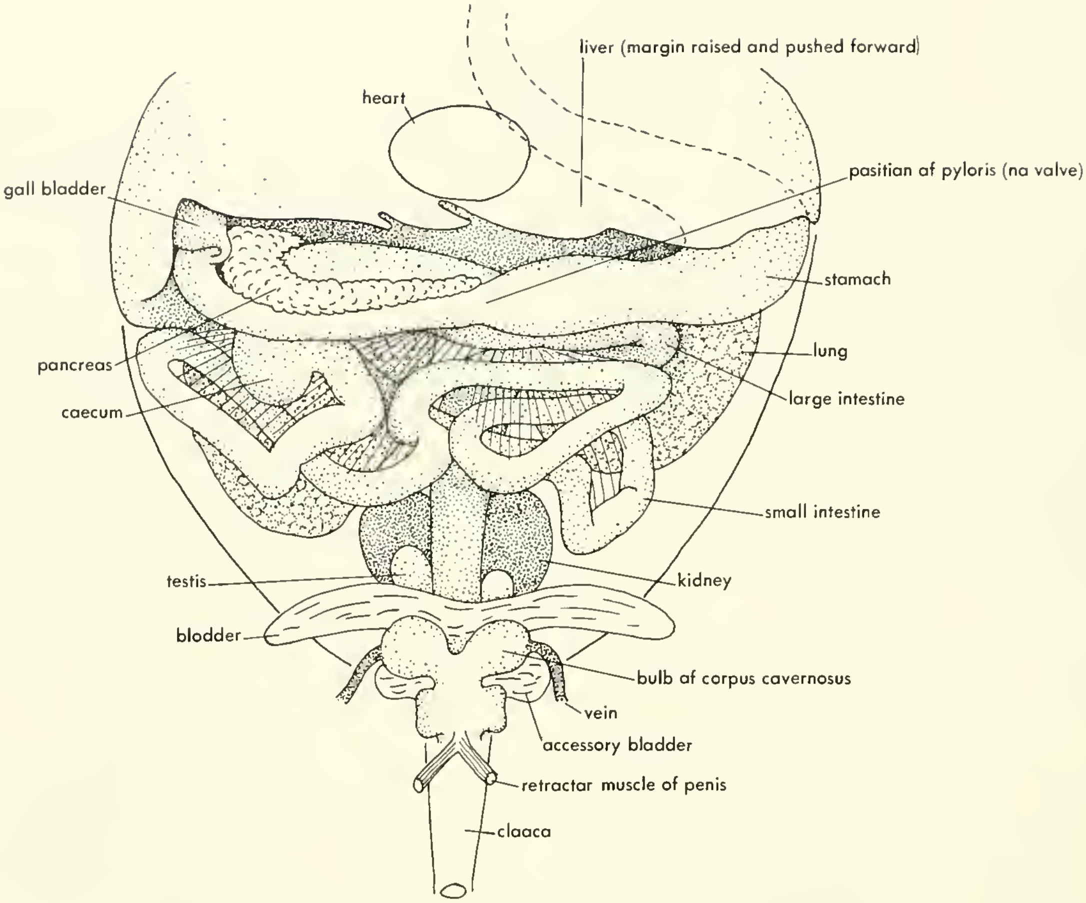


Figure 9-10. Ventral view of viscera of the turtle *Pseudemys*.

the large intestine which is involved and the loop is not attached to the stomach.

The liver is bilobed, and the gall bladder is to the right of the ventral midline. There is a ventral mesentery. The pancreas lies between the limbs of the closed duodenal loop; it is irregularly shaped and more evident above than below. The spleen is a small round body in the dorsal mesentery of the stomach near the dorsal body wall.

Embryological development The development of the gut of the bird, reptile, or mammal is much the same; that of the bird is well known. The form of the gut and its liver and pancreatic outgrowths can be observed in the several stages of the chick's development which are commonly studied.

Amphibians

In *Necturus* the pharynx tapers posteriorly to a constricted esophagus which opens almost immediately into the stomach (Figure 9-11). The stomach extends straight back to the pyloris or curves slightly to the right. The first part of the small intestine passes to the right and dorsally, and then posteriorly; this is the duodenum. Just before the posterior limb, the bile duct and pancreatic ducts enter the anterior or ventral aspect of the gut. From here the intestine describes a number of short loops in a semicircle around an area of dorsal mesentery in which the hepatic portal blood vessels lie. The anterior end of the large intestine is without a caecum and lies only a short distance behind the stomach. The large intestine extends back to the cloaca. The cloaca is a simple chamber into which the bladder opens ventrally; the ureters, the vasa deferens (nephric ducts), and Müllerian ducts enter dorsolaterally. Cloacal glands swell this region of the male at the reproductive time.

There is a ventral septum, the falciform ligament, below the liver. This is continued posteriorly as a strand enclosing the ventral abdominal vein. The liver lies below the gut and is attached to it by a band of tissue enclosing the bile duct, the hepatic portal vein, and the coeliacomesenteric artery. A gastrohepatic ligament (septum) is restricted to the anterior third of the liver. The dorsal mesentery is complete except for a section above the loop formed by the posterior end of the stomach and the first part of the intestine.

The liver is a single dorsoventrally flattened mass extending back, further on the right side, for more than half the length of the body cavity. Anteriorly it tapers to the hepatic vein. Its right and posterior margins are lobate. The gall bladder shows on the right side near the point of entrance of the bile duct into the duodenum. The pancreas is well developed, lying in the dorsal mesentery along the anterior margin of the gut between the pyloris and bile duct. At the bile duct, finger-like extensions follow the converging veins of the portal system. A small separate section ex-

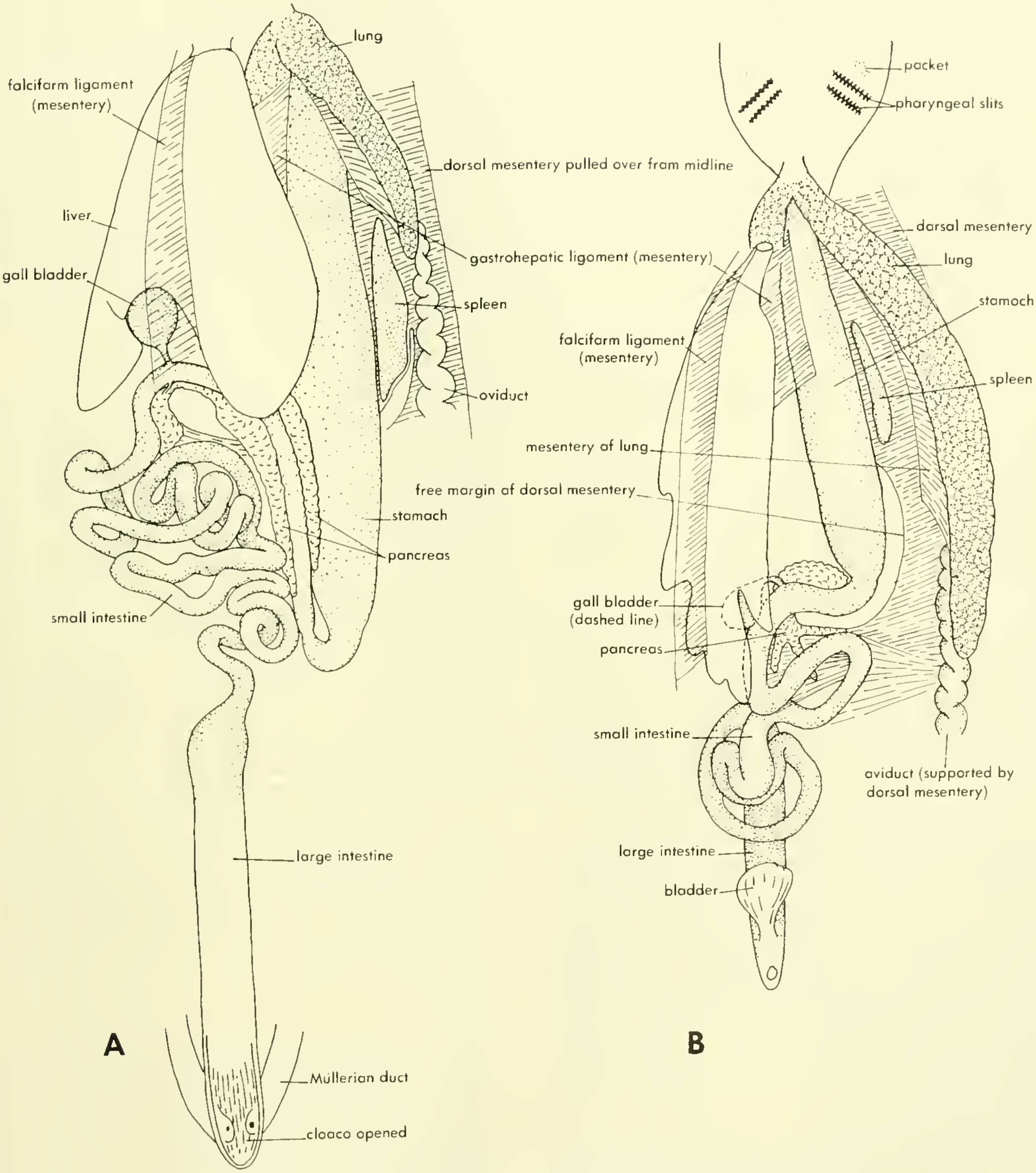


Figure 9-11. Ventrolateral views of the viscera of *Cryptobranchus*, A, and *Necturus*, B.

tends along the ventral aspect of the gut posterior to the bile duct. The spleen is an elongate body bulging to the left of the dorsal mesentery above the middle of the stomach.

Cryptobranchus has a long tubular stomach which ends posteriorly at the pyloris. The dorsal mesentery has a gap in the pyloric region, but the gastrohepatic ligament is complete as is the falciform ligament. There is no ventral mesentery for the intestine. From the stomach the duodenum extends anteriorly next to the stomach. The duodenal loop is open. Its first section extends forward, its second limb back. The remainder of the small intestine is thrown into a series of short open loops before entering the large intestine.

The liver is basically a single ventral mass with right and left lobes. The gall bladder lies just to the right of the midline in the notch between the lobes. There is no postcaval lobe in either *Cryptobranchus* or *Necturus.* There is a falciform ligament which extends posteriorly along the ventral body wall as a strand enclosing the ventral abdominal vein. The duodenum is broadly joined to the liver and stomach by the gastrohepatic ligament (mesentery). The pancreas is long and thin and lies along the first part of the duodenum, on the side away from the stomach. Patches of similar tissue lie between the stomach and duodenum. A part of the pancreas lies dorsal to the gut, just behind the entrance of the main bile duct. The two duodenal parts are joined by a narrow lymphoid stem.

The frog is similar to the salamander, but differs in that the stomach is hook-shaped. The spleen lies in the dorsal mesentery in the area of suspension of the looped intestine. In some anurans the large intestine has an anterior caecum (*Hyla arborea*).

Embryological development Several stages of development can be observed in commercially prepared serial and sagittal sections of the frog. The entoderm forms an ovoid mass in which the lumen of the gut is best marked in the pharyngeal region (Figure 7-7). In the 4-mm frog, the gut wall is several cells thick; behind the pharynx it is many cells thick below the lumen. All of the entoderm cells contain yolk and this is particularly abundant in the more ventral cells.

A stomodeal invagination of ectoderm forms the mouth. The pharyngeal pouches form and a liver diverticulum extends from the pharyngeal space down into the mass of yolk-filled cells. The posterior end of the gut is connected at first with the neural canal through the neurenteric canal (4-mm stage). This connection is next to the closing blastopore. The hindgut cavity extends ventrally below the neurenteric canal and lies near an invagination of ectoderm, the proctodeum. The cloaca is formed by union of these (4-mm larva) following breakdown of the separating membrane. The bladder is an anterior evagination from the hindgut portion of the cloaca.

With the establishment of a circulatory system, liver strands are formed. The thickness of the yolk-filled walls of the gut is continually reduced until the columnar epithelial of the older larva is achieved, but there is still much yolk in the cells of the looped gut of the 10-mm frog.

The pancreas first appears as a small, posteriorly directed diverticulum from the bile duct near its point of entrance into the gut. This is the ventral pancreas. Later this diverticulum divides into two and a dorsal diverticulum appears. These three outgrowths join to form a single mass which utilizes the ventral duct now opening just behind the bile duct.

The gut of the larval frog is interesting in that it is much elongated and forms a coil visible through the abdominal wall. At metamorphosis the gut shortens and attains the adult form. The difference in length is related to an algal versus an animal diet. Development of the salamander appears to be similar to that of the frog but is more direct.

In summary, the amphibian agrees in general with the least modified condition observed in the reptile, as for example in the alligator. This agreement suggests that this pattern is indeed similar to the ancestral vertebrate and that the rotated gut of the mammal, turtle, or bird is a specialization.

Choanate fishes

Actinistian *Latimeria* has a wide **esophagus** opening into a large **stomach.** This extends back to a tapered **caecum** which reaches to the posterior end of the body cavity. The **pyloric region** lies below the esophageal part and extends anteriorly to the **pyloric valve.**

The pyloric valve opens upward into a small chamber, the **bursa entiana** (see Figure 9-21 C), which in turn opens into the intestine extending posteriorly above the pyloric section and to the right of the caecum of the stomach. The intestine has a **roll-type valve** (see Figure 9-22) which makes nearly 20 turns and is attached to the ventral wall of the intestine. Behind the valve is a short section of gut extending back to the cloaca. The cloaca extends upward behind the point of entrance of the rectum, where it receives the urogenital papilla.

The liver has two large lobes: the right extends back about two-thirds of the body cavity length; the left is smaller. There is a gall bladder on the right. The pancreas is a band, triangular in section, lying along the right side of the pyloric region of the stomach and below the intestine. There is much hemopoietic tissue in the pancreas. The spleen is a compact body lying in the mesentery above the intestine and to the right of the stomach.

Dipnoan *Protopterus* lacks a distinct stomach (Figure 9-12). There is a constricted esophageal region into which opens the ventral glottis. Behind this is a slight enlargement displaced to the left; this can be viewed as a part of the stomach. From here the stomach leads back to the pyloric valve, which is a flap separating the stomach cavity from the intestine. The intestine contains a typhlosole, or spiral valve,

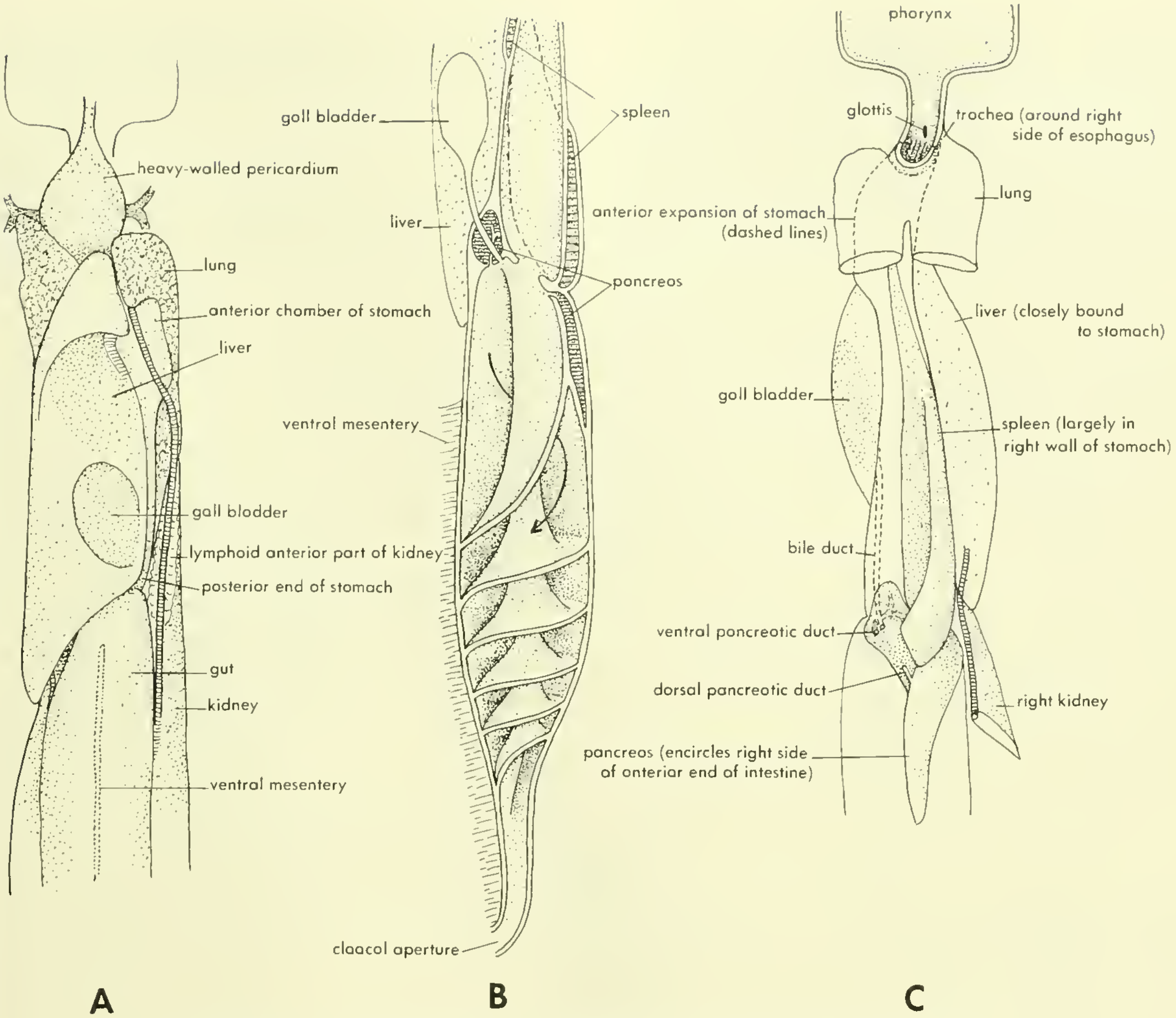


Figure 9-12. The viscera of *Protopterus*, a lungfish. A, ventral view of anterior organs; B, lateral view of digestive tract with left wall cut away to show interior (arrow indicates course of lumen); C, dorsal view of anterior organs.

beginning anteriorly near the opening of the bile duct (dorsally) and making about six and a half turns in a counterclockwise direction as it progresses posteriorly. It ends a short distance from the cloacal aperture attached to the ventral wall. Behind the valve is a short section of gut which opens into the cloaca. The cloaca extends upward to the urogenital papilla and then forward, above and parallel to the gut as a blind-ending bladder. The cloacal aperture is to the left of the median fin.

The liver is a single mass lying ventral and to the right of the stomach. It extends back to a rounded point on the right side. The gall bladder is large and lies in an embayment in the left-hand margin of the liver. The bile duct enters the gut on its ventral aspect just posterior to the gall bladder. The pancreas lies within the wall of the gut, beginning to the right of the entrance of the bile duct. Here there is a distinct mass which extends around the right side of the gut to the dorsolateral aspect, where it spreads out as a broad dorsal lobe. This lobe, still within the wall of the gut, extends back some distance and tapers to a rounded point. This dorsal portion is drained by a duct entering the dorsal midline of the gut at the point of the V formed by the pyloric valve.

The spleen is a large vascular mass in the right dorsolateral wall of the stomach. Posteriorly it connects with the pancreas and from here extends forward, tapering all the time to a point just below the anterior joined area of the lungs. A ventral mesentery attaches most of the posterior length of the gut to the ventral body wall. The other genera of lungfish agree in general with this description.

EMBRYOLOGICAL DEVELOPMENT The early stages of development of the lungfish (Figure 7-13) are like those of the amphibian with the exception of the spiral valve, which will be described for the following groups. The liver diverticulum arises early. According to Kerr (1919), one dorsal and right and left ventral pancreatic diverticula appear. The dorsal diverticulum appears first; it is solid in *Protopterus,* hollow in *Lepidosiren.* The ventral anlagen appear somewhat later and the two buds meet to fuse at the midline dorsal to the stem of the liver diverticulum. Still later the fused ventral mass grows upward to fuse with the dorsal mass which grows backward within the gut wall. The three ducts are retained in *Protopterus.* In *Neoceratodus* the left ventral bud remains rudimentary, and the dorsal part comes to drain through the duct of the right ventral diverticulum.

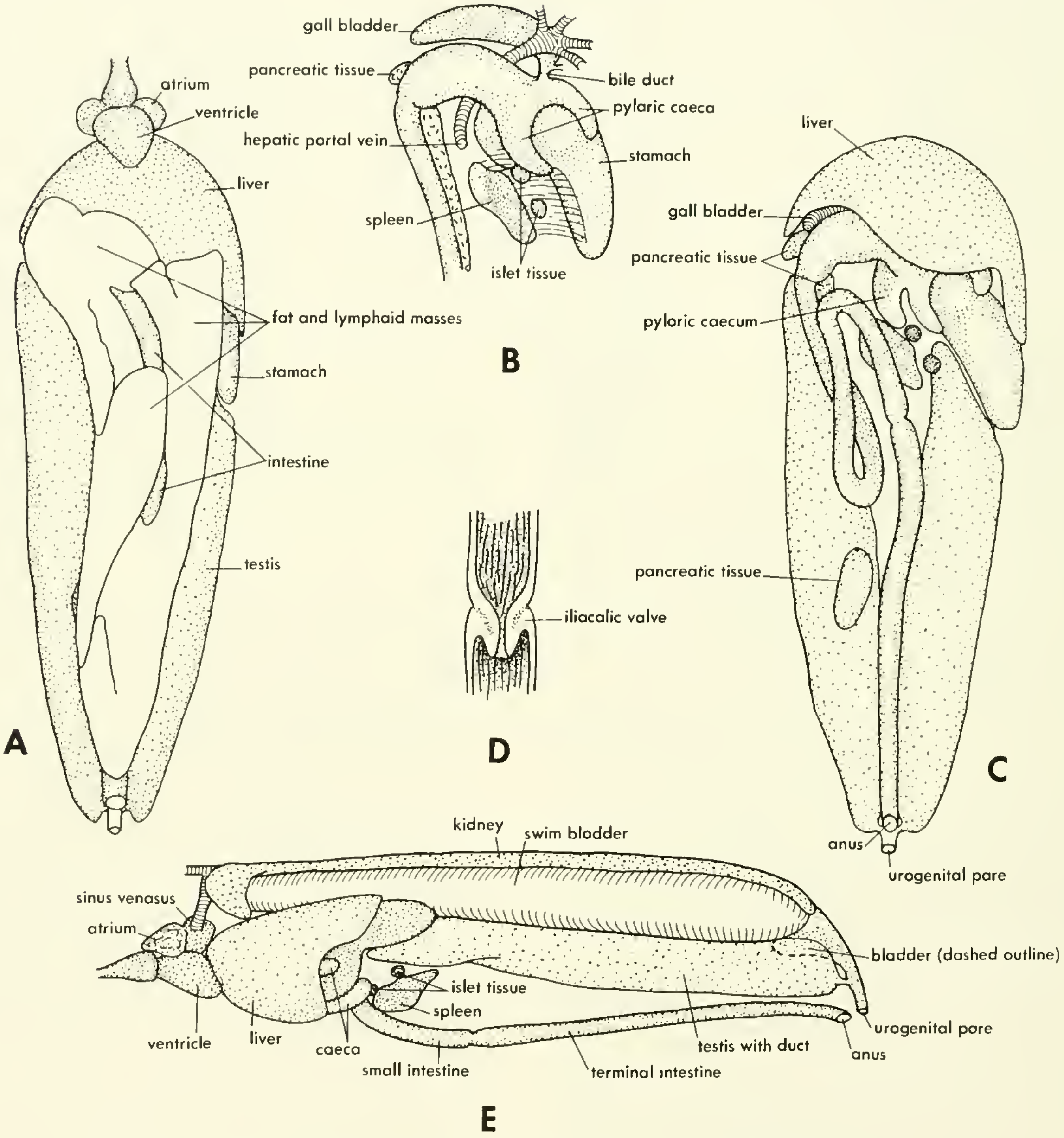


Figure 9-13. Viscera of the salmon. A, ventral view of general mass; B, details of relationships at anterior end of gut; C, ventral view of viscera with fat and lymphoid tissue cleared out; D, section through the ileocolic valve; E, left lateral view of viscera with fat and lymphoid tissues removed.

Islets of Langerhans, the insulin-producing cells observed in the pancreatic tissue of higher forms, have not been observed in the lungfishes.

Actinopterygians

Teleost The teleost fishes usually have a hook-shaped stomach extended posteriorly by a caecum. This is the case in the perch but not the salmon (Figure 9-13). The pyloric section of the stomach extends forward on the right ventrolateral aspect. There is a pyloric valve from which the duodenal loop extends forward and then posteriorly. The bile and pancreatic ducts enter the intestine near the pyloric valve. Pyloric caeca are present in most teleosts; in the perch there are three, opening at the pyloris, and many in the salmon. In the salmon these open into the ventrolateral aspect of either side of the duodenum throughout its anteriorly directed limb. These caeca form an irregular mass in which the separate tubes can be discerned.

The intestine is divided in the perch into anterior, including the duodenum, and posterior parts; these are separated by a distinct valve. In the salmon the valve is only slightly developed. The posterior part differs in having its walls thrown into occasional transverse folds. The gut opens to the outside separate from the urinary or genital systems. Lacking a cloaca is typical of the teleosts although there are some exceptions.

The liver is a single mass, somewhat larger on the left. The gall bladder lies dorsal to the liver and on the right. The pancreas is generally diffuse although scraps of this tissue can occasionally be observed in the general region of the entrance of the bile duct into the intestine. In the perch the pancreatic acini are mixed through a large ventral mass of lymphoid tissue in which the stomach and intestine are embedded. This mass extends back to the anus. In most teleosts the lymphoid tissue is more limited and forms a coating for restricted areas of the gut or strands between loops of the gut. In the salmon the pancreatic tissue forms a thin film over and around the pyloric caeca, and some strips along the bile duct, stomach, and intestine.

The spleen is a dark, regular-shaped mass between the stomach and the first loop of the intestine. The spleen is very small in some fishes and may be displaced posteriorly. One or two other small spherical masses, the islets of Langerhans, are usually seen above the liver and to the right of the esophagus or in the first loop of the gut. In the perch two small islets lie to the left of the spleen.

Polypterus The esophagus is fairly long and leads into an expanded stomach with a long posterior caecum (Figure 9-14). The pyloric section of the stomach extends forward and curves around to the right to enter the intestine. The intestine has a ventral pyloric caecum and a spiral valve which starts above the opening into the caecum. The bile duct enters the gut in a pocket between valve and caecum. The valve makes about five and a half turns in a counterclockwise direction as it progresses posteriorly. It tapers down and disappears on the right lateral wall one-third of the length of the intestine in front of the anus.

The liver is a single mass lying largely below the stomach. The pyloric part of the stomach loops forward below a median liver lobe, while a long, tapered intestinal lobe of the liver extends back and above and attaches to the intestine. The gall bladder lies above the right margin of the liver and anterior to the pyloric loop of the stomach. Its bile duct, accompanied by blood vessels and pancreatic ducts, enters the anterior end of the intestine dorsally. The pancreas is diffuse, but a small mass is exposed between intestine and stomach. Strands extend from here along the venous drainage from the ventral intestinal fat body and the stomach wall. The pancreatic mass passes around the left side of the gut to the area of the entrance of the bile duct. Pancreatic tissue is scattered in the tissue around the bile duct and extends into the medial lobe of the liver and back along the undersurface of the anterior third of the intestinal lobe.

The spleen is a long band, triangular in section, lying above and to the right of the stomach and extending down between the stomach and intestine. A fat mass hangs by a mesentery below the gut, and bilateral fat bands hang from the body wall to either side of the median (right) lung. Fat also rims the liver. The lung, attached to the dorsal wall, extends the length of the body.

A ventral septum is lacking below the liver and digestive tract. The gut is attached to the body wall for a short distance anterior to the anus.

Acipenser and Polyodon The stomach of *Acipenser* is of a simple tubular form, without a posterior caecum. In its course it makes a complete circle, curving to the left (and downward), then forward, and across to the right below the esophagus (Figure 9-15). The pyloric end has thick muscular walls forming a massive pyloric sphincter. The intestine is divided into two segments. The anterior segment has a tubular pyloric mass opening into it at its anterior end. The anterior intestine curves to the left, then extends back as a closed loop which enters the posterior intestine on the right. There is a valve-like constriction between these two parts of the intestine. The posterior section contains a spiral valve which makes about seven counterclockwise turns in its posterior course. The valve ends dorsally near the anal opening.

In *Polyodon* the anterior division of the intestine is S-shaped but much shorter than in *Acipenser.* Its constricted entrance into the posterior intestine is valve-like. There are about seven turns in the spiral valve.

The liver is bilobed, and the left lobe extends further back above the pyloric loop of the stomach. In *Polyodon* this lobe of the liver is not developed; thus, the right lobe extends somewhat further back than the left. Both genera agree in having the ventromedial margin of the right lobe notched to expose the gall bladder.

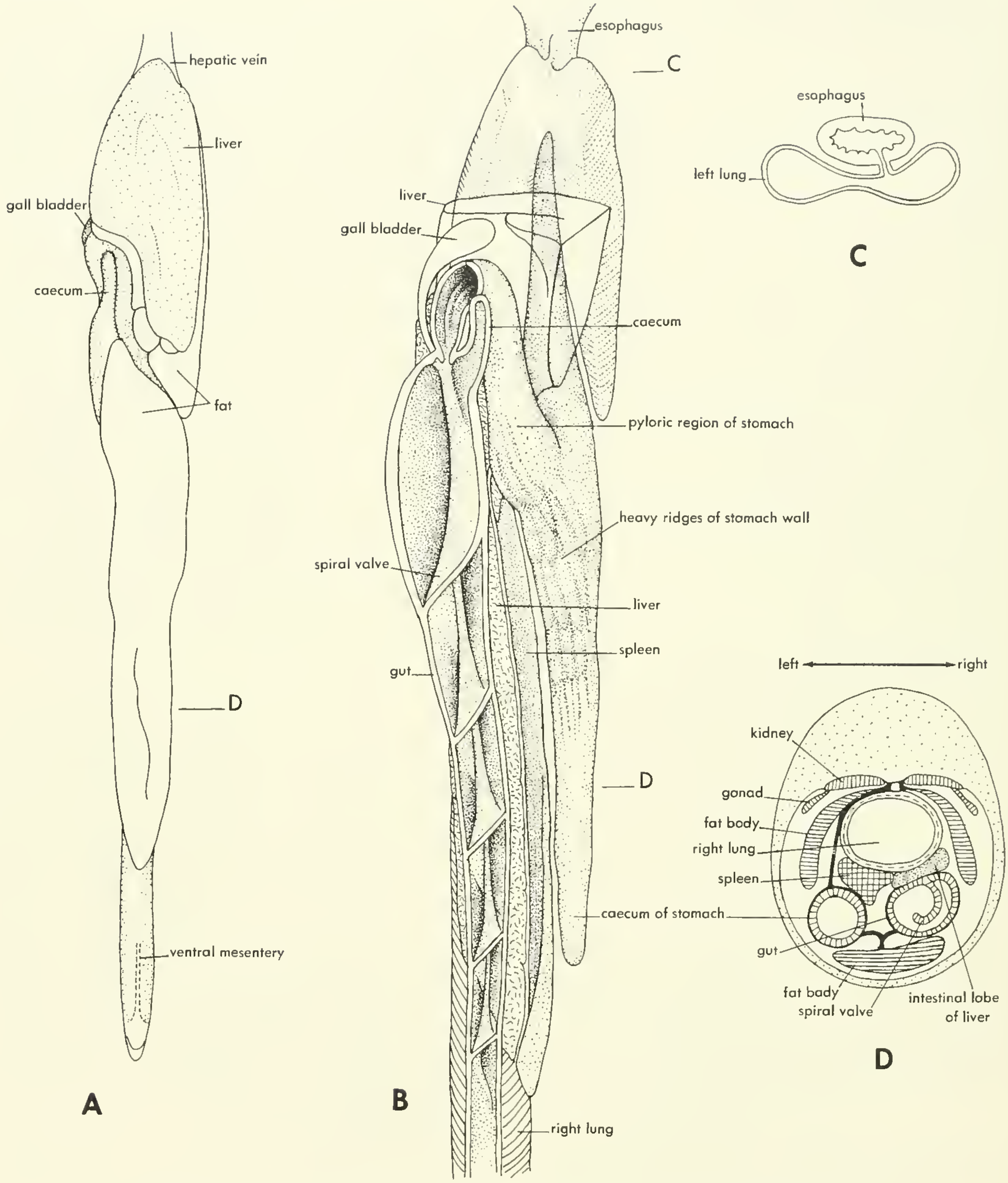


Figure 9-14. Viscera of *Polypterus*. A, ventral view of body cavity contents; B, anterior end of viscera with part of the liver shown as a ghost and with the ventral wall of the gut removed to show the interior; C, cross section of esophagus to show connection with lungs, right side to reader's right; D, diagrammatic cross section of body in region marked by horizontal line in A and B.

The pancreas is diffuse, but several wisps of this tissue can be observed along the course of the bile duct and back from there to the anterior right piece of the spleen. This part of the spleen is embedded in pancreatic tissue which continues back as a series of strands dorsal to the spiral intestine and along the two limbs of the anterior intestinal loop. There are no separate masses of islet tissue. In *Polyodon* the two parts of the spleen are embedded in pancreatic tissue lying dorsolateral to the spiral intestine. The spleen is many parted in *Acipenser,* two parted in *Polyodon.*

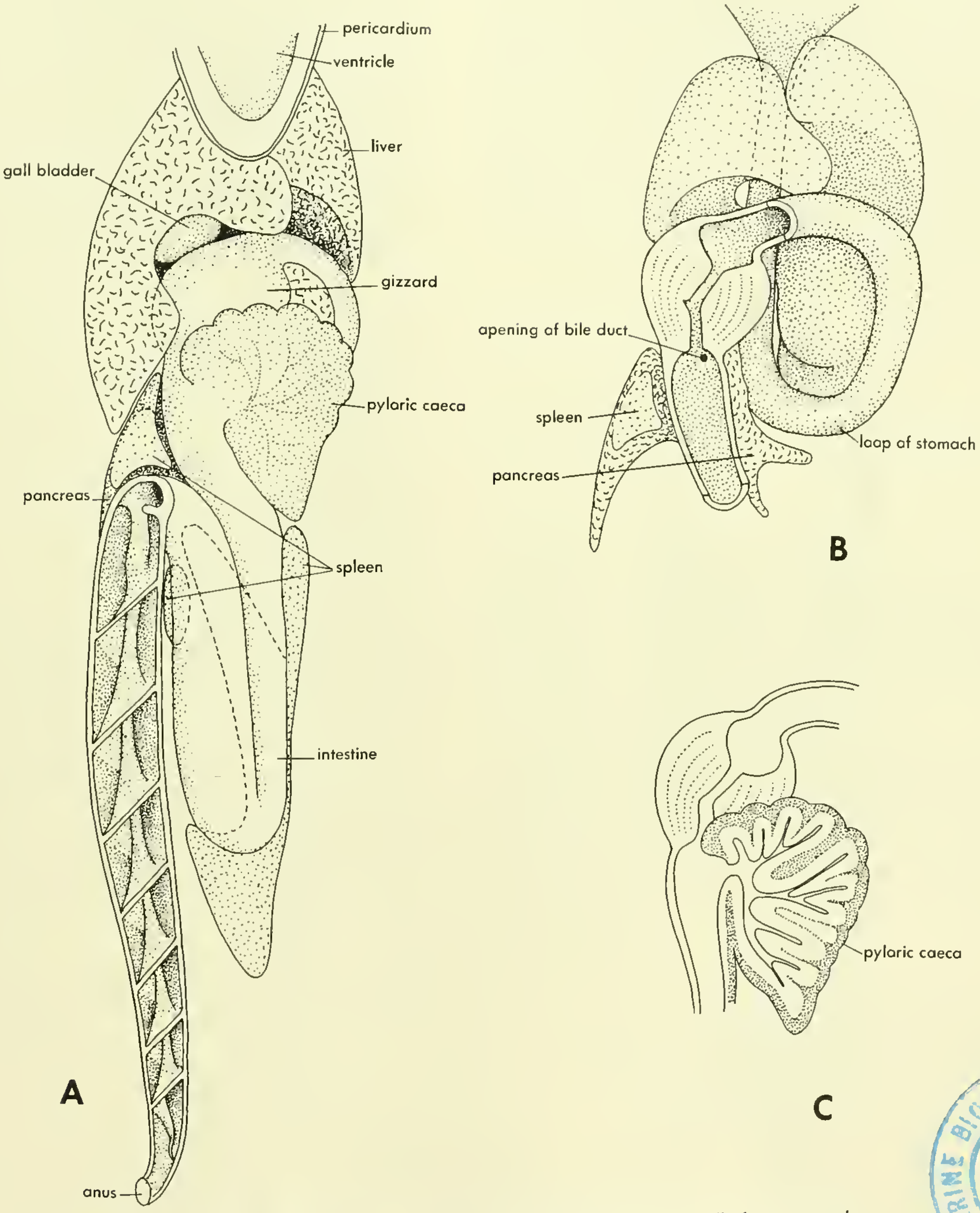


Figure 9-15. Viscera af the sturgean. A, ventral view af viscera with ventral wall af gut remaved ta shaw interiar; B, farm and relatianships af stamach laap as seen ventrally; C, sectian thraugh the pylaric caeca and gizzard.

Amia and Lepisosteus The stomach of *Amia* is large and sacculate, with a distinct posterior caecum (Figure 9-16). That of *Lepisosteus* is an elongate tube which posteriorly hooks to the right and forward to its pyloric valve. *Lepisosteus* has a mass of tubular pyloric caeca underlying the gut and opening into the posteroventral aspect of the intestine just behind the pyloric valve. *Amia* lacks pyloric caeca. In both genera the intestine is divided into anterior and posterior segments. The posterior segment is not separated by a valve from the elongate, looped anterior portion, but contains a spiral valve, which in *Amia* makes four turns and in *Lepisosteus* about two and a half turns in a counterclockwise direction as one follows it posteriorly. In both, the spiral valve ends on the right wall of the intestine a short distance anterior to the anus.

The liver is a single, elongated piece below the stomach in *Lepisosteus;* it is a bilobed mass in *Amia,* with the left lobe the larger. In both, the gall bladder lies to the right above the pyloric intestinal loop. The pancreas is diffuse. There is a distinct pancreatic strand along the bile duct in *Amia* which extends into the medial dorsal surface of the liver. This band continues back from the bile duct along the dorsal surface of the gut. In *Lepisosteus* the pancreas is more diffuse and not separable from the lymphoid and fatty tissue scattered among the loops of the gut.

The spleen lies to the right of the stomach in *Amia* and has a long lobe which extends back above the terminal part of the anterior segment of the intestine. In *Lepisosteus* the spleen is two-parted, lying in a position comparable to that of *Amia.* In both genera there are strands and masses of lymphoid tissue along the gut and in the mesenteries.

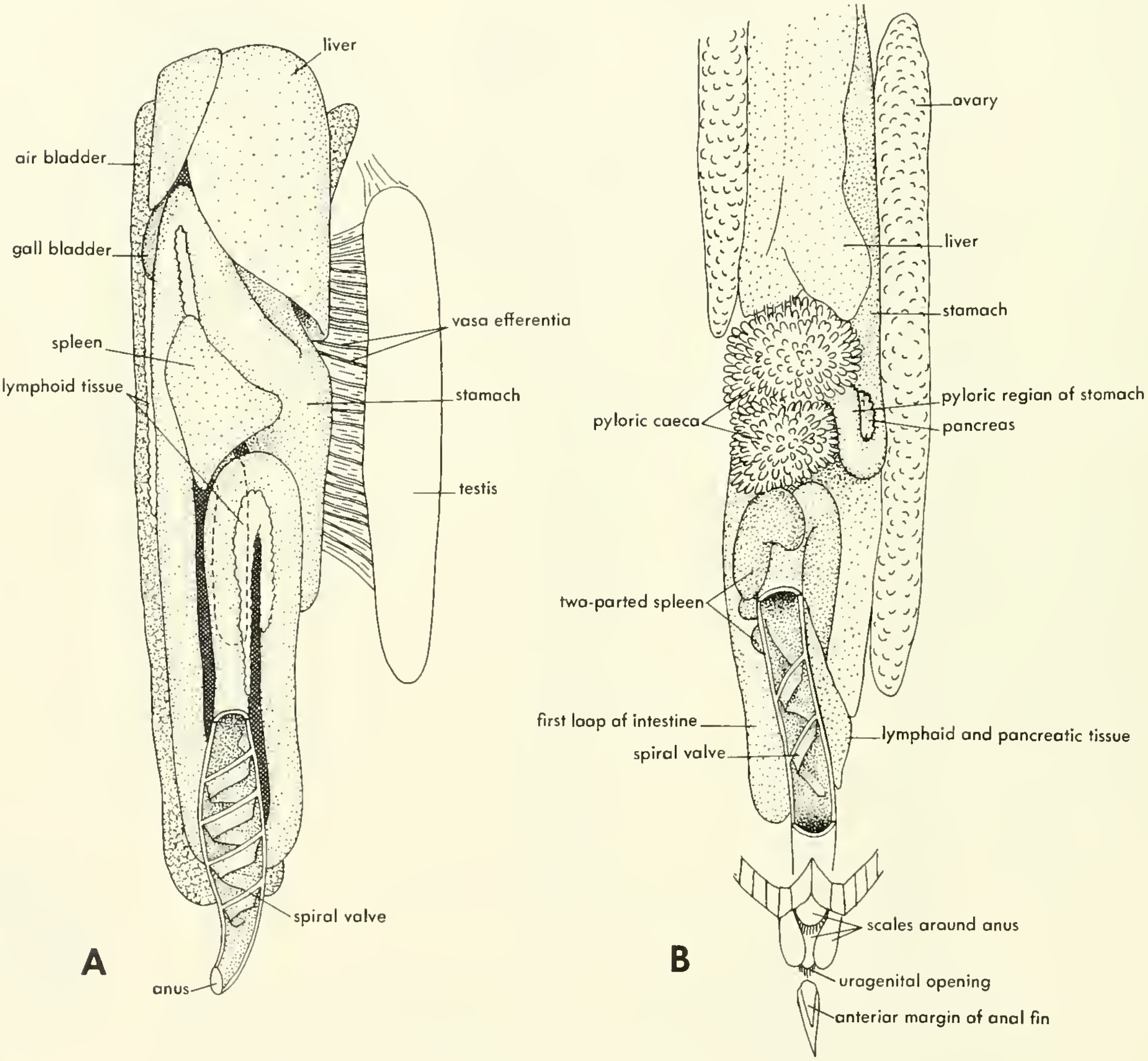


Figure 9-16. Ventral views of viscera of *Amia,* A, and *Lepisosteus,* B.

The liver and gut are not attached to the ventral body wall by a mesentery in any of the actinopterygian fishes.

Embryological development in actinopterygians The development of the telolecithal egg of the teleost resembles in some respects the development of the chick. In *Polypterus* and *Acipenser* the egg is nearly mesolecithal and the cleavage almost holoblastic (Figures 7-11, 7-12).

As the head fold is raised off the blastoderm, the foregut is developed. With closure of the blastopore, the tail fold and hindgut develop. The hindgut first appears as Kupffer's vesicle. The yolk stalk opens into the midgut. As the embryo increases in size and the yolk diminishes, the yolk sac becomes enclosed by an embryonic entodermal sac and is drawn into the body. The periblast diminishes with the yolk and disappears with that material as the last of the yolk enters the midgut and the sac is eliminated.

The liver and pancreatic diverticula develop anterior to the yolk stalk. The liver and gall bladder arise as in the higher forms. *Acipenser* is the exception to this course of development. A yolk sac is never formed; the yolk is contained within the foregut (stomach) anterior to the liver diverticulum (Figure 9-17).

In *Acipenser* four pancreatic diverticula have been described, two dorsal and two ventral. In *Amia* there are three diverticula; the dorsal one appears first, then the two ventral anlagen. In the 15-mm larva, and the adult, a single duct empties into the gut along with and behind the bile duct. In the salmon only the dorsal diverticulum develops; this lies behind the vertical of the liver diverticulum. There are two ventral diverticula from the bile duct where it enters the gut. The right ventral one becomes the duct of the definitive pancreas. All three diverticula are fully developed in some teleosts; the dorsal one gives rise in part to the islet, or islets, of Langerhans. The teleosts in general can be characterized as having separate islet masses. These are lacking in the holostean (*Amia* or *Lepisosteus*) and chondrostean (*Acipenser*) fishes.

The early development of the hindgut is of special interest; it grows in such a way that the typhlosole forms a spiral valve. In *Polypterus* the spiral valve extends through the entire length of the intestine, while in other actinopterygians less than half the length of the intestine is involved. Beginning posteriorly the gut lining is rotated through several turns. This rotation is adjusted for largely by shearing movement between the cells posterior to the valve. As a result the anterior end of the intestine is rotated in a counterclockwise direction, as viewed from the rear, about one half turn, so that the bile duct now opens into the gut dorsally.

In *Amia* the hindgut, with its typhlosole, lies at first close behind the yolk stalk (Figure 9-18). With the drawing in of the yolk sac, the midgut begins to elongate and to form a loop which extends up on the right side, across dorsally, down on the left side, then medially to the hindgut. The several segments of this loop are elongated in achieving the mature condition.

In *Lepisosteus* much the same sequence is observed, but here a pyloric caecum appears as a left ventral diverticulum from the gut (Figure 9-19). Other diverticula develop from this, and each comes to have many tubular extensions until the compact mass of the adult is formed.

In the actinopterygian the pyloric caeca develop late. In the salmon a few appear, then more and more until the full complement is achieved. Lack of caeca in *Amia* must be viewed as due to loss.

Chondrichthyes

Shark The shark has a wide esophagus and an expanded hook-shaped stomach, generally without a caecum (Figure 9-20). *Laemargus* (and *Spinax*) are peculiar in having pyloric caeca (Figure 9-21). There is a pyloric valve between stomach and gut and sometimes a bursa entiana between stomach and intestine (Figure 9-21 C).

The bile duct opens into the anterior end of the intestine, which has a spiraled (most sharks) or rolled valve (*Zygaena* —Figure 9-22). The spiral valve makes from four to fifty or more turns, depending on the species. The valve ends well anterior to the cloaca. A rectal or digitiform gland projects dorsoanteriorly, in the dorsal mesentery, from the terminal

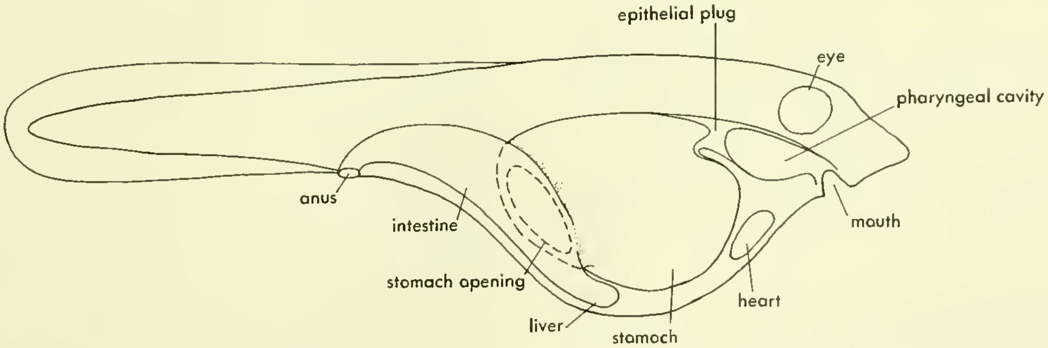


Figure 9-17. Early larva of *Acipenser*, the sturgeon, showing yolk-filled stomach and intestine and liver diverticulum.

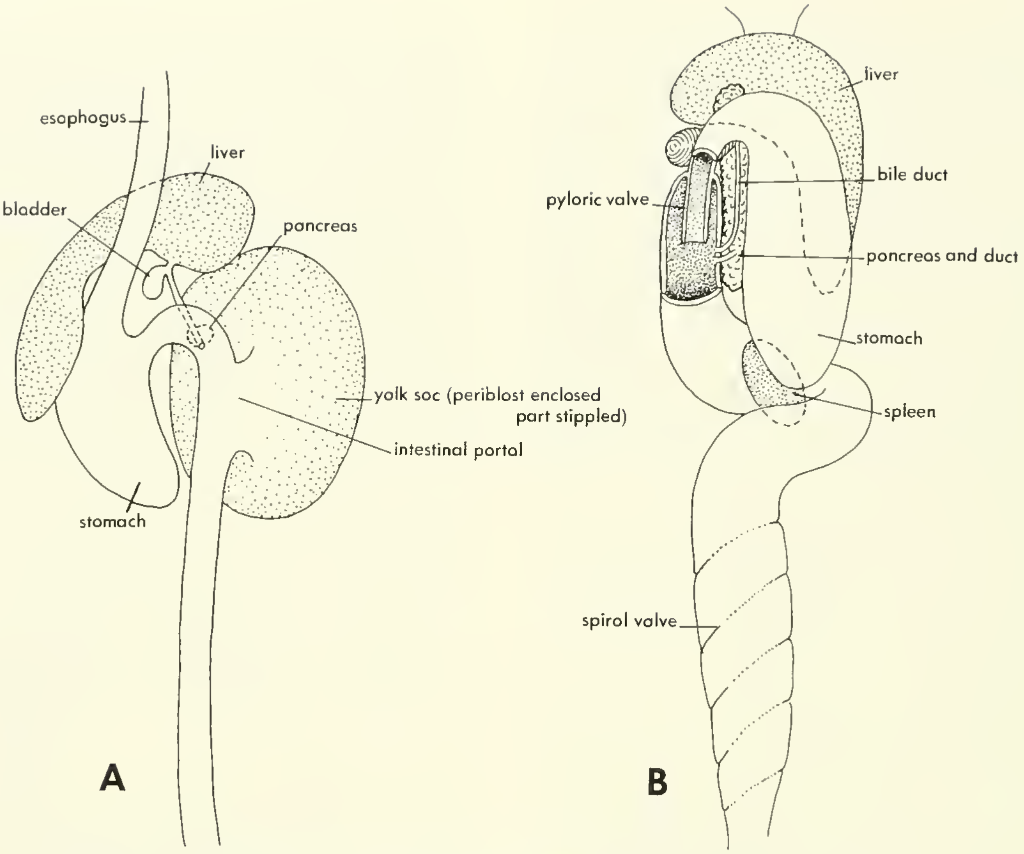


Figure 9-18. Two stages in the development of the digestive tract of *Amia*. A, early embryo in dorsal view; B, 22-mm embryo in dorsal view.

part of the intestine. This gland varies much in size; it is small in the rays, larger in the sharks. This compound tubular gland appears to function in control of blood salts.

The liver is bilobed; the lobes are joined anteriorly, ventral to the esophagus. The gall bladder is large and embedded in the right lobe near the ventral midline. The pancreas is compact but irregularly shaped and contains islet tissue. It lies below the anterior end of the intestine and extends from here to the left below the pyloris. The spleen lies dorsal to the posterior end of the body of the stomach and extends around, behind and below, or along the pyloric section of the stomach. The spleen may extend to the right to underlie the pancreas and pieces of the spleen may extend forward to the dorsal mesentery of the esophagus.

A dorsal mesentery is present for the stomach and the anterior part of the intestine, also for the rectal gland. There is no ventral mesentery. Lymphoid and fatty tissue, other than the large spleen, is not evident.

EMBRYOLOGICAL DEVELOPMENT The entoderm is divided early into a syncytial periblast on the surface of the yolk and the cellular entoderm of the blastodisc (Figure 7-10). The embryo develops at the posterior margin of the blastodisc but involves somewhat more complex movements than the actinopterygian.

Concrescence brings the cellular materials of the epiblast toward the midline of the posterior margin of the blastodisc, and this is accompanied by forward and lateral movements in the hypoblast. In the prechordal area the hypoblast is not already vertically delaminated into entoderm and mesoderm. As the embryo is added to posteriorly, this separation gradually appears. The mesoderm arises from the hypoblast along the midline, while the dorsal gut wall is produced by movements of the more lateral parts of the hypoblast medially below the mesodermal portion. In the actinopterygians the cells of the caudal node separate into entoderm and mesoderm as the embryo is laid down along the midline.

The foregut is formed by the separation and forward growth of the head fold, the hindgut by the formation and separation of the caudal end (Figure 9-23). As these two ends increase in length, the yolk sac constricts and comes to hang well below the developing animal on a slender stalk. At this time the "foetus" is developing in the egg shell or the uterus of the mother. Absorption of the yolk is accomplished by shortening of the sac and drawing it into the body. In *Squalus,* a second yolk sac is formed in the body and this too shortens until it is lost.

The development of the spiral valve involves torsion of the gut lining within the mesodermal cover (Figure 9-24). The first turns develop at the posterior end and extend forward as counterclockwise rotation continues. This torsion rotates the point of entrance of the bile duct to the dorsal surface of the gut. Unlike the typical actinopterygian a separate midgut does not form; it is included in the spiral intestine. The liver arises as a ventral diverticulum as in the higher forms, while the pancreas arises from dorsal and ventral diverticula.

Holocephalan *Hydrolagus* is without an identifiable stomach or pyloric valve (Figure 9-25). The esophagus, with its ridged epithelium, is constricted behind the pharynx and extends from here back and downward through a short arc to open directly into the intestine. The intestine receives the bile and pancreatic ducts dorsally at its anterior expanded end. There is a spiral valve which begins at the entrance of the bile and pancreatic ducts and extends, through four counterclockwise turns, nearly to the anus. The dorsal mesentery is largely missing, the ventral entirely so. A cloaca is lacking. There is no rectal gland (digitiform gland), but in the submucosa of the intestine are long branching glands which end blindly anteriorly and open posteriorly through the mucous lining.

The two lobes of the liver are connected by a narrow band ventral to the esophagus. The right lobe extends back to the posterior end of the body cavity and clasps the hindgut from above in a deep groove. The gall bladder lies below and to the right of the gut; its duct passes dorsally, then medially, and back to enter the dorsal aspect of the anterior

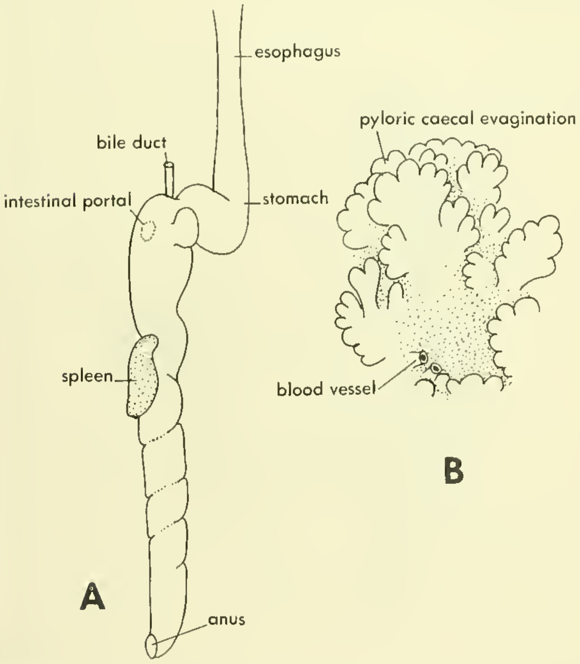


Figure 9-19. An early stage in the development of the gut of *Lepisosteus*, as seen in ventral view, A, and a later stage of pyloric caeca development, B. (After Jacobshagen, 1937)

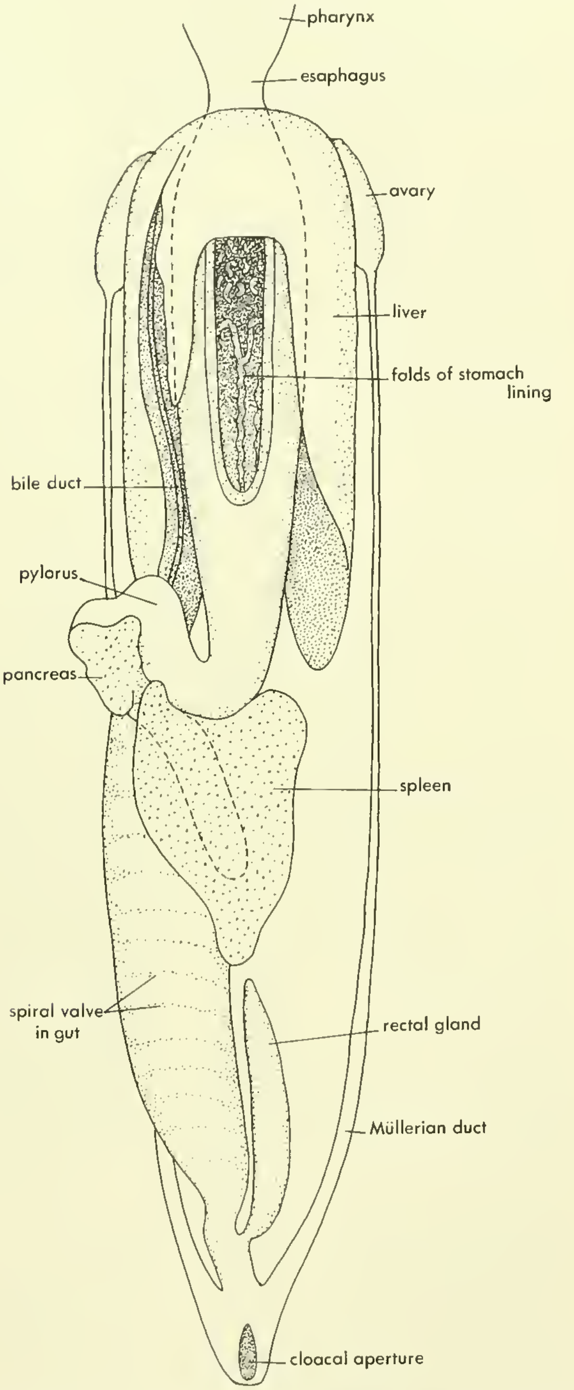


Figure 9-20. Ventral view of viscera of *Squalus* with part of stomach wall removed to show ridged lining.

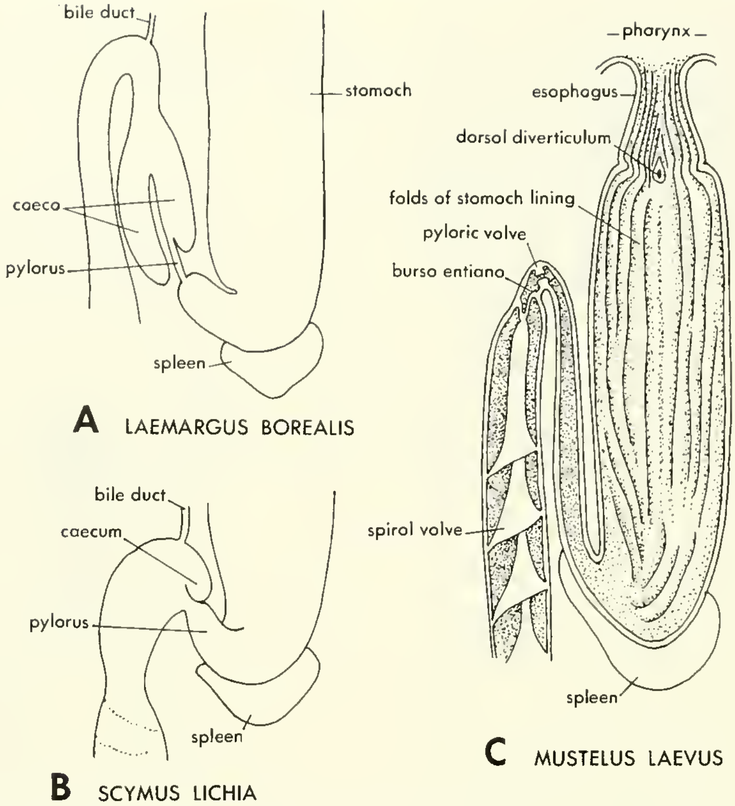


Figure 9-21. Pyloric caeca in *Laemargus borealis*, A, and *Scymus lichia*, B, and internal view of stomach and anterior end of gut of *Mustelus laevus*, C. (After Pernkopf and Lehner, 1937)

end of the midgut. The pancreas is a band-like mass lying along the hepatic portal channel, which drains the spleen and the wall of the gut. The intestinal vein from the spiral valve and anterior gut wall enters the hepatic portal stem at the anterior end of the pancreas. The pancreatic duct passes forward along this channel to enter the bile duct. The spleen is a triangular body lying above the gut and is attached to the pancreas anteriorly, with its tapered end directed posteriorly.

The holocephalan agrees with the shark in lacking a separate midgut and in having a compact pancreas. The lack of a distinct stomach has been considered primitive, but could as easily be the result of loss (a specialization). The development of the holocephalan is assumed to be like that of the shark but has not been fully studied.

General observations on gnathostome fishes

The intestines of the chondrichthyes, choanates, and *Polypterus* agree in lacking a distinct midgut—the spiral or rolled valve extends through almost the entire length of the intestine. *Bothriolepis,* an antiarch, is described as having a similar intestine with a rolled valve. The primitive members of the actinopterygian groups have a spiral valve in the

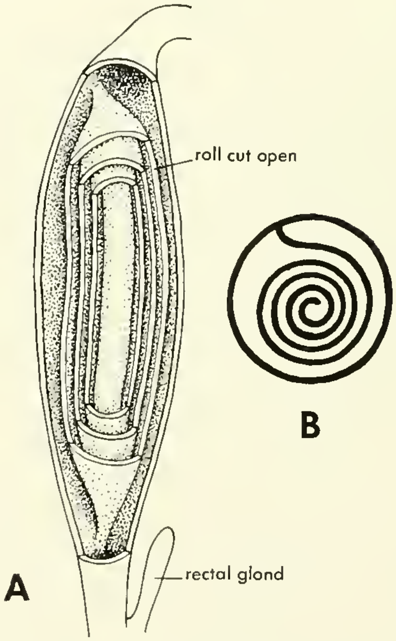


Figure 9-22. Rolled valve of intestine of *Zygaena*. A, ventral wall of gut removed to show the valve; B, cross section of gut and valve.

hindgut; this is lacking in the teleost, at least in the adult. The midgut region is much elongated in the ray-finned fishes, with the exception of *Polypterus,* and is sometimes separated from the hindgut by a valve.

The selachian and holocephalan resembles higher vertebrates in having a compact pancreas, while the actinopterygian is peculiar in having a diffuse pancreas and pyloric caeca. *Polypterus* agrees with the actinopterygian in this. In the dipnoan, the pancreas is concealed within the gut wall, as is the spleen, but both are separate compact structures in the actinistian. The lungfish and actinopterygian appear to be modifications away from an original condition.

Cyclostomes

Lamprey The mouth of the lamprey (Figure 9-26) is a circular opening set deep in a funnel-like sucker, armed with rows of horny teeth, and fringed with numerous fleshy papillae. The mouth opening itself is blocked by a tooth-bearing, rasping organ often referred to as the tongue. This tongue is an elongated muscular structure lying in the floor of the oral or buccal cavity and extending back below the branchial region. The tongue moves forward and back in helping create the suction by which the animal attaches to its prey or to rocks when moving upstream against a strong current. Other muscles move the teeth on the tip of the tongue up and down giving them a rasping action which cuts into the flesh of the prey. A pair of sac-like salivary glands, embedded in the tongue, open into the oral cavity at the base of the rasping teeth. These glands produce a secretion which prevents coagulation of the blood of the prey.

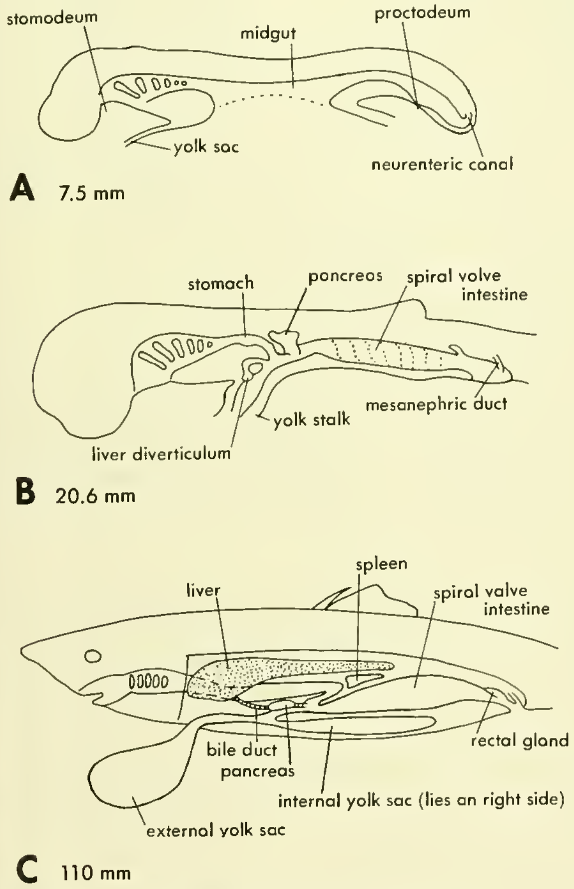


Figure 9-23. Three stages in the development of the gut and yolk sac of the shark, *Squalus acanthias.* (After Nelsen, 1953)

Behind the buccal cavity, the pharynx is divided into a dorsal tubular **pharyngoesophagus** and a ventral **respiratory passage.** On the anterior margin of this dividing septum, there are several forward-projecting tentacles supported by the cartilaginous rods of the velar skeleton. Below this tentacular margin and projecting posteriorly, is a flap of tissue on either side which serves as a **valve.** This valve eliminates backflow from the respiratory pharynx. In the larva the pharynx is undivided, but at metamorphosis the separation of the cavity occurs from behind forward. This process involves development of the rasping apparatus as well. The **velar tentacles** mark the position of the septum between the stomodeum and pharynx of the embryo.

The pharyngoesophagus is constricted posteriorly to a narrow opening, then widens out to open on the left through a longitudinal slit into the gut. This slit is extended by flaps on either side well into the gut cavity. This slit extends posteriorly into the anterior end of the typhlosole. Well behind this entrance the bile duct opens in a deep groove to the left, or above, the typhlosole.

The anterior end of the gut is expanded, while posteriorly it is of varying but reduced diameter. Most lampreys used in the laboratory are collected on their way to spawn at a time when they do not feed, so the gut is small. The gut lies free for much of its length in the body cavity. Anteriorly it is attached, right dorsolaterally, to the liver along a line extending much of the length of the expanded anterior part. The posterior fifth of the gut is attached dorsally by two or three vascular connections with the dorsal body wall. The anus opens into a cloacal slit in which lies the urogenital papilla.

The liver is a conical mass, hollowed above and rounded below. Anteriorly its base is attached all around to the body wall, and posteriorly it tapers to a rounded point below the gut. The gall bladder lies within the substance of the liver anteriorly at the midline; it is not conspicuous in sexually mature adults. The bile ducts join in the region behind the bladder and the main duct passes upward and medially to enter the gut near the posterior end of its anterior swelling.

Behind and above the entrance of the bile duct into the gut is an islet of Langerhans mass. A second large islet mass occurs above the constriction of the pharyngoesophagus at its opening into the gut. A third mass occurs midway between these. In the wall of the anterior part of the intestine are large patches of cells which resemble those of the pan-

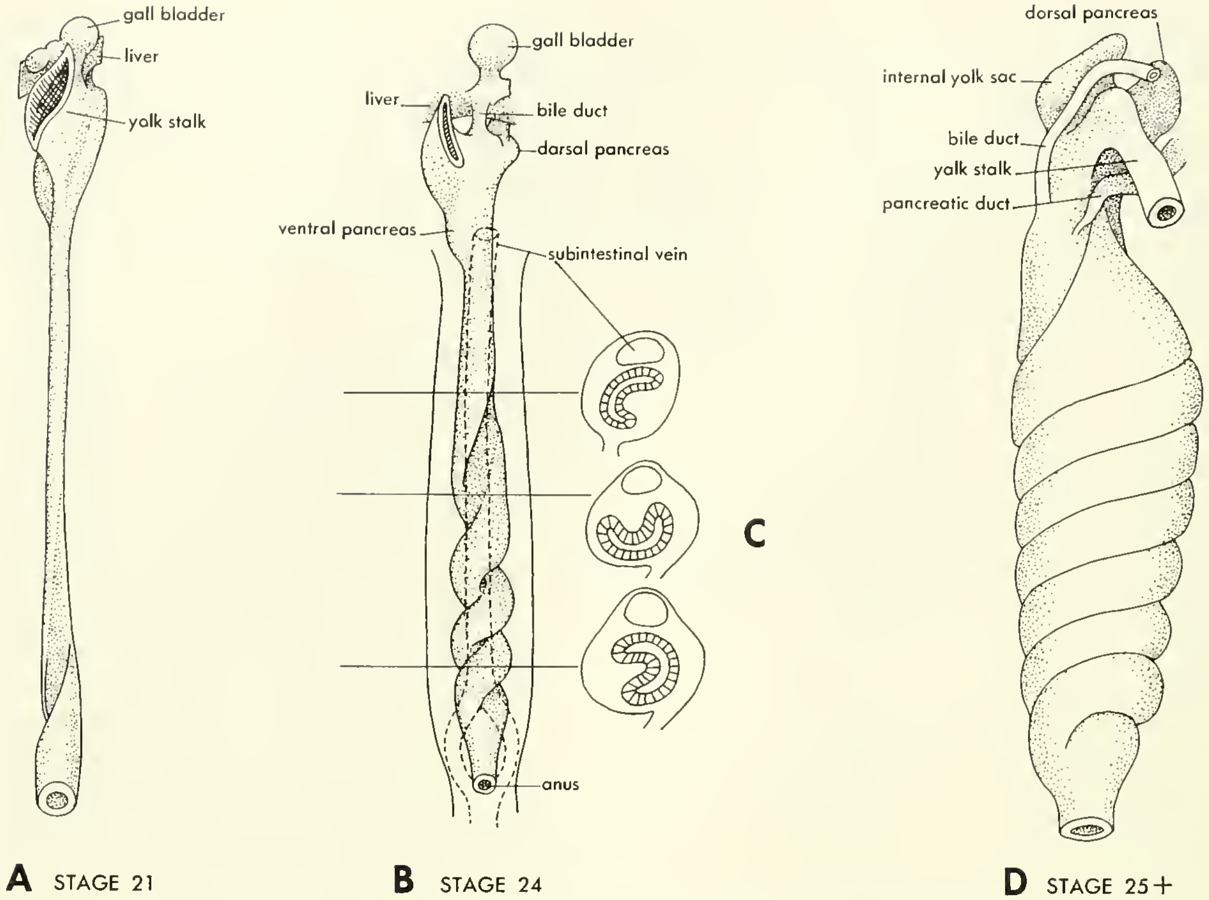


Figure 9-24. Three stages in the development of the spiral valve of the shark *Pristiurus*. The stippled tissues represent the lining of the gut, and several cross sections of stage 24 show the relationships of this lining to the rest of the wall of the gut and the subintestinal vein. (After Rückert, 1897)

creatic acini of higher forms. These patches can only be observed in prepared sections. The anterior pocket of the intestine has been viewed as a forerunner of the pancreatic diverticulum, but it might equally well be considered a pyloric caecum.

The development of the islet tissue can be observed in the 25 or 30-mm lamprey where small tubules extend out into the overlying connective tissue in the area of entrance of the bile duct. The tubules do not open into the gut cavity but connect only with the outer surface of the gut wall. Such tubules grow outward from the ventral, left, and dorsal aspects of the gut, and none is connected with the bile duct itself.

The typhlosole of the gut is generally described as a spiral valve, but it does not spiral in a way comparable to that of higher groups. In the lamprey this fold tends to lie along the left ventrolateral wall of the gut. In the adult the anterior end of the valve is left dorsolateral, so little rotation is evident. The gut, which lies free in the body cavity, appears to be twisted a turn or two in the region behind its middle. The valve tends to spiral, following it from behind forward, in a counterclockwise direction in the posterior third, and in a clockwise direction in the next third. The typhlosole of the lamprey is peculiar in that the mesenteric artery passes posteriorly through it, a situation not observed in higher forms.

EMBRYOLOGICAL DEVELOPMENT The lamprey egg undergoes holoblastic equal cleavage (Figure 7-6). The yolk is contained within the cells of the gut wall. At first the gut wall is many cells thick, and irregularly disposed spaces coalesce to form the definitive lumen. The blastopore remains as the anus, and there is no proctodeum. The liver appears first as a ventral evagination into the yolk mass from the anterior end of the archenteron or primitive gut. Later it is displaced backward and comes to lie behind the pharynx and in front of the yolk-expanded gut wall.

The development of the gut shows no rotation in the early stages. The typhlosole fold is filled by a mass of lymphoid or hemopoietic tissue.

Myxinid The mouth of the hagfish (Figure 9-27) is superficially like that of the lamprey, but the funnel is without teeth and papillae. There are four pairs of tentacles around the funnel, and a nasohypophyseal opening lies above it. There is a rasping organ, in the floor of the mouth cavity, armed with two semicircles of teeth, the anterior set larger than the posterior. There is a single tooth in the roof of the mouth above the rasping organ.

The nasohypophyseal canal opens into the mouth posteriorly, and behind this junction there is an enlargement of the pharynx, the velar chamber. From the roof of this chamber a velum is suspended from a midline frenulum. The lateral margins of this structure can be rolled and unrolled to produce a pumping action driving water back through the pharynx. The branchial pouches open to either side from the pharynx which leads back to the intestine.

The intestine is a straight tube of large diameter. There is no typhlosole, but the inner walls have longitudinal folds, as in the lamprey. The liver has a posterior left lobe and an anterior ventromedial lobe; the lobes are not joined (Figure

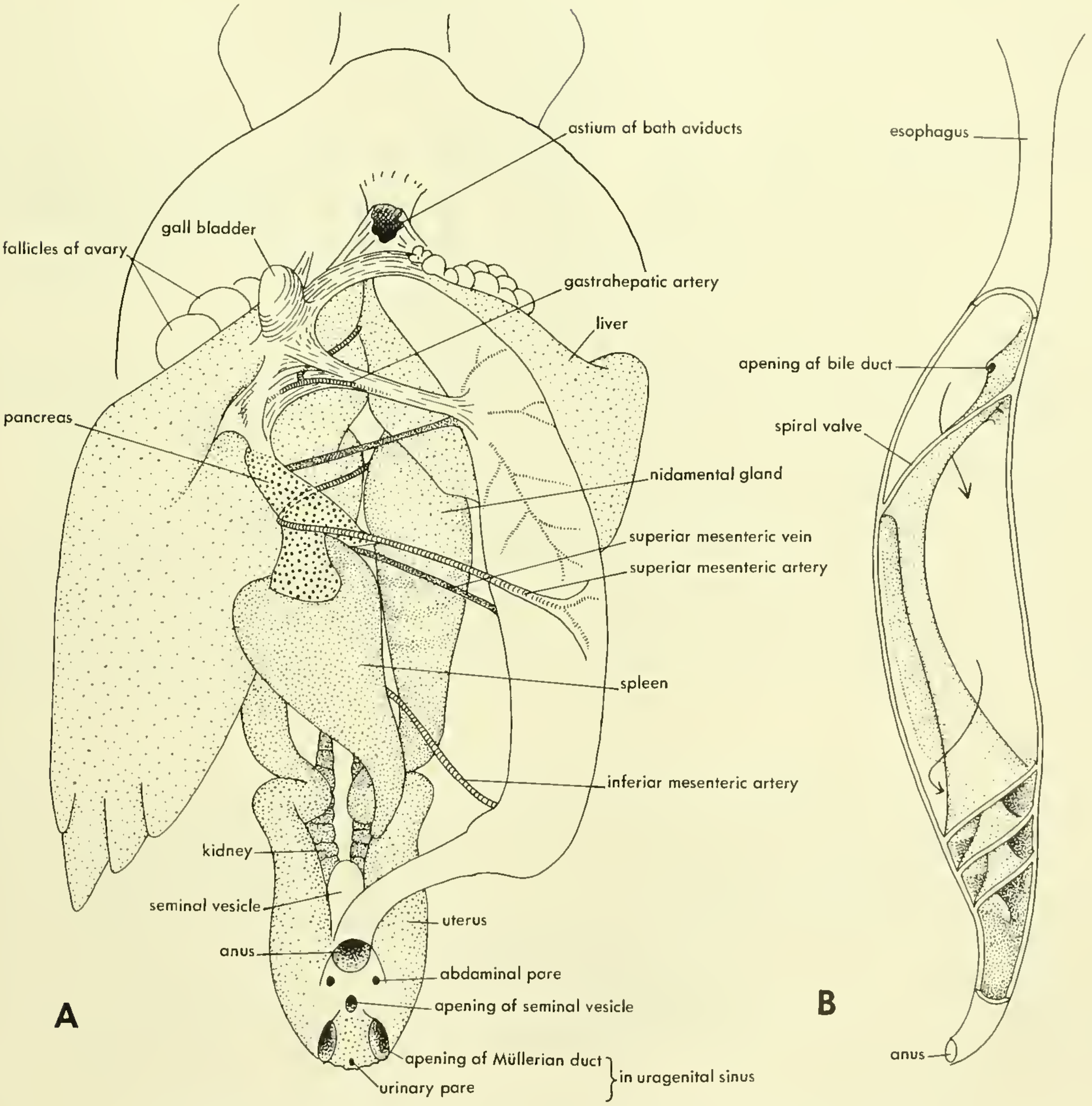


Figure 9-25. Viscera of *Hydrolagus*. A, ventral view; B, lateral view of gut with the left wall cut away to reveal the interior.

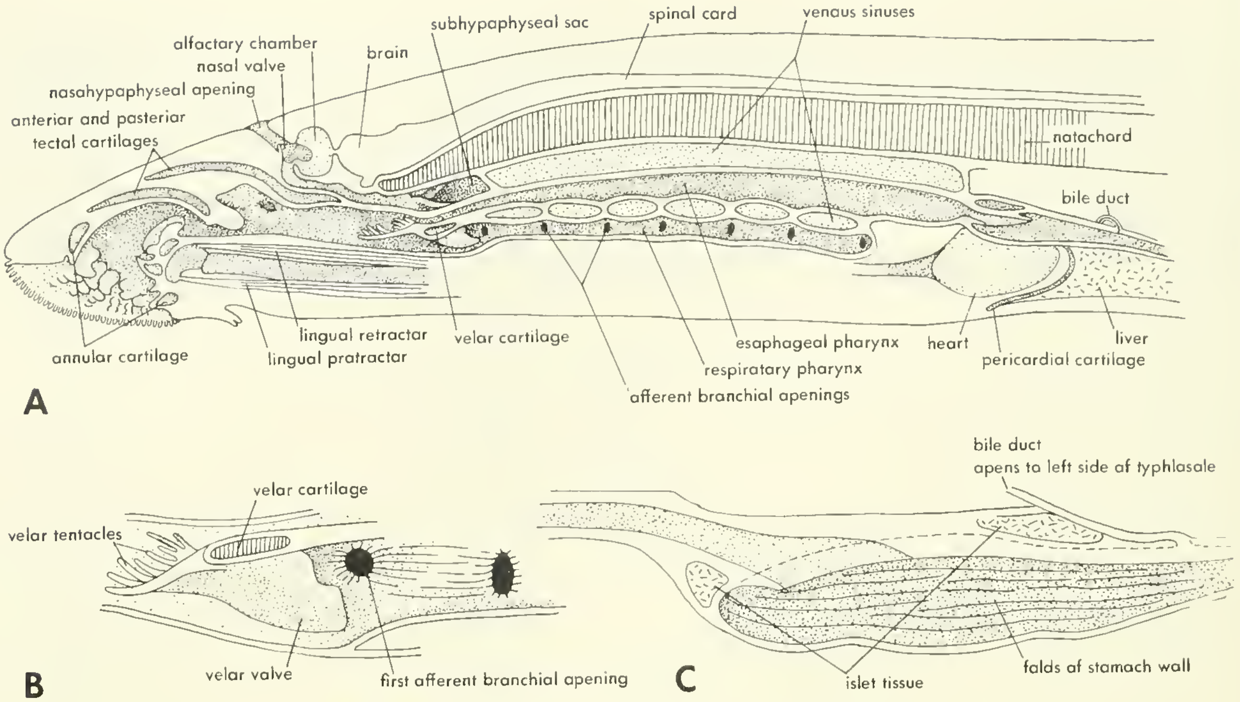


Figure 9-26. Sagittal section through the head region of a lamprey.

9-28). The gall bladder lies between these lobes, and its short duct extends forward to enter the intestine slightly to the left of the midline and well behind the union of the pharynx and gut.

At the point where the bile duct enters the gut, there is a swelling marking the mass of islet tissue of the pancreas.

There is no spleen in either *Myxine* or *Petromyzon*, although the latter has much lymphoid tissue in the typhlosole of the larva. The myxinoid has myeloid tissue in the submucosa of the gut, while the adult lamprey, on the way to spawn, has some cell production going on in the blood itself and in the kidney tissue.

The development of the myxinoid is not well known. The telolecithal egg develops much as in the shark or teleost (Figure 7-14). Development is direct, without metamorphosis.

General observations on fishes

The abdominal viscera of fishes show the same basic pattern as the tetrapod both in terms of adult parts and in the developmental stages of these parts. The diffuse pancreas of the actinopterygian and the internal pancreas of the dipnoan or cyclostome raise the question of the primitive condition. The fact that the shark, or holocephalan, and *Latimeria* have a well-developed pancreas suggests that this was the original

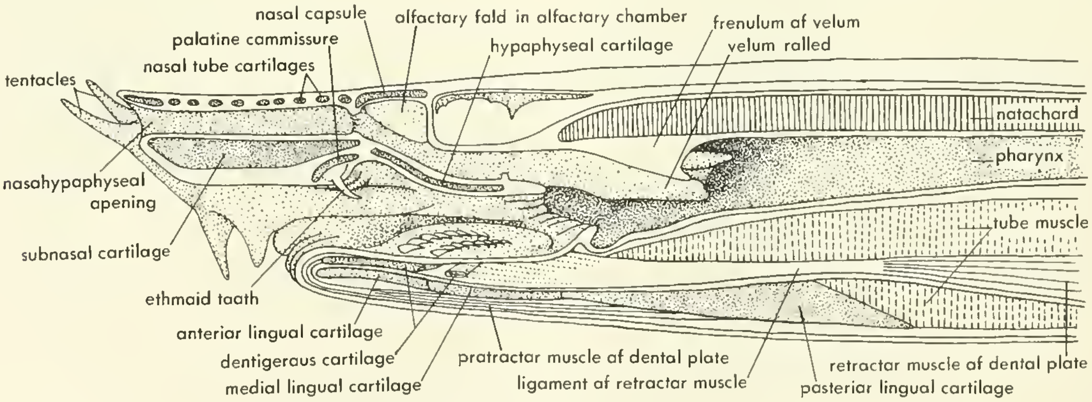


Figure 9-27. Sagittal section through the head region of *Myxine*.

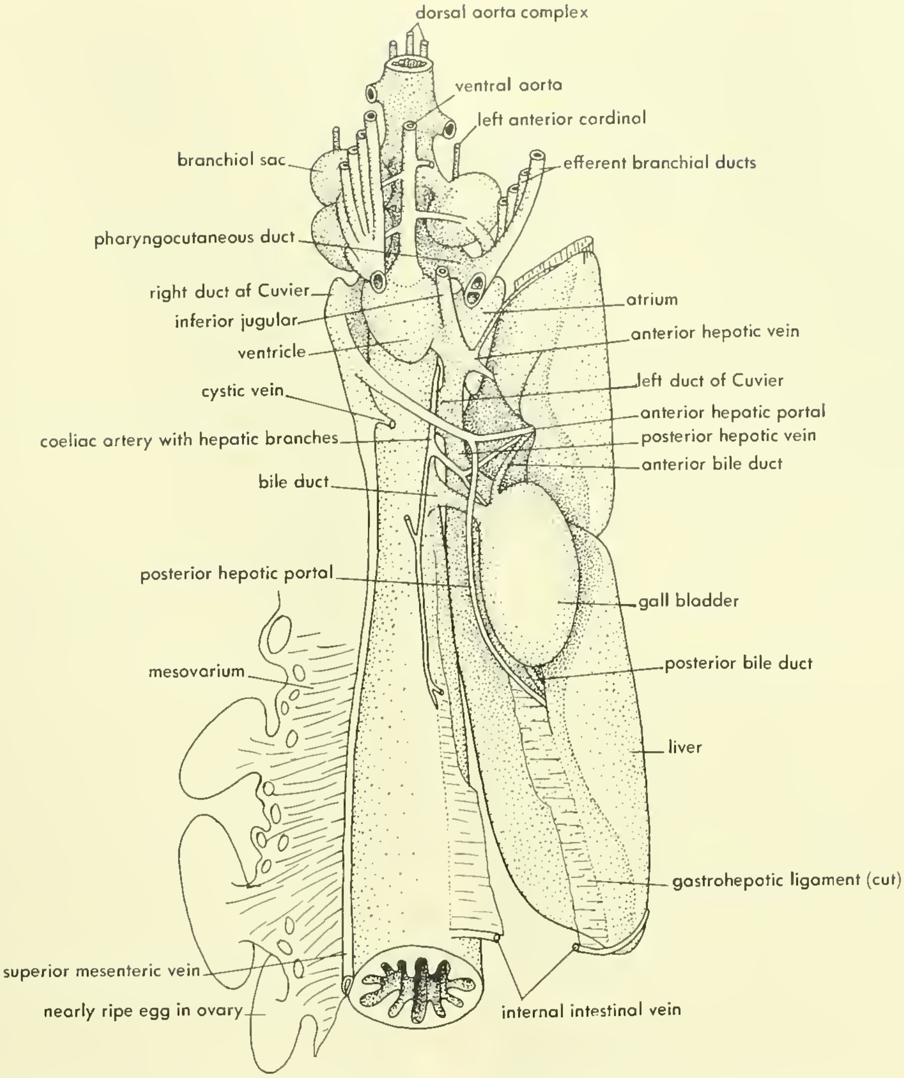


Figure 9-28. Anterior end of viscera of Myxine as seen in ventral view. The liver is displaced to the reader's right. (After Morenelli and Strenger, 1956)

condition. Diffusion of the pancreatic tissue in the actinopterygian appears to be related to the appearance and development of pyloric caeca. The origin of the pancreas in the several groups differs only in the number of diverticula; usually there are dorsal and ventral anlagen. In the lamprey a large number of tubules form, but these do not appear as evaginations of the gut wall. The manner of origin in this type is probably derived rather than primitive.

The liver is remarkably constant in its relationships with the gut and in having a gall gladder. The association of bile duct and pancreatic ducts is fairly constant. The segmentation of the gut into esophagus, stomach, and intestine is also consistent. The occurrence of two types of spiral valves suggests that at first there was only a simple typhlosole. Surface area was increased, for more efficient absorption, by growth of the free margin so as to form a rolled sheet or by increase in length so as to cause spiraling. In more advanced forms the spiral valve part of the intestine was reduced and a "small intestine" of increasing length developed. In the teleost the spiral valve is undeveloped and the intestine has small and large divisions separated by a valve. This development represents a parallelism to the situation in the tetrapod.

In the fishes the spleen does not have the same relationships that it has in the tetrapod, although that of the shark joins these extremes. The shark is peculiar in having a rectal gland, and comparisons of the shark and holocephalan are no better in this area of anatomy than they are elsewhere. Loss of the stomach in the holocephalan is a parallelism to the situation in *Protopterus* or the cyclostome. In the latter the lack of a stomach may reflect the specialized diet. Lack of a spleen is peculiar to the cyclostome.

Although the abdominal viscera do not sharply separate the agnath from the gnathostome, or define the several subgroups of the latter, they do contribute to the image of the primitive vertebrate. This ancestral form had a complex of organs rather similar to that of the lamprey but had in addition a stomach and pancreas, and perhaps a spleen.

THE RESPIRATORY SYSTEM

Respiration is usually defined as breathing, an act which involves the movement of air into and out of the lungs or the movement of water past gills, as in the fish. Respiration as a basic biological function is a much more sophisticated concept. For our purposes, respiratory systems involve organs specialized for the exchange of oxygen and carbon dioxide between the organism and the environment. Such a system includes a vascular contribution, since the exchange is between the environment and the blood.

Lungs

Mammals The **lungs** are bilateral lobulate structures, lying in the **pleural cavities** of the chest. The lungs are formed largely from the terminal sacculations of branching tubules stemming from the midline **trachea,** which opens into the pharynx through a T-shaped or ovoid **glottis.** Anterior to the glottis is the raised **epiglottis,** which folds back to help close the glottis. The epiglottis is part of the complex pharyngeal apparatus, the **larynx,** formed from cartilages of the **branchial arches.** The cartilages involved in this apparatus are the **epiglottis, thyroid, cricoid,** and **arytenoid.** The larynx contains the **vocal cords,** which function in speech.

Distally the trachea branches into two tubes, the **bronchi.** From these, **second order bronchi** branch irregularly into the lobes of each lung. The first few orders of bronchi are, like the trachea, supported by **cartilaginous semirings.** These successive branchings end with the **lobular** and the **respiratory bronchioles.** The latter divide into **alveolar ducts** opening into a large number of **alveoli** or into **alveolar sacs,** surrounded in turn by **alveoli.** The **alveolus** is the terminal division of this branching system and the site of gas exchange.

The **pulmonary arteries and veins** follow the branching of the air ducts. The pulmonary arteries stem directly from the right ventricle of the heart, while the pulmonary veins return to the left atrium.

The cavities in which the lungs lie are separated from that of the heart by the **pericardial sac,** and from the abdominal cavity by the **diaphragm.** The diaphragm is muscular and its contractions, along with those of the intercostal muscle, increase the thoracic volume. The lungs follow the volume changes of the thoracic cavity passively, so that air moves in and out of the air passages and body.

The air moving in and out of the body utilizes the nasal passages. These are separated from the mouth cavity by the secondary, or false, palate. In the nasal passages the air is sampled for odors by the olfactory sense. The nasal passages, with their intricate turbinals, condition the air in terms of temperature and moisture content for its entrance into the lungs.

Among mammals the lungs have a varying number of lobes; the right is usually more subdivided than the left. The left may be undivided, or both lungs may be undivided as in the whales. In whales the lungs extend back dorsally for nearly half the body cavity length; the diaphragm is powerful and obliquely oriented. The lungs function for hydrostatic purposes as well as respiration. In the whale there is a great development of arborized tubules supported by cartilaginous rings, but a reduced amount of alveolar tissue.

EMBRYOLOGICAL DEVELOPMENT The lungs appear first as a ventral diverticulum from the posterior floor of the pharynx, the **laryngotracheal groove** (Figure 9-6 D). This diverticulum extends back below the esophagus and branches to right and left in the tissue below the esophagus. The pair of **lung buds** thus formed bulge into the body cavity to either side, and, as development progresses, these bulges extend backward and outward separate from the esophagus (Figure 9-29).

The cutting off of the pulmonary spaces from the rest of the body cavity involves folds which grow inward from the body wall. The **pleuropericardial folds** form between the lungs and the pericardial space, while the **pleuroperitoneal folds** cut off the pleural cavity from the abdominal cavity. These folds join the **transverse septum,** which is associated with the anterior face of the liver, and the dorsal septum of the gut, the **mediastinum.** The latter supports the dorsal aorta, esophagus, and caval veins. The diaphragm is formed from the transverse septum and pleuroperitoneal folds attached medially to the mediastinum, and it is invaded laterally by its musculature.

Reptiles The lungs of reptiles and amphibians are similar, except that those of the former tend to be more complexly sacculated. In Sphenodon or the lizard, the right and left **bronchi** open into large **central cavities** surrounded by spongy alveolar tissue. The right lung is usually the larger. In turtles (Figure 9-10), the alveolar tissue may be very extensive with channels leading into it from the restricted central cavity. Alveolar tissue may enclose regularly arranged chambers with restricted openings into the central cavity. In the alligator the central cavity is little more than an extension of the bronchus into the alveolar tissue.

The lung of the reptile is supported by a mesentery from the dorsal mesentery. In most reptiles the lungs extend back into the abdominal cavity. In the alligator the somatic peritoneal membrane enclosing the visceral mass is muscular and separated from the body-wall musculature. From its

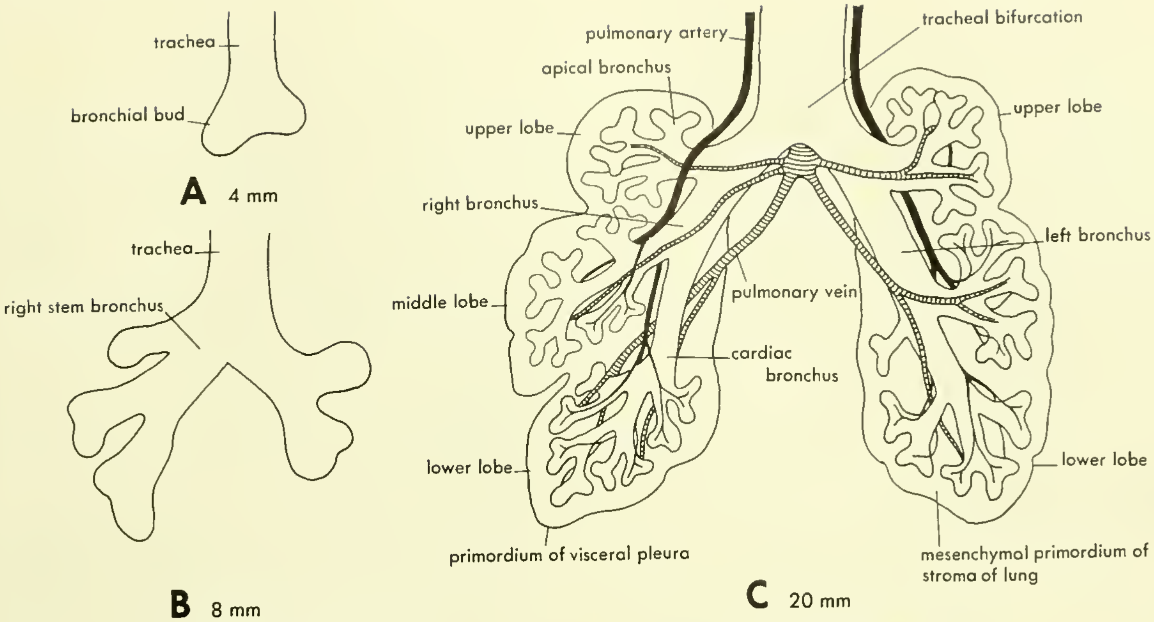


Figure 9-29. Three stages in the development of the lungs of a human. (After Patten, 1946)

origin on the pubes, this muscular sheet fans out and inserts on the free posterior margin of the liver. It draws the liver and heart mass backward, thus increasing the thoracic volume. A similar mechanism is observed in the turtle and in the lizard *Tupinambis*. Most lizards appear to respire by means of body-wall movements only.

Birds The lung of a bird (Figure 9-30) is an extremely compact organ broadly attached dorsally to the body wall as in the turtle. From the lungs five pairs of air sacs extend out through the remainder of the body cavity. These are the **cervical, clavicular, anterior** and **posterior thoracic,** and **abdominal air sacs.** (In the chameleon small sacs grow out from the lung proper and suggest the origin of the air sacs of the bird.) The air sacs of the bird extend into the large bones of the body and even into the vertebrae.

The volume of the body cavity is altered by movements of the ribs acting on the sternum and through the abdominal muscles. In flight, contraction of the pectoral muscles acting on the wings compresses the body. The lungs are separated from the rest of the body cavity by a membrane having the same associations as the pleuroperitoneal portion of the mammalian diaphragm. This membrane has several slips of muscle from the **internal oblique** series inserting on it, and these can act to pull the membrane backward and thus increase the pulmonary volume.

Air is drawn in with expansion of the body volume and it passes through the central cavity of the lung, the **mesobronchus.** The mesobronchus opens into a series of **dorsal** and **ventral bronchi** which branch outward to all parts of the lung. These are connected by numerous **parabronchi,** each of which is enclosed by a zone of **capillary loops** in which the gaseous exchange occurs. The capillary loops of one parabronchus open into those of the surrounding parabronchi. The mesobronchus leads back directly into the posterior thoracic and abdominal air sacs, while the other air sacs are connected with the ventral bronchi. With the exception of the cervical, each air sac has several recurrent bronchi which lead into the dorsal (or ventral) system of bronchi.

The flow of air through the lungs is not understood, but it is generally conceded that the air in the **respiratory capillaries** is essentially fresh and changed with each respiratory movement. The air in the sacs may be quite stale when the bird is at rest but is fresh when the bird flies.

Amphibians Among the salamanders the lungs are generally elongate, corresponding to the body shape (Figure 9-11). The effect of body shape is indicated also in the case of the snake. The central cavity is usually large and the alveolar tissues relatively thin, subdividing into progressively smaller spaces by distinct septa. In *Cryptobranchus* the lungs are quite small as compared with those of *Necturus*. In a few salamanders lungs are lacking (some species of *Ambystoma, Rhyacotriton, Salamandrina, Desmognathus, Leurognathus,* and the family Plethodontidae). The body surface is used for respiratory exchange in aquatic forms and in some of the lungless terrestrial types.

The lungs of the frog are ovoid sacs, whose walls are divided into progressively smaller spaces by septa. The lungs are supported by a mesentery attached to the dorsal mesentery of the gut. The posterior end of the lung projects

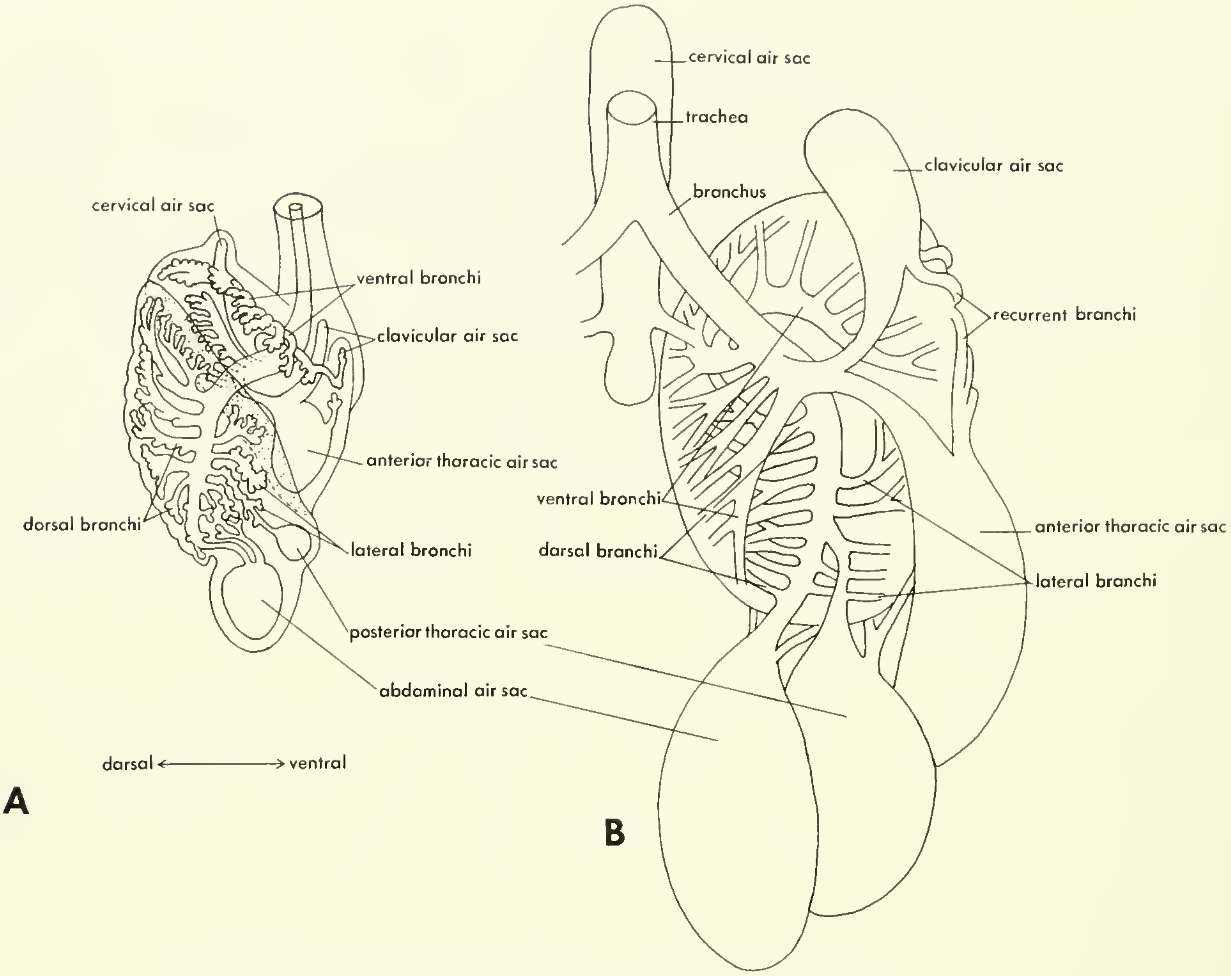


Figure 9-30. Semidiagrammatic lungs and air sacs of the bird. A, dorsolateral view of right lung of 9-day-old chick foetus; B, adult system in ventral view. (A after Witschi, 1956)

freely into the body cavity. Among anurans the body surface has an important accessory respiratory function.

Embryological development in reptiles and amphibians The lungs arise from the floor of the pharynx as in the higher forms. First a laryngotracheal groove appears in the floor of the pharynx, and from this paired outgrowths arise. The medial groove is later converted into the trachea, and the bilateral outgrowths become the lungs.

The alligator or bird parallels the mammal in the course of the development of the lung buds, which branch successively in the formation of the organ (Figure 9-31). In the bird the dorsal and ventral bronchi branch repeatedly to form the parabronchi; those of the dorsal and ventral bronchi meet midway between these two series along an oblique plane and fuse. In this way, what were blind-ending tubules come to form loops. In most reptiles and amphibians the lung buds merely expand, with a few knob-like diverticula, to form the definitive lung.

In the reptile a variety of membranes form an association with the lungs, and occasionally the lungs are nearly cut off from connection with the abdominal cavity, as is the case in *Tupinambis*. However, a diaphragm as such is never formed. In the amphibian there is no attempt to isolate the lungs from the remainder of the body cavity.

From their position and paired origin, it is generally assumed that the lungs represent a posterior set of gill pouches. In the case of *Hypogeophis,* there are eight pairs of pharyngeal pouches; the most posterior, eighth pair, gives rise to the lungs. In some salamanders seven pairs of gill pouches are presumed to occur; the lungs form from the seventh pair.

Swim bladder

In fishes respiration is usually carried on through the agency of **gills.** A hydrostatic organ, the **swim bladder,** may be used as a supplementary and emergency respiratory organ.

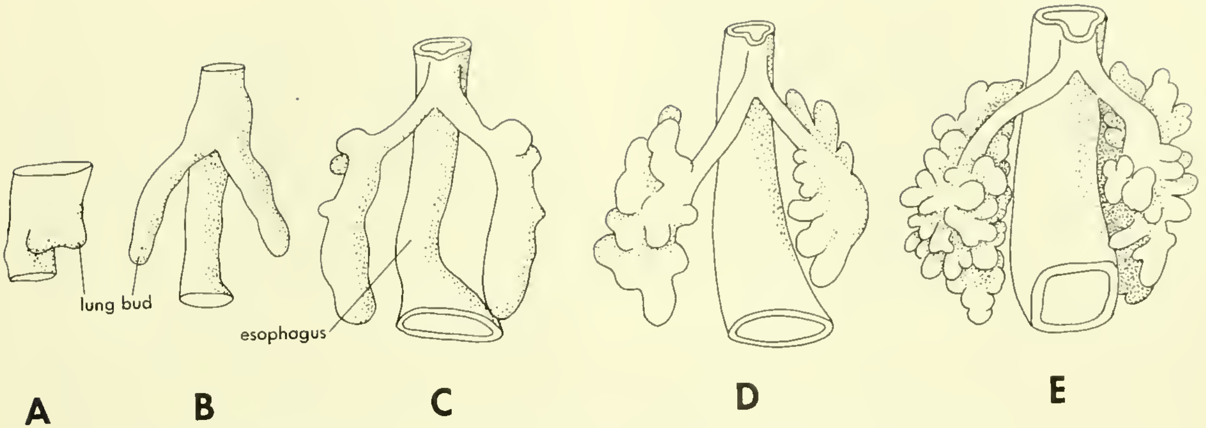


Figure 9-31. Five stages in the development of the lungs of the alligator. (After Broman)

It is generally assumed that the swim bladder is the homolog of the lung, although there are differences. The lung arises primitively from paired anlagen from the ventral wall of the pharynx, while the teleost swim bladder arises from an unpaired dorsal or dorsolateral diverticulum of the esophagus. The blood supply of the lung is from the sixth aortic arch, while that of the swim bladder is usually from the dorsal aorta.

Actinistia The swim bladder of *Latimeria* is attached anteriorly to the ventral aspect of the esophagus. From here it extends up and around the right side of the esophagus and stomach to a dorsal position, where it extends back in the dorsal mesentery the entire length of the body cavity. The gonads are suspended from its sides anteriorly, and below it hang the gut and its attendant organs. The walls of this bladder are much thickened with oil-filled cells, and only remnants of the lumen are observed. The vascular supply has not been described. The walls of this structure were calcified or ossified in the known Mesozoic fossil forms.

Dipnoan In two of the lung fishes, *Protopterus* and *Lepidosiren,* paired sac-like lungs extend the length of the body cavity. These have been rotated around the right side of the gut into a dorsal position, so that the original right lung is now the left. The stem of these lungs attaches to the ventral aspect of the "esophagus" just behind the expanded branchial chamber. There is a slit-like glottis opening into the pharynx or esophagus, depending on the definition of these terms. The lungs in these forms serve not only a respiratory function but also a hydrostatic one—ventral lungs would make it difficult to maintain an upright position, while an anterior lung would make it hard to maintain a horizontal position.

Although paired diverticula probably arise in the larva, only one retains its connection with the esophagus. Rotation of these sacs brings them in contact, with the result that their cavities become interconnected anteriorly. At the beginning of the development, the left lung is smaller than the right, but in the adult this same lung, now the right one because of rotation, is as large as the other.

In *Protopterus* the lungs lie retroperitoneally above the level of the kidney and the gonad (Figure 10-41), and they extend to the extreme posterior end of the body cavity. They are broad anteriorly, narrower midway along the body, and expanded in height posteriorly (Figure 9-12).

The lungs are served ventrally by the left pulmonary artery which passes below the esophagus and up the right side to reach the lung. Here the artery bifurcates to pass along the medial margin of both lungs. The right pulmonary artery bifurcates and extends back on the mid-dorsal surface of both lungs. The pulmonary veins lie along the lateral margins of the lungs and unite below the fused anterior part. The single stem passes down to the right of the esophagus, then along and to the right of the hepatic vein. From here it extends forward above the sinus opening of the right duct of Cuvier, then downward through a septum separating the recess of the sinus venosus to reach the auricular wall. It opens through the auricular wall to the left of the septum partially separating the cavity of the auricle into halves.

The left vagus nerve follows in part the same path as the left pulmonary artery; a second part passes dorsally to the embryonic left lung, now the right lung. The right vagus appears to lack a ventral division.

The **monopneumonous** condition of *Neoceratodus,* in contrast to the **dipneumonous** or paired lung condition, has been described as due to development of the right lung only, the left being rudimentary and lost in the pneumatic duct. Whether one or both lungs actually develop, the end result is the same in terms of the vascular supply. Thus, it appears that in *Neoceratodus* both lung buds fuse early and produce the single sac of the adult with its bilateral sacculations and blood supply. In *Protopterus* and *Lepidosiren* fusion occurs only anteriorly, but the left pulmonary artery serves the under side of both lungs just as in *Neoceratodus.*

Teleost The swim bladder of the teleost is a thin-walled, midline sac in the dorsal mesentery. It lies below the kidneys: the gonads lie lateral to it and the gut is suspended below it (Figure 9-13). The swim bladder may be connected with the esophagus dorsally, or this connection may be lacking in the adult (Figure 9-32). The salmon is an example of the first, **physostomous** condition, while the perch is an example of the second, **physoclystous** condition. This bladder generally has a hydrostatic function, but in some physostomes it is an air-respiratory organ.

In both physostomes and physoclists the swim bladder arises as a dorsal diverticulum from the esophagus. In the cod the swim bladder wall contains peptic (stomach) glands. In the physoclist the swim bladder undergoes modification so as to function as a hydrostatic, sensory, or sound-producing organ. There is an anteroventral secretory region, the **gas gland,** which contains a **retia mirabilis** (wonderful net) of blood capillaries, and a posterodorsal absorbing region, the **oval,** which develops from the degenerating pneumatic duct. These two parts may lie in nearly separated anterior and posterior chambers. The eel (*Anguilla*) is an intermediate type, retaining the pneumatic duct while having the oval and gas glands.

In physostomes, blood is supplied to the swim bladder through a branch of the coeliacomesenteric artery and is returned to the heart through a vein joining the hepatic portal system or the postcardinal vein (*Anguilla*). In physoclists the coeliacomesenteric artery supplies the retia mirabilis of the gas gland, the oval area, and the bladder wall. These structures also receive blood from the dorsal aorta. The blood returns from the gas gland through the hepatic portal stem, and the rest of the bladder is mainly drained through the posterior cardinal veins. Right and left branches of the vagus (Xth cranial) nerve innervate the structure, particularly the gas gland; the oval is innervated by sympathetic branches which parallel the vagus nerves.

In some teleosts (*Lampanyctus*) the walls of the swim bladder are thickened with oil-filled cells and the lumen is largely obliterated; however, a well-developed gas gland with a complex vascular rete may be retained. A few teleosts lack the swim bladder; these are usually specialized for lying on the bottom.

Amia, Lepisosteus, Acipenser In *Amia* and *Lepisosteus* the swim bladder extends nearly the length of the body cavity. Unlike the teleost, the walls of the bladder are sacculated laterally as in *Neoceratodus.* The pneumatic duct opens through a dorsal, slit-like glottis in the region of the esophageal constriction posterior to the pharynx.

In *Amia* arterial blood comes from right and left pulmonary arteries, while in *Lepisosteus* branches of the dorsal aorta descend at intervals along the length of the bladder. Venous drainage is into the left duct of Cuvier in *Amia,* into the right postcardinal of *Lepisosteus.* The teleost *Gymnarchus* is intermediate (Figure 9-33); the efferent branchial arteries of the third and fourth gill arches unite to form a root for the coeliacomesenteric and pulmonary arteries.

The swim bladder of the holostean arises as a single evagination from the foregut, well back from the pharynx. Bilateral anlagen have been described but only one is distinct, and this appears to be to the right of the midline. The relative position of its attachment shifts forward with growth.

In *Acipenser* the swim bladder is short and ovoid. The pneumatic duct enters the bladder ventrally, well behind the anterior end, and it joins the esophagus, or stomach, well back from the pharynx. The point of entrance into the esophagus is closed by simple constriction of the duct, and there is no glottis. Internally the bladder is smooth walled. The walls are fairly thick and fibrous—brittle in preserved specimens. Isinglass, a very pure gelatin, is produced from the swim bladders of sturgeons. The arterial and venous connections are with the dorsal body channels.

In the embryo, both left and right folds are said to arise from the roof of the esophagus, but only the right gives rise to the definitive swim bladder. Bilateral anlagen have been described for other fishes, and it has been assumed that sometimes the right and sometimes the left give rise to the swim bladder.

Polypterus *Polypterus* has bilateral air sacs joined anteriorly and opening through a ventral glottis to the right of the median line (Figure 9-14). It is assumed that these sacs arise as bilateral diverticula from the underside of the esophagus, just behind the pharynx. The left glottis is reduced to an epithelial strand or lost with the fusion of the anterior ends of the sacs. The left sac is short, one-fourth of the body cavity length; the right extends the entire body length, passing up to the right of the esophagus and stomach and back through the dorsal mesentery. In cross sections it is seen to be broadly attached dorsally between the kidneys with the gut suspended below it.

The inner epithelium of the sacs is smooth and partly ciliated. The walls are vascular and they are supplied dorsally by the pulmonary arteries and drained ventrally by pulmonary veins which join to enter the sinus venosus. The sacs are innervated by left and right vagi; the left has a branch extending above the esophagus to the right sac. Externally the walls of the sacs are covered by two layers of striated muscle fibers. The outer fibers run posteriorly and toward the ventral midline of each sac where they meet along a raphe; the fibers in the deeper layer are oriented at right angles to those of the outer.

The sacs of *Polypterus* contrast strongly with those of other actinopterygians (Figure 9-34). It is difficult to assume that the chondrosteans, holosteans, and teleosts were derived from a form with bilateral ventral sacs of which all trace has been lost except in *Polypterus.* It is equally or more difficult to assume that *Polypterus* is a modified choanate. The paired sacs of *Polypterus* give foundation to the theory of the separation of a brachiopterygian group from the actinopterygian.

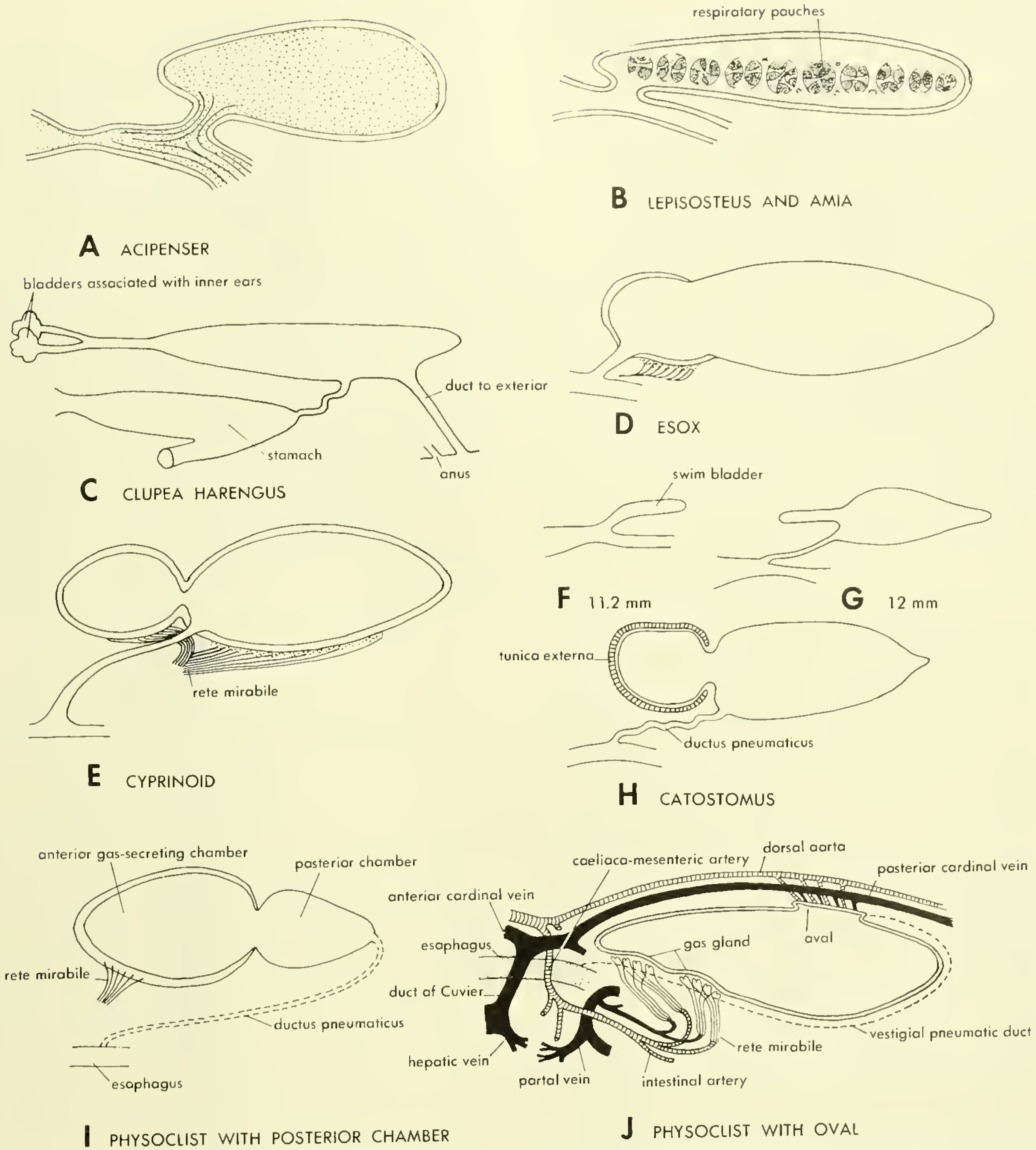


Figure 9-32. Variations in the structure and relationships of the swim bladder. F–H, three stages in development of the swim bladder of *Catostomus*. (C after Tracy, 1920; D, E, I, J after Goodrich, 1930; F–H after Nelson, 1959)

In the evolution of the Brachiopterygii, the bilateral pharyngeal pouches joined ventrally in a fashion parallel to that observed in the choanate. That parallelism is involved is suggested by the originally paired glotti, the muscular nature of the sac wall, and the lack of alveolar sacculations in *Polypterus*.

Other gnathostome fishes Miklucho-Maclay (1867) found a rudimentary dorsal diverticulum from the esophagus in embryos of *Galeus, Mustelus* (Figure 9-21 C), and *Squalus*. These rudiments were not generally observed by other workers, although Mayer (1894) found one in the adult of *Mustelus laevus*. Pits in the esophageal wall are observed in

Scyllium, Squatina, Carcharius, Pristiurus, Heptanchus, and rays. Wassnezow (1928, 1932) found one to three pairs of pits, dorso- and ventrolaterally behind the fifth pouch in *Trygon, Torpedo,* and *Pristiurus*. The most posterior of these in *Trygon* forms a dorsomedial pit comparable to that of *Mustelus*. In most adult sharks there is no evidence of a swim bladder, and, in the development of the shark, there is only this hint of a rudimentary swim bladder.

In the fossil antiarch *Bothriolepis canadensis*, casts of what appear to be lungs have been described. This interpretation has been objected to on the grounds that these structures lie too far forward and are thus casts of the gill chambers.

Cyclostomes In neither of the living cyclostomes is there any evidence of a swim bladder or lungs. Goethe (1875, 1905) observed in the lamprey a small pair of diverticula behind the most posterior gill pouch (the 9th). These were interpreted as lung rudiments. They might just as easily be interpreted as rudimentary gill pouches arising behind the branchial series, as is suggested in the myxinoids where the number of gill pouches is not a constant.

General observations There is little question that some sort of homology exists between the lungs of tetrapods and the swim bladders of fishes, but the exact degree is hard to determine. One can assume that these structures arose from a posterior pair of pharyngeal pouches, but little more than this. One cannot be sure that the same pair of pouches was involved in every case. It is suggested that in many primitive fishes such as sharks these pharyngeal sacs remained rudimentary or disappeared, while in others they became enlarged as a part of a pharyngeal air "breathing" system. In the ancestral actinopterygian the sacs appear to have joined above the esophagus and to have connected with the pharynx, or the esophagus; in choanates and in *Polypterus* the sacs joined below and connected ventrally. Thus there may have been at least four lines of evolution: loss, joining above, and joining below in both the choanate and, as a separate event, *Polypterus*. The possibility of *Polypterus* and the choanate representing a single line is remote since they differ in the nature of the "ductus pneumaticus." The fact that the lungs of some choanates rotated upward around the esophagus, as in the dipnoan, or passed upward to either side suggests the importance of hydrostatic factors in fishes (or amphibians); the resultant dorsal position is a parallelism to the situation in the actinopterygian. The same events occurred in the evolution of the line leading to *Polypterus*. What factors operated to produce a ventral connection are not known; there is the possibility that this is a secondarily achieved relationship. It has also been suggested that the dorsal connection of the ray-finned fish may have been derived from an original ventral attachment. This view is popular since it allows a monophyletic origin for both lung and swim bladder.

Gills

The gills of vertebrates involve special modifications of the aortic arches which are discussed in Chapter 11. Only a brief summarizing account will be attempted here.

Amphibians Gills occur only in the larva or as a neotenic feature of the adult in such salamanders as the axolotl or *Necturus* (Figure 7-23). In the adult of *Necturus* there are two **gill slits**; these lie between the first and second and the second and third branchial arches. These gill slits are margined internally by reduced **gill rakers.** There are no gill filaments on these arches, but there are three pairs of **external gills** extending outward from the epibranchial regions of the first three branchial arches. *Cryptobranchus* has a single pharyngeal slit between the first and second branchial arches (see Figure 4-18). There are neither internal nor external gills in this species. In the axolotl there are four gill slits (I-IV), three external gills in the adult, and an incipient operculum which extends from one side to the other across the throat.

In the larval frog three pairs of external gills form (Figure 7-24). The first pair before hatching, the second and third pairs at intervals. These are attached to the first, sec-

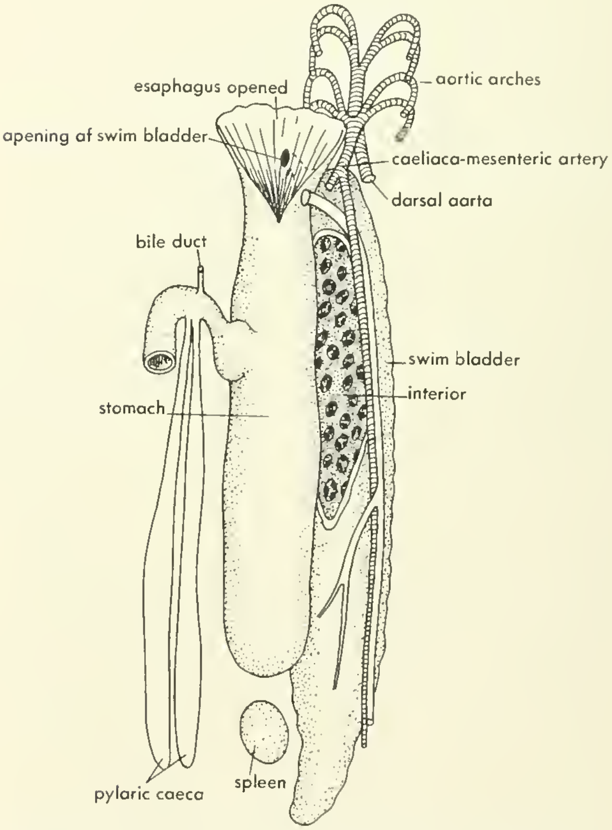


Figure 9-33. Swim bladder and its relationships in *Gymnarchus*, as seen in ventrolateral view. (After Hyrtl)

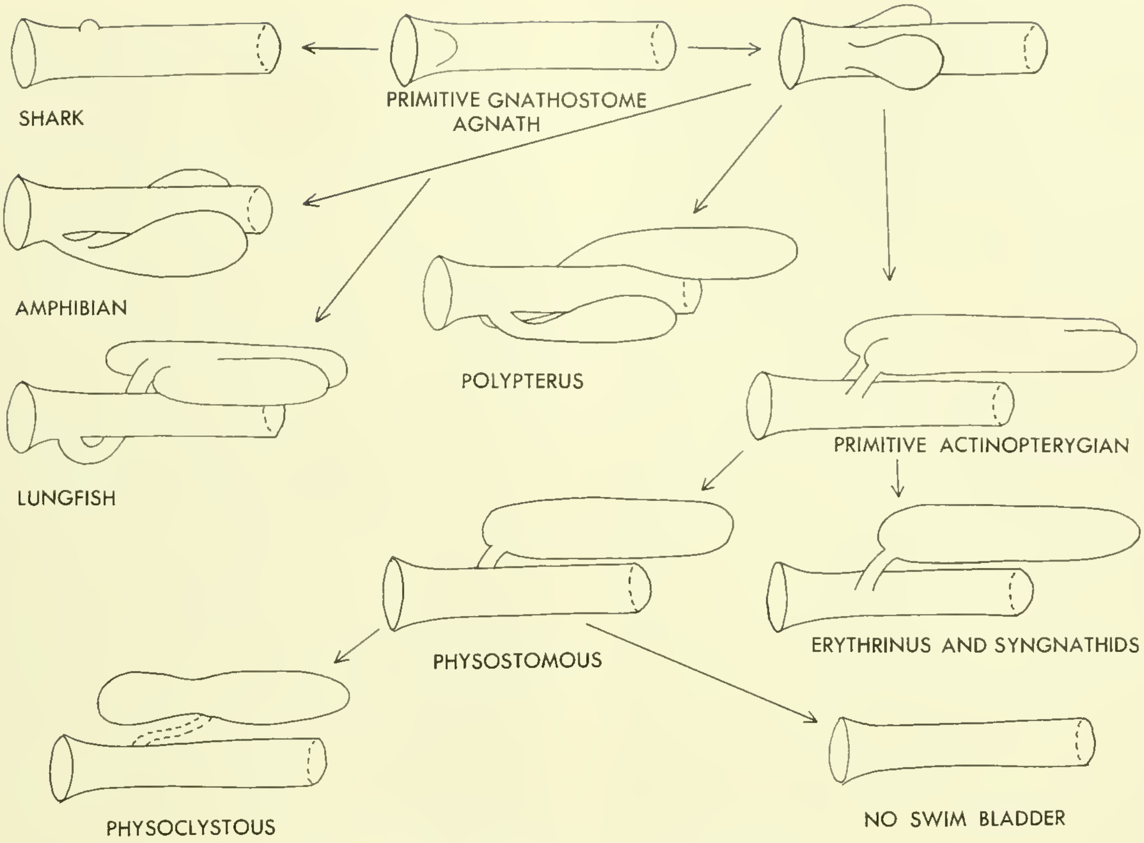


Figure 9-34. Possible phylogeny of the swim blodder.

ond, and third branchial arches and can be observed in the 7-mm frog. On each of these arches the external gill is reduced as the **internal gill filaments** form along the arch itself. The slit between the hyoid and first branchial arch is obliterated by the posterior growth of an **operculum.** The opercula of either side are continuous across the throat. The joined opercula grow back and attach behind the **branchial chambers** except for a slit on the left side. With enclosure of the confluent branchial spaces, only internal gills are now present. A **hemibranch** has appeared on the fourth arch behind the third and last gill slit; this condition is observed in the 10-mm frog. These gills serve the larva until, with metamorphosis, the lungs come into play.

Among fossil amphibians only the branchiosaurs and a few other types such as *Dvinosaurus* retain the gills and visceral skeleton. These types are presumed to be neotenic since the amphibian stage of evolution is defined as having functional lungs in the adult. Perhaps only some of the more advanced amphibians, as defined by other criteria, abandoned gills for lungs. One might assume that *Necturus* has come down from the beginning of the Amphibia without change in this feature. It is clear in the case of the axolotl that gills are a neotenic feature; *Necturus* is a parallel case where gills have been retained in the adult as a specialization for an aquatic life. Not all aquatic salamanders retain larval gills, as witness *Cryptobranchus.*

Choanate fishes *Latimeria* has a deep spiracular pouch without a mandibular pseudobranch on its anterior wall or an external opening. There is a small **hyoidean hemibranch,** on the posterior surface of the hyoid arch, and there are four **holobranchs,** gills along both anterior and posterior margins of an arch (Figure 11-18). The fifth branchial arch is reduced and without gills.

The lungfishes, similar in some respects, all lack the mandibular pseudobranch and have only a rudimentary spiracular pouch. *Neoceratodus,* the most aquatic of the lungfishes, cannot live out of water. It has an hyoidean hemibranch and four holobranchs (Figure 11-18). *Protopterus* and *Lepidosiren,* being given to aestivation periods during dry spells, appear to depend more on the lung. *Protopterus* has the hyoidean hemibranch, the fourth and fifth arches bear holobranchs, and the sixth has an anterior hemibranch. Vestiges of the external gills of the larva are retained in the adult.

In both *Protopterus* and *Lepidosiren* the first branchial or hyobranchial slit, that between the hyoid and the first branchial arch, is closed. *Lepidosiren* has holobranchs on arches two, three, and four, and there are no hemibranchs.

The branchial arches in this group have rudimentary gill rakers on their inner margins, and the gill filaments extend well beyond the narrow medial septa (Figure 11-17). No gill rays support the filaments and there are two efferent arteries in each arch, at least in *Neoceratodus.*

The larvae of *Protopterus* and *Lepidosiren* have four pairs of external gills early in life; these are replaced by internal gills when the operculum develops (Figure 7-22). *Neoceratodus* never has external gills, and the operculum appears early.

Actinopterygian fishes The teleost type has a mandibular hemibranch or **pseudobranch,** four holobranchs on the first four arches, and sometimes a fifth arch hemibranch. A hyoidean hemibranch is lacking. The **branchial chamber** is covered by the **operculum** laterally and opens posteriorly and ventrally. The opercula may overlap ventrally or fuse; the fusion may be extended to the isthmus, reducing the opercular openings to bilateral slits or round openings. In *Synbranchus* the opercular opening is restricted to a ventral midline fissure.

The pseudobranch shows various stages of reduction and covering. In the salmon it is well developed. In the perch the filaments are reduced and covered by the mucous epithelium of the pharynx, and this covering is carried to an extreme in the cod where the hemibranch is buried. This hemibranch is embedded in the roof of the pharynx of *Cyprinus* by closure of the pouch in which it lies.

The mandibular hemibranch is limited in function with the closing of the spiracle. Furthermore, it now receives only oxygenated blood from the hyoid or first branchial arch. The term pseudobranch refers to the lack of respiratory function of this hemibranch. The pseudobranch may function in regulating the pressure in the ophthalmic artery or serve an endocrine function; acidophile (acid staining) cells are found in this organ of some fishes.

In terms of its branchial structure, *Eurypharynx* represents an extreme of the teleost—if indeed it is a teleost. In this genus the branchial region has been moved far back from the hyoid arch as a result of the development of the enormous mouth gape. There are six branchial openings, the first of which lies in front of the first branchial arch, as indicated by the glossopharyngeal nerve passing behind it. There are five holobranchs. The pouch-like **external branchial chambers,** serving all of the gill slits of a side, open ventrally to either side of the swollen cardiac portion of the isthmus.

Teleosts show many respiratory modifications. Some have arborescent or labyrinthine organs in the branchial cavity which function as accessory air-breathing organs. In others such as *Saccobranchus,* there are lung-like outgrowths of the branchial cavity which extend back into the body musculature. In some, air is swallowed and oxygen absorbed through the gut wall.

The larvae of teleosts utilize the yolk sac or body surface for respiration until the internal gills develop. Attenuated filaments of the internal gills may extend well beyond the opercular margin as external gills in types such as *Gymnarchus.*

Amia differs from *Lepisosteus* in lacking the hyoidean hemibranch (Figure 9-35) and in having the pseudobranch reduced and covered by the mucous epithelium. There are four holobranchs in *Amia* just as in *Lepisosteus* (Figure 11-19). In *Lepisosteus* the hyoidean hemibranch ends in contact with the posteroventral end of the mandibular pseudobranch. Blood for the pseudobranch comes from the afferent hyoid artery and the efferent artery of the first arch. The vessels of the pseudobranch of *Amia* interconnect the orbital and ophthalmic stems; there is no direct efferent or afferent branchial connection. Neither *Amia* nor *Lepisosteus* have a spiracle and the spiracular pouch is reduced to a rudiment, a pore on the pharyngeal surface at the anterior medial end of the interarcual groove.

Acipenser is comparable to *Lepisosteus* except that the hyoidean hemibranch lies just inside the margin of the operculum and does not contact the mandibular hemibranch (Figure 9-35). The spiracle is present but the spiracular pouch is little more than a tube from the hyobranchial or anterior branchial groove. Since the mandibular hemibranch receives only oxygenated blood, it is a pseudobranch. *Acipenser* and *Lepisosteus* also agree in having the opercula joined across the midline but free from the isthmus.

In *Scaphirhynchus* the hyoidean hemibranch is reduced in size and there is no spiracle. *Polyodon* lacks the hyoidean hemibranch but is otherwise like *Acipenser;* it has a spiracle. The larvae of these fishes are like those of the teleost.

Polypterus has a wide spiracle. The inner surface of the pharynx has the hyoidean or spiracular pouch separated from the hyobranchial groove by a ridge of tissue. There are four branchial openings. The first three branchial arches have holobranchs and the last a hemibranch. There is no

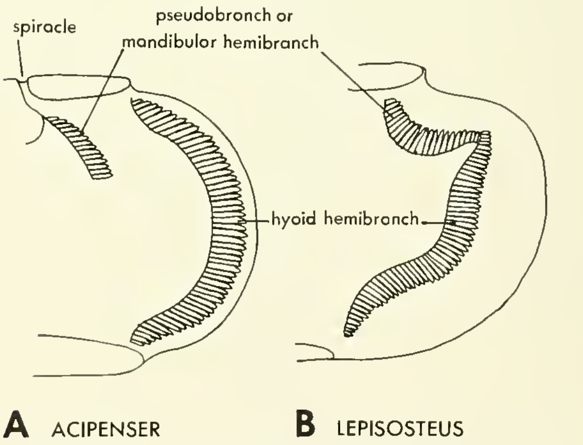


Figure 9-35. Internal view of the operculum showing the relationships of the hyoid hemibranch and the pseudobranch.

pseudobranch (mandibular hemibranch) or hyoidean hemibranch. The opercular structure, in terms of bones, is distinctive, as has already been pointed out.

The larva has a pair of large external gills which grow back from the hyoid arches—and receive their blood supply from those arches. This gill has dorsal and ventral rows of filaments. It appears before the branchial openings and persists relatively late in development, even after the formation of the operculum.

In terms of its respiratory apparatus, *Polypterus* appears to be quite distinct from the actinopterygians. Lack of the pseudobranch and hyoidean hemibranch could be explained as due to the respiratory function of the air sacs. However, the bilobed ventral "lungs" are also unique among actinopterygians, even if one discounts them as representing the primitive type from which the actinopterygians diverged. The larval gill of *Polypterus* is unmatched in any other type of fish (Figure 7-21). Again, it could be considered a primitive type of actinopterygian external gill which has been lost in all other members of this group.

Chondrichthyes Sharks have a spiracle with a mandibular pseudobranch, a hyoidean hemibranch and four, five, or six holobranchs (Figure 11-22). The posterior branchial opening lacks a posterior hemibranch. Each of the branchial clefts open separately to the outside. The medial septum extends beyond the gill filaments forming a flap covering the branchial slit behind. Muscle fibers extend down through this septum. A single row of gill rays supports the septum as compared with the double rows of gill rays supporting the two rows of filaments of the actinopterygian holobranch. *Polypterus* is like the actinopterygian in this feature, while the choanate lacks gill rays. This lack of gill rays is probably related to the reduction of ossification and development of the branchial system in the choanate group.

The branchial arches of the shark have one afferent arterial channel and bilateral efferent channels, as does the dipnoan *Neoceratodus*. *Acipenser* is intermediate with respect to the teleost, holostean, and *Polypterus,* in which there is one afferent and one efferent vessel.

The holocephalan is operculate. The opercula are joined below and with the isthmus. There are four branchial openings (Figure 11-24). The spiracular cleft is completely closed, although a spiracle is present in the young. There is no evidence of a pseudobranch in the spiracular pouch. The hyoid bears a posterior hemibranch fused to the inner surface of the operculum. The first, second, and third arches have holobranchs and the fourth a hemibranch. The gill filaments reach outward just beyond the septum. Each arch has only one efferent vessel and there are valves along its anterior and posterior margins. These valves act to close the branchial openings when the mouth is opened. The operculum serves this function in the actinopterygian.

The holocephalan thus differs from the shark or actinopterygian in its branchial organization.

Fossil gnathostome fishes Little is known about the branchial skeleton of the arthrodires and therefore of their gills. They are usually described as aphetohyoideans but, using the holocephalan as an example, this does not mean that there was a full mandibular slit or even a spiracle. The head shield extended back over the branchial region but did not form a movable (functional) operculum.

The acanthodians had three or four (rarely five) branchial arches and they too had a separate (not jaw supporting) and complete hyoid arch (the aphetohyoidean condition). There was a mandibular operculum supported by rays. The hyoid arch, and the more anterior branchial arches, may have had small dorsal opercular flaps.

Cyclostomes The lamprey has seven pairs of branchial pouches, beginning with the second branchial pouch—that one lying in front of the second branchial arch. Each of these pouches is lined with gill filaments and served by afferent and efferent arteries lying between the pouches. The pharynx of the adult lamprey is divided into a dorsal esophageal and a ventral respiratory passage (Figure 9-26). A narrow duct leads from the respiratory pharynx into the more or less spherical pouch. The pouch opens to the exterior through a small, round opening guarded by valves.

In the larval lamprey the pharynx is undivided and opens widely into or between the branchial arches. The pouches open to the exterior through small round ports. During metamorphosis the pharynx is divided and the constricted internal openings of the branchial pouches are developed.

The myxinoid is quite different from the lamprey, sharing only the pouch-like nature of the branchial clefts. (These fishes have been called the **marsipobranchs** on this account.) The number of pouches varies in this group: there are six pairs in *Myxine* and as many as thirteen to fifteen pairs in *Eptatretus.* The first branchial pouch never appears, the second develops, but degenerates as does another more posterior pair in the course of development. It is not known which pair of pouches becomes the most anterior of the adult, but the branchial apparatus is displaced far posteriorly. The myxinoid is peculiar in that a pharyngocutaneous duct leads from the pharynx to the exterior on the left side behind the last pair of gill pouches. In *Eptatretus* each gill pouch opens separately to the exterior, while in *Myxine* the excurrent channels join and open together behind the level of the gill pouches. The pharyngocutaneous duct opens with this left channel in *Myxine* (Figure 9-28).

The myxinoid differs from the lamprey in that the pharynx is undivided (Figure 9-27). The vascular supply of the pouches is also peculiar in that the afferent and efferent arteries serve a single pouch only—they are not spilt between two pouches as in the lamprey (Figure 11-26).

The functioning of the gill pouches of the lamprey and myxinoid is complex. When the mouth is attached or when the head is buried in a victim, as in the case of *Myxine*, some point of entry other than the mouth is necessary.

The spiracle serves as a point of entry for respiratory water in the case of the rays. The pharyngocutaneous duct might serve this purpose in the case of the myxinoid. In both kinds of cyclostomes the muscular pouches are capable of producing a pumping action with the result that water could enter the pharynx either from the mouth or the hypophyseal duct —the pharyngocutaneous duct in the case of the myxinoid. Water may be drawn into the pouch through its outer opening in the lamprey, then pumped from the pouch through the same port.

The branchial systems of the cyclostomes differ in their vascular relationships but agree in the general form of the pouches (restricted internal and external ports). The median septum of the arch in this group is a complex wall between pouches. It is possible that the marsipobranch type of pouch preceded the narrow branchial bars of the gnathostome, but it is just as likely that it represents a respiratory specialization related to the agnathan mouth. As a specialization it cannot be considered primitive or ancestral to the gnathostome.

Fossil agnaths The number of pharyngeal pouches and external branchial openings varies in the several fossil types. In the osteostracan there were 10 or 11 pouches and openings, the anaspids had from 8 to 15 openings, and the pteraspids 10 to 14 chambers all opening through a single external port. The pouches in these fossils, in terms of preserved skeletal clews, appear to have been like those of the living cyclostomes.

General observations A branchial system was probably present in the ancestral vertebrate, since pharyngeal slits are a basic chordate feature. The primitive system can be imagined as a series of slits of indeterminate number, probably not greater than seven, supported by some sort of connective tissue skeleton. It is possible that each branchial arch was a holobranch, with the exceptions of the first and last. The pouches of the agnath contrast sharply with the slits of the gnathostome and suggest that they are modifications, part of a pumping mechanism associated with the jawless mouth. The gnathostome retained the simple slits but produced an articulated branchial skeleton, a part of which was involved in the jaws. From this line of thought it seems plausible that both agnath and gnathostome types are divergences from the ancestral style.

The many variations in number of pouches or slits and in the details of structure indicate the plasticity of this region. The Osteichthyes are characterized as having five gill slits, as do most sharks and perhaps most of the arthrodires and acanthodians, but these are covered by an operculum. The actinopterygian differs from the choanate in having a pseudobranch. *Polypterus* appears to be quite distinct in most features.

One might ask here if there were two evolutionary lines of fishes, one without an operculum, the primitive state, and one with. Since the operculum is a part of a respiratory mechanism, which directs water in through the mouth and out past the gills, it is quite possible that this structure could arise in several lines. The opercula of the osteichthian, acanthodian, and holocephalan are distinctive in their structural details and, probably, in their action, and thus could be parallelisms. However, if the opercular skeletons and action of these opercula were developed late, then all could have come from a single ancestral source (monophyletic). The view that they are parallelisms (polyphyletic) seems more in line with the facts.

Body surface

The general body surface is frequently used by vertebrates, either as larvae or as adults, for respiration and in some has become the main respiratory system, along with the lining of the mouth. It is generally assumed that the most primitive vertebrates, based upon the porous nature of their dermal bones, had a rather rich capillary net associated with the outer part of the dermis and that this capillary net supplied a certain amount of the respiratory requirements for these organisms.

The amphibian stage apparently marked the dividing point for respiratory pathways. The living amphibians represent forms in which cutaneous respiration was continued or even further developed, as in the case of the lungless salamanders, while the reptiles represent a type in which the outer layer of the skin became cornified or keratinized and thus impermeable or only slightly permeable to the respiratory gases. This keratinization was important in combating drying. Whereas the moist-skinned amphibian would be limited to wet areas or places of high humidity, the dry-skinned reptile could seek food anywhere within the ranges of its temperature tolerances. This dichotomy of the vertebrate stem was extremely important in the evolution of this group.

RESUMÉ

The viscera of the vertebrates suggest some of the basic events of their phylogeny, However, this record is difficult to assess because of the functional plasticity of these organs and systems. Again the basic split into agnath and gnathostome is seen and the several groups of gnathostomes are suggested. The dissimilarity of shark and holocephalan is emphasized again as is the unique nature of *Polypterus*. Resemblance between the dipnoan and amphibian is slight because of the modified nature of the former. Comparisons would probably be better with a Devonian dipnoan. The tetrapod groups agree closely in most details.

10

The Urogenital System

Because of their close morphological relationship, the excretory and reproductive systems are described together. The relationship is particularly close in the male where tubules of the kidney are utilized for the transport of the sexual products. This area of comparative anatomy is generally given close attention and its contribution to our knowledge of vertebrate phylogeny is often stressed. Homer Smith believed that the fine structure of the vertebrate kidney indicated a specialization for the removal of water and that, therefore, the vertebrate group arose in fresh water. It may, however, have been a preadaptation making possible the invasion of fresh water. The urochordates and hemichordates lack any kidney and have apparently always been marine in habitat. Amphioxus has a large number of nephric vesicles, associated with clumps of solenocytes, in the pharyngeal region. The vertebrate system shows no agreement with that of the cephalochordate, so it can be assumed that this type of excretory system arose in the vertebrate group as an adaptation to some special condition, metabolic or environmental. The vertebrate reproductive system also probably arose independently since it is not indicated in the protochordates.

THE EXCRETORY SYSTEM

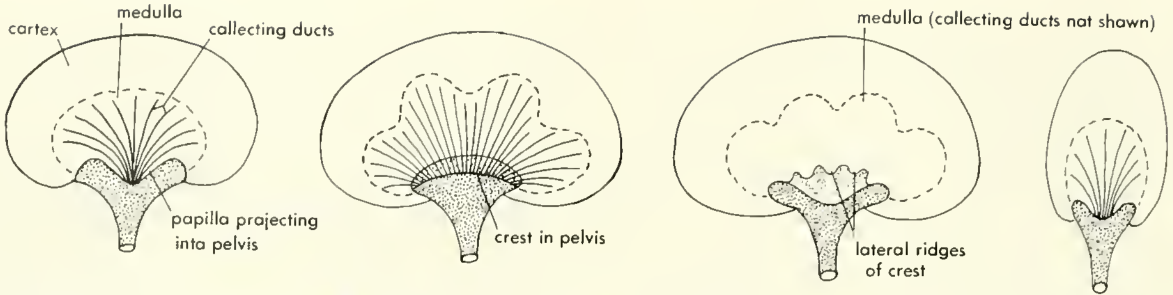
The function of the excretory system is to separate excess or waste materials from the blood. It consists of the kidney, the tubes draining this structure, and an exit from the body. Frequently there are storage structures associated with this system. Since the process of excretion is generally defined as removal of metabolic wastes from the body, this term would also include the removal of carbon dioxide by way of the respiratory system. The excretory system also is involved in water and salt balance, which are only in part related to metabolism; therefore, it seems best to use the rather indefinite statement "removal of excess or waste materials" in describing its function.

Mammals

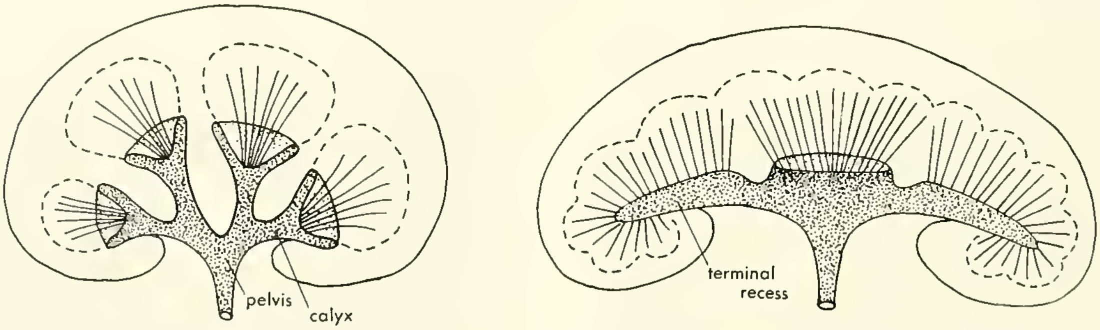
The kidneys in the mammal (or man) are fairly large structures lying **retroperitoneally** against the dorsal wall of the body cavity, to either side of the midline (Figure 10-3). Conspicuous **renal arteries** and veins enter the medial concavity (**hilus**) of the kidney. From the hilus exits the **ureter.** If the kidney is sectioned frontally, much of its interior structure can be observed (Figure 10-1). In its simplest form, as in the monotremes, small marsupials, edentates, bats, some rodents, insectivores, and some carnivores (cat), the ureter opens into a simple cavity or **pelvis,** into which projects a **papilla.** This is the **unilobular** (or **unipyramidal**) type of kidney. From the tip of the papilla numerous dark lines indicate the collecting tubules and collectively these form a pyramid. Capping the pyramid is cortical tissue in which dark granules, the knots of arterial capillaries called **glomeruli,** can be observed. The major blood vessels, which enter at the hilus, branch to either side between the outer **cortical material** and the inner **medullary** (tubular) **substance.**

In a more complex type of kidney, the tubules of a pyramid open along a **crest** or ridge instead of on a papilla. This crest projects into the cavity of the pelvis. Such a type occurs in the dog or sheep, as well as in many carnivores and cloven-hoofed mammals, the artiodactyls. The next step in increasing complexity of structure involves subdivision of the pelvis into a number of outpocketings, the **major** and **minor calyces.** Into each of these subdivisions a papilla projects. Each papilla has a pyramid with its cap of cortical tissue, and the whole forms a **lobule.** This type of kidney is described as **polylobular** and **compact.** The several lobules are enclosed and separated by connective tissue, the **columns of Bertin.** A compact polylobular kidney is observed in the pig, kangaroos, some carnivores, and some primates (man).

The variations of kidney structure are interesting when viewed in taxonomic terms. For example, among small carnivores, the weasel has a papilla, while the marten has a ridge projecting into the pelvis. The lion, cat, and lynx have a single papilla, while the tiger has a ridge. A specimen of **Hyrax** was observed in which there was a single papilla in

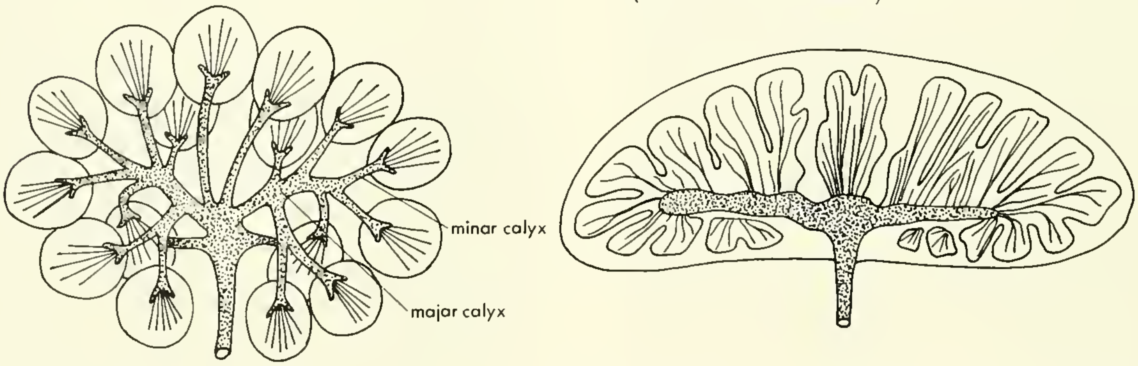


A UNILOBULAR WITH PAPILLA **B** UNILOBULAR WITH CREST **C** UNILOBULAR-PAPILLA WITH LATERAL RIDGES **D** CREST IN CROSS SECTION



E POLYLOBULAR COMPACT

F CENTRAL CREST WITH TERMINAL RECESSES (WEAKLY POLYLOBULAR)



G POLYLOBULAR LOOSE

H POLYLOBULAR WITH REDUCED PELVIS AND EXPANDED TERMINAL RECESSES

Figure 10-1. Variations in the internal structure and form of the mammalian kidney. (Mainly after Gerhardt, 1914)

one kidney and a crest in the other. Among primates, the chimpanzee has a papilla; the orang and gorilla have a crest, while man has a number of papillae opening into calyces of the pelvis.

Next in order of increasing complexity, the outer surface of the kidney reveals the individual lobules as in the cow, or the lobules may be even more distinct as in the seal. In the whale, *Physeter,* the lobules are quite separate within the capsule. Each lobule is a **renculus** ("little kidney") with the calyces appearing as tubules leading to the ureter (Figure 10-1 G). Another modification is observed in the kidney of the horse, which is indistinctly polylobular and compact with a crest extending into the pelvis. The pelvis, however, has tubular extensions, each called a **recessus terminalis,** reaching into the anterior and posterior parts of the elongated kidney. These extensions receive the collecting tubules of the indistinct lobules of the ends of this kidney. A similar type is seen in the Dugong (Sirenians), but here the lobuli are distinct and separated by columns of Bertin. The central pelvis is much reduced and inconspicuous, and the recessi are large spaces.

The ureter extends from the pelvis of the kidney to the bladder, which it enters. The bladder stores urine, which passes from here to the outside through the **urethra.**

Embryological development The development of the mammalian kidney can be described as a progressive event beginning with some small tubules at the anterior end of the body cavity and extending from here in a posterior direction. The stages as generally described are: the "first kidney" or **pronephros,** then a "middle kidney" or **mesonephros,** and finally the "last kidney," the **metanephros.** The pronephros and mesonephros undergo degeneration in turn, leaving only the metanephros.

The pronephros appears very early (2.5-mm embryo). Its first evidence is a series of thickenings of the lateral plate mesoderm in the sixth to twelfth metotic or **postotic** (behind the otic capsule) segments of the body (Figure 10-2). These structures appear lateral to the myotomes as knots of cells extending outward from the intermediate plate and lying just under the epidermis. These rudiments connect together to form a strand separated from the coelomic cavity by the somatic mesoderm. As the coelom extends medially, into the intermediate plate, the cord of cells is separated from the somatic mesoderm and contacts it only at segmental intervals. The solid rudiments now begin to hollow out and form **funnels** opening into the coelom at points of contact with the somatic mesoderm (Figure 10-3). The anterior rudiments begin to degenerate as the more posterior ones reach full development. The latter appear to be displaced backward as they form, so that a large number of them will lie within three or four somites (8 in a Echidna associated with spinal ganglia 4 to 6; 14 to 16 in the marsupial *Trichosurus* associated with spinal ganglia 6 to 8). The elements of somites 9 to 12, from the 5th cervical posteriorly, produce rudiments from which a **nephric duct** develops and grows posteriorly (Figure 10-3). The nephric duct is variously referred to as the pronephric duct, mesonephric duct, and wolffian duct. The nephric duct extends posteriorly by multiplication of the cells of its tip, not by segmental contributions. It reaches the cloacal area in the 4.3-mm embryo. The mesonephros extends from the 8th cervical to the sacral region in the 5.4-mm embryo.

not so, acc. to J. Overta

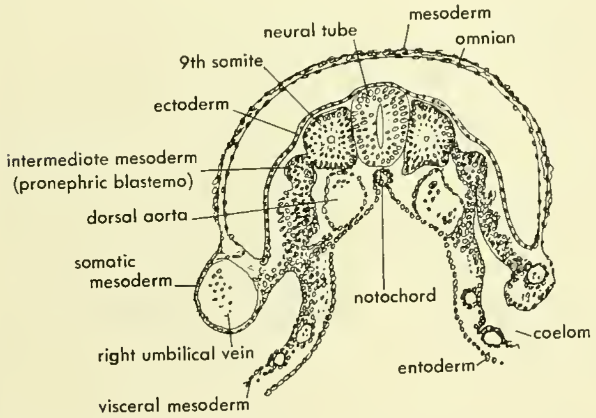


Figure 10-2. Cross section of a 10-somite stage human showing the relationship of the pronephric blastema to the rest of the mesoderm. (After Torrey, 1954)

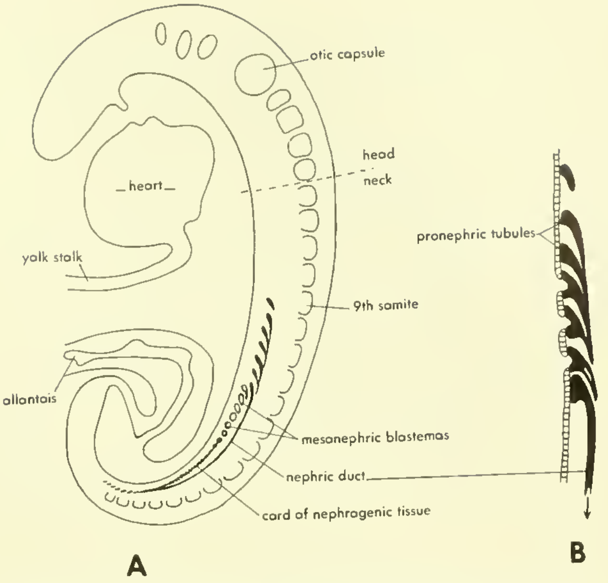


Figure 10-3. The pronephric and early mesonephric rudiments of the human. A, general appearance and relationships of kidney rudiments in a 2.5-mm embryo; B, pronephric area enlarged. (B after Ihle et al. 1927)

The tubules of the mesonephros arise from clumps of cells formed in the nephrogenic cord lying along the nephric duct (Figure 10-4). The nephrogenic cord of cells arises from the intermediate plate mesoderm in much the same way as the pronephric end of the nephric duct (Figure 10-3). It derives its name from the fact that it "gives rise" to tubules. A few tubules of the mesonephros develop anterior to the 14th somite, thus perhaps overlapping the posterior part of the pronephros. About 30 to 40 tubular units in all develop, two or three per segment. These are not symmetrically placed. In marsupials and monotremes, this kidney becomes functional. The mesonephros of the human is histologically in between the functional type of the hoofed mammals and the nonfunctional type of the rat, mouse, or dog which never develop glomeruli. Many of the mesonephric tubules of the human develop **peritoneal funnels,** which are rudimentary or lacking in the mouse or dog.

The posterior end of the mesonephros is fully developed at about 15 mm (head-rump length of embryo). Meanwhile, the anterior part has started to degenerate. Regression then begins posteriorly, as well as continuing from the anterior end, until only a small middle region persists. This is connected with the male reproductive system and is modified into the **epididymis** or retained as a nonfunctional vestige, the **epoöphoron,** in the female.

The metanephros of man begins to develop at about the 5.4-mm stage, as a small diverticulum from the posterior

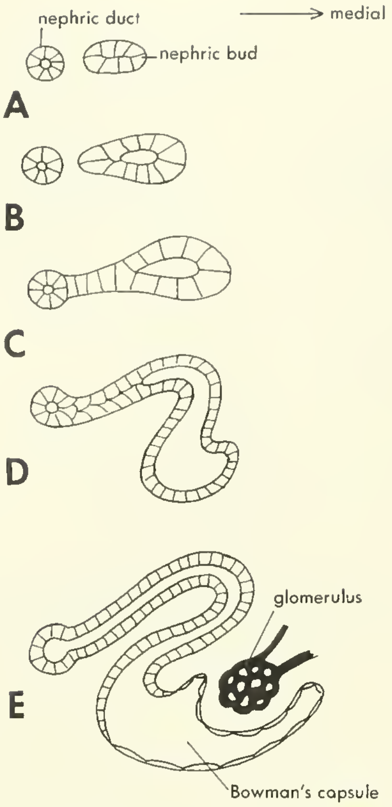


Figure 10-4. Five stages, (A to E), in the development of a mesonephric tubule. (After Ihle et al, 1927)

end of the nephric duct (Figure 10-5). This outpocketing enters the nephrogenic cord; it forms the ureter and from it grow the calyces and several generations of collecting tubes. The nephrons develop from the nephrogenic cord in a sequential fashion as new generations of collecting tubes are produced (Figures 10-6, 10-7). Although the first few generations of nephrons are resorbed, at least 12 generations are present at the time of birth. This means more than one million nephrons are present in each kidney. In the later stages of development, the kidneys move forward, or upward in the case of man, beneath the peritoneum until they near the diaphragm. The kidneys of monotremes remain in the posterior part of the body cavity.

The ducts of the kidney, the ureter, and the nephric duct switch positions during development, so that the ureters enter the bladder, while the nephric duct, which is now the male **vas deferens** (degenerate in the female), enters the urethra. The latter extends from the bladder to the outside. The bladder is formed from the **allantois.**

At this point a few definitions appear to be in order, based on structure. The pronephros is composed of tubules formed segmentally at the anterior end of the body cavity. These may open into the coelomic cavity by way of funnels. The tubules unite distally to form a part of, or give rise to, the entire nephric duct. The mesonephros can be defined as having tubules formed from buds of nephrogenic tissue lying medial to the nephric duct. These tubules later establish entrance into the nephric duct. There may be several of these tubules per segment; the two sides of the animal are asymmetric. Peritoneal funnels may develop in relation to these tubules. The metanephros is made up of a system of collecting tubules which grow out from a single evagination from the posterior end of the nephric duct. Blastematic buds of nephrogenic tissue form tubules which enter these collecting ducts and thus form the functional metanephric kidney. No peritoneal funnels develop in relation to metanephric tubules.

In the mammal the pronephros is never functional. The mesonephros is functional in the monotremes, marsupials, and many placentals until the metanephros comes into action. The mesonephros of some mammals is never functional, for

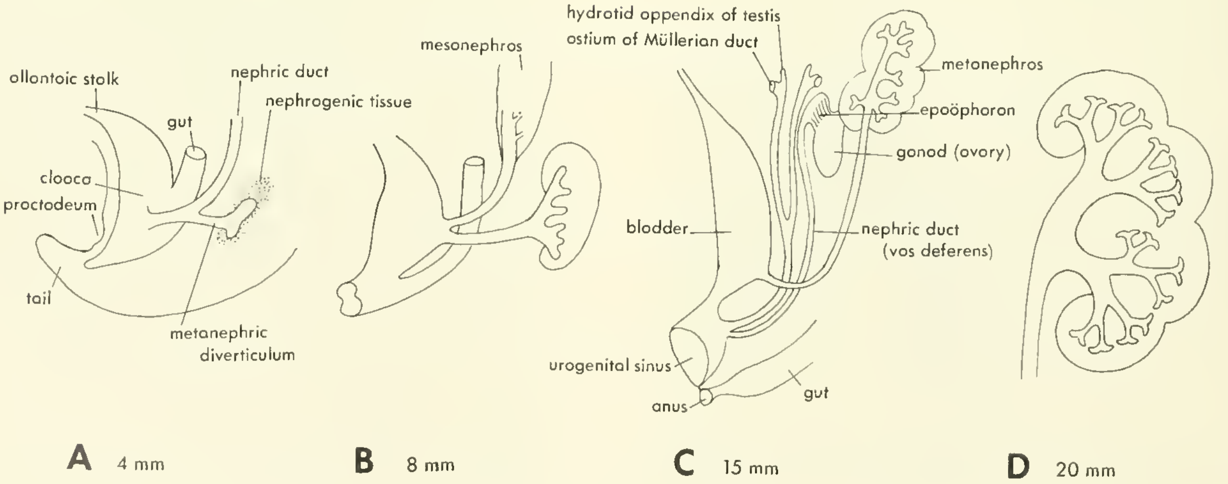


Figure 10-5. Four stages in the development of the human metanephros. (After Patten, 1946)

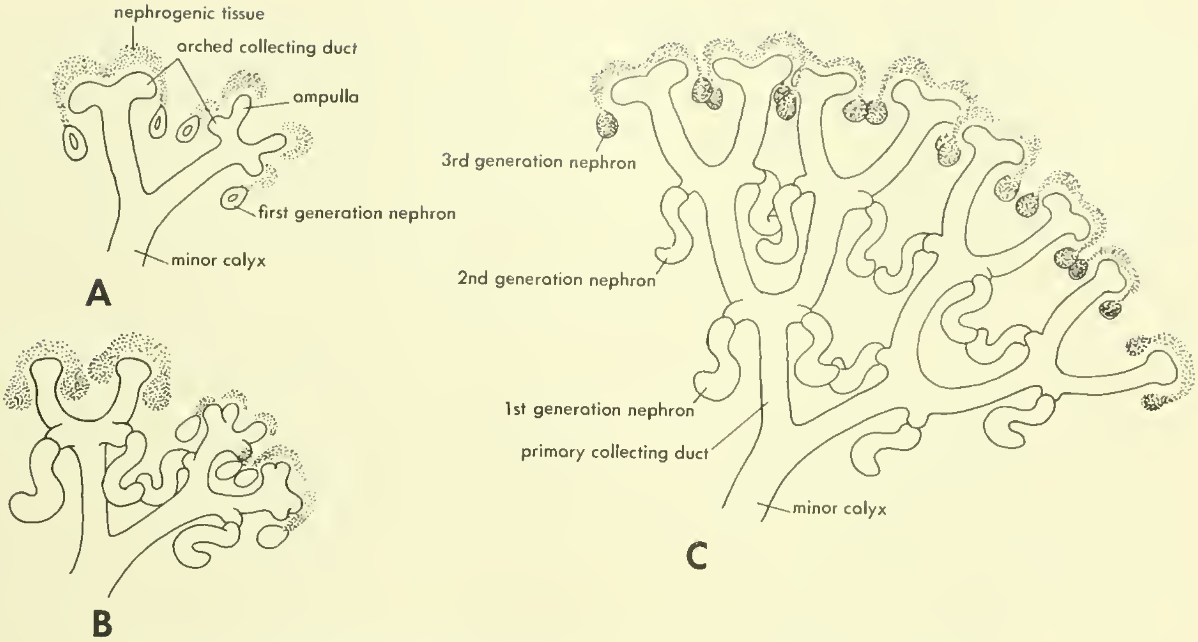


Figure 10-6. Three diagrammatic stages in the development of successive generations of tubules in the mammalian metanephros. (After Patten, 1946)

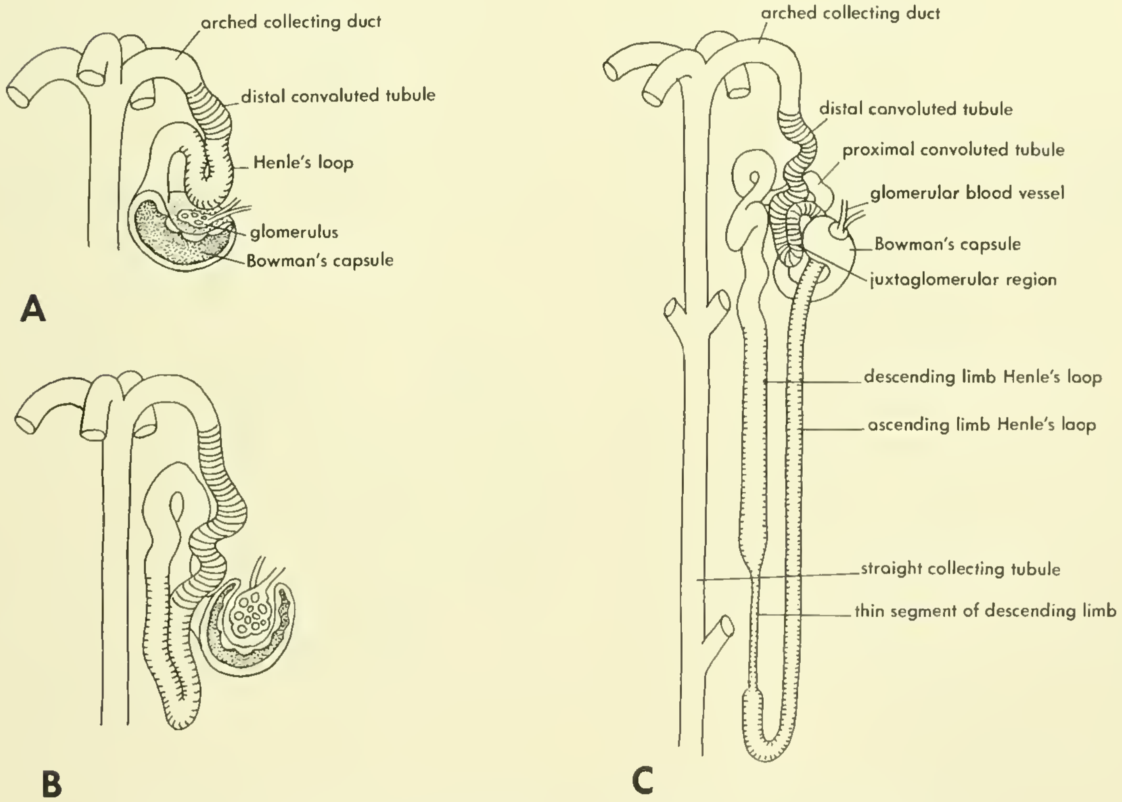


Figure 10-7. Three stages in the differentiation of a single metanephric tubule. (After Patten, 1946)

the placenta makes such function unnecessary. Degeneration of the mesonephros sees part of its structure modified into sexual ducts: epididymis and vas deferens in the male, the **epoöphoron** and **Gartner's duct** in the female (Figure 10-35).

Reptiles and birds

The adult **kidney** of the turtle, Sphenodon, or lizard is a **metanephros** of relatively small size, lying well back in the body cavity (Figure 10-8). The shape of the kidney reflects somewhat the body shape; long and thin in snakes, short and thick in turtles. In some lizards fusions occur at the midline in the posterior region of the kidneys. The surface of the kidney may be strongly lobate, ridged, or folded with wrinkles. The kidney is drained by a **ureter** which may extend along the entire structure and continue posteriorly to its entrance into the **cloaca,** as in the snake, or it may be very short, arising at the middle of the kidney and extending posteromedially to the cloaca, as in some lizards. The

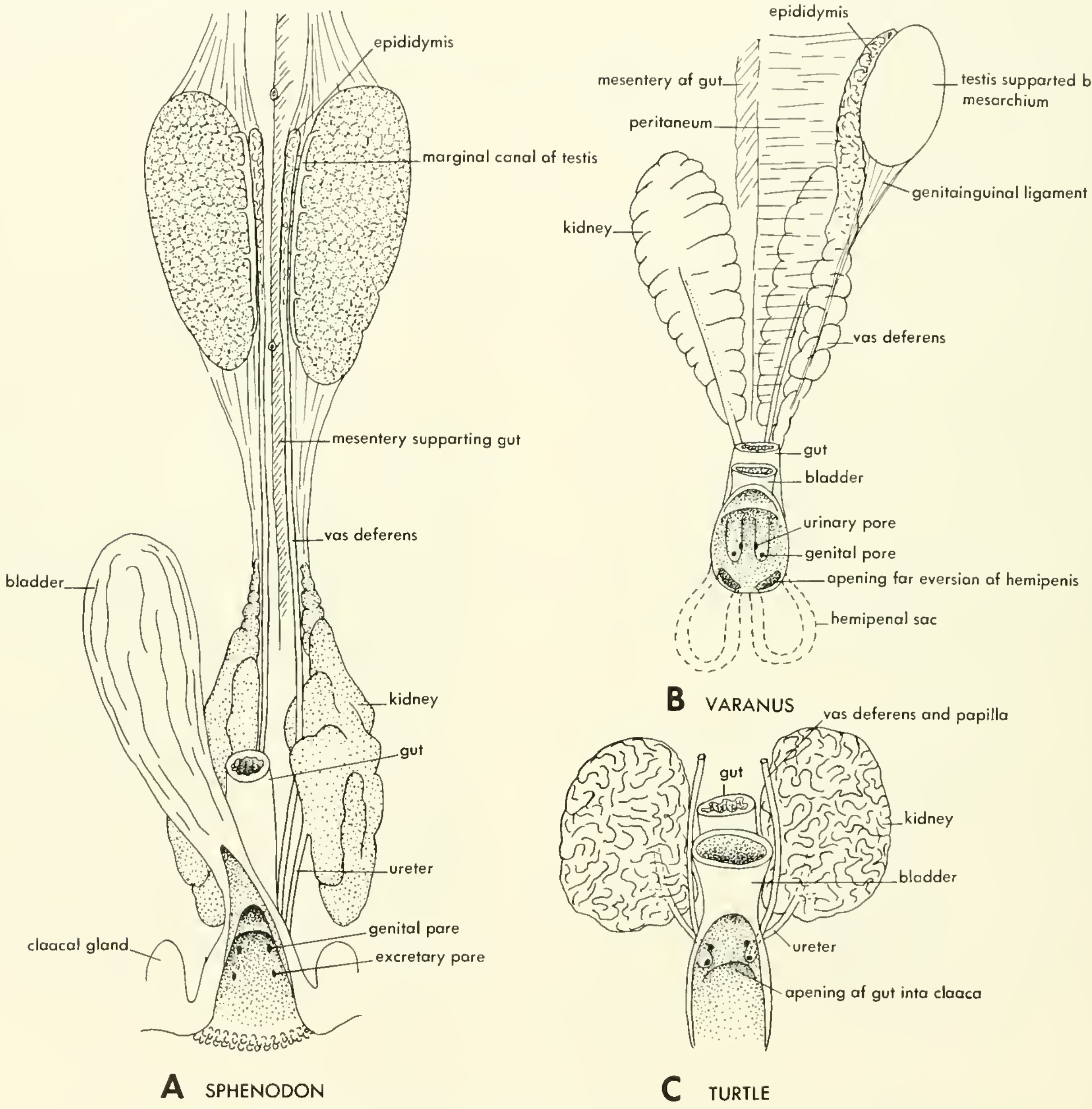


Figure 10-8. Urogenital systems of reptiles. A, ventral view of Sphenodon; B, of *Varanus*; C, of a turtle (*Testudo*). (After van den Broek 1933, 1938)

ureter may join the vas deferens before entering the cloaca or the two may open separately. In the turtle the **urogenital sinus** lies below the **rectum.** In the lizard, Sphenodon, and snake the **bladder** has remained in its ventral position, but the ureters and sex ducts open dorsally into the cloaca. The alligator and bird are like the lizard but have no bladder (Figures 10-9, 10-10).

The fine structure of the reptilian kidney (or bird) differs from that of the mammal in lacking the pyramids of collecting tubules, and in having the kidney divided into a very large number of small units. These units are related to the blood in quite a different way than the pyramids. Both venous and arterial blood enter the kidney. The arterial blood serves the **zone of glomeruli** at the center of, or along one side of, the unit. The arteries are paralleled by **efferent veins** draining the units. At the periphery of the unit, or along the side opposite the artery, is the **afferent renal vessel** bringing venous blood into the unit. The **collecting tubules** of the unit parallel the afferent veins (see Figure 10-12).

Embryological development: reptile The first rudiments develop in myotomic segments 3 to 10 or 12. The **funnels** or cords of cells appear first in segments 3 and 4 and later in the more posterior segments. The most anterior rudiments disappear, leaving those in somites 5 to about 10 or 12 (10 to 11 in the turtle *Chrysemys*). The anterior two or three of these open into the coelom through ciliated funnels. The more posterior cords separate from the somatopleure and contribute to the nephric duct cord which extends back from the anterior funnels. The tubular duct like the funnels is produced by hollowing out of the cell cords. The posterior end of the nephric duct now grows posteriorly, without segmental contribution, to enter the cloaca. In the turtle (*Chelonia*) and the alligator, a midline coelomic glomerulus develops. A number of nephrocoels fuse and enclose this **glomus** (or glomerulus). The pronephros begins to degenerate early (6-7 mm).

The mesonephros arises in somites 12 to 31, plus or minus a few, according to the species. Each primary canal appears first as a clump of cells which hollows out; then it develops a renal corpuscle and gains entrance into the nephric duct. The number of tubules anteriorly is fewer than posteriorly and their interrelationships are simpler. The tubules are not segmentally arranged; there are several per segment. The anterior part becomes connected with the testis by tubule outgrowth from the **Bowman's capsules** of the **Nephrons** or kidney tubules (Figure 10-7) and from the testis.

The metanephros appears first as an evagination of the extreme posterior end of the nephric duct. This evagination grows outward capped by nephrogenic tissue; it branches forward and posteriorly to form the ureter and primary collecting branches. By further subdivision and branching of these, as in the mammal, the metanephric kidney is formed, utilizing the nephrogenic tissues associated with somites 32 and 33. The number of nephrons formed in reptiles is far less than in mammals, 1500 to 2000 per kidney as opposed to about a million. The earlier generations of nephrons are retained, so even the larger collecting tubules have nephrons entering them. With the establishment of the metanephros, the anterior part of the mesonephros degenerates down to the epididymis of the male or the vestige observed in the female.

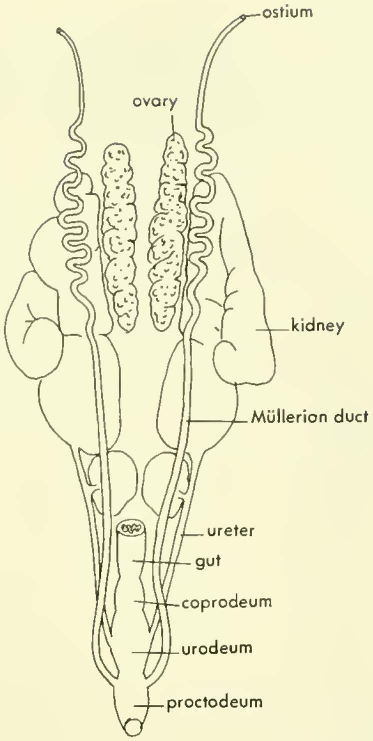


Figure 10-9. Ventral view of the urogenital system of a young female alligator. (After Reese, 1915)

The urinary bladder when present is formed as in the mammal, from the allantoic outgrowth of the hindgut.

Embryological development: bird The embryological development of the bird is much better known than that of the reptile and can be studied using standard embryological preparations, the 48, 72, and 96-hour chick serial sections. The pronephric elements first appear between 40 to 48 hours of incubation. The most anterior one is in the third postotic somite, and the units extend posteriorly for about 12 segments. Of these, the more anterior ones soon degenerate.

In many vertebrates the pronephric tubules lie anterior to the ducts of Cuvier, usually in an anterior cardinal sinus. In the 48-hour chick, the most anterior tubules lie behind the level of the ducts of Cuvier (7th to 8th somite), the large venous channels draining the dorsal body-wall vessels (the cardinals) into the heart (Figure 11-28). The anterior tu-

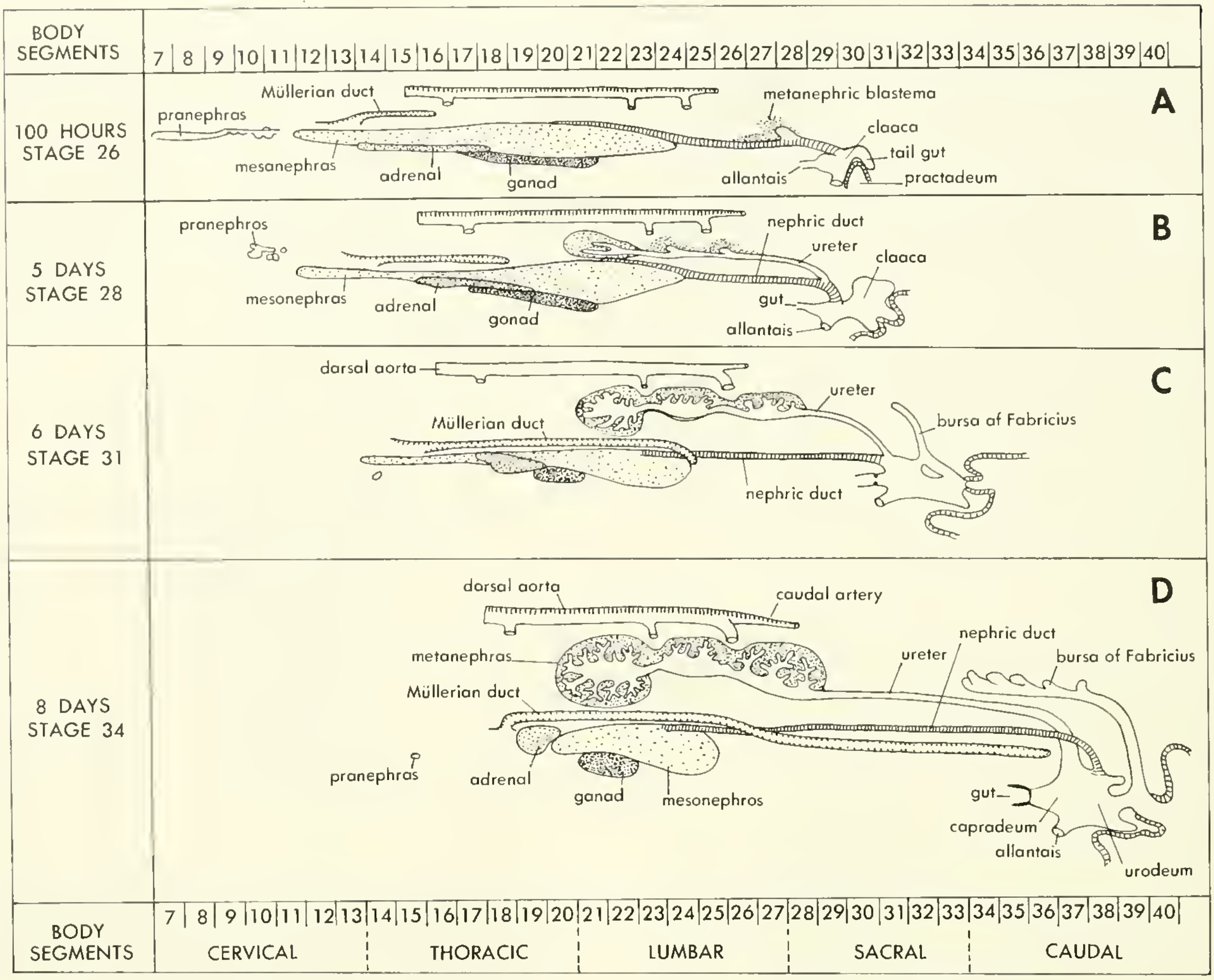


Figure 10-10. Developmental stages of the urogenital system of the chick in terms of somite position and age. (After Witschi, 1956)

bules are little more than cords of cells extending from a slight funnel to a small vesicle. At first the vesicle of one segment does not attach to that of the next. From about the fourth or fifth vesicle back they join as the nephric duct which lies just below the posterior cardinal vein. The pronephros has about 10 tubules at this stage and extends posteriorly to about the 15th somite. The most posterior tubules are S-shaped like those of the mesonephros.

At the posterior end of what appears to be the pronephros (funnels indicated for each tubule), the posterior cardinal is inconspicuous and the nephric duct moves outward and upward to lie above the mesonephric blastema. Here the nephric duct expands and knots of nephrogenic cells appear ventromedial to it, just behind the level of the vitelline artery. Some tubules are developed and enter the nephric duct. The nephric duct extends back to the last conspicuous (27th to 28th) somite. Glomeruli are not apparent at this stage, although at the anterior end of the pronephros a few swellings into the body cavity, adjacent to the aorta, are observed.

In the 72-hour chick the pronephric elements are still present; two or three asymmetric funnel remnants and vesicles lie to either side, above the coelomic cavity in the region of the lung buds. The nephric duct begins a few somites back from the first vesicle. Funnel remnants are apparent at intervals. At the posterior end of the pronephric region, two or three complete S-shaped tubules are present with open funnels. Behind these, several tubules have detached (separate) funnels. Distinct glomeruli are lacking but bulges for them lie medial to the peritoneal funnels.

In the 96-hour chick small glomeruli project into the cavity above the lung buds (somites 9 to 10), but the pronephric rudiments are inconspicuous. The pronephros now consists of bits of tubules lying in the 6th to about the 15th somites, and some vestigial glomeruli in the 12th to 16th somites. The nephric duct lies below the anterior cardinal from the fourth pair of glomeruli back. The first pair of glomeruli is associated with small tubules. The glomeruli increase in size until the third or fourth pair, when internal glomeruli begin to be present; from here back the external glomeruli dwindle, over a distance of one or two segments, and the internal ones increase in size and number.

The pronephric elements intergrade with those of the mesonephric area (Figure 10-10). Each mesonephric tubule has an internal glomerulus but no peritoneal funnel. From the 16th to the 22nd somite there are about 12 primary asymmetric tubules. With the appearance of new tubules each segment comes to have 2 to 5, usually 4, units in it. These lie in a lateral to dorsal-medial progression and each unit opens separately into the nephric duct. The nephric duct evaginates to meet the later tubules and these outgrowths become collect ducts.

In the metamorphosing bird, the fourth or fifth day or later, depending on the species, the pronephros is nearly regressed. The mesonephros is a distinct body stretching from about the 12th to the 24th somite; its nephric duct enters the cloaca in the sacral region at about the 29th or 30th somite. Degeneration of the anterior end of the mesonephros continues, while the more complex posterior part completes development of all its units and becomes functional (there is evidence of nitrogen excretion on the fifth day of development).

The metanephros appears at the time of metamorphosis as an evagination from the nephric duct at the level of the 29th somite. This evagination enters the nephric blastema and grows rapidly forward, dorsolateral to the nephric duct. This evagination induces tubule formation in the cap of nephrogenic tissue lying dorsal to the posterior cardinal. Three distinct lobes form, and in these the collecting tubules extend outward from the metanephric duct (ureter). The organ now extends from the 20th somite to the 28th. The ureter opens separately, in front of the opening of the nephric duct into the cloaca, at the 37th or 38th somite.

The mesonephros continues to function till the time of hatching, when the metanephros is well differentiated. The anterior part has degenerated back to about the 20th segment. At hatching, only the tubes involved with the testis are retained, and their glomeruli are lost. This area of tubules is transformed into the epididymis.

The **Müllerian duct,** the female sexual duct, appears on the lateral aspect of the anterior end of the mesonephros next to the nephric duct. It appears first as a thickening of the epidermis, then as a groove which closes over to form a tubule with an anterior **ostial opening** (**ostium**). The tubule extends posteriorly until it reaches the cloaca. The development of this tubule in a bird or in the reptile is the same as in the mammal.

Amphibians

Salamander In *Necturus* or *Cryptobranchus* the **opisthonephric kidney** is long and thin. An opisthonephros is a kidney which is assumed to incorporate both mesonephric and metanephric materials. It can also be defined as an adult kidney—not a developmental stage—which is primarily, if not entirely, of mesonephric origin. The anterior half is partly modified in the male into an **epididymis** which connects with the elongate **testis** (Figure 10-11). The nephric

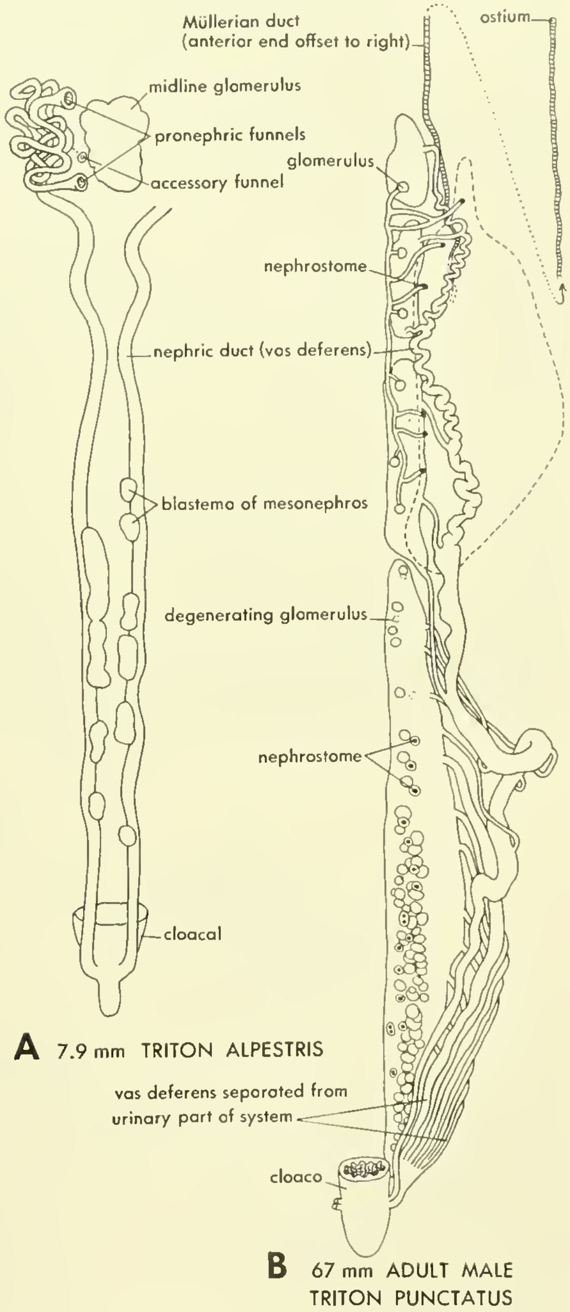


Figure 10-11. Two stages in the development of the kidney of the salamander *Triton*. A, 7.9-mm larva; B, 67-mm (adult) male. (After Kindahl, 1938)

duct of the male extends anteriorly a short way as well as posteriorly from the epididymis. It is very swollen and convoluted in the region of the epididymis.

Posteriorly the nephric duct drains the enlarged and excretory part of the opisthonephros. There are no separate posterior **ureters** in *Necturus*, but in *Cryptobranchus* a series of these is developed in both males and females. These drain the posterior, excretory part of the kidney directly into the **cloaca.** The nephric duct is thus separated as a **vas deferens.** The opisthonephros of the salamander is peculiar in that **peritoneal funnels** are present in the adult. In the males these regress in the anterior epididymal part of the kidney at the time of reproduction. The kidneys of frog and salamander receive both venous and arterial blood; in this respect they resemble the reptile (Figure 10-12).

EMBRYOLOGICAL DEVELOPMENT Pronephric development begins with the appearance of cell masses (**pronephric crests**) bulging from the anterior **nephrotomes** (intermediate plate of mesoderm). Segmental **nephrocoels** form in these segments and connect with the **coelom** (Figure 10-15). These segmental cavities soon become lost in the coelom. Funnels form in postotic segments 4 and 5 (spinal segments 1 and 2). The number of pronephric funnels shows some variation; there are four in *Cryptobranchus* and the apodan *Hypogeophis* has even more. These funnels open into a pronephric duct formed by the confluence and hollowing out of the segmental pronephric crests. This duct is continued posteriorly by similar segmental nephrotomic contributions until it reaches the cloaca.

The pronephric tubules become quite elongated and looped as does the pronephric duct. These tubes come to lie in the sinus of the anterior cardinal vein. The two ciliated pronephric funnels of the typical salamander (Figure 10-13) become associated with a large medial glomerulus projecting on either side of the median septum into the coelom.

The opisthonephros develops from the segments behind the pronephros but is separated from the pronephric area by a gap. This is explained by the fact that the more posterior pronephric segments do not produce funnels. Furthermore, the most anterior segments of the mesonephros are only slightly developed and tend to degenerate early.

The sequence of tubule formation is from anterior to posterior, but the most anterior elements are somewhat retarded and tend to abort early. The tubules arise from small masses of blastema which hollow out to form S-shaped tubules, each with a Bowman's capsule medially and an attachment to the nephric duct laterally. These tubules develop a ciliated peritoneal funnel as an outgrowth from the rudimentary capsule.

The anterior end of the mesonephros never becomes excretory. Its tubules develop secondary and tertiary side branches which end blindly and the renal corpuscles of some tubules abort when connection with the testis is achieved. The efferent ducts of the apodan, however, retain the glomeruli. Some of the mesonephric tubules lie anterior to the efferent ducts and these degenerate in later stages.

In the posterior part of the kidney the primary tubules are not segmentally arranged and are quite erratic in number and position. These tubules are followed by secondary, tertiary, and higher orders which use the primary ones as collecting ducts. The connections of these primary tubules tend to be displaced posteriorly in some salamanders and thus give rise to the ureters which may open into the neph-

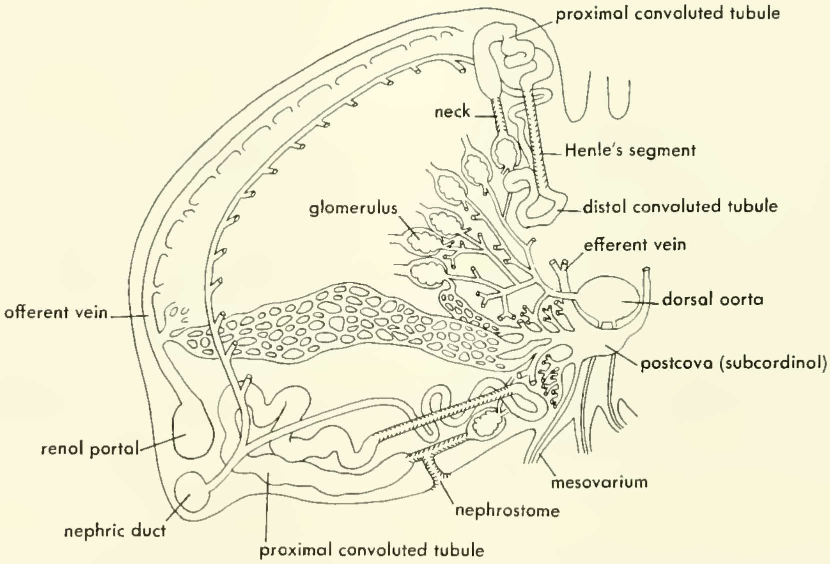


Figure 10-12. Cross section of kidney of *Necturus maculosus* showing relationships of the tubules to the blood supply. (After Chase, 1923)

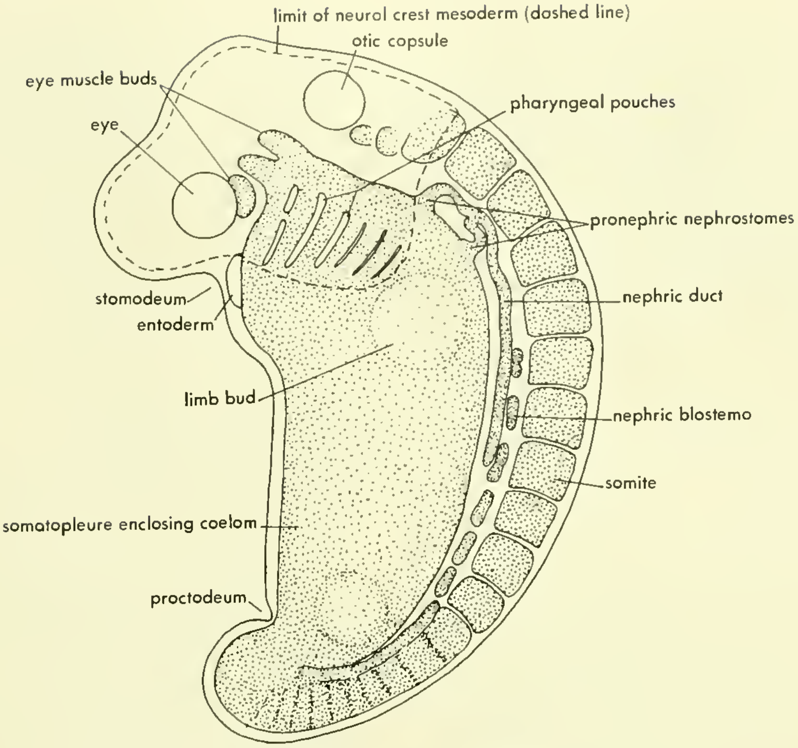


Figure 10-13. Mesodermal components in a larval salamander. (After Witschi, 1956)

ric duct, open separately into the cloaca, or join together as a single ureter to enter the cloaca. The development of this posterior part of the opisthonephros in no way suggests the metanephros. The pronephros degenerates with the development of the posterior part of the opisthonephros.

In the posterior part of the kidney of the apodan amphibian, the primary tubules connect with outgrowths from the nephric duct. These outgrowths resemble in their origin the single diverticulum of the metanephric system of the amniote. As a note here it should be pointed out that Brauer's (1902) work with the apodan *Hypogeophis* is a classic study of the development of an amphibian kidney, and from this a pattern for the differentiation of the mesoderm has been derived (Figure 10-14). This pattern suggests that the funnels of the pronephric tubules are not homologous to the peritoneal funnels of the mesonephric tubules and that the nephrocoel in the more advanced tubules has been reduced to the Bowman's capsule.

The Müllerian duct first appears as a thickening of the epithelium lateral to the nephric duct; this thickening forms a groove which closes over and gradually extends posteriorly, in both sexes, to open into the cloaca in the adult stage.

Frog The opisthonephros of the frog is a compact elongate ovate body. It is drained by the nephric duct lying along its outer margin. This duct also serves the testis of the male as a vas deferens. Relationships with the testis are variable among anurans (Figure 10-15). In a few species a ureter is developed. Peculiar to the anuran is the **ampulla** of the nephric duct, a swollen glandular section just before the tube enters the cloaca. Peritoneal funnels are present in the adult but are unique in that they open into the venous sinuses (Figure 10-17).

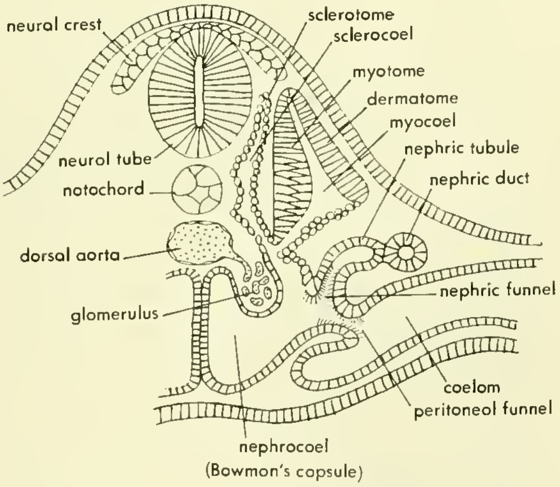


Figure 10-14. Mesodermal components as suggested in the development of *Hypogeophis*, an apodan amphibian. (After van den Broek, 1938)

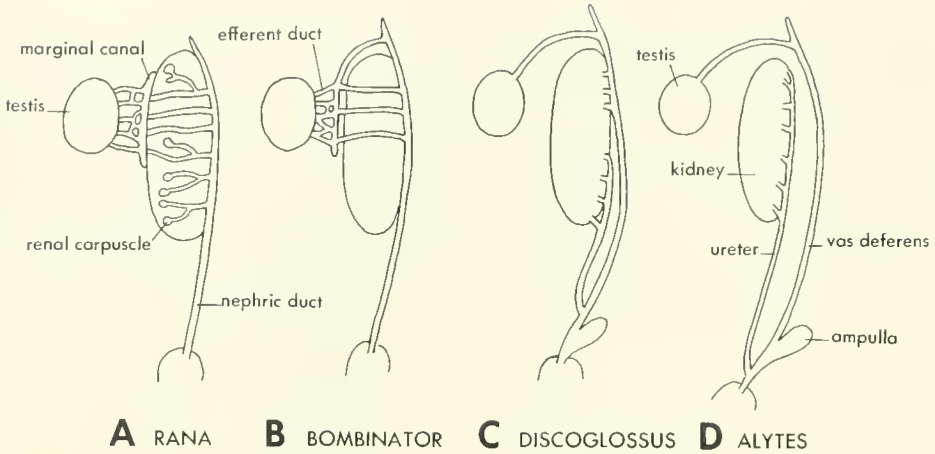


Figure 10-15. Connections between the testis and the nephric duct in amphibians. (After van den Broek)

EMBRYOLOGICAL DEVELOPMENT In the frog there are three pronephric funnels; the first is at the level of the second myotome and the third visceral arch (Figure 10-16). These funnels develop from the somatic layer of the intermediate plate in the usual fashion. The nephric duct is continued posteriorly by segmental crest contributions until it reaches and opens into the cloaca. The anterior nephrocoels fuse and open widely into the coelom. In this process the most anterior funnel is moved back into the next segment.

These funnels are associated with a large medial glomerulus which can be observed in the 10-mm frog. The convoluted tubules of the pronephros lie in the anterior cardinal (venous) sinus. At the 10-mm stage there are no mesonephric elements, but the blastemas of these can be observed dorsomedial to the nephric duct. The nephric duct has already extended posteriorly to the cloaca. As development progresses, the pronephric funnels may fuse into a single unit.

The "mesonephros" arises from about the 6th myotomic segment back to the 11th; it is doubtful that any metanephric materials are involved. The tubes of segments 9 and 10 are very advanced as compared with those in front or behind. The number of units increases anteriorly and posteriorly up to about a dozen, but these have no segmental correlation.

The most anterior tubule or two loses its **renal corpuscles** (glomerulus and Bowman's capsule), becomes connected with the testis, and carries only sperm (Figure 10-13). The next three or four primary tubules lose their corpuscles and conduct sperm, but their secondary tubules are excretory. More posteriorly the primary tubules degenerate to collecting ducts serving many **nephrons** (excretory tubules). More posteriorly these collecting ducts become complexly convoluted. In the most posterior part of the kidney some of the orders of nephrons open into the nephric duct and cross connections develop between the collecting ducts. New generations of nephrons continue to appear until full growth is achieved, a matter of several years in some species.

Peritoneal funnels develop in relation to the tubules of the mesonephros, but they either lose connection with these tubules or develop completely separate from them. These peritoneal funnels, and second or higher funnels, open into the venous sinuses of the kidney (Figure 10-17). The beat of their cilia is toward the sinus; therefore we can assume materials (coelomic fluid) pass into the sinus.

The connection between testis and kidney develops by outgrowth from the capsules of the primary tubules. These outgrowing tubules unite distally to form a **marginal canal.** Outgrowths from the **central canal** or network of the testis, the **efferent ducts,** grow through the mesentery to reach the marginal canal (Bidder's canal). The connection reflects the common origin of the mesonephric blastema and the medullary part of the gonad. At first, kidney and gonad are broadly connected; later this is reduced to strands of tissue which form the efferent ducts.

In some anurans the anterior sexual part of the kidney is reduced or lacking, and the testis is connected directly to the nephric duct anterior to the definitive kidney. This relationship is understandable in terms of the observation that the anterior end of the indifferent gonad of the anuran is modified into the fat body (Figure 10-40). The extension connects by an efferent duct with an anterior tubule which becomes isolated by degeneration of the enclosing kidney and vascular tissues.

Some male anurans develop a **ureter** by anastomosis of the collecting tubules and extension of this common collecting duct nearly to the cloaca by gradual separation from the nephric duct.

It has been suggested that the ampulla of the nephric duct, which contains many tubules, represents a modification of the most posterior part of the nephric tissue. An alternate view is that it represents only a glandular development of the terminal part of the duct. The suggestion that not all of the nephric material is utilized in the opisthonephros finds some support in the reduced number of segments seemingly

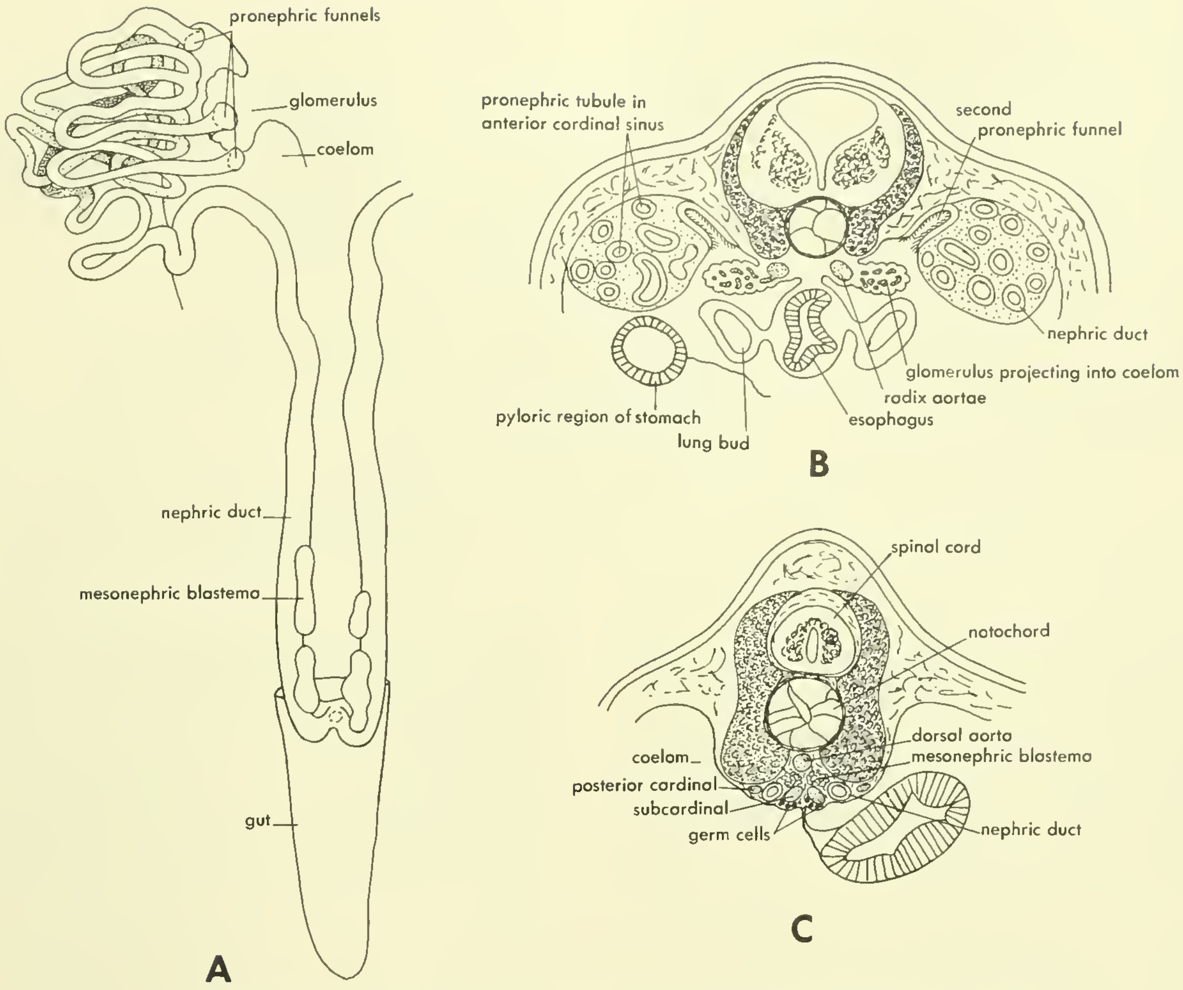


Figure 10-16. Pronephric system of the larval frog. A, ventral view of entire system in a 12-mm larva; B, cross section of a 10-mm larva at the vertical of the second pronephric funnel; C, cross section of 10-mm larva showing mesonephric blastema and germ cells. (A after Kindahl, 1938)

involved in the kidney, as suggested by the number of primary tubules, and the fact that development continues for such a long period. These facts also support the view that this is a much modified kidney as is attested to by the nature of its peritoneal funnels.

The pronephros degenerates with the establishment of the excretory functioning of the mesonephros. The opisthonephros, or adult kidney, appears to be entirely of mesonephric origin. The Müllerian ducts arise as in the salamander.

Choanate fishes

Actinistian The soft anatomy of the crossopterygian is known only for *Latimeria*. Here the kidney is a short, thick, medial mass lying in the postcloacal part of the abdominal cavity, not against the roof, but rather on the floor. Laterally, the margins of this mass extend up along the walls of the body cavity. From it come paired ureters which are dilated dorsally as the urinary bladders. These ducts open into a urogenital sinus which opens at the tip of a papilla in the cloaca.

The kidney of this fish, by its position and the fact that it is not associated with the testis, is comparable to the posterior part of the opisthonephros of the amphibian. Histologically, it lacks the extensive lymphoid (blood-filtering) and hemopoietic (blood-cell producing) tissue of the other fishes and has many clumps of large glomeruli from which long looped tubules extend.

Dipnoan The kidney of the dipnoan is an opisthonephros. The band-like organs of either side are fused posteriorly (Figure 10-41). Many vasa efferentia from the testis enter throughout the length of the definitive kidney of *Neoceratodus*—which

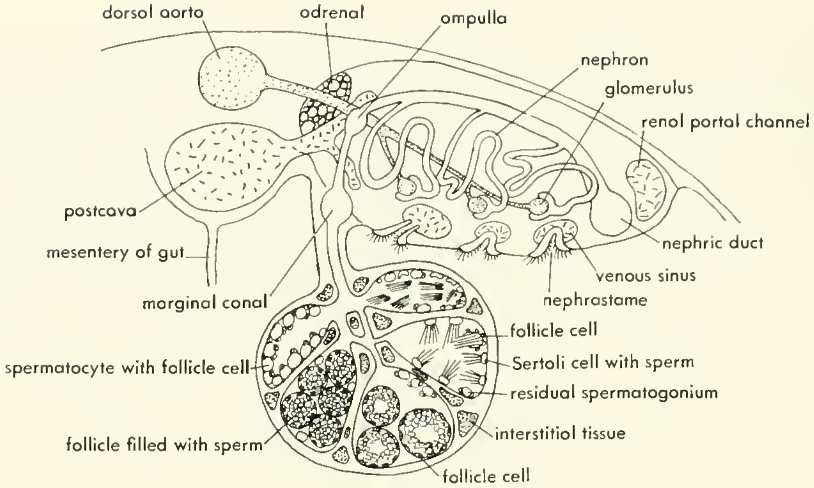


Figure 10-17. Cross section of an opisthonephros of the frog showing relationships with the blood supply and the testis. Nephrostomes opening into the venous sinuses are shown. (After Witschi, 1956)

appears to be only the posterior half of the larval structure. Within the kidney the efferent ducts connect with some of the capsules of the nephric tubules. The arrangement is similar to that of the sturgeon or *Amia* and differs from the frog in that the glomeruli of the sperm-carrying tubules are retained. The nephric ducts unite posteriorly and the **urinary sinus** thus formed opens into the cloaca along with the Müllerian ducts and the gut. A **cloacal bladder** extends forward above the rectum.

In *Protopterus* and *Lepidosiren* the central net is extended from each testis to the midline where it fuses with that of the other side; the median canal continues posteriorly nearly to the posterior end of the kidney. In *Protopterus* a few efferent ducts enter the kidney and connect through a large number of glomerulus-retaining tubules of the last two segments of that structure; the efferent ducts connect with tubules of the last few (5 to 6) segments in *Lepidosiren*. The nephric ducts extend back to the cloaca, whose roof they enter just posterolateral to the midline tubercle of the female genital ducts. In the male of *Protopterus* the nephric ducts unite and open at the tip of a distinct midline urinary papilla which retains bilateral openings into the cloaca. The cloaca extends forward above the gut as a midline urinary bladder.

EMBRYOLOGICAL DEVELOPMENT The pronephros involves about eight segments, of which two anterior ones produce funnels. The funnels lie in metotic (postotic) somites 4 and 5 in *Protopterus* and *Lepidosiren*, 5 and 6 in *Neoceratodus*. The nephric duct arises as a ridge from the segmental nephrotomes. This ridge separates from the lateral plate and lies dorsolaterally just below the epidermis. It is extended by segmental contributions, which lie just below the epidermis, to the cloaca (somite 42).

The pronephric funnels open into the pericardial coelom, dorsolateral to a large medial glomus. Occasionally accessory funnels are present. The pronephros is later reduced to a single funnel, the posterior one or a fusion product of both original funnels. The Müllerian duct arises in connection with this funnel in *Neoceratodus* and grows posteriorly, just medial to the nephric duct.

The mesonephros begins to develop relatively late in larval life. The tubules appear far back from the pronephros, in somites 23 to 38 (the cloaca lies in about the 42nd somite). The most anterior tubules are somewhat behind those further back in their stage of development. The primary tubules are neither symmetrically nor segmentally arranged. As development proceeds, the number of tubules increases. In the anterior part of the kidney, at 52 mm, only the primary tubules are present, whereas in the posterior two-thirds, there are primary, secondary, and tertiary tubules, in a ventrodorsal sequence. The glomeruli are clumped together, while the groups of peritoneal funnels are joined by a groove. The primary tubules of *Neoceratodus* and *Protopterus* may be interconnected at different points. Later generations of tubules arise from balls of cells budded off from the primary tubules. The several generations of tubules have renal corpuscles and peritoneal funnels.

In *Protopterus* up to six orders of tubules have been described for the hind part of the opisthonephros, each draining into the order preceding it. A glomerulus may be shared by two or three nephrons. In this genus, and *Lepidosiren*, the urinary bladder is said to arise as an anterior diverticulum from the urinary sinus, but such a bladder is not present in a 200-mm larva. The bladder is probably of cloacal origin.

Actinopterygians

Teleost The teleost kidney is sometimes a **holonephros**, that is, one made up of pronephros and opisthonephros

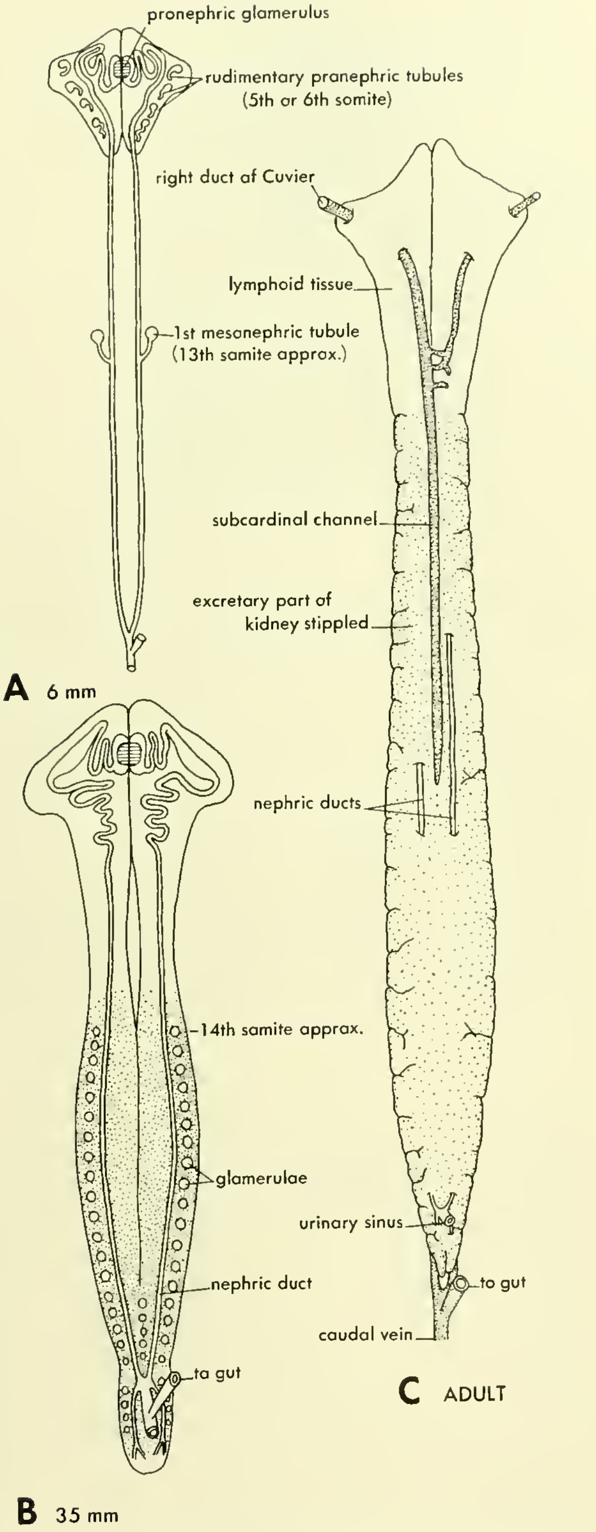


Figure 10-18. Three stages in the development of the kidney of the salmon. (After van den Broek et al., 1938)

(Figure 10-18). In the salmon the pronephros is retained as a lymphoid area containing suprarenal tissue (see Chapter 12). In a teleost such as the lantern fish *Lampanyctus,* the pronephros is developed much like the posterior part of the kidney. There are four pairs of looped pronephric tubules, each with a glomerulus, in this species. These tubules lie in the anterior cardinal channel. In some teleosts the pronephros degenerates and the adult kidney is an opisthonephros.

The opisthonephros is generally a simple organ with primary, irregularly arranged, tubules and sometimes what appear to be secondary and tertiary tubules. Where the opisthonephros extends behind the vertical of the anus, an independent duct or tube drains this part on each side. The nephric ducts join above the area of the anus and the midline sinus has a large, forward-extending outpocketing which functions as a bladder. The urinary duct opens to the outside through a urinary papilla.

The extremes of the group appear to be *Lampanyctus,* with its holonephric kidney and lymphoid tissue; *Cyclothone,* which has only a pair of pronephric tubules extending posteriorly as the nephric ducts—undoubtedly a case of neoteny in a fish which looks like a larva in many respects—and several marine teleosts in which the tubules of the opisthonephros are aglomerular or reduced to small branching diverticula of the nephric duct (Figure 10-19). Functionally the kidney in teleosts is phagocytic, blood-cell producing and excretory. In some fishes, the stickleback, posterior tubules produce a secretion used as a glue in nest building; in other species such tubules are modified into seminal vesicles, producing a sperm-maintaining fluid.

EMBRYOLOGICAL DEVELOPMENT In the salmon the pronephros develops in the 3rd to the 7th or 8th metotic segments. The nephrotomes (intermediate plate of mesoderm) have nephrocoels which do not open into the coelom. The roof of the nephrocoel invaginates upward forming a funnel and the pronephric ridge or cord associated with these funnels hollows out as the pronephric duct. The nephrocoels of one or more pronephric tubules now form a single pronephric chamber, not connected with the coelom, which leads into the pronephric duct by a single large funnel, representing an original funnel or a fusion product of several of the original funnels. Bilateral pronephric glomeruli develop and complete the pair of pronephric elements. In *Lampanyctus* four pronephric tubules, each with a glomerulus, develop and remain separate.

The pronephric canal is extended posteriorly by formation of a crest followed by separation of a band of cells from the outer layer of the intermediate plate, which is continuous with the somatic mesodermal lining of the coelom. The nephric duct eventually reaches and opens into the cloaca.

In the salmon the pronephric area is largely lymphoid and hemopoietic. It becomes completely so with the degeneration of the pair of pronephric elements. This lymphoid area involves 12 to 13 somites, the more posterior

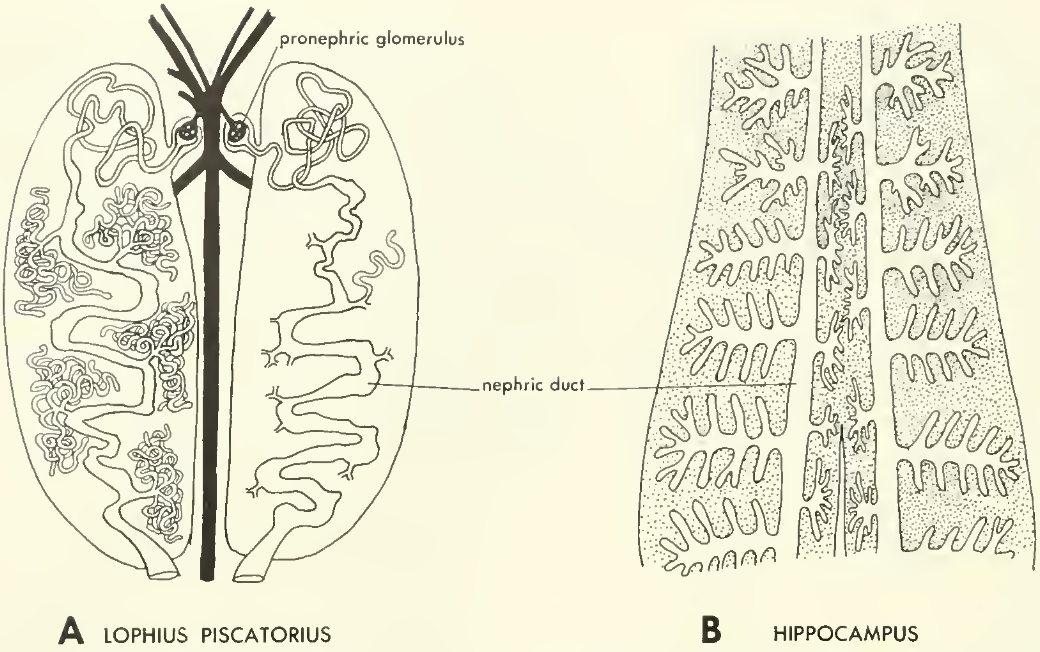


Figure 10-19. Tubules of aglomerular kidneys in two teleost fishes. A, *Lophius*, and B, *Hippocampus*. (After Gérard, 1954)

ones of which produce rudimentary tubules which abort. The functional kidney lies from the 14th somite back to about segment 38; four segments of this are postcloacal. The excretory regions of the kidneys fuse across the midline. Like the higher groups, except the mammals, the blood entering the kidney is both arterial and venous.

Polypterus The opisthonephros of this type is long and thin, and the organs of either side are not joined posteriorly (Figure 10-45). The nephric duct is distinct from the genital duct in both the male and female. The nephric ducts are expanded and joined to form a urinary sinus, which opens into the cloaca.

EMBRYOLOGICAL DEVELOPMENT The pronephros is formed by seven to nine nephrotomes, each having a nephrocoel (Figure 10-20). The outer layer of the nephrotome evaginates to form a pronephric crest and a funnel (Figure 10-21);

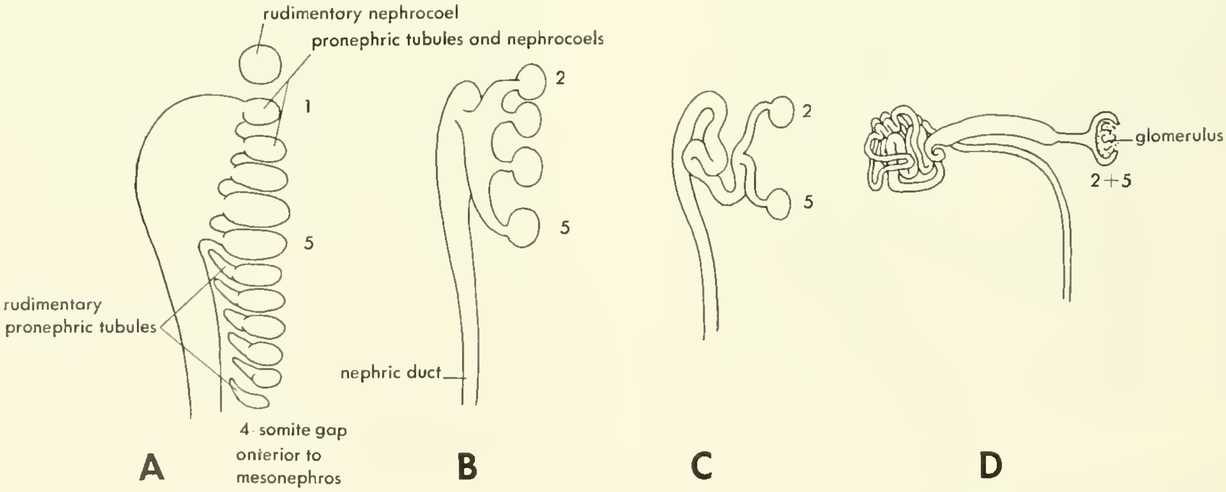


Figure 10-20. Four stages in the development of pronephros in *Polypterus*. (After van den Broek, 1938)

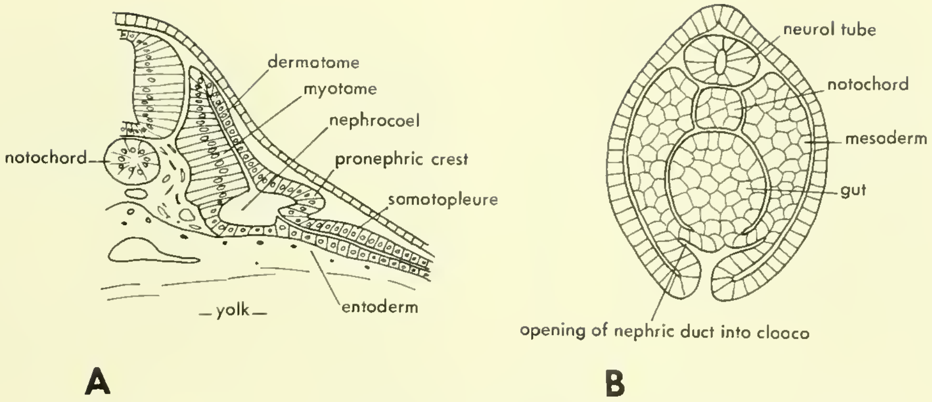


Figure 10-21. The origin of the pronephric tubule in *Polypterus* from the outer layer of the intermediate mesoderm, A, and the opening of the nephric duct into the cloaca, B. (A, after von den Broek, 1938; B, after Goodrich, 1930)

the anterior five rudiments have funnels and their crests join as the precursors of the nephric duct. Several more posterior funnels are formed but abort, and the crests of these segments are added to the nephric duct. The nephric duct continues to be extended posteriorly by crest contributions, separated from the intermediate plate, until it reaches the cloaca (Figure 10-21). The most posterior contributions appear to represent the entire intermediate plate, which then hollows out.

As segmental coelomic spaces develop, only the second and fifth pronephric funnels remain, and their nephrocoels open laterally into the coelom through peritoneal funnels. Each of these remaining tubules develops a renal corpuscle. With further growth the two units of a side fuse to form a single element having a single glomerulus and a very convoluted tubule. As this process of fusion goes on, the connection between the nephrocoel (now Bowman's capsule) and the coelom is lost. This single pronephric tubule lies in the fifth somite.

The mesonephros develops from segmental clumps of nephrogenic tissue, beginning about four somites behind the single pronephric tubule and extending through the 39th somite. The primary tubules differentiate and enter the nephric duct. In the anterior somites of the mesonephros there are usually two glomeruli and as many tubules. In the caudal half there are more glomeruli (as many as five) with the same number of tubules. In the 20th to 36th somites there are peritoneal funnels for each of the tubules.

The pronephros has disappeared in a 90-mm larva and peritoneal funnels are present as late as 150-mm but are lacking in the adult. The number of tubules has greatly increased and many use a single collecting duct.

Acipenser The kidney of this fish is long and tapered, thin anteriorly and widened posteriorly where the two organs are fused (Figure 10-45). The anterior end is continued forward into the region of the pronephros, under the posterior end of the chondrocranium. The kidney is possibly a holonephros; that of *Polyodon* is said to be a holonephros.

The nephric duct increases in diameter posteriorly and is suddenly expanded laterally as a bladder which extends most of the length of the fused portion. Posteriorly the two ducts unite to form a midline sinus. In both sexes a large ciliated funnel joins the nephric duct near the anterior end of the expanded bladder portion. This funnel serves for passage of the eggs in the female but is not a genital duct in the male.

In *Polyodon* this funnel enters the posterior part of the expanded bladder portion of the nephric duct, just anterior to the midline urinary sinus. In young specimens it ends blindly. In one female the duct had failed to form on one side.

The testis of the male is connected with the kidney tubules by a large number of vasa efferentia. These enter a **marginal canal** from which a number of ducts pass into the substance of the kidney and enter the capsules of some of the tubules. More than the anterior half of the kidney length is involved in the cross connection between testis and nephric duct; about one tubule in three is involved in sperm transport and these retain their glomeruli.

EMBRYOLOGICAL DEVELOPMENT The pronephros arises in postotic segments 4 to 8 or 3 to 10 (Figure 10-22). As already observed in the salmon, the outer layer of the intermediate plate, or the somatic mesodermal layer, evaginates upward and laterally to form a crest. The crests of the several pronephric segments join to form a ridge or strand which is continued posteriorly by comparable contributions from the intermediate plate of the more posterior segments, all the way to the cloaca. The ridge separates from the lateral plate and hollows out to form the nephric duct.

The first five to seven of the pronephric segments develop a nephrocoel in the intermediate plate as well as a funnel. The first several nephrocoels open into the coelom. The most anterior funnel becomes vestigial very early. Later the

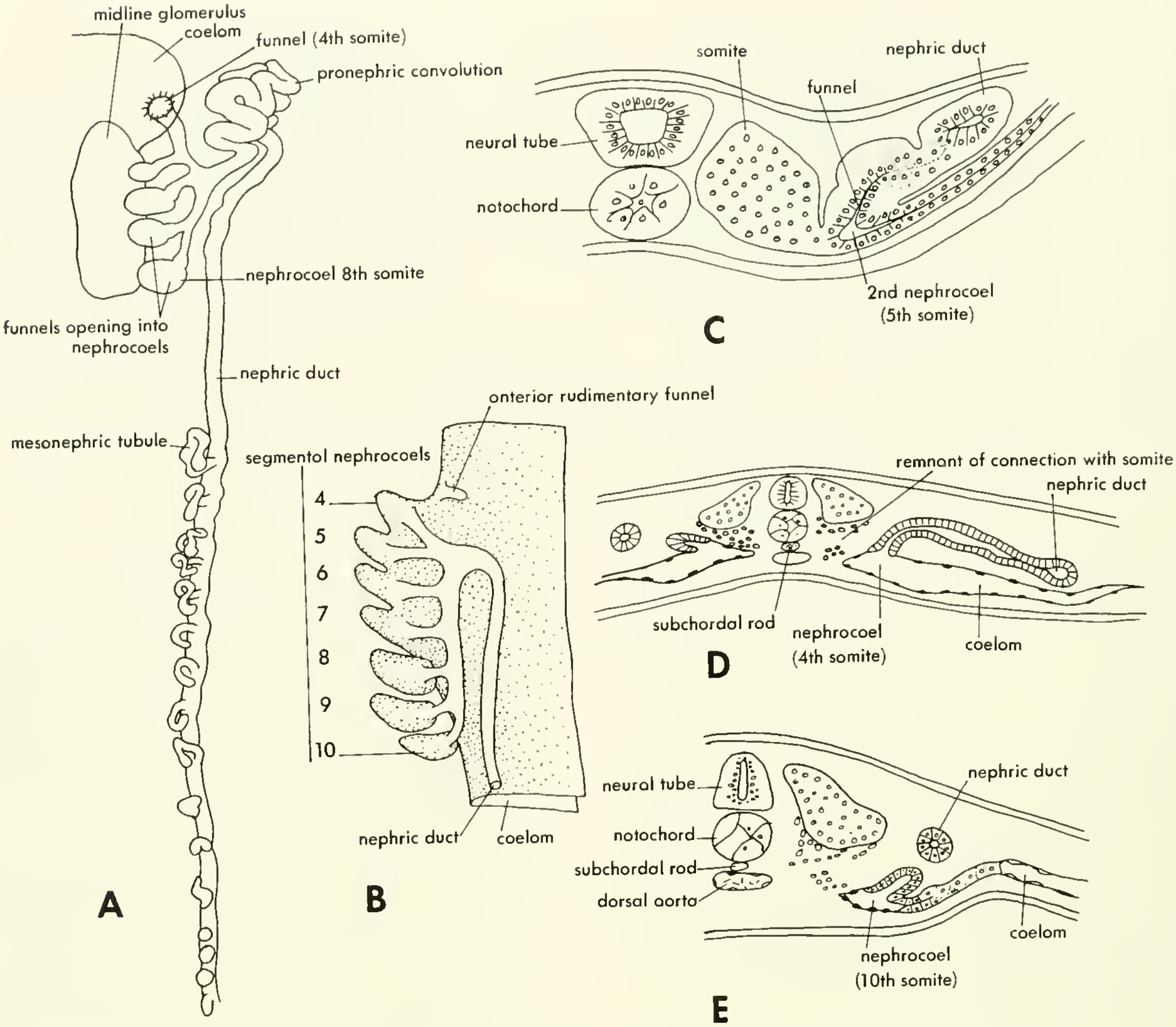


Figure 10-22. Development of the kidney in *Acipenser*. A, entire pronephric system with mesonephric beginnings in 13-mm larva; B, pronephric tubules opening into general coelom or coelomic pockets at 26-hr stage; C, D, and E cross sections showing relationship between pronephric elements and coelom. (A, after Kindahl, 1838; B–E, after Moschkowzeff, 1926)

remaining funnels, with the exception of the most anterior one, lose their coelomic connection. The several pronephric tubules become associated with glomeruli lying just ventrolateral to the dorsal aorta. The more anterior segments of the pronephros now appear to undergo some posterior displacement. The glomeruli unite to form a single large median glomus lying immediately below the dorsal aorta, and the nephrocoels fuse into a single cavity on either side of this. At this time the pronephros undergoes degeneration, but possibly passes through a stage with a single pair of pronephric units formed by fusion of the several earlier ones.

The mesonephros is developed from segmental blastemal knots. These form tubules which join the nephric duct. Each tubule has a renal corpuscle and a peritoneal funnel. Multiplication of tubules occurs through secondary and tertiary (and higher) generations which use the primary tubule as a collecting duct. The peritoneal funnels are lost in the adult, but the genital duct, which is similar in both male and female, may functionally replace them.

It has been suggested that the genital duct (of the female) is developed from the rudimentary peritoneal funnels of the secondary tubules or even by division of the nephric duct. It appears to be comparable to that of *Lepisosteus* and develops in the same way.

Amia and Lepisosteus The adult kidney of *Amia* is an opisthonephros. These organs are fused posteriorly into a single mass which extends behind the anal opening. Anteriorly each is a narrow band extending forward, then out, to the duct of Cuvier. In the male, the testis connects by numerous long efferent ducts through the mesorchium with the anteromiddle part of the kidney and through this with the nephric duct. The female has a large funnel opening into the nephric duct just where that duct turns ventrally to form the urogenital sinus (much like *Acipenser* or *Polyodon*).

The connection between oviduct and nephric duct is of interest. The oviduct ends blindly in the connective tissue sheath of the nephric duct and may bulge into it. Just anterior to this tip is a small slit or pore connecting these ducts. *Amia* has a urinary bladder projecting forward from each nephric duct just before that duct enters the urogenital sinus. This sinus opens into a small fold a short distance behind the anus.

Lepisosteus has a much more elongate but similar kidney (Figure 10-46). There is no marginal canal for the connection with the testis. As in *Amia,* the nephric duct extends along the lateral margin of the kidney. Posteriorly the nephric duct increases in diameter and has elastic walls serving as a urinary bladder. The oviduct of the female opens into the anterior end of this expanded part. The nephric ducts form a midline urinary sinus which opens to the outside behind the anus.

EMBRYOLOGICAL DEVELOPMENT In its development, *Lepisosteus* is much like *Acipenser.* The fourth to seventh metotic segments develop funnels. The most anterior one opens into the coelom, the others into their separate nephrocoels, which in turn connect with the coelom. What appear to be accessory funnels so develop that the tubules are connected with the coelom not only through the nephrocoel but also through additional funnels (true peritoneal funnels). A single median glomerulus develops from the several pairs of glomeruli, and the several nephrocoels fuse to form a single cavity for the several tubules. In a 40-mm larva there were an anterior coelomic funnel, three funnels associated with the glomerular capsule (space around glomerulus), and a peritoneal funnel associated with the tubules from this capsule.

The pronephros is still present, although degenerating, at 70 mm; soon thereafter it has degenerated and is largely replaced by lymphoid tissue.

In *Amia* the pronephros has three nephrocoels at the beginning; the anterior one of these opens into the coelom. A compound midline glomus forms and the two posterior tubules fuse. The pronephric duct is somewhat more convoluted than in *Lepisosteus.* The nephric duct appears to be continued back from the pronephric region as a ridge formed from the intermediate plate mesoderm and then separated as a cord of cells.

The mesonephros develops as in other forms (Figure 10-23). In the early stages, secondary and tertiary tubules open into the nephric duct. Ciliated peritoneal funnels are present up to about 100 mm; however, many tubules lack funnels, while others have two. Some funnels end blindly in the kidney substance. With the development of the oviduct, some funnels open inside of this tube in both *Amia* and *Lepisosteus,* as in *Acipenser* and *Polypterus.*

General observations The actinopterygians, including *Polypterus,* agree in having a multifunnel pronephros which is associated with a median anterior glomus. The number of tubules associated with the glomus tends to be reduced both by fusion and degeneration, so that a single anterior tubule results in *Polypterus, Amia,* or the teleosts. The pronephros generally degenerates, although the whole or its most posterior part may be retained as a lymphoid strand. Occasionally a functional pronephric tubule is retained in teleosts and in *Polyodon.* In the teleosts, mesonephric peritoneal funnels are lacking even in the early stages. Such funnels are lacking in the adults of all actinopterygians.

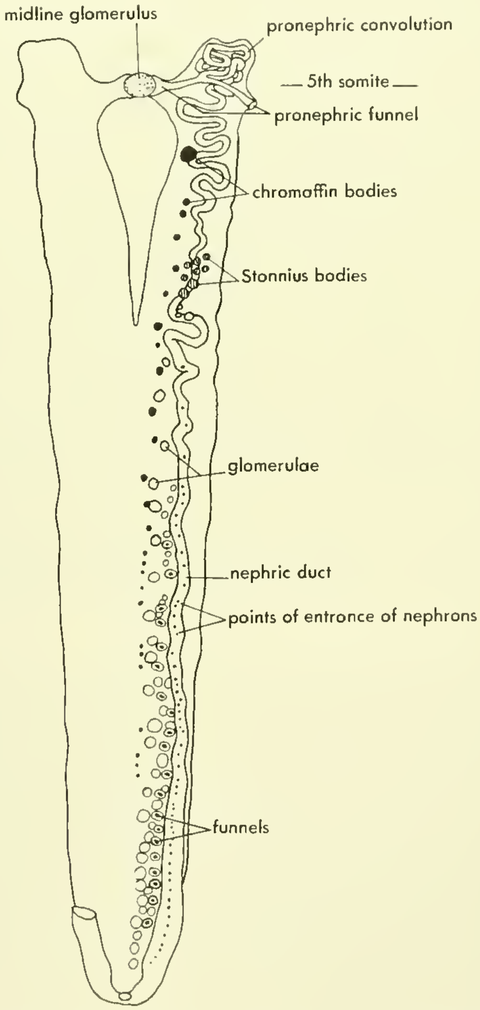


Figure 10-23. Ventral view of kidney of 22-mm *Amia* showing pronephric elements, nephric duct, positions of mesonephric glomerulae and funnels, and Stannius and chromaffin bodies. (After Kindahl, 1938)

Chondrichthyes

Shark The kidney of the shark is an opisthonephros, a long band increasing in dimensions posteriorly (Figure 10-48). Its surface is irregular and in some species distinctly lobed. In the sexually mature male, the anterior part is converted into an epididymis. The nephric duct becomes hypertrophied and very looped and coiled, acting as a ductus deferens—the anterior part of the nephric duct of the female shows a tendency in this direction. Posterior to the tubular epididymis, a part of the kidney of the male is modified into the *Leydig's gland.* Behind this is the expanded excretory part of the kidney. The kidneys of either side are in contact posteriorly but not joined.

The nephrons of the epididymis portion each have a renal corpuscle and a coiled tubule. With establishment of connection with the testis, the renal corpuscle is lost and the lumen of the tubule is increased. The Leydig's gland portion is formed of functional nephrons in the young, but these become aglomerular and secretory in the adult. They produce a secretion which acts in the formation of spermatophores (bundles of sperm) and in the transport and conditioning of the sperm. In the female, with the exception of the extreme anterior end which degenerates (epididymis area), the entire opisthonephric band is functional.

The nephric duct in some sharks (*Squalus*) is converted into a vas deferens in the male, and the posterior excretory part of the kidney is drained by a separate duct, the ureter. All stages of separation of vas deferens and ureter are shown among sharks. Some species have several ureters opening into both nephric duct and cloaca. The least modification is observed in females of *Squalus* where segmental ducts from the entire length of the definitive kidney enter the nephric duct; posteriorly one or two segments may be drained by a separate ureter. In some sharks (*Torpedo*) the female is like the extreme of the male; the anterior Leydig's part is nonfunctional and attached only to the nephric duct, while the separated posterior part of the opisthonephros is expanded and lobate, and is drained by a separate ureter into the cloaca.

Peritoneal funnels are present throughout life in some sharks. These have been related to the presence or absence of abdominal pores—the funnels act as a substitute for these pores. In some sharks these funnels are present only in the young. *Squalus* has such funnels throughout life along with abdominal pores. These funnels can be demonstrated by staining with Flemming's fluid, a mixture of chromic, acetic, and osmic acids. This is allowed to stand in the abdominal cavity for a time, then flushed out. The funnels are stained by an accumulation of osmic acid and lie near the midline or on the mesenteries which anteriorly support the gonad or posteriorly the rectum.

The peritoneal funnels of both the Leydig's region and functional excretory region lead into a mass of lymphoid tissue and end at a vesicle. The funnels are not connected with the nephrons. This is probably true even in the case of *Scyllium.* The lymphoid tissue of the kidney may be well marked as segmental patches around the lateral vesicles of the funnels (*Squatina*) or may diffuse within the kidney substance.

EMBRYOLOGICAL DEVELOPMENT The pronephros of the shark is reduced and never functional. As a general proposition, the pronephros of embryos with large yoke masses is never functional, at least in terms of fluid passing down the nephric duct to the cloaca—see myxinid.

The number of pronephric rudiments varies from four to eight and these lie in metotic segments 7 to 10 or 7 to 14. In *Squalus* there are about six somites involved (7 to·12). The nephrotomes (intermediate plate area) of these segments develop nephrocoels which connect with the coelomic spaces laterally. The roofs of these nephrotomes are evaginated upward as funnels and the pronephric crests (Figure 10-24). The thickenings join together to form a ridge which hollows out as a pronephric duct. Funnels are formed which open into the coelom. Glomeruli are lacking.

The nephric duct grows posteriorly from the pronephric region without drawing materials from the overlying ectoderm or the underlying splanchnopleure (or nephrotome) and thus the shark resembles the reptiles and mammals. The pronephric funnels tend to fuse and form a single large funnel on either side. In *Pristiurus* or *Squalus* these bilateral funnels move downward over the wall of the gut, meet below the gut, and fuse. This median funnel (or bilateral funnel) is part of the definitive Müllerian duct system of the reproductive apparatus. In some sharks, only a single pronephric funnel appears to be involved in the ostium of the Müllerian duct. There is a distinct resemblance here between shark and dipnoan.

The mesonephros extends back from the pronephric region through 35 to 37 somites (37 pairs of canals in *Squalus*). In *Squalus* there is a tubule in each segment built of two components. The first is a peritoneal funnel leading into a tubule which arches up and laterally; this represents the nephrotome opening into the coelom. The second part is an outgrowth from the nephric duct toward the blind end of the first; this is a collecting tubule. The tubules develop, as a generality, in an anterior-posterior sequence; the most anterior ones, however, are somewhat behind those further back and do not develop very far. The first seven or eight degenerate, as may the most posterior ones. There are 25 to 30 segments in the definitive kidney (23 to 24 pairs of peritoneal funnels in *Squalus*). The most complex tubules and the greatest number of generations of tubules develop in the posterior half.

As the **peritoneal funnel tubules** develop, the middle section of each expands and separates into a rudimentary capsule, for the distal part, which is now a first order nephron, and a sacculate **lateral vesicle,** which can be identified as the nephrocoel (Figure 10-50). This division is followed by

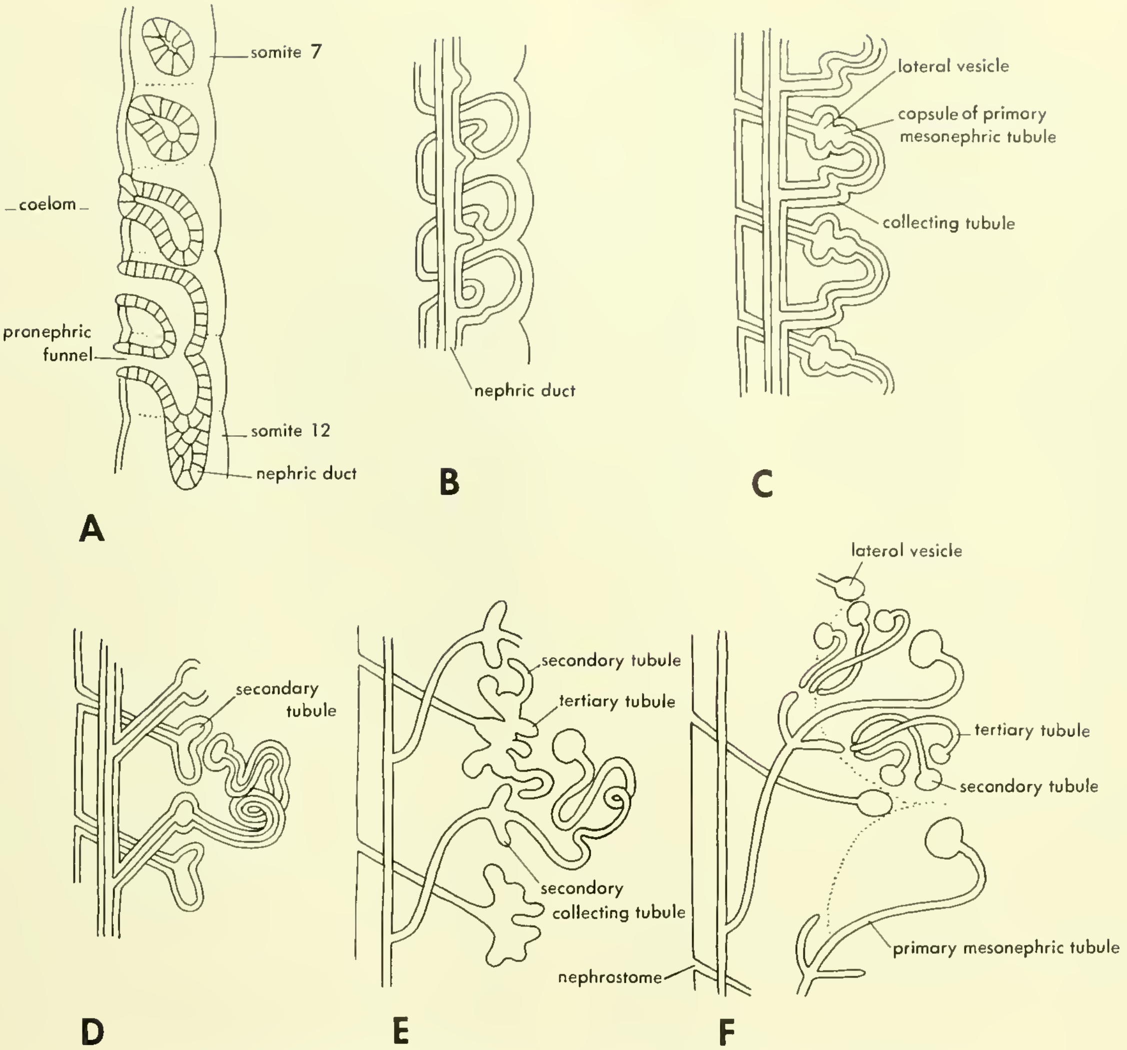


Figure 10-24. Stages in the development of tubules in *Squalus*. A, pronephric area of 5-mm embryo of 25 to 27 somites; B, beginning of tubule formation in mesonephric region; C–F, progressively later stages. (After Borcea, 1906)

the formation of secondary and tertiary tubules which are budded off in pairs from the lateral vesicle. The new generations of tubules enter secondary collecting tubules evaginated from the region of junction of the primary collecting duct and the primary nephron, the segmental collecting duct. The more posterior collecting tubules of some sharks, including *Squalus*, tend to move their point of attachment on the nephric duct more and more posteriorly. Concurrently the Müllerian duct is separating from the anterior end of the nephric duct. In the female this separation continues in a posterior direction until the Müllerian duct opens separately into the cloaca.

In *Pristiurus* the segmental tubules form individual units; the expansion becomes a Bowman's capsule enclosing a glomerulus (Figure 10-25). Each segmental tube gives rise to several generations of tubules which have a common collecting tubule. The bunches of segmental tubules form the segments of the definitive kidney. In the adult, connection between tubule and funnel is probably lost.

In the later stages of development of the male, the most anterior part of the mesonephros is modified into the epididymis. About six segmental tubules are involved in the transport of sperm from the testis to the nephric duct. Their glomeruli and peritoneal funnels disappear. The way the connection between testis and kidney develops is not known, but it involves either the conversion of the peritoneal funnels into the **ductuli efferentia** (certainly the funnels disappear) or more probably it involves independent tubular extensions from the glomer-

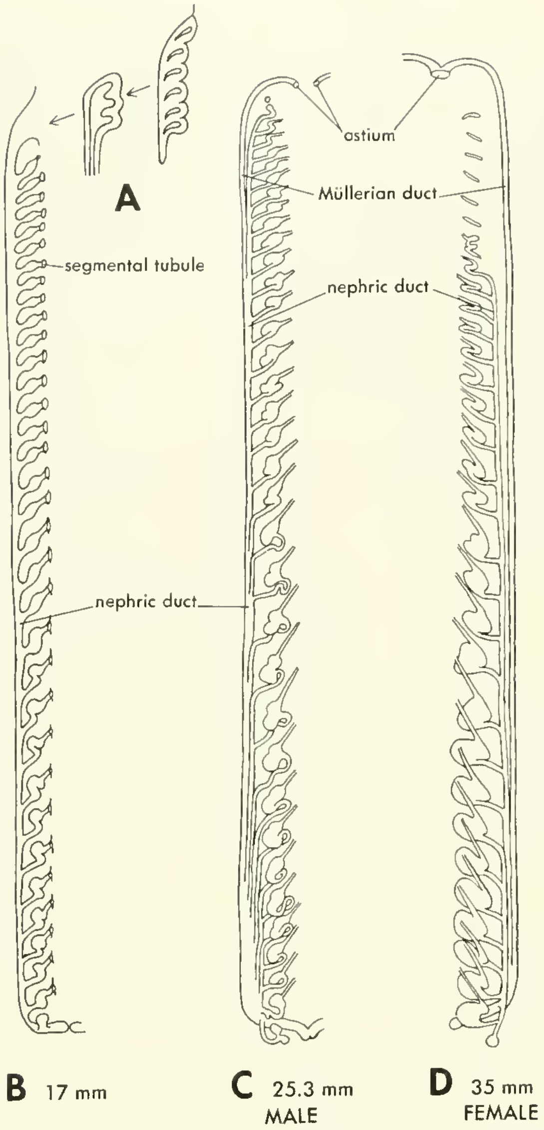


Figure 10-25. Two stages of kidney development in *Pristiurus* (the sawfish). A, progressive fusion of pronephric funnels to form ostium of Müllerian duct in the early stage; B, C, D, later stage of male and female. (After van den Broek et al., 1938)

uli to a marginal canal and independent extensions of the central net of the testis, through the connective tissue bands of the mesorchium to the kidney and into the marginal canal.

The nephric duct of the male also is modified in forming the **ductus,** or vas, **deferens.** Behind the epididymis, 10 to 15 segments are modified into the Leydig's gland. Behind this, 10 or 11 segments remain as the definitive kidney.

Holocephalan The kidney of the holocephalan resembles that of the shark (Figure 10-49). It is an elongate band, narrow anteriorly, somewhat expanded posteriorly. The most anterior part in the male is an epididymis; behind this is a Leydig's gland followed by the functional kidney. Since Leydig's gland and the kidney cannot be differentiated macroscopically, the term Leydig's gland is applied loosely to the narrow anterior part. On the basis of collecting tubules, there are six to eight segments in the Leydig's gland, which is excetory in the young male but becomes aglomerular and secretory in the adult. The most anterior lobules of the functional kidney drain into the much convoluted vas deferens which then expands into a thick-walled ampulla for most of the length of the functional kidney. The greater part of the functional kidney, eight or nine lobules, drains through a series of ureters. Some of these ureters have complexly looped sections and the first six or so enter the ampulla dorsally. The last two enter the urinary sinus behind the ampulla. The nephric ducts fuse posteriorly to form a urogenital sinus. In the mature male there is a small glandular mass, the urogenital gland, projecting forward from the urogenital sinus just before that sinus opens from the body. There are no peritoneal funnels in the kidney but abdominal pores are present. There are vestigial Müllerian ducts in the male.

The kidney of the female is like that of the young male except that the most anterior part degenerates (there is no epididymis). The extreme posterior ends of the kidneys may fuse, but they are essentially separate bands between which the interrenal gland lies. The nephric duct and four of five ureters join and empty into a thick-walled (muscular) urinary sinus which extends forward as a bladder. The Müllerian ducts are well developed and posteriorly open into a slightly developed urogenital sinus (Figure 10-50).

The development of the kidney of this group has not been described. It is assumed that in the young female the urogenital sinus opens into a cloaca. The urogenital sinus has a pouch-like outgrowth. As this urogenital sinus everts, the Müllerian ducts, the excretory pore, and a more anterior "seminal receptacle" come to open almost separately.

General observations There is a close resemblance between the shark and the holocephalan in terms of the excretory system, at least in the intricately looped and knotted vas deferens. One item of difference lies in the fact that the urogenital system opens behind the anus. Another item is the forward-projecting "seminal receptacle" of the female holocephalan which is suggestive of the bladder in higher forms and the rectal gland of the shark; that is, it is a rudimentary allantois. Both shark and chimaerid have abdominal pores opening posterolateral to the anal or cloacal opening.

The development of the shark kidney differs markedly from that of the other fishes and tetrapods in that the tubules of all segments, not just the pronephric region, arise directly or indirectly from funnels. The mesonephric tubules arise as several generations of evaginations from a nephrocoel (lateral vesicle). The collecting ducts arise as outgrowths from the nephric duct in the mesonephric area as

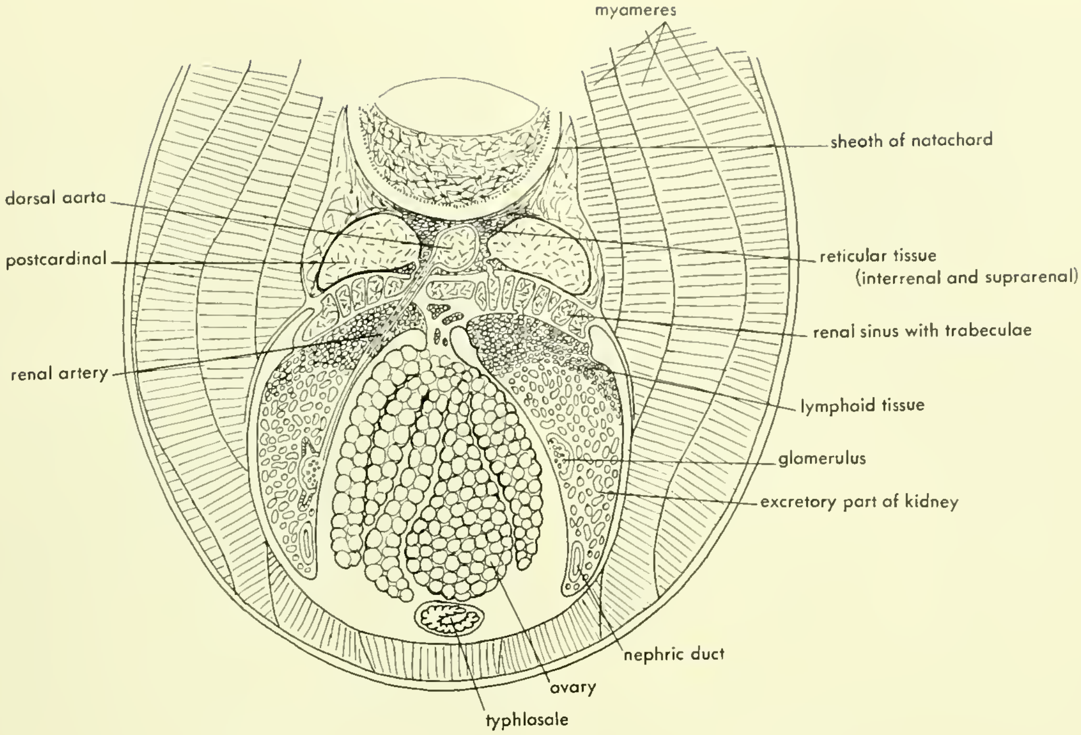


Figure 10-26. Cross section of adult lamprey to show interrelationships.

well as in the posterior "metanephric" region. The origin of the Müllerian duct by the splitting of the nephric duct is also unmatched elsewhere.

Cyclostomes

Lamprey The kidney of the adult lamprey is an opisthonephros. It is band-like, hanging down on either side of the body cavity (Figure 10-26). That of the left side is larger. Anteriorly each kidney is narrow, beginning at the duct of Cuvier (posterior end of the pronephric region) where it is only a band of tissue in the roof of the coelom; posteriorly it increases in depth. Near the anal region it tapers to the nephric duct. The nephric ducts of either side join just before reaching the tip of the urogenital papilla which extends into the cloaca (Figure 10-27).

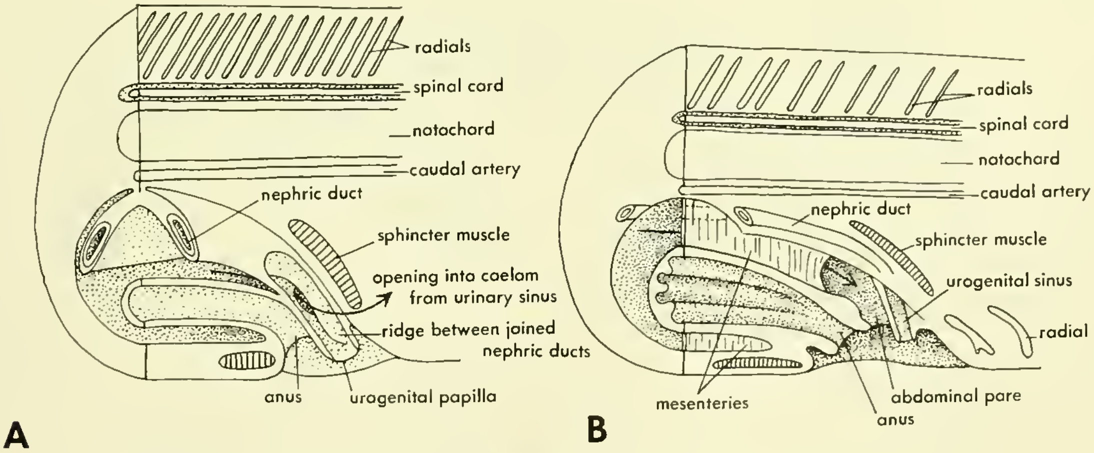


Figure 10-27. Semidiagrammatic sagittal sections of the cloacal region of the lamprey, A, and Myxine, B.

As seen in longitudinal section, the kidney lies below the large posterior cardinal vein into which its venous sinuses open. In the medial wall of the kidney fold is a longitudinal glomerular band served by nearly segmental arteries. The capsules associated with the glomerular band are all coalesced into a common cavity from which numerous nephric funnels extend in every direction (except directly medially). The nephric tubules are complexly looped and join the nephric duct in the ventral margin of the kidney fold.

Further details of structure can be seen in a cross-section cut from a preserved specimen (Figure 10-26). Below the **notochord** is the dorsal aorta and to either side of this the **posterior cardinal veins.** Separating these vessels from the kidney is a thick layer of connective tissue which appears to be perforated only by the occasional **renal arteries** serving the **glomerular band.** Below this connective tissue plate is a thick-walled **suprarenal sinus** which extends to either side of the midline and is crossed dorsoventrally by numerous **trabeculae** of connective tissue. Where renal arteries pass down, they are enclosed in broad connections between roof and floor. The trabeculae and the larger connectives enclosing the arteries form bilateral anteroposterior bands. These bands support the mesentery of the median **gonad.**

The kidney tissue lies below the suprarenal sinus to either side. It is divided into a dorsal, darker part and a larger, ventral, lighter colored region. The dorsal part is lymphoid in nature, producing blood cells, while the white part is the tubular excretory portion. The excretory tissue extends through about half the length of the body cavity, from the 40th or 45th myotome to the 75th or 80th myotome. The lymphatic tissues extend the entire length of the body cavity; anteriorly the lymphatic bands end to either side of the sinus venosus, about somite 20, in the region of the late larval pronephros—see below. The suprarenal sinus extends the entire length of the kidney.

Circulation in this kidney involves direct arterial supply to the glomerular band from which the blood percolates among the tubules into the reticulum of the lymphoid part. From here it passes through slit-like openings in the floor of the suprarenal sinus. From the suprarenal sinuses it passes through similar slits in the roof. These slits open into a loose tissue lying along the ventromedial walls of the posterior cardinals. Perhaps this is a phagocytic tissue along with the interrenal tissue. The blood leaves this tissue by round openings, several to a segment, and enters the posterior cardinals.

EMBRYOLOGICAL DEVELOPMENT The pronephros arises in metotic somites 4 to 19, approximately (Figure 10-28). The nephrotomes develop interior hollows, the nephrocoels, which later, in segments 7 to 11 or 12, open laterally into the segmental coelomic spaces (Figure 10-29). The outer layer of the nephrotomes of these segments, and those posterior to them, evaginate upward to form a pronephric crest. These crests join from segment to segment. In the most anterior segments, 4 to 6, regression occurs early, but in somites 7 to 11 funnels are formed which extend upward into the pronephric ridge. Behind these the pronephric ridge separates as a cord of cells which later hollows out as the nephric duct. The nephric duct is continued posteriorly by segmental contribution from the nephrotome or intermediate plate mesoderm, and in embryos of 34 or 35 somites it reaches the cloaca.

The tubules of the definitive pronephros vary in number from four to six. They lengthen rapidly and become complexly looped (Figure 10-29 B,C). The whole pronephric

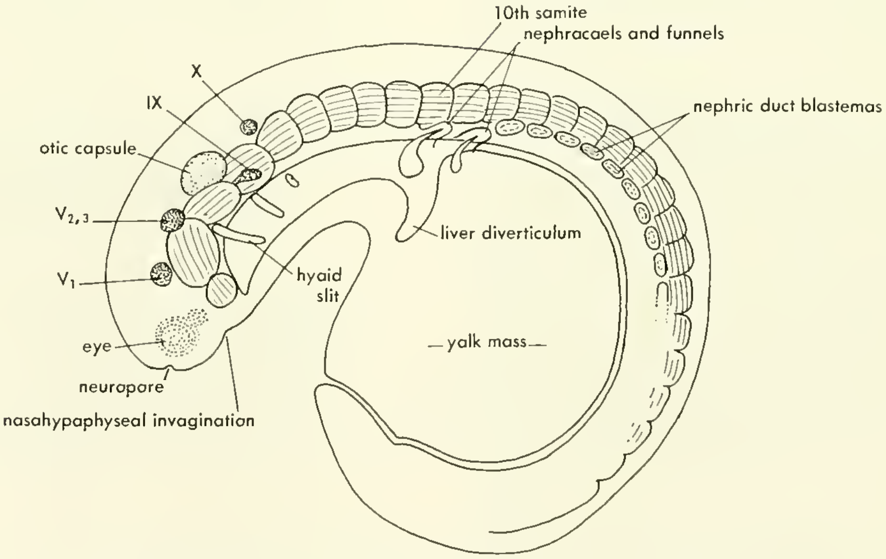


Figure 10-28. Lamprey larva of 26 to 28 somites. (After Damas, 1944)

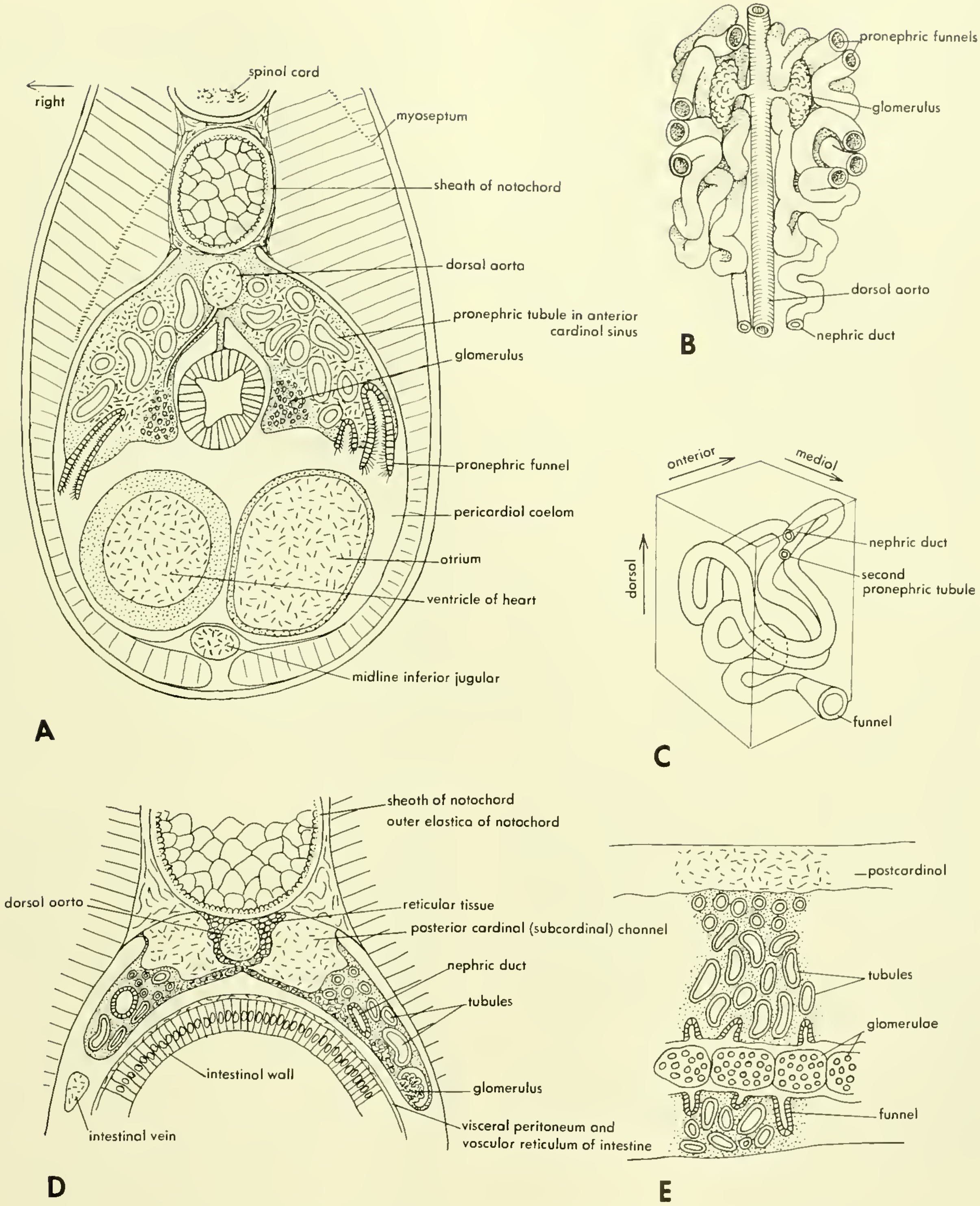


Figure 10-29. Development of the kidney of the lamprey. A, cross section of 15-mm larva; B, ventral view of pronephric tubules as they lie in the pronephric sinus; C, stereodiagram of the anterior pronephric tubule of a 15-mm larva; D, cross section in the mesonephric region of a 15-mm larva, about middle of body; E, parasagittal section of a well-developed mesonephros. (E after Gérard, 1954)

structure bulges into the pericardial cavity as a sac through which the blood of the anterior cardinal vein courses to reach the sinus venosus. The pronephric tubules extend back not only into the duct of Cuvier but even into the posterior cardinal channel. The funnels have flaring ciliated margins. The funnel cilia create a current into the tubules. The funnel extends into the pronephric sac a short distance, and joins the tubule which has less intensely staining cells with a ciliated inner surface. On the inner surface of either pronephric sac is a single large glomerulus.

The pronephros is an active excretory structure in the early larval period. It increases in size (well developed in the 30-mm larva) proportionally as the animal grows, and it does not degenerate until the larva reaches a size of about 100 mm. As the larva increases in size and the branchial apparatus expands posteriorly, the pronephros is displaced back into segments 18 to 23, approximately.

The mesonephros is represented at first (10-mm larva) by a thin, irregular blastema of cells arranged around the wall of the lower half of the postcardinal and medial to the nephric duct. The kidney anlage lies ventrolateral to the posterior cardinal and bulges slightly into the body cavity. This ridge increases rapidly in size and forms a band projecting down into the body cavity (Figure 10-29 D). In the 15-mm larva about four mesonephric tubules have appeared, about five or six myotomes back of the pronephric area. At their appearance these tubules are quite flexed. The nephric duct lies in about the middle of the kidney band, while the glomeruli are in the ventral margin. In front of and behind these tubules the kidney is lymphoid in nature; dorsally it is not marked off from the posterior cardinal.

The mesonephros adds new tubules posteriorly with increasing size. The most anterior tubules, about 20, regress and disappear, being replaced by lymphoid tissue. As development proceeds, the number of myotomes between head and cloaca is about doubled. Each segment appears to have a glomerulus and a single initial tubule. There are no peritoneal funnels. Secondary tubules appear, as do tertiary and perhaps more generations. With multiplication of tubules new glomeruli are produced by subdivision of the initial one. In this way a band of four or five glomeruli is produced and is served by a segmental artery (Figure 10-29 E). Occasionally segmental arteries extend into the next posterior segment.

The nephric ducts extend about five myomeres beyond the posterior ends of the kidneys. Here they unite as an excretory sinus into which open, to either side, the posterior pockets of the body cavity. The common duct opens to the exterior through a pore on the tip of the urogenital papilla.

Myxinid The adult of *Eptatretus* has a pronephros consisting of a small mass of tubular tissue just anterior to the duct of Cuvier (the 31st to 33rd somite) and above the heart. The right pronephros is larger than the left and lies somewhat anterior to it. In section, many small funnels are observed opening from the coelom into a central mass of cells. The central mass lies inside a pronephric vein. Occasionally channels from funnel to vein are observed. At the posterior end of the pronephros, there is a renal corpuscle opening into the coelom through a funnel and into the central mass by a duct. Occasionally two glomeruli occur.

This head kidney lies well anterior to the opisthonephros (Figure 10-30). The latter is little more than the nephric duct, a thin, slightly looped band beginning at the vertical of the 33rd to 35th myomere and extending for much of the length of the body cavity. The opisthonephros of the male is thicker and somewhat more looped than in the female. Posteriorly the nephric ducts join and form a urinary sinus opening to the exterior through a papilla (Figure 10-27). The lumps along the length of the opisthonephros represent renal corpuscles and short tubules (Figure 10-30). About four such lumps are crowded at the anterior end, and their arterial and venous connections indicate that they have been displaced backward. The most anterior tubule may lead directly back into the nephric duct, or a vestige of the nephric duct may extend anteriorly beyond the point of entrance of this tubule. Although the renal corpuscles are irregularly spaced, in terms of distribution along the nephric duct or one side as compared with the other, there appears to be one pair of tubules for each muscle segment, in all about 35 pairs.

The tubules are very simple in structure (Figure 10-30 B). There is no peritoneal funnel and cilia are lacking. A thin neck section opens from the capsule into the tubule which is histologically similar to the main nephric duct. In a few specimens of *Eptatretus,* an elongated neck region opened directly into the nephric duct. The glomerulus is served by a small branch from the dorsal aorta and is drained directly into the postcardinal vein by a short vessel.

EMBRYOLOGICAL DEVELOPMENT The development of this type is only partly described. In the earliest embryos, with the same number of somites as the adult (101 to 102), a series of segmental nephrotomes is present in somites 13 to 74. Each is a vesicle, separated from the somite, of dark staining cells enclosing a small nephrocoel. The lateral mesoderm is mesenchymatous at this stage: it is not segmental nor is it divided into somatic and visceral layers.

New nephrotomes appear posteriorly as those at the anterior end of the series open laterally into the coelomic spaces. The coelom at first has distinctly segmental cavities medially, but laterally it appears as irregular spaces. All of these spaces unite to form the body cavity, which opens medially into the nephrotomes. Distinct nephrotomes form back to about the 76th somite; behind this are four indistinct nephrotomes in which cavities do not develop, although four less dense areas are indicated. These four incipient nephrotomes complete the nephric band back to the cloaca.

The nephrotomic vesicles of segments 12 (10 to 13) to 30 give rise to pronephric crests dorsally. These crests and the vesicles coalesce; the vesicles as separate entities are now

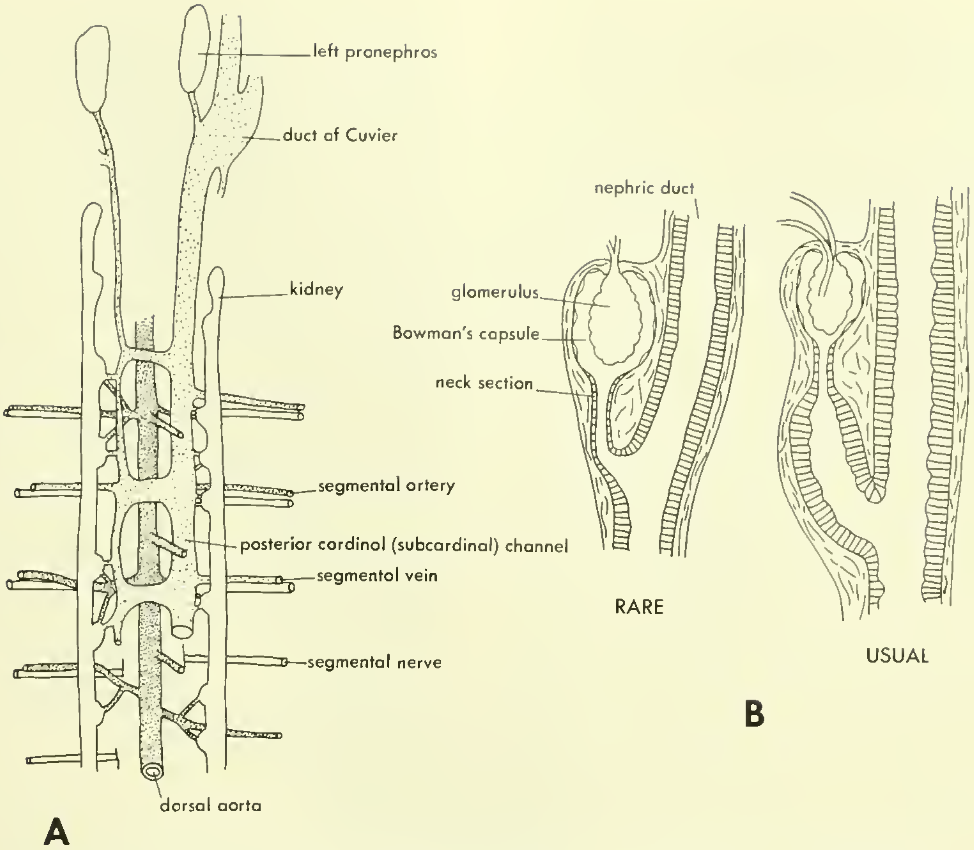


Figure 10-30. Kidney of *Myxine*. A, anterior end of kidney as seen from below, and relationships to blood vessels; B, two types of tubules observed in the adult kidney. (A after Marinelli and Strenger, 1956; B after Conel, 1917)

lost and the coelom extends to what was their medial walls. Segmental funnels form and the cavities of these extend into the pronephric ridge or cord to form the nephric duct.

Posterior to the 30th somite a different process occurs: there is a transition from one process to the other in the region of the 30th somite. The second process involves retention of the nephrocoels as separate spaces opening into the coelom laterally. The roof of the nephrotome is evaginated upward as a pocket, and the outpocketing of adjacent nephrotomes join dorsally as a continuation of the nephric duct. These segmental outpocketings can be viewed as enlarged funnels. Occasional less developed segments temporarily break the continuum of the nephric duct from front to rear. Nephric elements arising in this way extend back to about the 70th somite. The most posterior elements are rudimentary and abort early; they do, however, contribute to the nephric duct which thus reaches the cloaca.

In the opisthonephric region, behind the 30th somite, the nephrocoel of each segment is cut off from the coelom by closure of its lateral wall. This process extends gradually but irregularly posteriorly. With the nephrocoel isolated from the coelom, a glomerulus begins to form medial to the funnel. The entire nephrotome, except the part involved in the nephric duct, is now reorganized into the adult tubule. The nephrocoel forms the Bowman's capsule. The most posterior tubules degenerate early. Posteriorly there is a continued degeneration of units in an anterior direction, until the definitive kidney is achieved, the last opisthonephric unit lying in about the 70th somite.

Anteriorly the pronephros has been pushed posteriorly by the development of the branchial pouches. In this process it has also become compressed. What had extended through segments 12 to 30 now lies in segments 31 to 33. How many of the original elements are retained is not known, perhaps five to seven units. In this shortening process the nephric duct breaks down and in its place a fibrous mass of tissue develops; this is the central mass which now lies in the blood of the pronephric sinus. A pair or two of glomeruli appear and at first bulge into the body cavity below the pronephric mass. Later each of these is enclosed in a pronephric chamber with a peritoneal opening into the coelom. The tubules of the shortened pronephros now begin to multiply by a budding process until the adult condition of hundreds of small funnels and tubules is attained.

Fossil agnaths In the cephalaspids a fossa in the rear wall of the head skeleton is thought to have been formed by a pronephric mass.

General observations Comparisons of the lamprey and myxinid kidneys are difficult. They agree in having the kidney extending through a large number of body segments; this is related probably to their eel-like form. They agree in having the nephric duct formed by segmental contribution rather than by growing back from the pronephric area. They agree in lacking "mesonephric" peritoneal funnels.

They differ, however, in many ways. The pronephros of the lamprey is never a blood-cell forming area, while the opisthonephros contains much hemopoietic tissue. The pronephros of the myxinid appears to function largely in blood-cell production and phagocytosis and is not connected with the excretory part of the kidney. The opisthonephros of the lamprey is quite complex in its structure with a suprarenal sinus separated from the excretory-lymphoid tissues of the kidney below and the postcardinal vein above. The glomerular band of the lamprey is a unique feature. The opisthonephros of the myxinid is simple, consisting of segmental tubules with glomeruli. The nephric duct is similar histologically to the tubule and apparently functions in **athrocytosis** (phagocytosis of certain large molecules), **resorption**, and **secretion.** The blood supply of the tubule has not been described, but probably there are small channels in the connective tissue sheath which are supplied by the renal arteries and drained by the renal veins.

The development of the kidney of the myxinid is unique and it is the simplest of the vertebrates. There is superficial agreement with the shark in that funnels form in all segments. However, the funnels are not the same, being pronephric throughout in the myxinid and peritoneal in the mesonephric region of the shark. The myxinid is peculiar in that an entire nephrotome is consumed in forming a definitive tubule and a part of the nephric duct. The simplicity of this kidney is probably related to the marine habitat and is not an indication of primitiveness.

The kidney of the lamprey is also specialized since funnels, of any kind, are not formed in the mesonephric region. The multiplication of glomeruli and the great hemopoietic development also suggests modification.

General observations on the excretory system

A clear picture of the evolution of the vertebrate excretory system is still lacking. It is usually suggested that the primitive system was a holonephros, with one or more tubules per body segment, extending the length of the body cavity. This view has some justification; however, there are other alternatives. It is quite possible that the original kidney was essentially a pronephros, each tubule functioning in the recovery of materials from the coelomic fluid as well as from the glomerular filtrate. The early appearance of this anterior region in ontogeny preadapted this kidney to serve the larvae of more advanced vertebrates, while progressively more posterior parts of the nephrogenic cord, still largely or entirely undifferentiated, developed into more elaborate and complex kidneys adequate for a larger and more active organism. Another view would be that the pronephric kidney is a larval specialization. It developed progressively more anteriorly, as a reponse to the advantage of the earlier differentiation of that region, with the result that it was able to satisfy the needs of larval forms with longer and longer periods of growth and differentiation. Differentiation included the production of a more complex kidney in the primitive kidney region situated well back from the pronephros.

The excretory system of Amphioxus as well as the general story of kidney ontogeny supports the first view, while the fact that the functional kidneys of all living vertebrates lie well back in the body cavity, separated by a gap from the pronephric region, gives some support to the latter. The holonephros theory appears to be largely a compromise supported by the developmental stages of some sharks and the myxinoids, types which do not seem to be particularly primitive in terms of their kidney structure.

THE REPRODUCTIVE SYSTEM

Mammals

The male The male reproductive system consists of **testis, efferent ducts,** modified tubules of the kidney, the nephric duct—now called the **vas deferens**—and accessory glands developed from the vas deferens (Figure 10-31).

The testis is a rounded mass whose interior is filled with lobules of looping and interconnected **seminiferous tubules** (Figure 10-32). Each lobule is encapsulated, along with the whole testis, in connective tissue, the **tunica albuginea.** The outer surface of the testis is smooth, without indication of the internal lobules. Several seminiferous tubule loops unite and enter a marginal network of tubules, the **central canal** or **rete testis,** by way of a **tubulus rectus** or straight tubule. Connecting the rete testis with the embryonic mesonephric kidney is a series of efferent tubules which pass through the supporting mesentery, the **mesorchium,** and enter the remains of a part of the mesonephric kidney. The modified kidney tubules, or **tubuli mesonephroi,** along with a part of the nephric duct, the **ductus epididymidis,** form the **epididymis.** The vas deferens leading back from the epididymis differs from its precursor, the nephric duct, in having an investment of smooth musculature. The vas deferens leads into the **urogenital sinus,** or **urethra,** through an enlarged area, the **ampulla.** Above or anterior to the entrance of the vas deferens into the urethra is the bladder. Also at this junction are the **seminal** vesicles and the **prostate gland.** The urethra distally passes through an intromittent organ, the **penis.** Bilateral **bulbourethral** or **Cowper's glands** enter the urethra behind the erectile tissue of the penis.

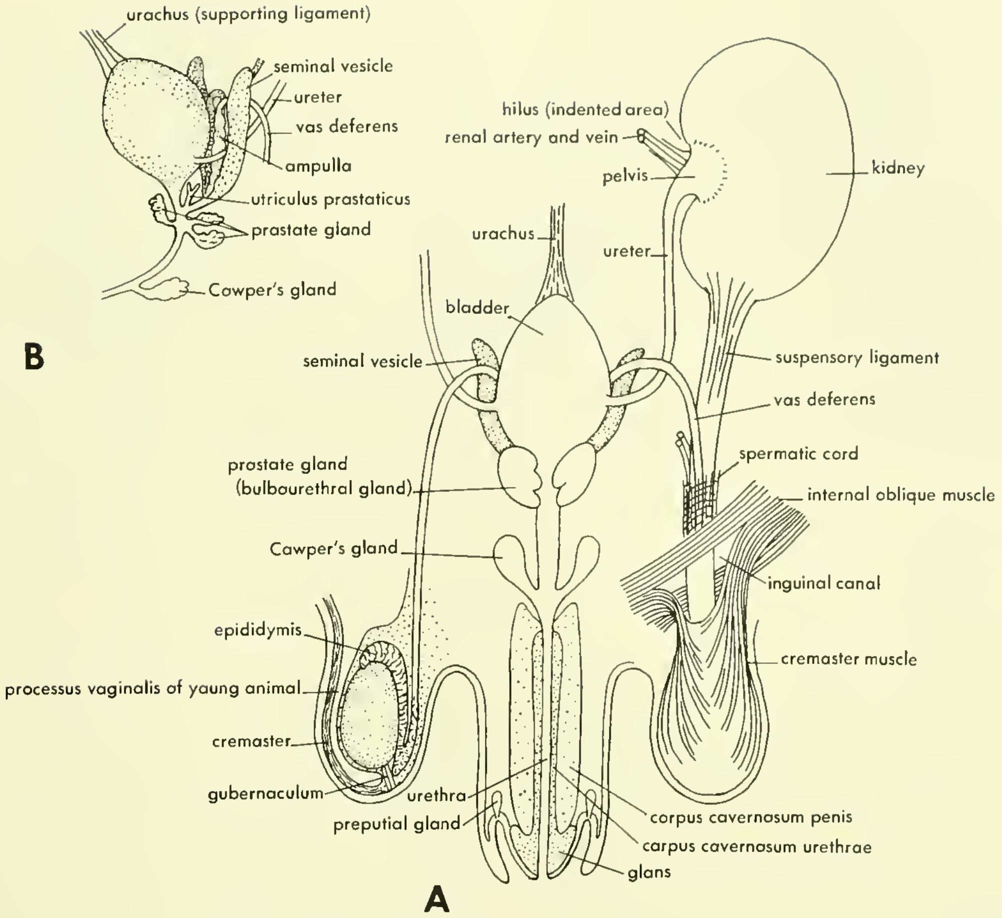


Figure 10-31. Urogenital system of a male mammal (man). A, semidiagrammatic system as seen fram below (or in front); B, lateral view of bladder region showing interrelatianships.

The embryological development of the male system is indicated in the above description and in the previous account of the kidney. Not mentioned are other remnants of the nephric ducts, the **appendix** of the epididymis and the **paradidymis** (Figure 10-32).

Müllerian ducts are rudimentary in the male. The anterior end remains as the **hydatid appendix** of the testis, while a bit of the midline tubule, where it enters the urogential sinus, remains as the **prostatic utriculus.**

Mammals characteristically have the testes in a **scrotum** outside the body cavity. The process of descent into the scrotum in man involves movement posteriorly (toward the caudal end) along the line of the genital ridge and between the peritoneum (lining of the body cavity) and the body musculature (Figure 10-33). This movement continues caudally, then across the posterior wall of the body cavity, and out through the muscular body wall at the inguinal canal (Figure 10-31). In this emergence from the body cavity the testis is accompanied by an outpocketing of the coelomic lining, the **processus vaginalis.** The testis carries strands of the

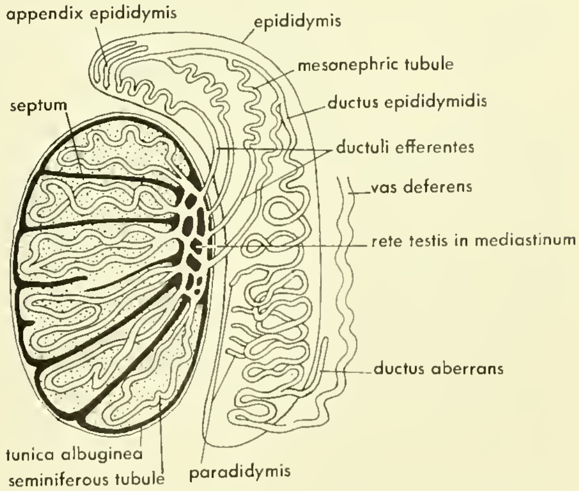


Figure 10-32. Testis tubules and connectians with nephric duct in man. (After Ham, 1957)

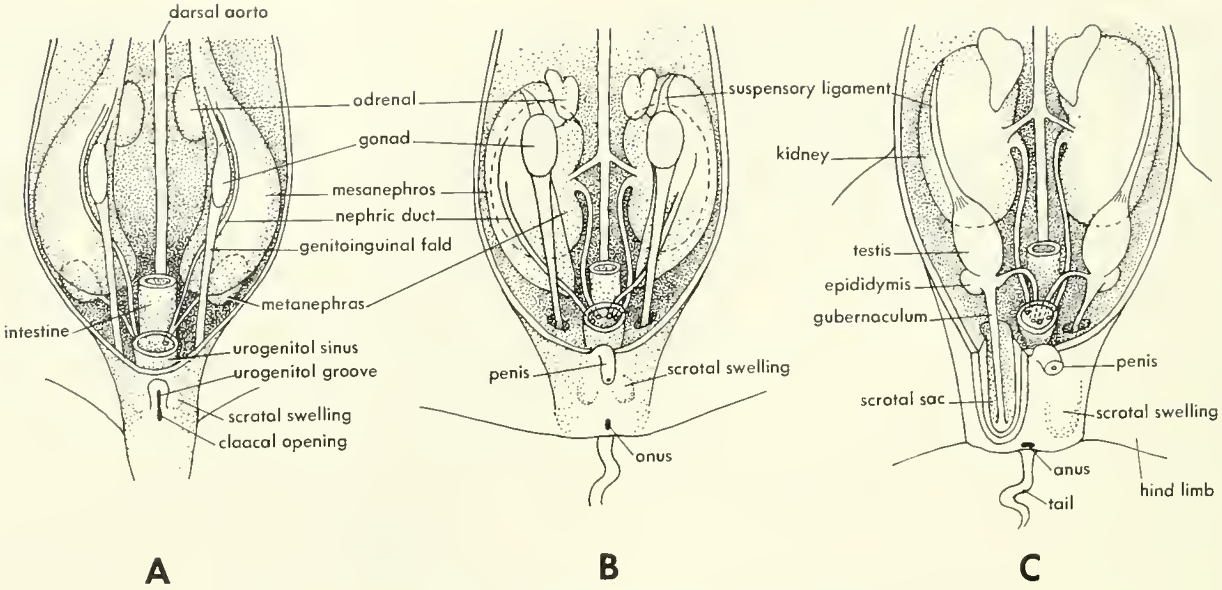


Figure 10-33. Three stages in the descent of the testes in the pig. (After Nelsen, 1953)

body-wall musculature before it, the **cremaster.** The testis now lies between the skin sac of the scrotum and the nearly enclosing processus vaginalis of the coelom. It is anchored to the scrotal wall by a ligament, the **gubernaculum testis,** and supported from the body cavity by the **spermatic cord.** This cord is a bundle of connective tissue anchored to the kidney region, and it encloses the ureter and the nerves and blood vessels passing from the body cavity into the scrotum. The processus vaginalis is closed off late in development from the body cavity at the inguinal canal.

Although the scrotum is characteristic of the mammal, it does not occur in all nor is the relationship between penis and scrotum the same. In the placental the scrotum lies behind the anteriorly directed and exposed penis, while in the marsupial the posteriorly directed, sheathed penis is behind the scrotum. In some mammals (many rodents), the testes descend into the scrotum during the reproductive period, while in others the testes are retained in the body cavity. This last is described by the term **testiconda.** Some of the placentals appear to have always been testicondate, whereas others may have secondarily returned to this condition.

The extreme of mammals is observed in the monotremes (Figure 10-34). In these the testes are retained in the body cavity in the primitive position, ventral to the kidney (Figure 10-37 A). The Müllerian ducts are complete although small in size, and the ureters and vas deferens open at the same level dorsal to the opening of the bladder. These openings may be on separate tubercles (Echidna) or on the same one (Platypus). The penis is an erectile tissue tube sheathed by the epithelium of the floor of the cloaca. The urinary sinus opens both through the penis and into the cloaca anterior to the penis. The glans is bifurcate at the tip, and the central canal opens through many small tubules on either division of this tip. The prongs of the glans are covered with small horny spines.

The marsupial agrees with the monotreme in lacking seminal vesicles. They are intermediate in that the penis may lie in a pouch in the cloaca (*Perameles*) or just below the nearly or quite separate anal opening (most marsupials) —the two openings are, however, enclosed by a common **sphincter muscle.** The penis may be tubular (*Perameles* and many marsupials) or may have a dorsal groove for passage of the sperm (*Didelphis,* the opossum). In the opossum the excretory duct is no longer connected with the cloaca; it opens at the base of the grooved penis. In the kangaroo the penis is like that of the placental, tubular and serving both excretory and reproductive products. The glans of the marsupial penis is usually bifid, but not in *Dasycercus.*

The female The female system of the mammal consists of the **ovary,** the **oviducts,** the **uterus,** and the **vagina** (Figure 10-35). The vagina opens directly to the exterior in most mammals between the urethral opening and the anus. In front of the urethral opening is a clitoris, which represents a rudiment of the penis, and to either side are **labia** representing the folds between the urogenital and anal divisions of the cloaca and the outer margin of the cloacal aperture.

The ovary in its development differs from the testis in that the **medullary cords** are poorly developed, while the **cortex** becomes the dominant tissue in which the **germ cells** develop. The medullary cords are of mesonephric blastema origin, while the cortex is produced by thickening of the epithelium overlying the **genital ridge.** The cortex retains a thin overlying germinal epithelium. The large germ cells lie at first in the epithelium but later penetrate the gonad as it differentiates and separates from the mesonephros.

In the male the medullary cords, infiltrated with germ cells, form the seminiferous tubules, while in the female the medullary cords are repressed. Clumps and strands of cortical cells, with germ cells among them, become partly enclosed by thin strands of medullary cells. The medullary strands supply **thecal** (encapsulating) **cells** to the cortical cords in which the nests of female germ cells develop. Late in development the ovary moves posteriorly below its peritoneal cover. Its suspensory ligament marks this movement. It still remains in contact with the body wall, but the oviduct now loops below and in front of it (Figure 10-37).

The **Müllerian ducts** form the tubular portion of the female system, conducting the egg from the ovary, supplying it with the proper environment for its development (uterus), and aiding in fertilization by means of a copulatory pouch, the vagina. The Müllerian ducts appear relatively late (20 mm) in man and develop by a process of infolding, beginning at the anterior end of the mesonephros and extending posteriorly. It should be noted that the ostium of this tube lies well anterior to the genital part of the mesonephric kidney.

The first evidence of this duct is a thickening of the epithelium of the kidney next to the nephric duct. This thickening forms a groove (Figure 35 A) which closes over, except at its anterior end, the **ostium.** This process of invagination and tubulation extends back along the kidney through the **genitoinguinal fold** to the midline anterior to the urogenital sinus. Here the two ducts unite and extend back to enter the urogenital sinus just in front of the nephric duct (see Figure 355, Patten, 1946). The genitoinguinal fold has been modified by the medial movement of the posterior end of the Müllerian ducts. From the anterior end of their fused area a fold now extends to the inguinal region, passes out through the inguinal canal, and ends in the labia majora. This is the **round ligament** of the uterus, corresponding in part to the gubernaculum of the male.

The vagina represents the terminal part of the fused Müllerian ducts. This region is separated from the thick-walled, glandular uterus by the **cervix.** The uterus opens laterally into the two tubes (oviducts or Fallopian tubes). These tubes open into the body cavity through a flaring ostium with **fimbriated** (frilled) margins. Remnants of the

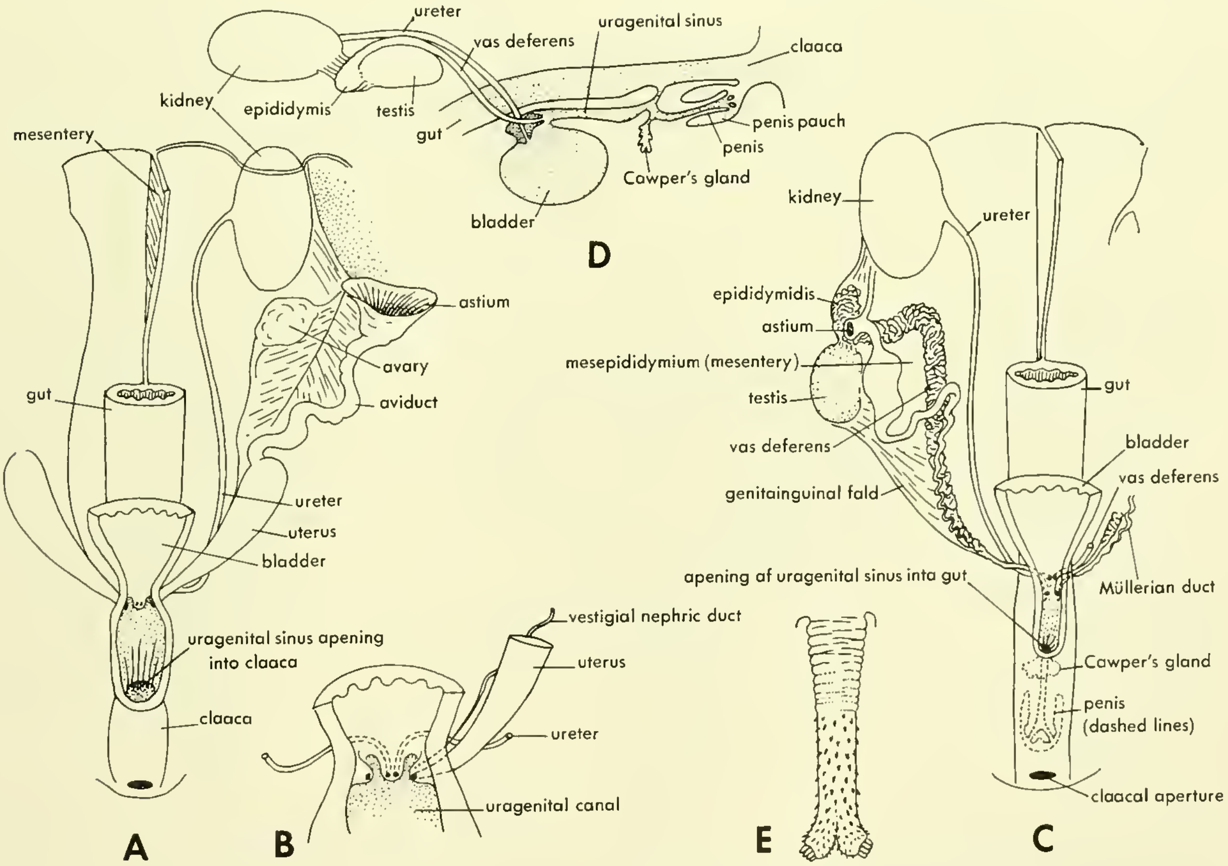
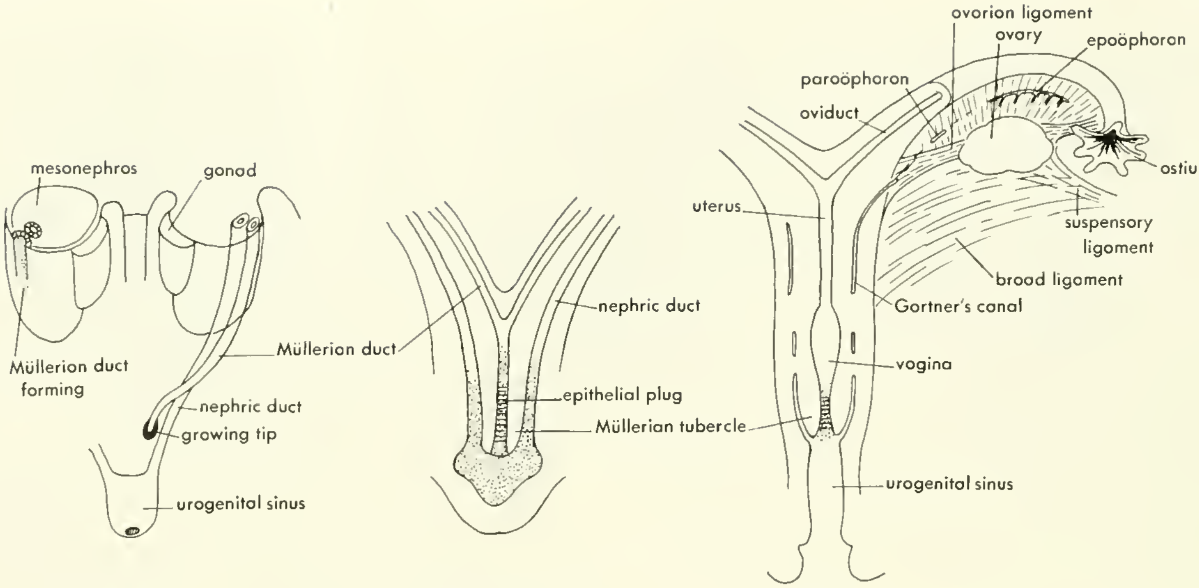


Figure 10-34 Uragenital systems in bath sexes af the Echidna (*Tachyglassus*). A, female in ventral view; B, details of tubes apening inta uragenital canal; C, male in ventral view; D, male in lateral view; E, bifurcate, spinaus penis. (A, after van den Braek, 1933; E, after Grassé, 1955)

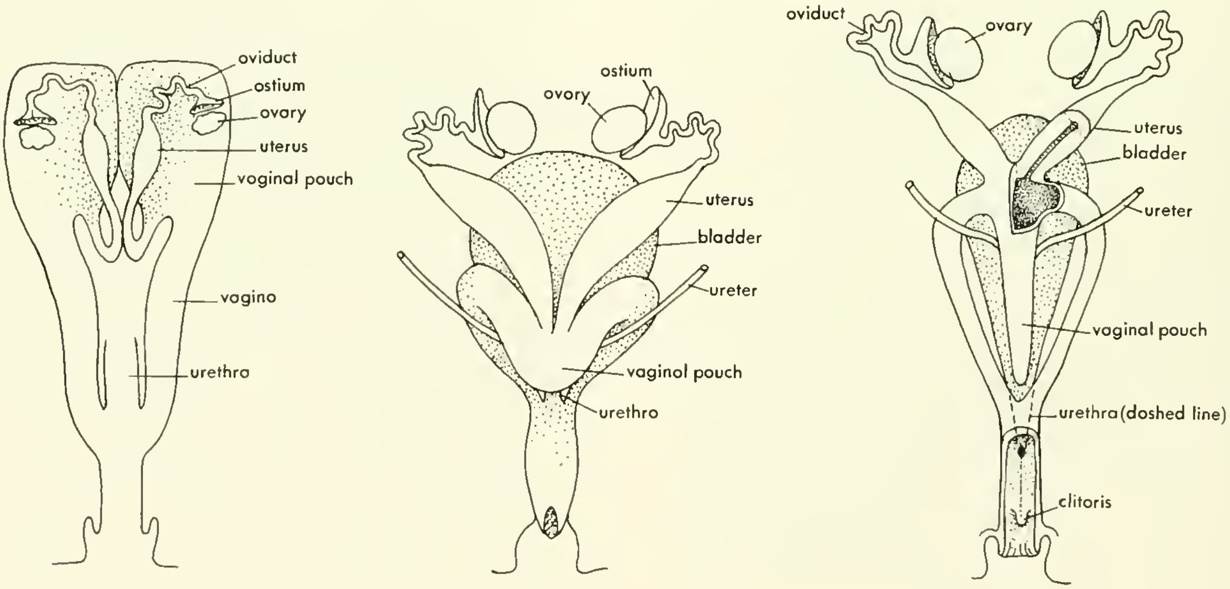


A 23 mm **B** 32.9 mm **C** 69 mm

Figure 10-35. Three stages in the development of the human female reproductive tract. (After Patten, 1946)

mesonephric kidney are evidenced in the **epoöphoron, paroöphoron** of the young, and **Gärtner's duct** (part of the nephric duct) in the early foetus.

Like the male, the females of mammals show marked variations. The monotreme lacks a vagina, using the urogenital sinus and the cloaca as a copulatory tube (Figure 10-34). The two uteri open laterally into the urogenital sinus well anterior to the cloaca. A vestigial nephric duct is



A **B** **C**

Figure 10-36. Female tracts of three kinds of marsupials as seen from below. A, *Perameles;* B, opossum; C, *Halmaturus* or *Macropus.* (A After Grossé; B in part from Bolk et al, 1933; C after van der Broek, Bolk et al, 1933) retained. The oviduct in this group secretes albumin and applies a shell to the eggs as in the reptilian antecedents of the mammals.

The genital tract of the marsupial is similar except that the cloaca is much reduced (Figure 10-36). The urogenital and anal openings, the former below the latter, are contained in a shallow cavity closed by a sphincter. The genital system is bipartite. The terminal part of the Müllerian duct, opening into the urogenital sinus, is differentiated into a thin-walled vagina. Each vagina forms an S-shaped loop, coursing first laterally, then posteriorly, then medially and anteriorly. Anteriorly the vaginae usually meet at the midline above the bladder and fuse. The vaginae remain separate in *Perameles* and the wombat and also in some species or individuals of opossums. In the Virginia Opossum or in *Dasycercus*, fusion occurs only between the posterior parts of the medial limbs, while in the kangaroo and many other species fusion produces a large medial chamber or pouch into which the uteri open. This medial pouch extends forward and may contact the urogenital sinus and even open into it as a medial vagina. In some species, such a medial opening is formed only at the time of birth of the young when the young rupture through the walls of the pouch and sinus. A similar event occurs in the wombat where young can rupture from either vaginal loop into the urogenital sinus.

The thick-walled uterus continues the duct forward and laterally from the vagina or from the medial vaginal pouch. The duct has a tube section and a fimbriated ostium.

Among placental mammals there is some variation of structure. Most have a single medial vagina opening to the exterior separately, or nearly separately, from the urethra, the exceptions being the sloth, anteater, armadillo, the rodent *Pedetes,* and the rabbit-like pika. The tubular uteri may open separately into the median vagina as in the rat; this is the **duplex** condition. The uteri may be fused posteriorly and open together into the vagina, while anteriorly they extend as separate tubes to either side; this is the **bipartite type** (pig). When the uteri are more extensively fused and have but short lateral extensions, this is the **bicornuate type** (horse, cat). Complete fusion without distinct horns—with only the thin-walled tubes extending away to either side—identifies the **simplex type** (man).

The gonad of the male or female arises from a genital ridge associated with the kidney. This interrelationship in the two sexes and the different kinds of mammals is summarized in Figure 10-37.

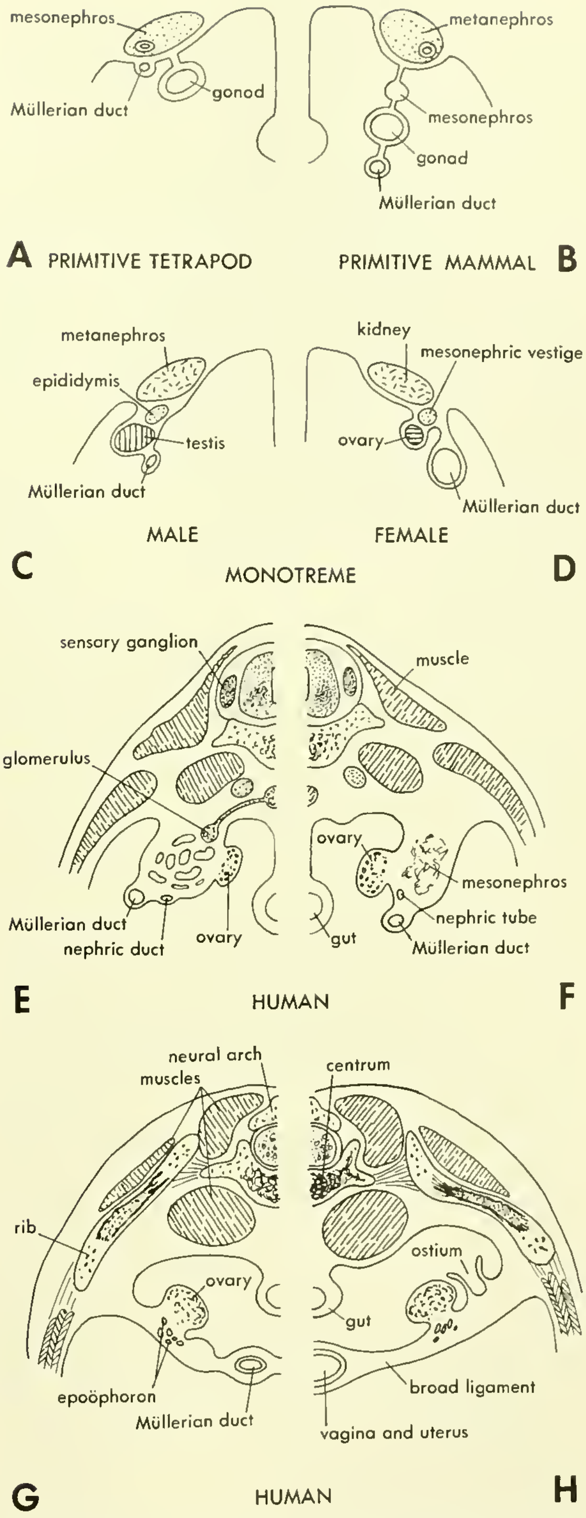


Figure 10-37. Cross sections of a hypothetical primitive tetrapod and several kinds of mammals to show the interrelationships between the kidney stages and the reproductive tracts of males and females. (After van den Broek, and Patten, 1946)

Reptiles and birds

The male The male reptile has the testis suspended in the body cavity like the primitive mammal (Figure 10-8). In the interior of the testis, the looped, but not anastomosing, seminiferous tubules open into a central net or canal which connects through the efferent tubules with the marginal canal of the mesonephric kidney. From the marginal canal the coiled tubuli mesonephroi lead to the ductus epididymidis, the anterior end of the nephric duct. The many variations in the testis-kidney connections suggest great plasticity of development in this area.

The epididymis is well developed and may extend far posteriorly before giving way to the slightly convoluted vas deferens. The deferent duct joins the ureter of its side, and they open together at the tip of a urogenital papilla. The ducts of either side open through separate papillae. In some reptiles the ureter and vas deferens open separately into the urogenital sinus. The urogenital sinus may be only a pocket of the cloaca lying behind the openings of the anus and the ventral bladder. A vestigial Müllerian duct lies along the body wall lateral to the testis and reproductive tract in general.

Two different kinds of intromittent organs are found in reptiles, but Sphenodon lacks such a structure. The lizards and snakes agree in having **hemipenes.** These are bilateral sacculations of the cloaca (Figure 10-8 B). These sacs extend posteriorly below the skin. When everted, one at a time, they protrude through the cloacal aperture. The distal end is large and rounded, and the stem tapers to a narrow base which attaches at the anterolateral cloacal wall. The structure is grooved to conduct the sperm from the cloacal cavity of the male to that of the female, into which it is everted. The surface of the everted hemipenes is studded with spines.

In turtles and crocodilians there is a grooved penis in the floor of the cloaca (Figure 10-38). This contains fibrous and perhaps erectile tissue, a **corpus fibrosum.** The penis of the turtle is suggestive of that of the primitive mammal, except that it is not sheathed in a pouch. That of the crocodile is simpler and like that of the bird.

The testes of the bird are comparable to those of the lizard (Figure 10-10). The testis lies below the anterior part of the kidney rather than anterior to the kidney. Connection with the kidney tubules involves an irregular cavity, the **antrum,** into which the tubuli recti of the seminiferous tubules open on the one side and from which on the other side a number of efferent ducts (10 to 12) pass into the epididymis. The antrum represents the rete testis.

The deferent duct opens posteriorly into the proctodeum, just as in the crocodilian. In the males of most of the perching birds, the terminal part of the duct becomes quite elongated and coiled at the breeding time. A "glomus," or tubular mass, is thus formed, which, along with the terminal ampulla of the duct, causes the cloacal aperture to bulge outward.

In the bird, but also in reptiles and many mammals, the testes undergo a drastic change in size during the course of the year. In the nonbreeding period they are much smaller than at the breeding time.

The female The ovary of the reptile differs only in that very large, yolked eggs are produced (Figure 10-9). As a re-

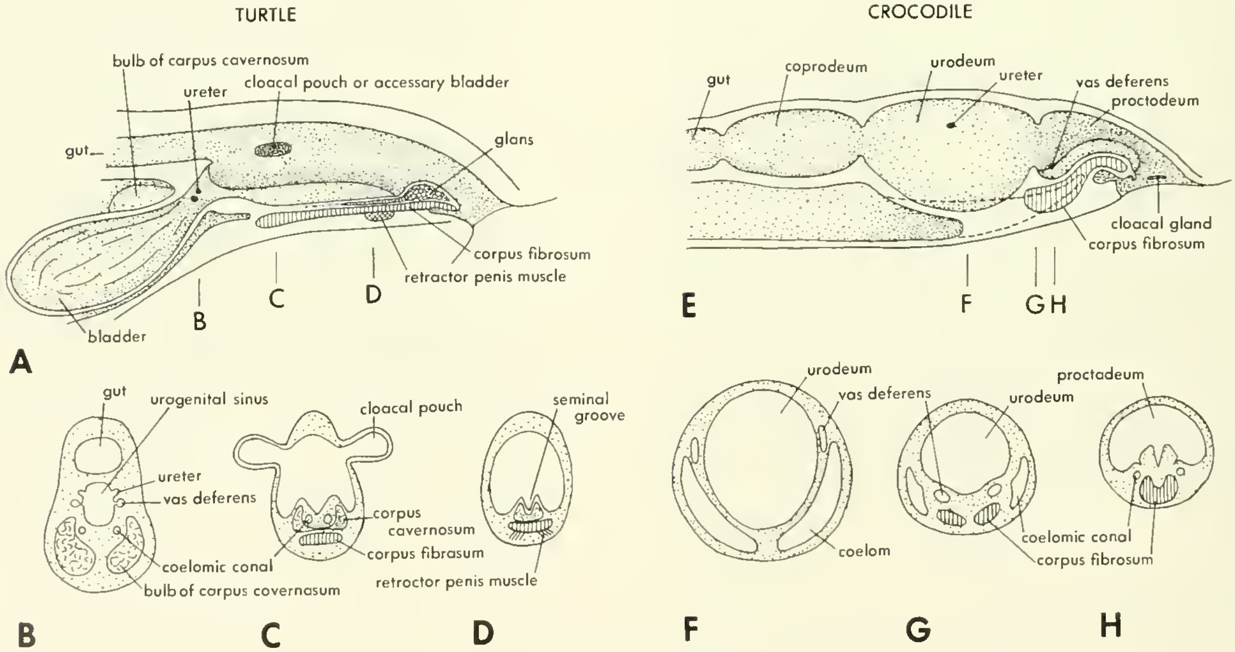


Figure 10-38. The penis of the turtle and crocodile. A, sagittal section through cloaca of turtle; B, C, D, three cross sections (indicated in A) showing interrelations of parts; E, sagittal section of cloaca of crocodile; F, G, H, three cross sections (indicated in E) showing interrelations of parts. (After Ihle et al, 1927)

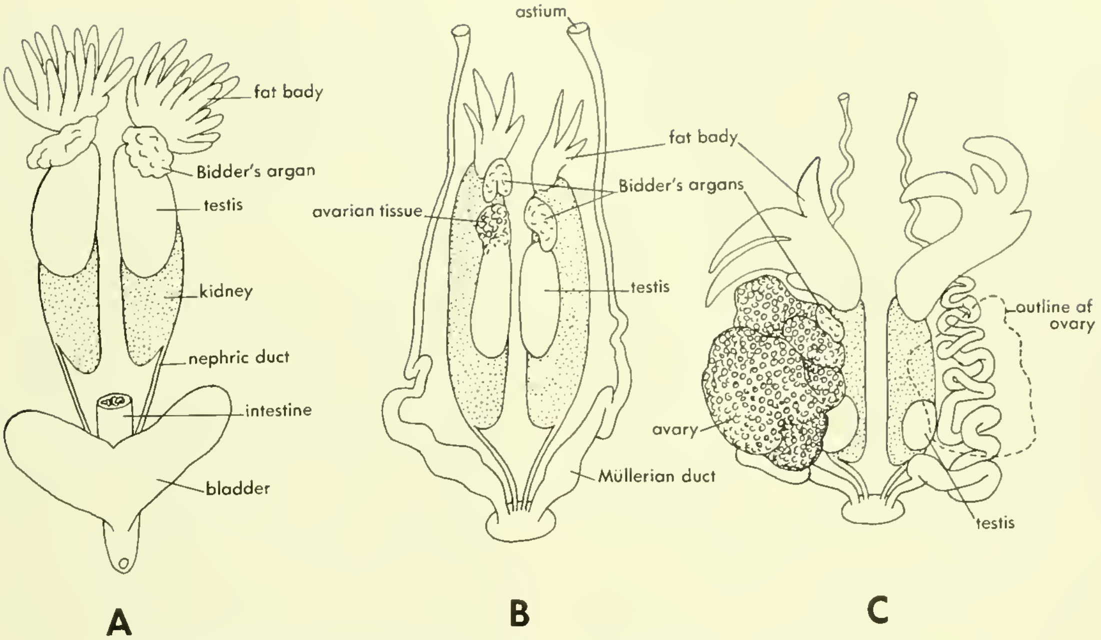


Figure 10-39. Reproduction system of the toad (*Bufa vulgaris*). A, normal male toad; B, hermaphroditic male; C, hermaphroditic female. (After van den Broek, 1933)

sult, single follicles are frequently larger than the entire inactive ovary. The Müllerian ducts consist of five sections: ostium, tube, isthmus, uterus and vagina. The **ostium** opens anterior to the ovary and leads into the **tube portion,** which is folded and pleated and loops anteriorly, then medially, and then back. The tube tapers to the narrow third part, the **isthmus** which leads into the thicker-walled **uterus.** The terminal, thin-walled **vagina,** extends to the cloaca into which it opens separately from that of the other side. The urogenital part of the cloaca lies posterior to the gut opening. This posterior portion, the urodeum, is produced by upward and backward movement of the point of entrance of excretory and reproductive ducts.

The bird differs in that the right ovary is usually rudimentary, the left producing all the ova. Paired ovaries are present in only a few birds of prey. The right oviduct is also vestigial. Vestigial deferent ducts are sometimes present in the female.

Amphibians

The male The testis is a smoothly rounded mass in the anuran (Figure 10-39), but in the salamander it may be elongated (Figure 10-11), divided into two or more lobes, or even separated into a longitudinal series of **testicules** as in the apodan and salamander *Desmognathus.* In the development of such strands of testicules, new units bud off toward the head; one for each year in some species.

In the bufonids (the toads), there is a **Bidder's organ** at the anterior end of the testis, and in front of this a digitiform (with finger like extensions) **fat body.** In the frogs only the fat body is present. In salamanders and apodans fat bodies occur medial to the gonad or ventral to the gonad.

The internal anatomy of the testis is like that of the reptile but less complex. The short seminiferous tubes have a wide lumen and end blindly; in some species they can be described as ampullae. Several ampullae or tubules converge to a ductus rectus, which in turn enters the central canal lying along the line of the supporting mesentery. The efferent ducts are of varying number and extend to the marginal canal of the kidney. This canal is derived from outgrowths from the capsules of the primary tubules of the anterior part of the mesonephric kidney—but not the most anterior part. The tubuli mesenephroi, or mesonephric tubules, extend to the epididymal duct. The efferent ducts develop from the strands of mesonephric blastema left behind in the separation of gonad and kidney. The kidney tubules carrying sperm retain their glomeruli in the apodan and the salamander *Spelerpes* but lose them in most amphibians. A distinct epididymis is developed in *Necturus* but not in all salamanders. The nephric duct may be quite thickened and may enter the cloaca separately without an ampulla. A Müllerian duct lies along the nephric duct in the male.

The female The ovary is an irregular, elongate mass in which there is a single cavity (urodele) or many (10 to 30) cavities (anuran). The eggs are not ruptured into the central cavity of cavities but into the body cavity. The Müllerian duct of the young female is not much larger than that of the male. In the mature animal it becomes swollen and very convoluted; it extends through the entire length of the body cavity. The eggs enter the ostium and traverse this duct, where they acquire their jelly coating in oviparous types. In viviparous types the eggs develop in this tube. Several species of *Salamandra* and *Spelerpes fuscus* are viviparous, as are the apodans *Typhlonectes compressicauda* and *Dermophis thomensis.* The tubes can be divided into an ostium, an infundibulum (with a thin wall, wide lumen, and no glands), a tube (with glands in those forms which lay eggs, or no glands but mucous cells in the viviparous types), a uterus (with a much folded epithelium forming a reticular pattern and a wide lumen), and a vagina. The last is a short section between uterus and cloaca. The Müllerian ducts open into the cloaca on a papilla lateral to the opening of the nephric ducts. These ducts arise as in the higher forms.

General observations In the development of the amphibian gonad, the **genital ridge** forms on the ventromedial or medial aspect of the mesonephric kidney bulge. This ridge extends much of the length of the mesonephros and may be considered as having three areas: anterior **progonalis,** middle **gonalis,** and posterior **epigonalis** (Figure 10-40). The definitive gonad develops from the middle area in all tetrapods. The **fat bodies** of urodele and apodan represent a part of the entire band, whereas in the anuran, only the progonalis gives rise to the fat body.

Bidder's organ develops in all males and some females of the toad family, Bufonidae. This organ develops from the gonalis section just anterior to the definitive gonad. The function of the organ is not known but is assumed to be endocrine since this structure undergoes an annual cycle of size change, decreasing in size prior to the reproductive period. This change in size is more marked in the female than in the male, but since females of only a few species have the organ while all of the males have it, this difference in size change is not as meaningful as might be assumed at first glance. Bidder's organ is known also to have the capability of developing into an ovary when either sex is castrated.

In the development of the gonad, germ cells first appear as a band just dorsal to the enteron (gut cavity), ventral to the aorta, and between the two lateral mesoderm plates. This band of yolk-laden germ cells lies at the dorsal root of the gut mesentery and can be observed in the serial sections of the 10-mm frog (Figure 10-16 C).

The germ ridge separates into two strands which move laterally and form slight folds on either side of the median line. These folds constrict basally so that a suspensory ligament is formed. As seen in cross section, each gonad consists of one or two large, yolk-laden germ cells with a few small heavily staining peritoneal cells around them. The whole is enclosed by the germinal epithelium.

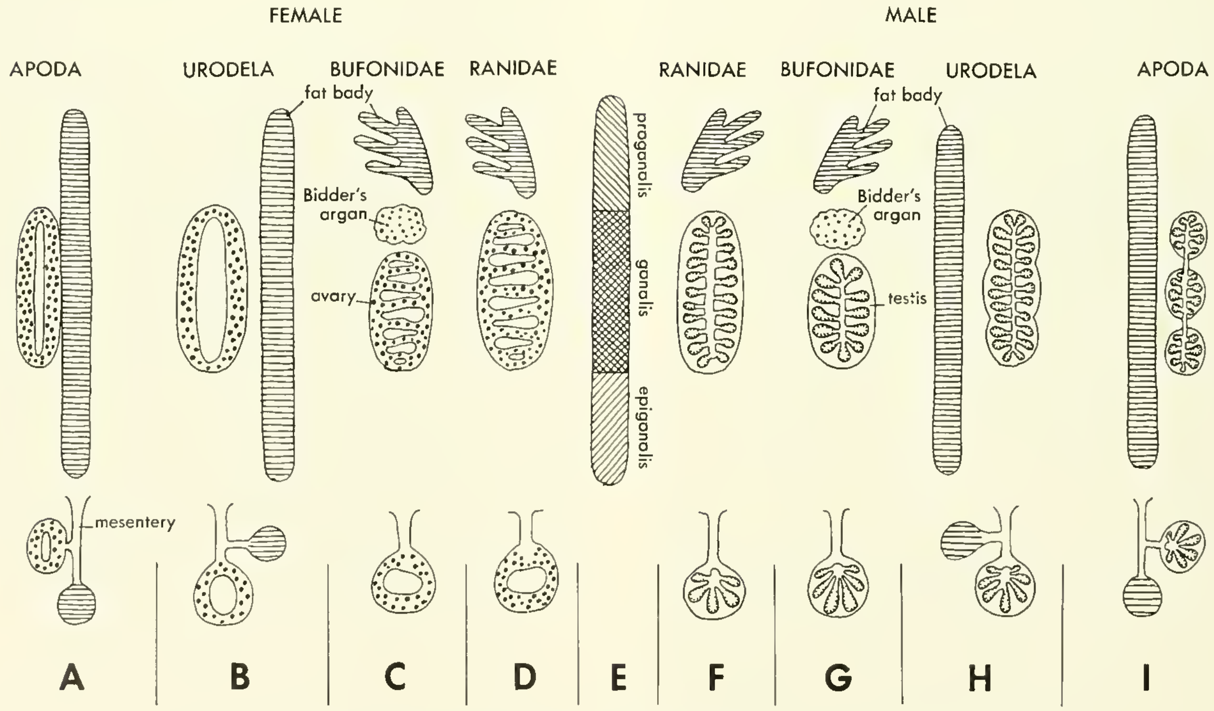


Figure 10-40. Relationships of gonad, fat body, and Bidder's organ derived from gonadal ridge in amphibians. Cross sections show interrelationships to mesentery of gonadal ridges. For orientation, the midline of the page corresponds to the midline of the animal and the margins are lateral. (After van den Broeck, 1933)

The gonad ridge increases in size both by division of the contained cells and also by migration of cells from the medial border of the mesonephros. These migrating cells move down through the supporting mesentery and enter the gonad. The migrating cells form segmental masses which fill the interior of the indifferent gonad, which now has a **cortex** of germ cells embedded in epithelial cells and is enclosed in a thin epithelium. At the anterior and posterior ends of the gonad, the progonal and epigonal portions, sex cells are lacking.

Near the center of the gonad, small openings or rifts appear between the cortical mass and the medullary sex cords. These soon widen and join to form the genital cavity or **gonocoel.** The simple gonocoel is essentially retained in the development of the ovary, while in the testis it is replaced by tubular channels arising within the mass of **sex-cord** or **medullary cells.**

In the development of the ovary, the amount of mesonephric tissue entering the gonad is small. As growth proceeds, this medullary tissue forms relatively less of the organ although it does increase in absolute amount. The cortex develops from the single layer of germ cells of the indifferent gonad to one with several layers; large **oocytes** form clumps, or **egg nests,** within this cortex. The **ovocoel** (gonocoel of ovary) is divided into many compartments enclosed by medullary cells.

The testis may develop directly or indirectly. In direct development the germ cells move out of, or are taken out of, the thin cortex by the sex-cord strands and as a result lie scattered throughout the interior of the gonad among the medullary cells. After the sex cells form clumps, a rift appears in each clump, forming the cavity of the ampulla, which is enclosed by the sex-cord cells. The ampulla elongates to form a tubule which is connected with the rete testis formed in the medullary mass along the **hylus** of the gonad, next to the supporting mesentery. The efferent tubules arise from strands of mesonephric cells in the mesentery connecting the rete with the marginal canal of the kidney.

Indirect development occurs in many races of frogs where it may be the only method or only a rare aberration. In this type of development, a gonad appears which at first tends toward cortical development; it produces lobules of cells comparable to the egg nests of the ovary. This gonad also has medullary tissue, enclosing the gonocoel, and this tissue contains sex cells. In form it is elongated like the ovary but is somewhat more irregularly shaped. The female tissues are better developed anteriorly and essentially undeveloped posteriorly. Later the central sex-cord area, enclosing the now subdivided gonocoel, develops along with its enclosed germ cells. The cortical material aborts as this process goes on and a definitive testis results.

Hermaphroditism (Figure 10-39) is occasional in adults as a result of failure of the sex-directing mechanism to convert the indifferent gonad to one sex or the other. In these, the anterior part of the gonad is female, while the more posterior parts are male. This agrees with the anterior-posterior sexual gradient observed in bufonids.

Choanates

Actinistian In *Latimeria* the right testis is two or three times larger than the left but both produce sperm. The right testis extends through the middle quarter of the body cavity ventrolateral to the swim bladder. The epididymis is small and leads to the vas deferens, which enters the cloaca separate from the urinary sinus.

The ovary of the female has a central cavity. The Müllerian ducts have not been described. In both sexes, masses of hemopoietic tissue are associated with the reproductive tract as well as with the viscera in general. In this respect the coelacanth resembles the other fishes.

Dipnoan

THE MALE The testis of *Lepidosiren* is an elongate mass, round in cross section and enclosed in fatty tissues. It lies somewhat lateral to and below the kidney; its anterior half is in contact with the body wall, while its posterior half is suspended by a mesorchium.

Internally it is formed from a large number of radially arranged ampullae opening into a central net of canals lying along the dorsomedial margin next to the supporting septum. The central net extends back as an elongate band of tubules closely bound to the kidney tissue. From this band, efferent tubules extend into several of the posterior segments of the kidney; these connect with the glomeruli of the nephric tubules at the time of breeding. The cranial end of the Müllerian duct, with an ostium, is present in the young male but is lacking in the adult.

The testis of *Protopterus* is proportionally larger than that of *Lepidosiren* (Figure 10-41). It extends the entire length of the body cavity as a thick band, closely and broadly bound to the kidney above and hanging free in the body cavity below. Anteriorly it is bound to the body wall and appears to be largely lymphoid in nature. The right gonad is attached anteriorly to the liver. The left gonad extends forward to the region of the duct of Cuvier. Posteriorly it is rounded off but has a short tubular extension. The seminiferous tubules are much longer than the ampullae of *Lepidosiren.* The tubules enter a central canal which extends along the dorsomedial margin of the organ and beyond the posterior end of the testis. The canalicular or rete extensions of right and left testis unite to form a median tube, which ends blindly just anterior to the urinary papilla (Figure 10-41 B). From this terminal pocket, efferent ducts enter the kidney to right and left and connect with a large number of renal capsules of the last two segments. The cranial and caudal ends of the Müllerian ducts remain; the remnants fuse at the midline but do not enter the urinary sinus.

The testis of *Neoceratodus* is long and thick, tapered ante-

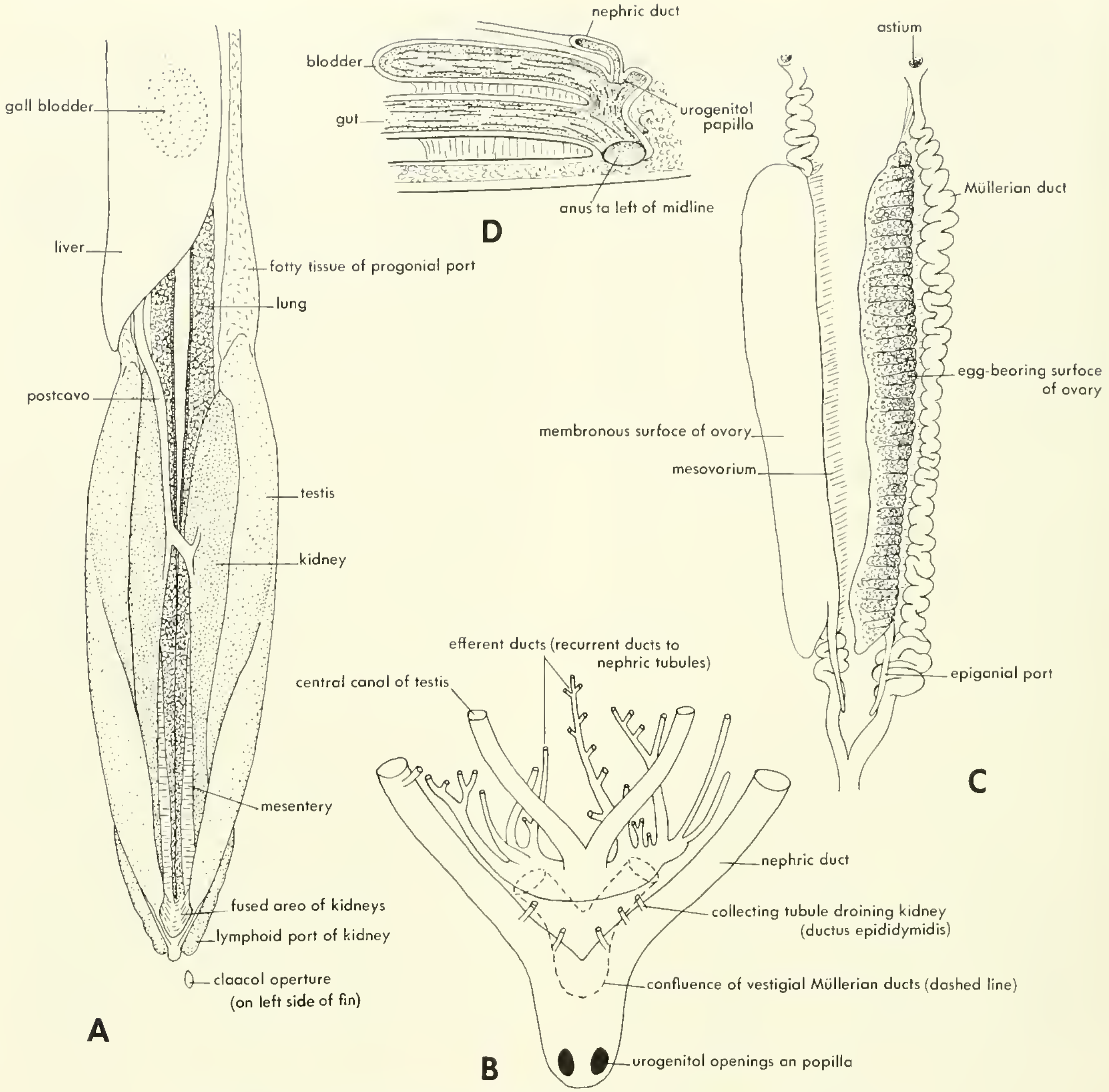


Figure 10-41. Urogenitol system of lungfishes. A, ventrol view of *Protopterus* with gut removed; B, details of tubule relotionship of posterior end of A; C, sogittol view of cloocol region of A; D, femole system of *Neoceratodus*. (B, ofter Kendohl, 1938; D, ofter Gunther, 1871)

riorly and posteriorly, and triangular in section. The right testis is attached to the tip of the liver. The testis of either side is supported by a short mesorchium, its posterior half lying below the anterior half of the kidney. The seminiferous ampullae are long, radially arranged, and open into a central (dorsomedial) canal. Many efferent ducts extend from the central canal into the kidney and connect with capsules of the nephric tubules. The renal corpuscles of these tubules are retained and apparently remain functional as in the other lungfishes.

The Müllerian duct is present, lying along the broad, dorsolateral surface of the testis. Posteriorly the Müllerian duct passes below, then lateral to the nephric duct, and from here to the midline where it fuses with that of the opposite side. The common sinus thus formed ends blindly in front of the cloaca.

THE FEMALE The ovary of *Protopterus* or *Neoceratodus* is long and hangs down from the body wall as a band; the eggs are shed from its lateral aspect. There is usually a distinct epigonal extension. In *Neoceratodus* the ovary is bound anteriorly to the dorsal body wall (Figure 10-41 D); in *Protopterus* it is suspended by a short mesovarium. The convoluted Müllerian duct lies lateral to the ovary; its slit-like fringed ostium opens into the anterior end of the body cavity. Posteriorly the duct has a straight expanded section, the uterus. The two ducts unite to form a short median vagina which enters the urogenital sinus through the tip of a papilla.

The ovary in the dipnoan agrees with that of fishes but differs from the sacciform ovary of the amphibian, where the eggs are shed from all surfaces.

Actinopterygians

Teleost

THE MALE The testes of the teleost are long and rounded in section; they extend nearly to the cloacal region. In texture they are finely granular as opposed to the coarsely granular or distinctly egg-laden ovary of the female. In fine structure there is usually a central cavity into which radially arranged short pouches (ampullae) or tubules open. The tubules may join together as they extend posteriorly, so that a central cavity as such is not present. In syngnathids the testis is a simple tube.

The testis is not connected to kidney tubules, rather the central canal, of whatever form it takes, extends posteriorly lateral to the swim bladder and urinary bladder (Figure 10-43). Eventually the ducts of either side join and open to the outside between the anus and excretory openings. In the cod the posterior ends of the testes are joined and a single duct extends to the genital opening. In some fishes the more posterior tubules of the testis are secretory and may be identified as seminal vesicles (Weisel, 1949).

The opening of the male genital sinus sometimes differs from what has been described. It may open into the urinary bladder as in muraenids and *Anableps;* into the excretory sinus in blennies, the salmon, perch, and many others; into the anal margin in *Lota;* and into the joined anal and excretory opening in syngnathids (i.e. into a cloaca).

THE FEMALE Ovaries in the teleosts are of two types: simple bands hanging down into the body cavity, or saccular. The latter are of two varieties: the **parovarial** is formed by the free margin of the genital fold bending laterally and fusing with a fold from the body wall (Figure 10-42 A); the **endovarial** type is formed by the ventral margin curling laterally to meet a fold from the upper margin of the gonad (Figure 10-43). This folding of the genital ridge is observed in the ovary of the salmon and in the region posterior to the ovary where a separate oviduct is produced in the salmon or *Osmerus*.

The oviduct can be of the endovarial variety (Figure 10-43 B), attached to the lateral aspect of the swim bladder in front and the urinary bladder behind. Both swim and urinary bladders are suspended in the medial septum. In either position, body wall or down on the swim bladder, the oviducts unite to form a genital sinus opening to the outside between anus and urinary apertures. In the cod the two ovaries join posteriorly and utilize a single oviduct. Not all females have saccular ovaries with oviducts. In the salmon the ovary is a free band, or parovarial. The eggs pass from the body cavity into a funnel lying above the rectum and below the urinary bladder; this funnel opens between the anus and excretory pore (Figure 10-44). The funnel is formed by membranes extending out and upward from the terminal part of the intestine to the body wall; the dorsal mesentery of the gut is lacking in this region. In the muraenids the ovary is a simple fold; the eggs form on the lateral aspect and are shed into the coelom. Exit from the body cavity is by bilateral slit-like openings behind the anus. These openings are in the general position of the abdominal pores of other fishes.

Polypterus The male has an elongate testis closely connected with the kidney (Figure 10-45). The central canal begins anteriorly and in the thin posterior continuation there is an interconnected set of channels. Posteriorly a single duct emerges and, following the wall of the nephric duct, opens in the urinary sinus.

The male of *Polypterus* appears to be comparable to the male teleost in having the central canal extended posteriorly through the epigonal region, not to a separate pore, however, but to the cloaca. The posterior part of the male duct has been assumed to have arisen in a parovarial style.

The female has an elongate, band-like ovary hanging down into the body cavity from its mesovarium (Figure 10-45 B). There are numerous ridges on the outer surface from which the eggs are shed into the body cavity. The oviduct lies lateral to the mesovarium, in the region of the posterior half of the ovary. It follows the course of the nephric duct to the posterior end of the body cavity, where it opens into the urinary sinus almost where that sinus opens into the cloaca. The oviduct is like that observed in the following actinopterygians.

Amia and Lepisosteus In males of *Amia* and *Lepisosteus* the testis is long, band-like, and rounded at either end (Figure 10-46). It is attached by a broad mesorchium through which numerous efferent ducts pass into the kidney. The nephric duct shows no modification as a vas deferens.

The ovary is suspended by a broad mesovarium in which there are strands of tissue resembling the efferent ducts of the male. The ovary of *Amia* differs markedly from that of *Lepisosteus* in that it hangs free in the body cavity. From its lateral, ridged surface the ova are shed into the body cavity and carried to the cloaca through the large membranous

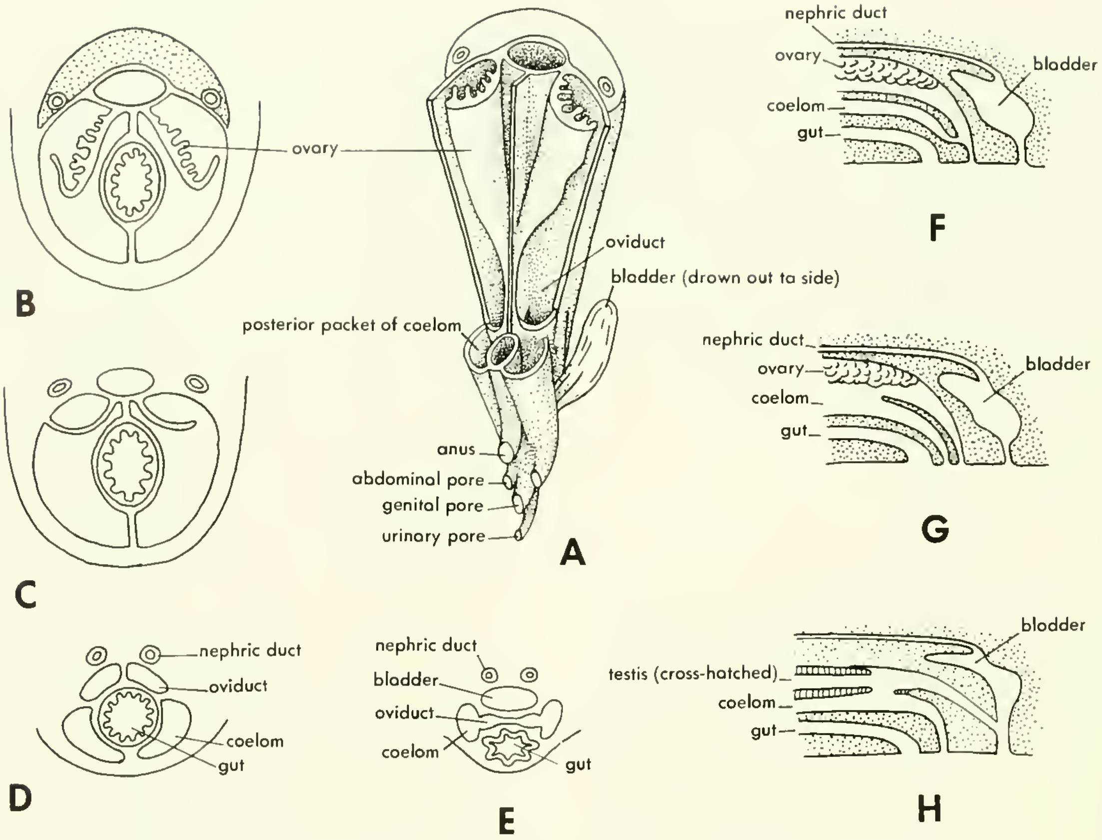


Figure 10-42. Structure of the reproductive tracts of teleosts. A, semidiagrammatic ventrolateral view of typical female system; B, C, D, E, cross sections at the levels indicated in A; F, sagittal section of typical female; G, sagittal section female salmon; H, sagittal section of male salmon. (After van den Broek, 1933)

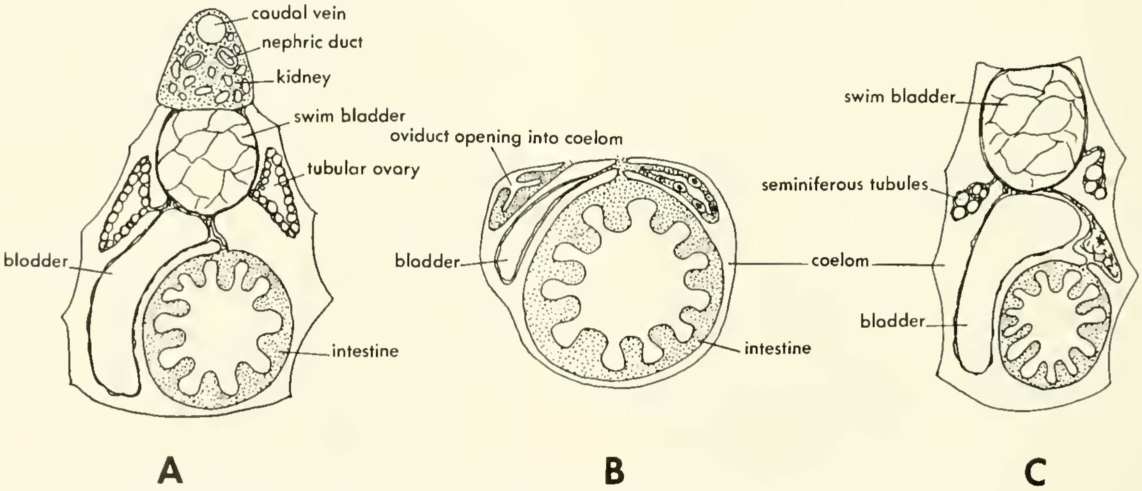


Figure 10-43. Three cross sections showing interrelationships of parts of female, A and B, and male, C, of the lantern fish *Lampanyctus leucopsarus*.

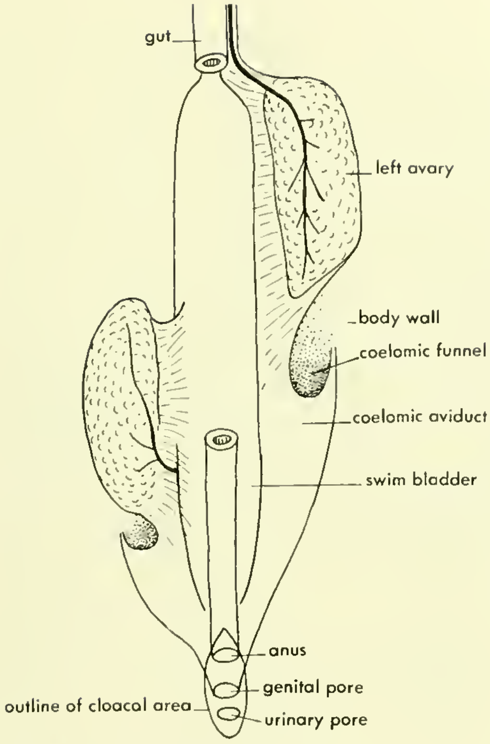


Figure 10-44. Ventral view of female system of the Smelt, *Osmerus eperlanus.* (After Huxley, 1883)

funnel. The oviduct lies lateral to the mesovarium and below the nephric duct. The oviduct enters the nephric duct where the latter turns downward toward the urogenital sinus. The ovary of *Amia* is like the testis in having a distinct vascular drainage which passes along the middle of the medial aspects and connects anteriorly with the main vascular channels.

In *Lepisosteus* the ovary is more elongate than that of *Amia.* It is sacculate and attached in its middle part by a dorsally tapering, membranous funnel, in part formed from the mesovarium. This funnel leads into the oviduct lying along the body wall below the nephric duct, as in *Amia.* Posteriorly the oviduct enters the nephric duct in the region of its swollen bladder portion.

The parovarial ovary of *Lepisosteus* is formed by folding of the genital ridge to meet a sheet extending down from the body wall. The ovary and its oviduct suggest the situation observed in teleosts but could be a parallelism.

Acipenser *Acipenser* and *Polyodon* are peculiar in that both sexes have large, funnel-like ducts extending anteriorly, between the mesentery of the gonad and the body wall, almost to the middle of the gonad (Figure 10-45 C,D). The gonads are long bands of tissue, irregularly thickened but thickest in their posterior half. They extend from the region of the heart, back nearly to the cloaca. The testis has a distinct bundle of tubular tissue, the central net, running along the middle of its lateral aspect. This band passes just below the margin of the coelomic funnel. Anteriorly the testis lies in contact with the body wall, and posteriorly it is suspended by a short mesorchium. The vasa efferentia extend from the central canal band dorsomedially to the margin of the kidney. The nephric duct is not modified as a vas deferens.

The ovary is similar in form. Its eggs rupture from the lateral surface into the body cavity and pass down the coelomic funnel.

Embryological development The development of the gonads of actinopterygian fishes is only partly known. The germ cells migrate into the body and come to lie in two bands near the midline mesentery, below or medial to the nephric ducts. These germ cells are surrounded by cells of epithelial and mesenchyme origin, and the whole is enclosed in a thin epithelium. The germ mass now extends down into the body cavity as a genital fold. Development of the swim bladder in the dorsal mesentery tends to move the genital ridges laterally, and thus they are now supported from the sides of that bladder. When the swim bladder contacts the body wall laterally, the genital fold comes to lie below the bladder, but well away from the median septum. Multiplication of germ cells and **stroma** (filling-in) cells follows, and an irregular cavity, the gonocoel, forms. This cavity is formed from splits in the gonad tissue.

From the indifferent gonad, male and female organs develop. Both sexes apparently utilize the internal cavity of the indifferent organ. The female differentiates earlier, with some of the germ cells, the ovogonia, enlarging as ovocytes and the stroma forming a thick outer capsule. The central cavity is now lined by an epithelium and extends back through the epigonal part of the ridge as the oviduct. The oviduct eventually reaches the exterior at the genital pore or enters some other tubular structure.

In the male the testis is indicated by clumps of germ cells, the spermatogonia, which arrange themselves in the walls of diverticula from the lined central cavity. In this way the tubular or ampullar system is formed. The central canal, or system of canals, extends posteriorly through the epigonal region to form the male duct.

In some, perhaps most, teleosts the ovocoel opens laterally by a split into the coelom. Thus an ovarian groove is formed. This groove extends posteriorly through the epigonal area as the oviducal groove. This groove becomes lined with epithelium and then closes secondarily to produce the entovarial or parovarial ovary along with its posterior oviducts. In some fishes a dorsolateral opening remains in the oviduct even in the adult. This slit is functionally closed by contact of its edges with the body wall (*Lampanyctus*).

General observations The origin of the oviducts of the primitive types of fishes, such as *Polypterus, Acipenser, Amia,* and *Lepisosteus,* has not been satisfactorily worked out, but it

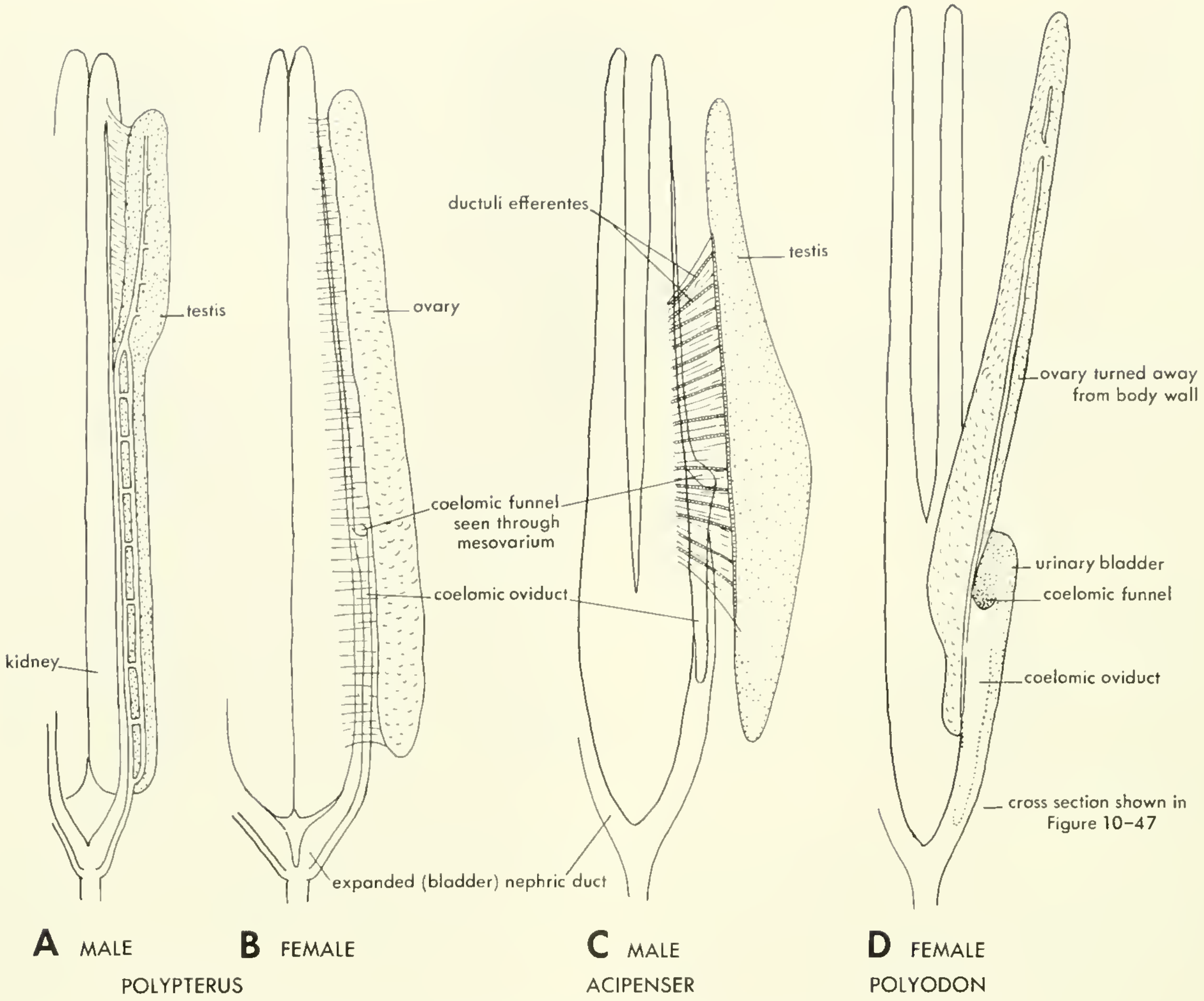


Figure 10-45. Reproductive systems of *Polypterus*, A and B; male of *Acipenser*, C, and female of *Polyodon*, D, as seen in ventral view. (A and B after van den Broek, 1938)

is certain that the anterior part of the oviduct is a chamber of the coelom closed off by a peritoneal fold between the body wall and the genital fold. The peritoneal funnels of the margin of the opisthonephros open into this space. The posterior termination of this space lies in contact with the nephric duct and at maturity opens into that duct (Figure 10-47). It has usually been assumed that this coelomic tube grows posteriorly through the tissue underlying the nephric duct and that this extension represents the Müllerian duct. The position in which the oviduct opens into the nephric duct does not suggest any such posterior growth; the entire tube can be considered as coelomic in origin.

Balfour and Parker (1882) have argued the pros and cons of considering this tube a new structure or a modification, at least in part, of the Müllerian duct. The greatest difficulty is to account for the acquisition of an opening between this coelomic funnel and the nephric duct. A possible solution would be the enlargement of a peritoneal funnel within this coelomic duct. Direct opening of such a funnel into the nephric duct seems improbable. The problem becomes a more general one in view of the evidence of the parovarial and endovarial ducts opening through the body wall between the anus and the excretory pore. There is some sort of developmental factor here which is not as yet understood. It appears certain, however, that no actinopterygian has any remnant of the Müllerian duct.

The fact that *Polypterus*, *Acipenser*, and *Amia* share the coelomic type of oviduct suggests that this type is more primitive than the completely parovarial system of *Lepisosteus*. The endovarial and parovarial systems of teleosts, in which peritoneal funnels are always lacking, would appear to be modifications of the *Lepisosteus* system, achieved by a gradual shift from the parovarial type to the endovarial. The oviduct becomes a posterior outgrowth of the ovocoel, which

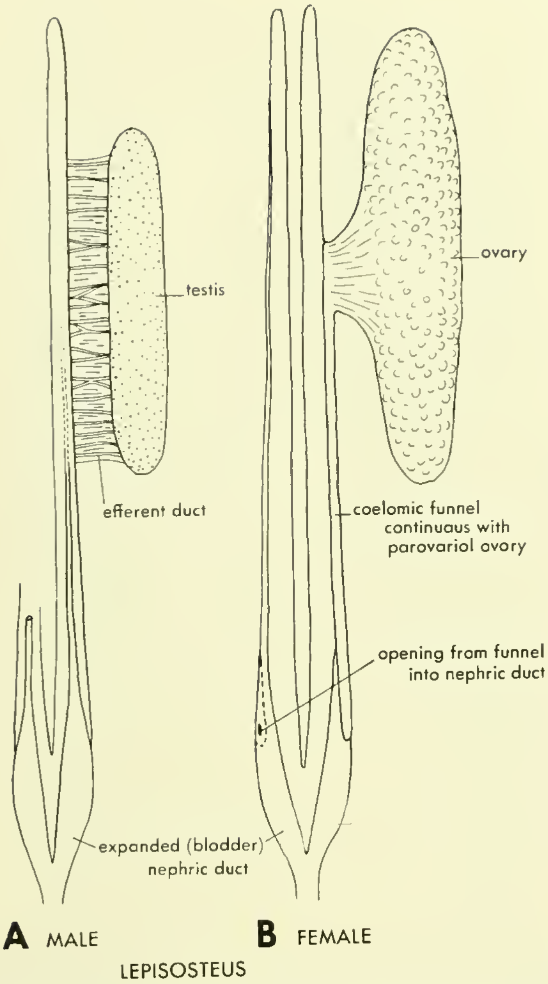


Figure 10-46. Reproductive tracts of male and female of *Lepisosteus os* seen in ventral view. (In part after van den Broek, 1938)

acquires new connections posteriorly, but usually opens by a genital pore.

The salmon type of system is the result of reduction of the primitive oviducts. In the young salmon the ovary shows a slight lateral fold ventrally but remains free of the body wall. The genital ridge extends posteriorly first in the swim bladder, then on the mesentery of the gut. It disappears near the posterior margin of that mesentery but reappears on either side of the terminal part of the gut. Here it extends out and up to fuse with the body wall, thus forming the floor of the posterior, midline funnel serving for exit of the eggs from the body. This funnel breaks through to the exterior between the urinary pore and the anus at spawning time.

The similarity of sexual ducts in male and female teleosts suggests that they are the same. Actually the male duct is the result of posterior extension of the central canal through the genital ridge, while the female duct is the result of a folding or invagination process, i.e. the oviduct lying above the lateral to the primitive ridge. An interesting situation is observed in *Lestidium affine,* where the hermaphroditic gonad has both male and female ducts, the former dorsomedial to the latter. The male ducts enter the urinary sinus separately; the female ducts unite and exit between the excretory pore and anus.

The genital ridge of the teleost is also peculiar because it contains no obvious mesonephric blastema; it is essentially cortical. There is the possibility of inclusion of some mesenchymatous cells which arose near or in the mesonephric blastema. These cells appear to form part of the stroma, a tissue mass enclosing germ cells, and as such are not localized as in the gonadal ridge of higher forms, where there is a cortex and a medulla. Some teleosts are hermaphroditic and in these the ovarian part lies anterior to the testicular part.

Chondrichthyes

Shark

THE MALE The testis is large and suspended by a broad mesorchium (Figure 10-48). The position in the body cavity varies from far anterior back to about the middle. The right is usually larger than the left.

In *Scyllium* there is a sequence of developmental stages of seminal ampullae. This sequence starts from the ventral free margin where new follicles are forming and progresses toward the dorsal attachment. At the time of breeding, a set of ripe ampullae connects through narrow ductuli recti with the central canal, which lies along the attached margin of the gonad. Many of the ampullae observed along the canal are empty; these are spent ones of previous reproductive periods.

The testes of most sharks are made up of typical ampullae, each connected with the central canal and each giving rise to repeated generations of germ cells. In some sharks the testis is associated with an **epigonal organ** which is lymphoid in nature. This extends back to the cloaca in *Galius;* it may be relatively small as in *Heptanchus* or absent as in *Squalus.* Perhaps as an epigonal extension, the testes of *Scyllium* meet and fuse posteriorly.

The central canal, which may form a reticulated set of channels, is drained by one or a few anterior efferent ducts. These enter the epididymis. Peritoneal funnels may remain in this part of the kidney but lose connection with the modified nephric tubules. The epididymis is highly developed and associated with the Leydig's gland (see description of shark kidney).

The nephric duct is distinctly modified for sperm transport and may be separate from one or several ureters carrying the excretory fluid to the cloaca. Its posterior third, approximately, is expanded as a glandular ampulla which has a reticulum of folds on its inner surface. A terminal evagination from the nephric duct occurs in some species (*Scyllium*); this is the **vesicula seminalis.** In both sexes of

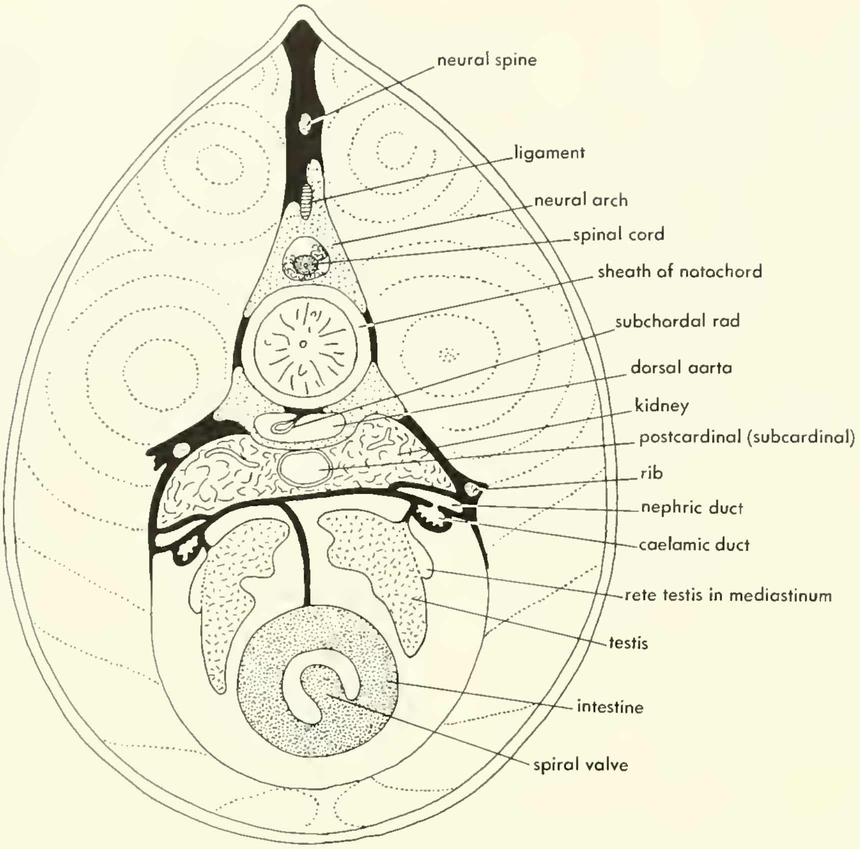


Figure 10-47. Cross section of male of *Acipenser fulvescens* showing connection (on reader's right) between the nephric duct and the coelomic duct.

Squalus there is a short, bladder-like expansion of the nephric duct here. The nephric ducts join as a urinary sinus, which also serves the ureters when present, and this opens through a papilla into the cloaca. From the cloaca the **spermatophores** (bundles of sperm) are forced by the action of **siphons**, muscular sacs underlying the skin and extending forward from the cloaca, through the grooves of the **claspers** into the cloaca of the female.

In some sharks a rudiment of the Müllerian duct enters the cloaca near the nephric duct; this is the **vagina masculina.**

THE FEMALE The ovary is generally shorter than the testis. Usually there are right and left ovaries, but in some sharks the left may be rudimentary (*Scyllium, Pristiophorus, Carcharias, Galeus, Mustelus, Zygaena*). An epigonal organ may be associated with the ovary (*Scyllium, Heptanchus*). The eggs are shed into the body cavity and carried to the exterior through the Müllerian ducts. The common funnel of these ducts lies at the anterior end of the body cavity, below the esophagus and just behind the heart. In some sharks there are paired ostia in the region of the pronephros. The Müllerian duct consists of the usual segments: funnel, tube, isthmus, uterus, and vagina. In oviparous forms there are two specialized zones in the tube which secrete albumin, and a horny shell to enclose the egg; these zones form the **nidamental gland.** Fertilization apparently occurs in this area. *Squalus* is viviparous as are many sharks. In these the fertilized egg undergoes development in the uterus, most of the posterior half of the oviduct. The developing young may recieve nourishment from the maternal tissues in some species (metaviviparous). The vagina is the terminal section connecting with the cloaca; it opens dorsolateral or dorsal to the urogenital sinus.

Holocephalan The testes of the male chimaerid lie far forward in the body cavity (Figure 10-48 E). The efferent ducts differ in that they are more numerous and form an anastomosing network in the mesorchium. The epididymis is well developed as is the Leydig's gland. The nephric duct is partly separated from the ureters and its terminal half is expanded as a glandular ampulla. Several ureters open into the ampulla, along its length, and into the urinary sinus formed by the fused posterior ends of the nephric ducts. The urinary sinus opens by a small pore behind the anus. Distinct Müllerian ducts occur in the male. These can be followed from the region of the heart, along the ventrolateral walls of the

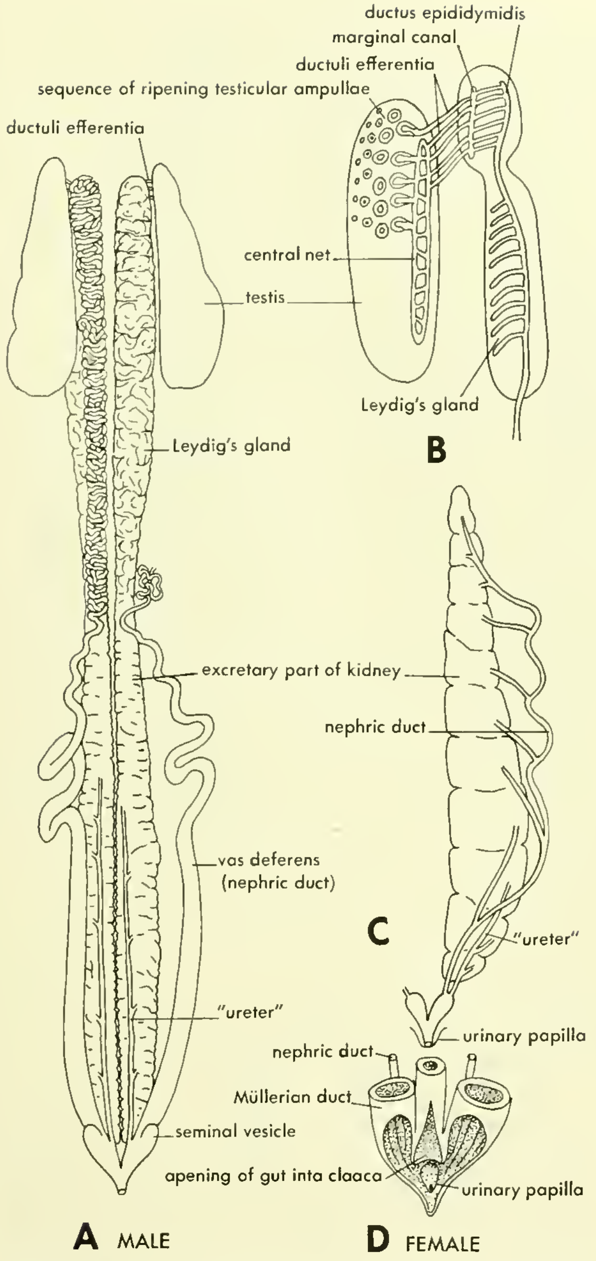


Figure 10-48. Uragenital systems af the shark. A, male *Squalus;* B, relatianship af *testicular ampullae* and tubules in *Scyllium canicula;* C, urinary system af female *Scyllium;* D, uragenital ducts and claaca af female *Squalus.* (A and D after Marinelli and Strenger, 1959; B and C after van den Braek, 1933)

ampullae to the urogenital sinus where they end blindly above the **urogenital gland.** In the very young the urogenital gland is small; it is larger in the adult although it may be embedded in connective tissue and not apparent. The male has anterior and posterior pelvic claspers utilized in copulation (Figure 10-49).

The female (Figure 9-25) is similar to the shark in the position of the ovary, the general nature of the oviduct, and the large, shelled eggs. The Müllerian ducts have a common midline ostium, below the esophagus, and each has an expanded nidamental gland area. Also there are regions identified as the isthmus, uterus, and vagina. The oviducts open individually, lateral to the excretory pore in a shallow urogenital sinus. Anterior to the excretory pore and behind the anal opening is an opening into a blind-ended sac which has been called the **seminal receptacle.**

The young female is presumed to have a more marked urogenital sinus. The anterior wall of this sinus forms a forward-extending bladder or sac, the seminal receptacle. In the mature female, with the partial eversion of the urogenital cavity, the sac comes to open anteriorly, while the Müllerian ducts open lateral to the excretory pore (Figure 10-49). The small urogenital gland of the male may be the homolog of the seminal receptacle of the female.

General observations Only the middle part of the genital ridge develops in sharks. The genital fold hangs down into the body cavity with no tendency for its margin to roll laterally (Figure 10-50). The germ cells lie on the lateral surface of the fold. The same relationships of cortex in the female and medulla in the male, as observed in amphibia and higher forms, appear to hold.

Heptanchus is described as having a rudimentary testis in females; the testis lies above the ovary along the line of attachment of the mesovarium. In a number of immature males of this shark, rudimentary ovaries were observed lying below the testis and fused at the ventral midline. The Müllerian ducts of these males had a single midline funnel but reached only part way posteriorly. The relationship of male organ to the attachment area of the gonad and the female organ to the more ventral cortical part of the ridge agrees with observations in the higher forms.

The origin of the Müllerian ducts from the pronephric funnels and the splitting of the nephric duct appears to be distinctive for this group. The fairly close agreement in this area of anatomy between the holocephalan and sharks, which in other respects seem to be so diverse, suggests that they are indeed derived from a common anestor, an ancestor having Müllerian ducts in the female and a Leydig's gland as well as an epididymis in the male.

Cyclostomes

Lamprey The gonad of the lamprey is an irregularly lobate mass suspended by a midline mesentery (Figure 10-26), and, in the ripe condition, it may even fold around the intestine. The gonad, whether testis or ovary, extends almost the entire length of the body cavity. There are no reproductive ducts.

The germ cells appear in the early larva on either side of the body and migrate to the midline where they form a

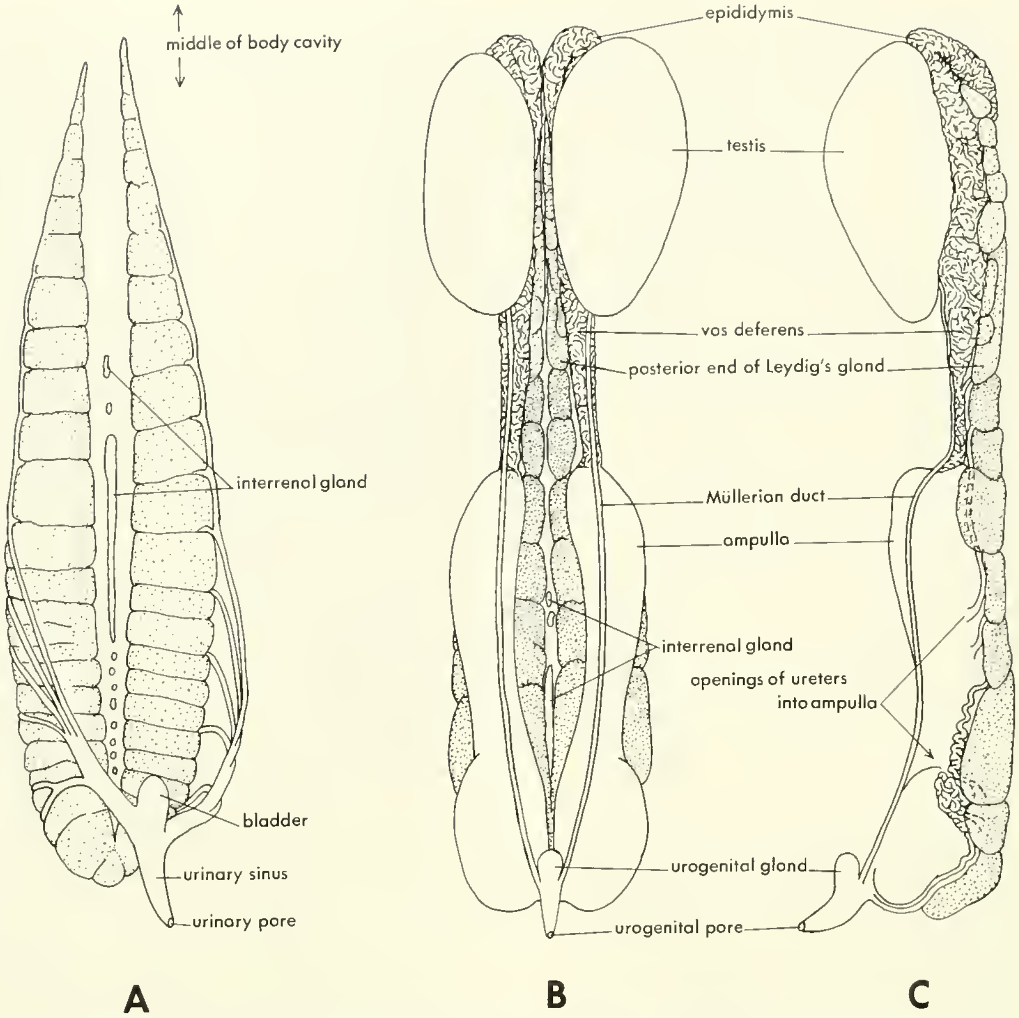


Figure 10-49. Urogenital systems of the chimaerid, *Hydrolagus*. A, kidneys of adult female (see Figure 9-25 for relationships to reproductive tract and viscera in general); B, ventral view of male systems, showing testes lying in anterior part of body cavity; C, lateral view of male systems.

single band (25 to 30-mm larva). The stroma surrounding the gonocytes, or germ cells, appears to be of epithelial origin but could include cells from the mesenchyme of the kidney anlage. The gonadal ridge extends through the posterior two-thirds of the body cavity, reaching almost to the posterior end. According to Lubosch (1903), about 25 per cent of the larvae have hermaphroditic gonads but later become males by loss of the ovocytes. Of adults, approximately half are of either sex. In the male the clumps of germ cells form follicles, which when ripe rupture into the body cavity. In the female the germ cells become surrounded by follicle cells of the stroma which contribute to the development of the egg. The eggs rupture into the body cavity at maturity.

The sex cells leave the body by way of the abdominal pores. These bilateral apertures in the wall of the urogenital sinus are similar in the two sexes. They open a few weeks before spawning. Injection of oestrone or anterior pituitary will cause perforation of these pores in the young lamprey.

Myxinid The single gonad appears late as a structure attached to the gut just to the right of the mesentery. The anterior part develops first and produces ovocytes; the posterior part develops first and produces ovocytes; the posterior part produces spermatocytes. In fish less than 20 cm long, none can be identified as males, but by 24 cm the two sexes are defined. However, both have a rudimentary area

In the adult the gonad stretches nearly the entire length of the body cavity. Its supporting mesentery is attached to the gut wall to the right of the mesentery. The testis is folded and lappeted; the sperm-producing follicles are numerous, the mature follicles at the surface, the younger follicles deeper in the stroma. When ripe, the follicles rupture into the body cavity.

The ovary is sparsely spotted with follicles of which the smaller ones are near the free margin. As the eggs become larger they hang down into the body cavity below the level of the free margin (Figure 9-28). The eggs are shelled while still in the follicle; a small micropile, opening through the shell, allows for fertilization. Not all of the large follicles observed develop to mature eggs; some develop at the expense of others which atrophy. The mature eggs are shed into the body cavity and leave the body by way of the coelomic pore, which is the same in both sexes. It is an opening between the urinary pore and the anus (Figure 10-27 B).

Some individuals of Myxine, about 13 per cent, are sterile; they are either without male or female elements in the gonad band or, if these develop, degeneration occurs before mature sex products are formed.

Myxinids, like the lampreys, are not **protandrous hermaphrodites** or **hermaphroditic. Protandry** refers to being male first and later becoming female. Certainly, lampreys are potentially hermaphrodites with development continuing into one sex or the other—the exception being sterile individuals where neither sex seems to have the upper hand.

General observations on cyclostomes The cyclostomes resemble the actinopterygians in that there is little or no nephric contribution to the gonad. They differ in that the bilateral bands, the more primitive condition, of other groups are here fused into a single midline mass. Differentiation of the early gonad band into anterior female and posterior male parts agrees with the situation of other groups.

Müllerian ducts are lacking as is any kind of sex duct. This state might be compared with that observed in Amphioxus. However, if one assumes some sort of basic interrelationship between the vertebrate kidney and gonad, then comparisons cannot be made with Amphioxus. This relationship might also suggest that the primitive pathway for the germ cells of both sexes was through the kidney. The kidney pathway, however, appears to be secondary—the cyclostomes are thus primitive, while the actinopterygians and the other living gnathosomes represent two pathways to increased efficiency in the transport of germ cells.

General observations on the reproductive system

As in the case of the excretory system, a comparative analysis of the reproductive system of the various kinds of vertebrates tends to raise questions regarding phylogeny rather than to answer them. Certainly there is a basic reproductive system plan common to all but plastic and open to modification in terms of ducts in the several groups.

The germ cells appear to arise in much the same way and to migrate into bilateral epithelial folds or germinal ridges in the gnathostomes, or into a single midline or asymmetric ridge in the agnath. The latter appears to be the derived

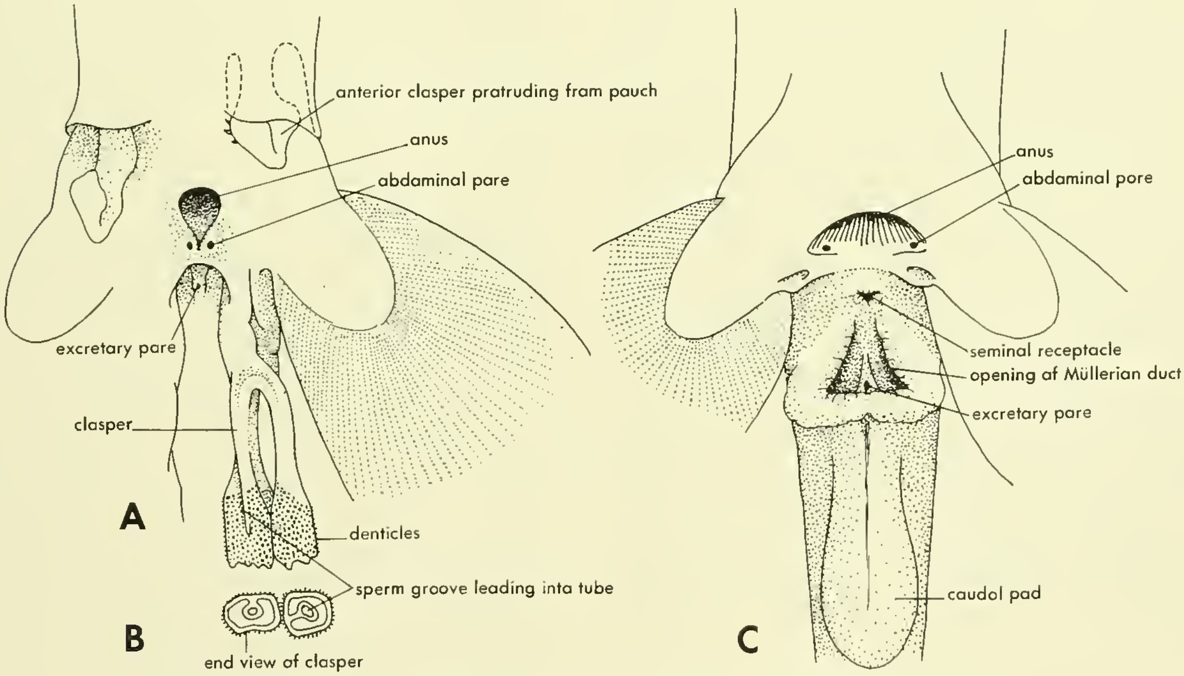


Figure 10-50. Ventral views of pelvic region in male *Hydrolagus*, A, and female, C. A, shows both anterior and posterior pelvic claspers of the male; B, end view of posterior pelvic clasper.

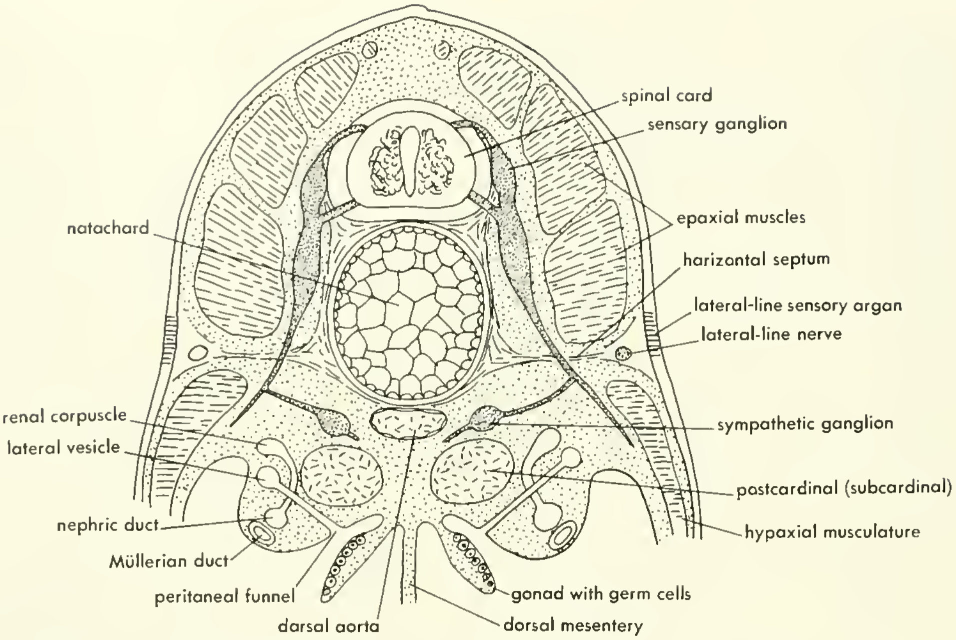


Figure 10-51. Crass section af a 33-mm *Scyllium conicula* shawing interrelatianships between kidney tubules and genitol ridge. (After Goadrich, 1930)

condition, not the primitive. The more anterior part of the ridge has female potential, while the male section lies more posteriorly. The cortical region, or ventral margin of the fold, is female, while the region of mesenteric attachment, or medullary invasion, is masculine. Central cavities or tubular interiors are general; the latter is always the case in the testis. The ray-finned fishes and cyclostomes differ from the other vertebrates in lacking a distinct medullary component in the gonad.

The definitive gonads of gnathostomes are associated with ducts of nephric origin except in the actinopterygian fishes. The ducts of this group develop either as a posterior outgrowth of a hollow within the gonad ridge or a hollow produced by folding of that ridge. Although the ducts of both sexes involve similar events, these are separate ducts when both gonads are present in a single individual.

The Müllerian ducts which serve the females of other fishes and tetrapods arise in the chondrichthian from a pronephric funnel and the splitting of the nephric duct from front to back. In higher forms the ostium does not usually appear as an expanded pronephric funnel but probably was derived from one, as is indicated in *Neoceratodus*. The anterior end of the definitive tube is formed by invagination, at the anterior end of the mesonephric kidney, of a thickened area of epithelium next to the nephric duct. Development proceeds toward the posterior connection with the cloaca.

That the chondrichthians share Müllerian ducts with the higher forms seems quite puzzling in view of the apparent absence of these structures in actinopterygians. This paradoxical situation has caused most zoologists to accept the assumption that the coelomic tubes observed in ray-finned fishes must be, at least in part, Müllerian ducts. Lack of any proof of this assumption leads to the first clear evidence of a gap within the osteichthian fishes. The many similarities in kidney and gonad development between actinopterygian and choanate fish lose significance when it is observed that the sharks are more like one than the other in terms of these reproductive ducts.

Since it is usually assumed that the primitive condition is one lacking sex ducts (as in the cyclostome, which has bilateral gonads), an early radiation of the vertebrates into three lines is suggested: an actinopterygian line which did not utilize the nephric ducts, a chondrichthian line having the usual kinds of ducts as well as Leydig's glands, and a choanate line with typical ducts but without the Leydig's glands. It is necessary, if the evidence of the previous chapters is to be given any credence, to view the similarity of shark and choanate as a parallelism. This opinion is supported by their lack of agreement in terms of Leydig's glands as well as by the obvious parallelisms of egg structure, nidamental glands, and viviparity. This parallelism is made possible, in the case of the female, by the availability of pronephric funnels, with their capacity for posterior tubular extension, and in the case of the male, by the proximity of mesonephric and testicular tubules.

11

The Circulatory System

The nature of the parts and the pattern of the circulatory system characterize the vertebrate, although the system is suggested in the cephalochordate. This system is described as being composed of a heart and a series of vessels, the arteries carrying blood away from the heart and the veins returning blood to the heart. Connecting the main arteries and veins are vessels decreasing in diameter to the capillaries and increasing again to the veins. All of the tissues of the body are permeated by the capillaries, and no cell is at a great distance from such a channel.

Both the parts and the pattern of the circulatory system show some variation from one group to another; much of this variation is of a functional nature and has little relationship to the phylogeny of the group. Several areas of this system can be examined in search of modifications of a phylogenetic nature.

THE HEART

Mammals

The heart of the mammal has four chambers; two ventricles and two auricles (or atria—singular, atrium). Functionally it represents two hearts, serving separate and parallel pulmonary and systemic circulations, each with a contractile auricle and ventricle. The heart and its history is best understood in terms of its embryological development.

The heart appears first as irregular clusters and chords of mesenchymal cells lying between the splanchnic mesoderm and the endoderm in the region below the pharynx. These cells become organized into two strands lying to either side of the anterior intestinal portal. Each strand acquires a lumen and thus becomes an **endocardial primordium.** These tubes extend beyond the cardiac region into the head fold and posterolaterally on to the yolk sac. Meanwhile the splanchnic mesoderm has become thickened in the region of the heart and this thickening tends to wrap around the tubes. As the anterior intestinal portal moves posteriorly, these two tubes approach each other at the midline, meet, and fuse to form a single channel, the endocardium or lining of the heart; the enclosing splanchnic mesoderm now forms the **myocardium,** the muscular part of the heart.

As the endocardial tube is formed, it becomes flexed in a sigmoid curve. Anteriorly the first two **aortic arches** extend outward and upward; posteriorly the **vitelline veins** (or the **omphalomesenteric veins**) extend out onto the yolk sac. A series of constrictions now appear dividing the tubular heart into segments. Anteroventrally and to the right is the **truncus arteriosus** (bulbus cordis) which widens into a conus at the reflexed **ventricle;** the endocardial primordia first meet and fuse at the anterior end of the truncus. The ventricle is separated by an **atrioventricular** constriction from the anterodorsal **atrium,** and behind the atrium is the **sinus venosus** formed by the junction of the two large vitelline veins (Figure 11-41).

Meanwhile other blood vessels have appeared: **anterior cardinals** drain the head region, and **posterior cardinals** drain the posterior part of the body. These unite to form the paired **common cardinals** (or **ducts of Cuvier**) which descend to enter the sinus venosus. The opening of the sinus venosus into the atrium now lies dorsal to the ventricular portion. The atrium has pouches extending out to either side and down around the truncus and the anterior end of the ventricle. The latter now shows bilateral posterior bulges, precursors of right and left ventricles.

Looking at the interior of the heart, one sees the beginning of an interatrial septum between the two outpocketings of the atrium; the sinus venosus opens through a slit to the right of the interatrial septum (Figure 11-1). The two ventricular pouches are slightly separated by an **interventricular septum.** The wide atrioventricular canal is divided by dorsal and ventral cushions into an I-shaped opening. As development progresses, both the interatrial and interventrical septa grow toward each other, and then the atrioventricular cushions meet and divide the **atrioventricular canal** into right and left passages. **Osteum I,** between the interatrial septum and the atrioventricular cushion, closes as **osteum II** develops in the upper part of the septum and a **secondary interatrial septum** begins to appear.

While the right and left sides of the heart are separating, the truncus arteriosus begins to be divided into **pulmonary** and **systemic channels.** Division begins by a ridge forming

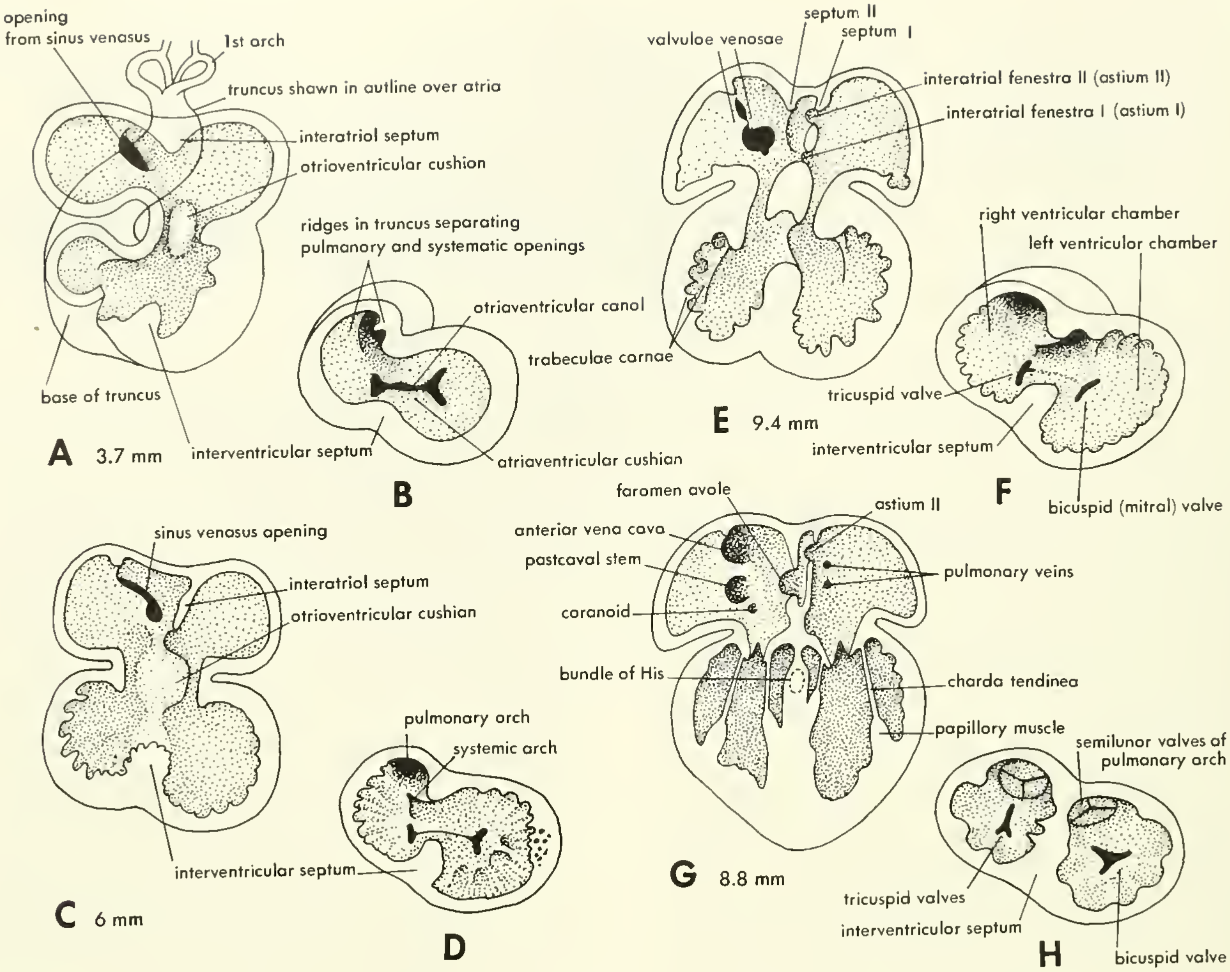


Figure 11-1. Development of the mammalian heart. A, semidiagrammatic frontal section of the heart of a 3.7-mm pig; B, anterior half of A as seen from behind; C, 6-mm pig; D, anterior half of C; E, 9.4-mm pig; F, anterior half of E; G, 8.8-mm human; H, anterior half of G. (After Patten, 1946)

between the openings into the fourth and sixth aortic arches. These ridges are extended backward along the truncus wall in a clockwise course of just over one-half turn. The right lateral ridge comes to lie left ventrally in the conus opening, and the left ridge is right dorsal in position. The edges of these extend outward until they meet, thus dividing the truncus. The fused ridges then join the interventricular septum which has also fused with the atrioventricular cushion to complete the separation of the ventricles.

Concurrently the sinus venosus is drawn into the wall of the right auricle until the now formed **anterior** and **posterior venae cavae** open separately, the former in front of the latter. (The development of these vessels will be described later in this chapter.) Then a coronary vessel opens behind the posterior. The sinus tissue is represented by the **sinuatrial node** of the adult heart.

The second interatrial septum develops until only a small foramen ovale remains. This foramen is not in line with the osteum II of the primary interatrial septum. The cushions margining the openings between the atria and ventricles now begin to develop as flaps supported by **chordae tendineae** and **papillary muscles.** These braces for the valves are sculpted out of the thick muscular walls of the ventricle. Valves develop from the cushions at the base of the pulmonary and systemic trunks, three in each of these. The pulmonary drainage has appeared and has entered the left auricle. These pulmonary openings appear as new developments; their origin from the original venous entry into the right atrium is not indicated.

Among mammals, the heart appears to be constant in its structure, varying only in such details as the pattern and points of origin or exit of the coronary vessels. Of functional interest is the fact that some of the heart muscle tissue has been modified into a conducting system for coordinating the action of the heart. This system is formed of a **bundle of His** and **Purkinje fibers,** and it includes the sinu-atrial node in which the heart contraction is initiated. Another modification of the heart tissue is the "skeleton" found at the bases of the main vessels from the heart. In different species this may be fibrous, partly cartilaginous, or ossified.

Reptiles

The heart of the reptile is basically three-chambered but retains a bit of the sinus venosus. This heart differs from the mammal in that three vessels exit from it: two systemic trunks, the right bearing both carotids, and a pulmonary trunk.

In *Tupinambis* (Figure 11-2) the two atria are completely separated; they enter the ventricle to either side of a valvular apparatus from which a large knob-like process extends out on the left side. This process is hollowed below and rounded above and can be pressed upward to cover the openings into the two systemic vessels. The opening of the pulmonary trunk lies in a pocket separated from the systemic portals by a muscular flap.

The mechanism of operation is assumed to be as follows: blood from the right atrium enters the ventricles. This is oxygen-poor blood. This blood is directed into the cavum pulmonale by the process of the atrioventricular valve. The blood from the left atrium, which is oxygen rich, enters the main part of the ventricular chamber, swelling it outward. With contraction of the ventricle the first blood to leave is that from the right atrium, which is directed into the cavum pulmonale by the atrioventricular valve blocking the exit into the systemic openings. As the pressure in the ventricle increases, the muscular flap separating the systemic and pulmonary chambers is pushed outward closing the pulmonary exit. The atrioventricular valve is now pulled to the left exposing the systemic exits which receive the oxygenated blood. Thus there appears to be a functional mechanism for separation of the blood in this lizard.

The heart of the alligator is more complex than that of the lizard or the turtle (Figure 11-3). There is complete separation of right and left atria and ventricles. The only connection between the two sides of the heart is through the **foramen of Panizza** which connects the left and right aortic trunks. The most peculiar feature is that the left aortic and pulmonary trunks leave the right chamber of the heart, while the right aortic trunk, bearing the carotid arches, comes from the left chamber.

The heart of the bird is similar to that of the alligator; however, there is no connection between the right and left sides. The bird has lost the left systemic trunk and arch; all

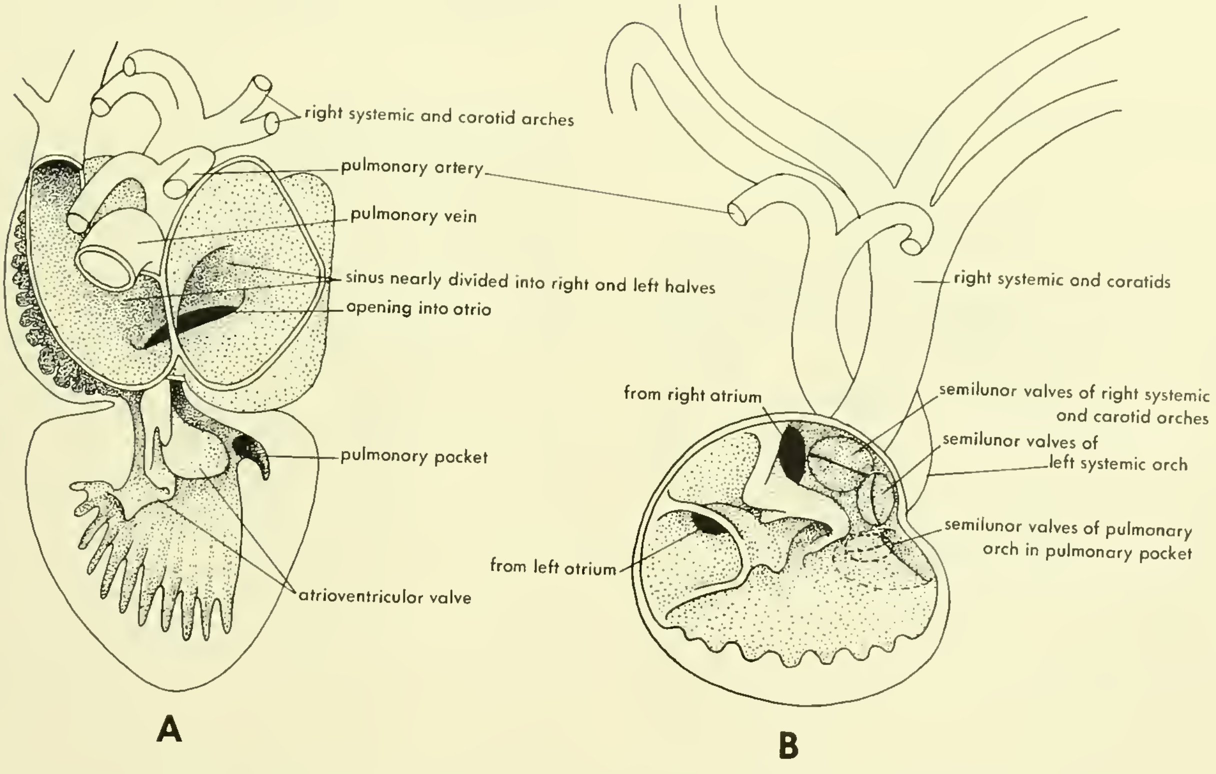


Figure 11-2. Dorsal view of heart and main blood vessels of *Tupinambis*, A, and anterior half of heart as seen from behind, B.

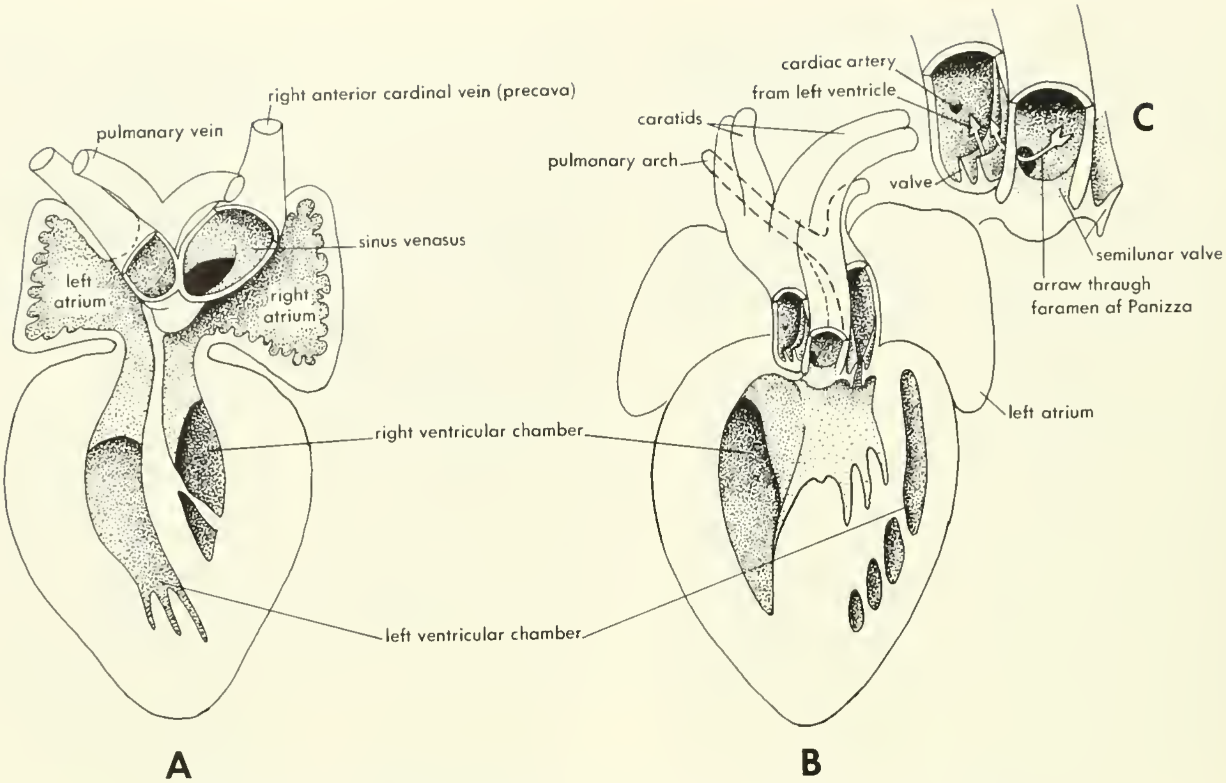


Figure 11-3. Dorsal view of heart and main blood vessels of the alligator, A, as seen from below, B, and details of foramen of Panizza, C.

systemic blood passes through the right trunk, which leads into the carotid arches, and the right systemic arch.

Embryological development The development of the reptile's heart is much like that of the mammal's. The heart tube is formed of bilateral components and flexed. Posteriorly the vitelline veins form a sinus venosus. Anterior to the sinus, constrictions delimit an atrium, a ventricle, and a truncus. The flexion continues until the atrium lies dorsal to the ventricle. The atrium becomes divided by an interatrial septum into right and left chambers connected by perforations through the septum. There is no evidence of an interventricular septum (in *Lacerta*), but a fold arises from the ventral ventricular wall to separate the cavum pulmonale from the main ventricular cavity. This fold may represent a modified interventricular septum.

The truncus of the reptile is subdivided into three parts rather than two. A series of folds appear which spiral around the wall of the truncus in a clockwise direction from front to rear. These folds arise at the base of the arches and extend posteriorly. At the heart end, there is a large dorsolateral fold on the left side and a smaller ventrolateral fold on the right. Smaller folds now appear dorsolaterally on the right and ventrolaterally on the left. The large left dorsolateral fold extends gradually across the chamber and meets the opposite fold to subdivide the truncus into pulmonary and systemic channels. This septum extends the length of the truncus from the arches to the ventricle. The right dorsolateral fold also develops and subdivides the systemic channel into right and left halves. This subdivision extends only through the proximal part of the truncus. Semilunar valves form at the base of these trunks. The several arches at the end of the truncus are some distance beyond the ends of the spiral channels within the truncus.

In the bird heart, the sinus venosus is greatly reduced. The right atrioventricular valve is muscular as contrasted with the membranous valve of the lizard or the alligator. The systemic channel is not subdivided into right and left parts. The left systemic arch disappears so that the entire channel, which has no connection with the right ventricle, serves the right systemic and carotid arches (Figure 11-11). These apparent changes in relationship between the trunk openings and the interventricular septum help explain the difference between the lizard, or turtle, and the crocodile.

Reduction of the sinus venosus in the reptiles appears to be a parallelism to the situation in the mammal. The resemblance of the four-chambered avian heart to that of the mammal is superficial and misleading. A comparison of the avian and crocodilian heart shows that they are built on the same plan and agree in almost every detail. The crocodilian is the more primitive since it preserves the left systemic arch and trunk.

On the basis of the developing heart, Goodrich (1930, p. 577) suggested that there are two lines of reptiles: one leading through the therapsids to the mammals and the other to the living sauropsids. This dichotomy, which unites the turtles with the eureptiles, seems to be a very basic one, and, in terms of the differences observed between the pelycosaurs and the other early reptiles, it may have extended back to the first radiation of reptiles. Perhaps the dichotomy took place among the amphibian ancestors of the reptiles, as suggested by Watson.

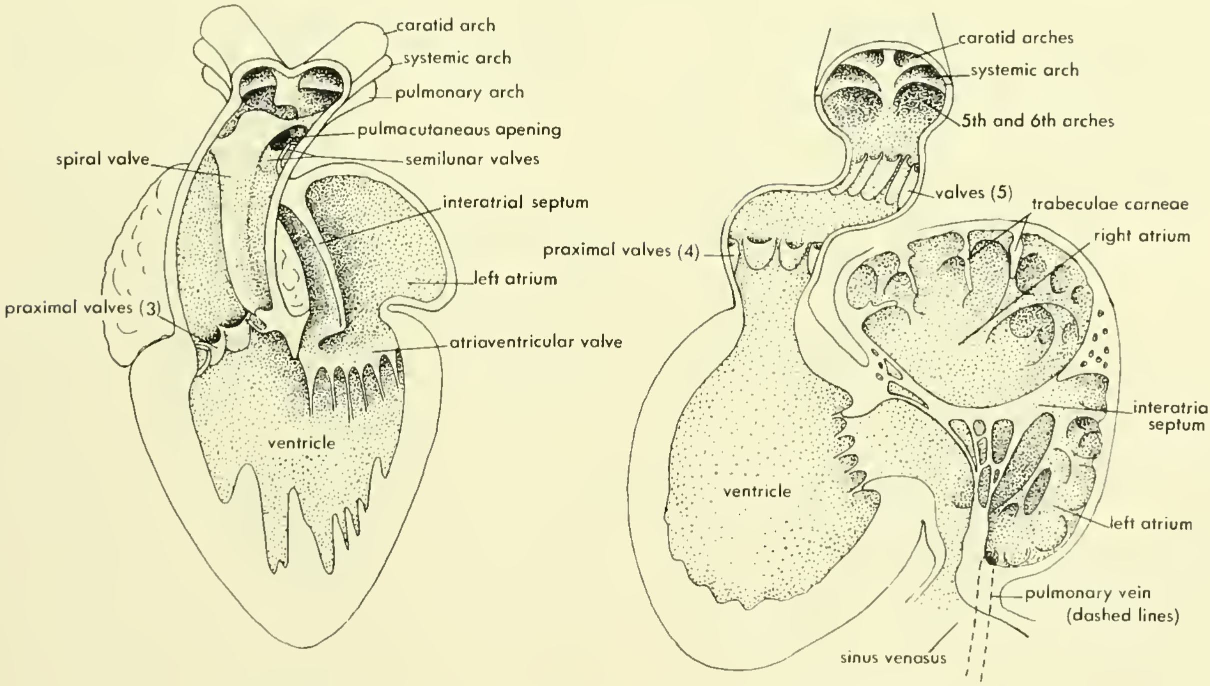
Amphibians

The heart of the amphibian whether anuran or urodele is usually five-parted. From behind forward, these parts are the sinus venosus, two atria, a ventricle, and a truncus (Figure 11-4). The latter is expanded anteriorly into a "bulbus." The truncus, as in the previous groups, is not contractile—it is elastic, but here it is undivided. The limits of the heart are marked by the pericardium.

The truncus contains a valvular apparatus of one sort or another which acts to separate the two types of blood poured into the ventricle from the auricles. In the case of the frog, there is a large **spiral valve** which begins on the left lateral wall, passes up and across the dorsal wall, and ends distally at an enlargement. Distal to the spiral valve are openings for the **carotid** and **systemic arches** of either side and above these, lateral to the base of the spiral valve, is an opening into the **pulmocutaneous arches.** Behind the pulmocutaneous opening is a **semilunar valve** and a similar valve lies opposite this on the ventral lateral wall of the truncus. There are three semilunar valves separating the truncus from the ventricle.

In the frog the atrial openings lie to the left of the opening of the truncus, the systemic blood enters next to that opening, and the blood from the pulmonary circuit enters further away. It can be assumed that the oxygen-poor blood is more concentrated to the right, the oxygenated blood to the left. As the ventricle begins to contract, it is the oxygen-poor blood which goes first, passing over the spiral valve into the pulmonary arches. As the pressure increases, the valve is pushed over to the left, closing the entrance to the pulmonary channel and thus directing the blood which is oxygen rich into the systemic circuit.

The heart of the frog is perhaps the most elaborate of the amphibians. In salamanders the same number of chambers is present except in the lungless forms or in those with an aquatic (neotenic) specialization. In the plethodontids, where the lungs and pulmonary veins have been lost, the left atrium is missing. In *Necturus* and *Cryptobranchus* the interatrial septum is very thin and perforated. The truncus is much simpler; there are four or five **proximal valves,** next to the ven-



RANA CRYPTOBRANCHUS

Figure 11-4. Hearts of *Rana* and *Cryptobranchus* as seen from below and with the truncus opened to show the valves.

tricle, but no spiral valve. There is a **distal ring** of valves in *Cryptobranchus*. The distal end of the truncus is much expanded in some salamanders, as a **bulbus arteriosus**; this term is also used sometimes for the conus area of the truncus. In *Salamandra* there are proximal and distal series of valves and a very small spiral valve.

The amphibian heart differs from the reptilian or mammal heart in that the sinus venosus is retained. In the previous groups it has been reduced or lost. In the amphibian heart one can observe the **trabeculae carnae,** the strands of muscle tissue making up the muscular walls. These trabeculae are best observed in the atrial walls where they are separated by membranous areas.

Embryological development The amphibian heart develops much like that of the preceding groups. There is a sigmoid flexure in the vertical (sagittal) plane. The sinus venosus and atrium are dorsal, and the ventricle posteroventral with the truncus leads forward from it. A fenestrated interatrial septum appears which extends toward the atrioventricular opening. The atrioventricular cushions margin this opening above and below and give rise to the flap valves extending into the ventricle. The pulmonary veins develop along with the interatrial septum. At first they open into the sinus venosus, but this opening moves to the left so that an entrance into the left auricle is effected. In the plethodontids (lungless salamanders), neither interatrial septum nor pulmonary veins develop. In the aquatic types, the septum remains incomplete and fenestrated or degenerates in the adult.

Choanate fishes

The heart of *Protopterus* or *Lepidosiren* is four-chambered (Figure 11-5). The sinus venosus leads by way of the broad opening into the auricular chamber which is expanded on either side of a thin, perforate septum. The blood from the sinus enters to the right of the septum, the blood from the pulmonary vein to the left. There is a large opening below the auricles leading to the ventricle; in this opening is a large cushion mass, the ventral atrioventricular cushion. This cushion continues into the ventricle as a partial interventricular septum. Anterior to the interventricular septum is a single ventricular cavity.

The truncus is large with a sharp bend in it. There are three rows of proximal valves. The spiral valve begins ventrally, curves around the right side to the dorsal wall, and then extends forward along the dorsolateral wall to the anterior end of the truncus. The spiral valve is the equivalent of the left dorsolateral fold observed in the reptile

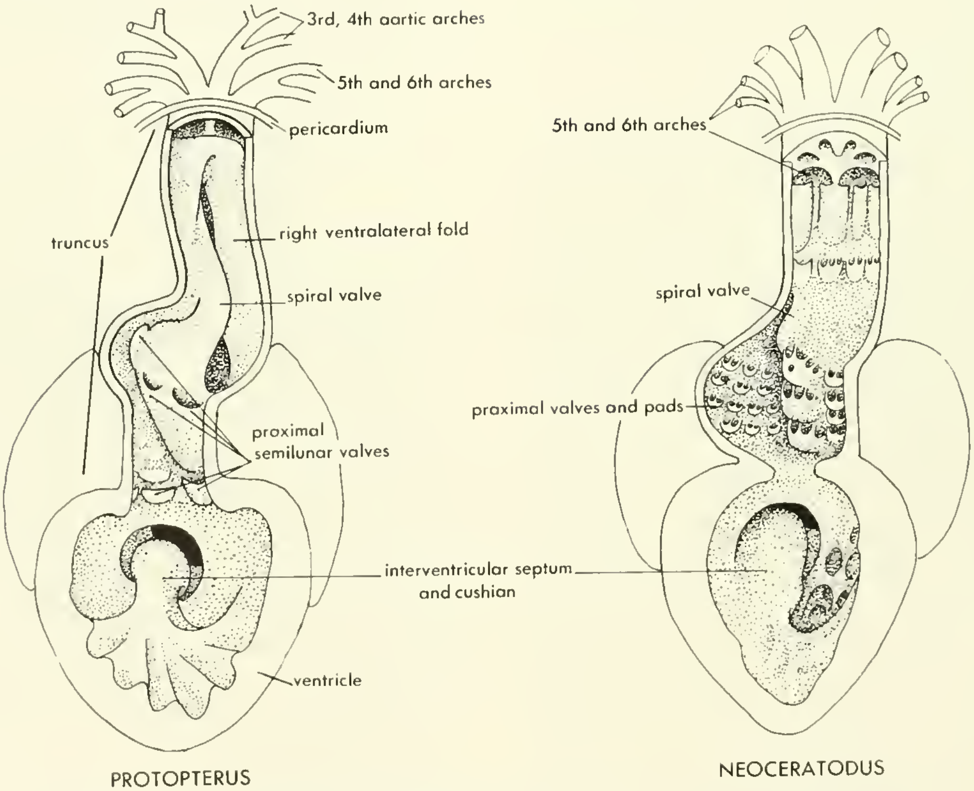


Figure 11-5. Hearts of *Propterus* and *Neoceratodus* as seen from below and with the truncus opened to show the valves. (In part, after Goodrich)

and the mammal. There is also a right ventrolateral fold. This lies in the distal straight portion of the truncus on the left dorsolateral wall opposite the spiral fold. The two fuse distally and overlap midway along their course—the margin of the spiral valve lying below the margin of the second valve. The pulmonary opening (arches 5 and 6) lies dorsal to the fused portion of the two valves, the systemic exits (arches 3 and 4) lie ventral. There are no apparent distal valves in the case of *Protopterus* or *Lepidosiren.*

Neoceratodus is different in that a spiral valve is lacking, but a row of large semilunar valves marks its course. There are several rows of proximal valves and two rows of distal valves. The amphibians and the lungfishes are, thus, very much alike in that a well-developed spiral valve may be present or the truncus may have rows of semilunar valves proximally and distally or throughout its entire length.

The heart of *Latimeria* is much like that of the embryo tetrapods. It consists of a posterodorsal sinus venosus, an atrium, a ventricle, and a truncus. The truncus continues forward from the pericardial cavity as the ventral aorta. The truncus has four longitudinal rows of endocardial thickenings on its inner wall which represent pseudovalves or reduced valves.

The heart of *Latimeria,* like that of the lungfishes, is contained in a spacious pericardial cavity with a thick wall. In the amphibians, reptiles, and mammals the pericardial sac is a thin membrane. The heart of the lungfish is peculiar in having a ventral fold extending upward which partly subdivides the ventricular cavity, forms a cushion valve for the atrioventricular opening, and continues as the interatrial septum. The lungfish also lacks a ventral aorta; the several arches arise from the truncus just outside the pericardial cavity.

Actinopterygian fishes

In the actinopterygian fishes there is a four-parted heart having a sinus venosus, atrium, ventricle, and truncus. The truncus is muscular and contractile at its proximal end, the conus (sometimes called the bulbus). In this group there is some variation in the number of valves in the truncus and the length of the contractile portion. Generally, the valves are limited to the proximal end. In *Lepisosteus* or *Polypterus,* the valves, lying within the contractile portion, extend far forward, nearly to the base of the aortic arches. There is never a spiral valve in this group, neither is there a separate pulmonary circulation.

It can be assumed that the primitive actinopterygian had a contractile truncus lined with many rows of valves as in *Lepisosteus.* In the more advanced or modified forms, the number of rows has been reduced: there are three in *Acipenser* (one distal, two proximal), two proximal in *Amia* and *Albula,* and one proximal in *Salmo.* A single set of proximal valves in a muscular, ring-like conus is typical of the teleost.

In this feature as in many others, *Lepisosteus* is quite distinct from *Amia. Acipenser* does not appear to be as primitive as *Lepisosteus* or *Polypterus.* The heart of *Gymnarchus niloticus* is unique in that a partial division of the atrium into systemic and pulmonary halves takes place in the early stages of development. This division must be regarded as a parallelism to that observed in the choanate group.

Chondrichthyes

The heart of the shark forms the usual sigmoid curve. There is a sinus venosus and an atrium dorsally, a ventricle and truncus ventrally (Figure 11-6). In most of the sharks, there are only a few rows of valves in the contractile truncus, three in the case of *Squalus.* In *Heptanchus* there is a distal row and three proximal rows, a condition suggestive of that of *Acipenser.* The truncus, its anterior end marked by connection with the pericardium, leads into a ventral aorta.

Agnaths

The heart of the lamprey is four-chambered, having a sinus venosus, atrium, ventricle, and truncus (Figure 11-7). The openings between divisions are guarded by valves. The blood enters the sinus dorsally through the right common cardinal, the left having been lost in development, and ventrally from the inferior jugular and hepatic veins. The elastic truncus has a single pair of valves at its proximal end, the conus.

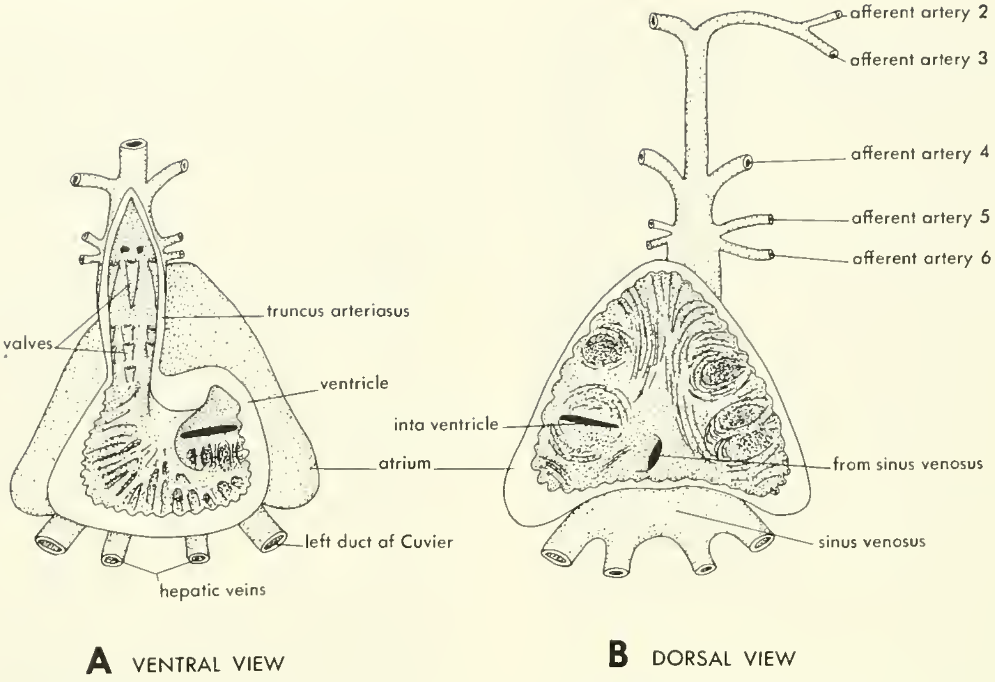
The heart of *Myxine* (Figure 11-7) is quite like that of the lamprey with the exception that the left common cardinal is retained and the right is modified into a portal heart pumping blood to the liver. The valves are similar, and only a single pair of semilunar valves guards the entrance into the truncus.

The pericardial sac of the cyclostome is thick-walled—that of the lamprey is supported by a cartilaginous skeleton.

General observations on the heart

The practice of numbering the chambers of the heart is quite confusing, as are the meanings of truncus, bulbus, or conus. The heart of the fish has four contractile chambers, as does the heart of the mammal. The mammal is better described as having a double heart, two atria and two ventricles, as contrasted with the fish which has but a single atrium and ventricle. This functional difference is the important concept.

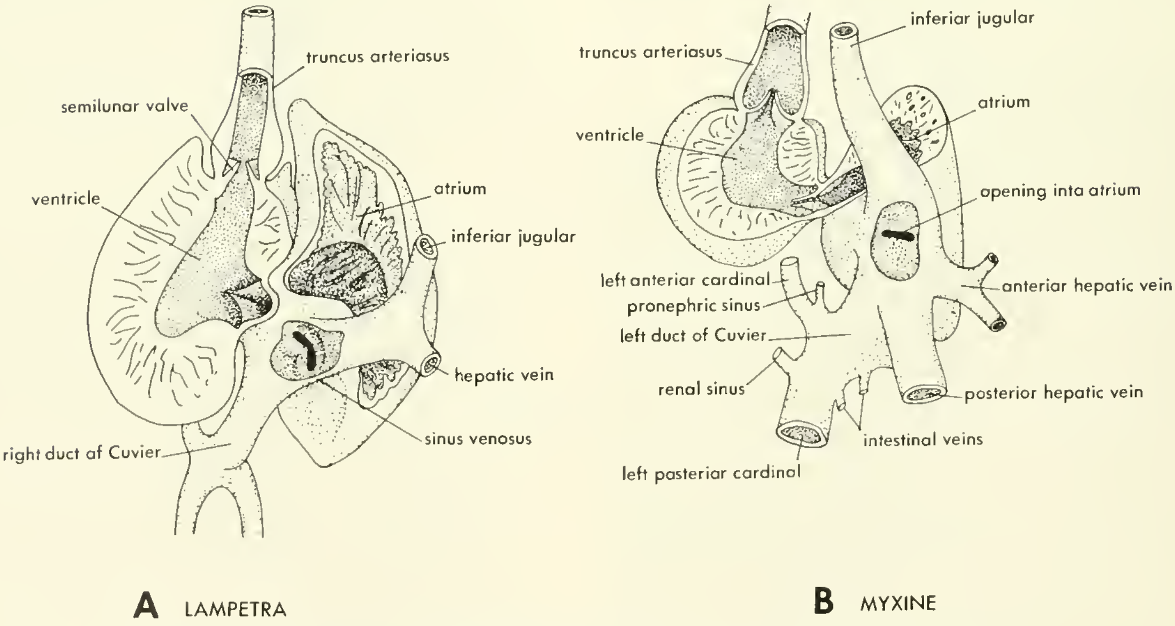
The heart does not appear to supply any basic comparative information; it can be assumed that primitively it was a linear structure, with a sigmoid curve, made up of sinus, atrium, ventricle, and truncus, lying in a pericardial cavity. All of the chambers were separated one from another by valves which gave the blood a directional flow. The truncus primitively was contractile and had a number of rows of semilunar valves in it. The functional value of many rows



A VENTRAL VIEW

B DORSAL VIEW

Figure 11-6. Heart of *Squalus acanthias* as seen from below with ventral wall removed, A, and from above with roof of sinus venosus removed, B. (After Marinelli and Strenger 1959).



A LAMPETRA

B MYXINE

Figure 11-7. Ventral views of the heart of the lamprey, A, with the several chambers exposed, and of *Myxine*, B. (After Marinelli and Strenger, 1954, 1956)

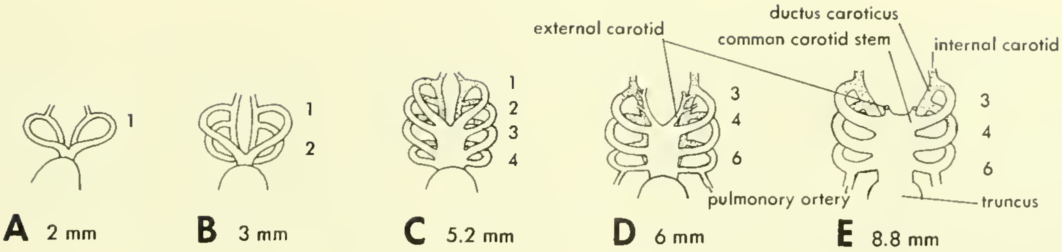


Figure 11-8. Five stages in the development of the aortic arches of man. (After Kramer, 1942)

of valves in the truncus is not apparent. From these rows of valves the four ridges observed in the higher forms developed and made possible the subdivision of the truncus.

THE AORTIC ARCHES

Mammals

The pharynx of the mammal in the course of its development produces a series of **branchial pouches.** These pouches do not break through to the exterior, but they do resemble the pouches which give rise to the gill clefts in fishes. Related to these pouches are a series of arteries, the **aortic arches.** These connect the ventral aortic trunk (**ventral aorta**) with the dorsal posteriorly conducting trunk (**dorsal aorta**) or trunks (**radices aortarum**).

In development the first arch is followed shortly by the second (Figure 11-8). The arches lead into separate dorsal radices which further posteriorly fuse and form the midline dorsal aorta. The third and fourth arches now appear, while the first and second arches undergo reduction. By the time the sixth arch has appeared, the first and second are greatly reduced. The third and fourth arches are large, the fifth very small (Figure 11-9). The sixth sends a posterior branch back to the lungs and connects with the dorsal aorta by a **ductus arteriosus** (ductus Botalli).

The first and second arches disappear, and their basal stem becomes the **external carotid** (Figure 11-10). The third arch becomes the base of the **internal carotid.** Dorsal connection between the third and fourth arches (carotid duct) is reduced and eventually lost. The left fourth arch, the **systemic,** continues to develop, while that of the right side disappears. The fifth arch disappears shortly after its appearance if it appears at all. The ductus arteriosus of the sixth arch atrophies at the time of birth, thus directing all of the blood of this arch through the lung. In terms of the adult, the systemic trunk extends to the left as the base of the systemic arch. The right fourth arch remains as the right **subclavian artery.** It has lost its connection with the dorsal aorta. The right subclavian and the right **common carotid** arise from the aortic stem by a common vessel, the **brachiocephalic (innominate) artery.** The left common carotid and subclavian arise separately from the aortic arch.

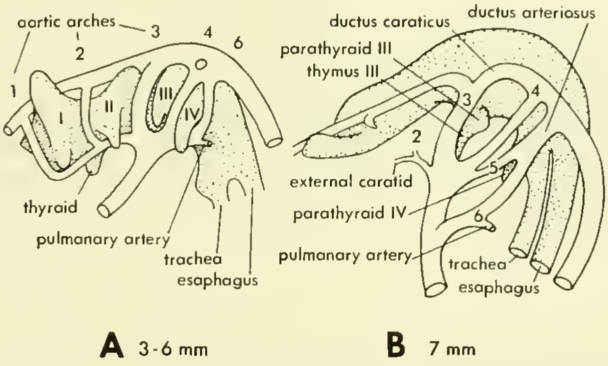


Figure 11-9. Two stages in the development of the aortic arches of man as seen from the side. (After Prentis and Arey, 1917)

Reptiles and birds

The aortic arches of the reptile pass through the same basic stages as those of the mammal. The primary difference lies in the fact that both systemic arches are retained as continuations of separate divisions of the truncus (Figure 11-11). The subclavian arteries pass to the limbs from the systemic arches and the carotid duct is usually retained (*Iguana* but not *Varanus*). The pulmonary arches are like those of the mammal, the ductus arteriosus being closed at the time of hatching with the result that all blood is directed to the lung. The exception to this is *Sphenodon* which sometimes retains this connection.

In the bird, the reptile pattern of development is maintained The right fourth arch becomes the systemic arch, the left disappears. The fifth arch, as in the mammal, appears only briefly if at all (Figure 11-12). The **carotid duct** of the left side loses connection with the left radix aortae and becomes the left **ductus Shawi,** which, along with the right one formed later, sends branches to the syrinx, bronchi, lungs, and esophagus. The left radix aortae develops a new, more medial connection with the pulmonary arch as the ductus arteriosus atrophies. Just before hatching, the right ductus caroticus loses its connection with the systemic arch and the ductus arteriosus of that side is lost (may form a ligament). The left radix aortae now becomes ligamentous.

It is usually presumed that the left systemic arch would be associated with the pulmonary stem as it is in the croc-

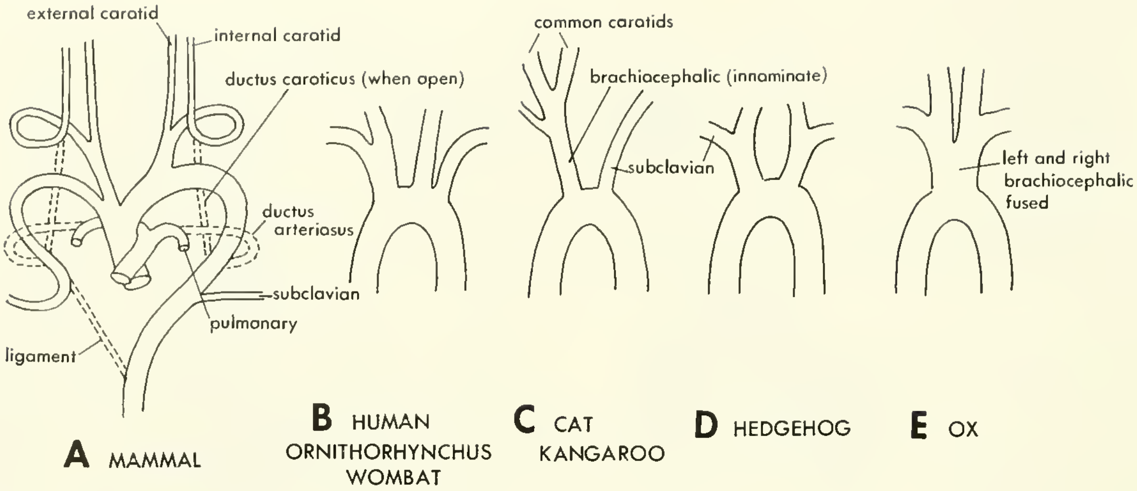


Figure 11-10. Variations in the arterial roots of mammals. (After Romer, 1955, and Owen, 1868)

odile, but this has not been observed. The loss of this arch results in the functional separation of pulmonary and systemic circulations in the bird, a parallelism to that observed in the mammal.

As a result of the elongation of the neck and the posterior displacement of the heart, relationships between the carotids are altered. In the foetus of 6 to 7 days, a commissure connects the external and internal carotids near the head, and the external carotid stem may lose connection with its cranial extreme. The stem is now called the **ascending esophageal** or superficial cervical.

The internal carotids come to lie next to each other at the midline in a hypophyseal canal. In some the carotids fuse, and the left or right root for this common vessel may be the larger. In other species, only the left carotid is retained. The variations of the carotids were used by Garrod (1873) in the classification of birds. The changes observed in the bird parallel those in the crocodilian in which only the left carotid is retained and the external carotid stems (collateralis colli) maintain their distal connections.

The posterior displacement of the heart is also reflected in the subclavian arteries. The subclavian arises as a segmental artery from the dorsal aorta posterior to the pharyngeal region. About the sixth day the heart is moved back in relation to the limb; a new subclavian stem develops from the external carotid region (ventral radix aortae) of

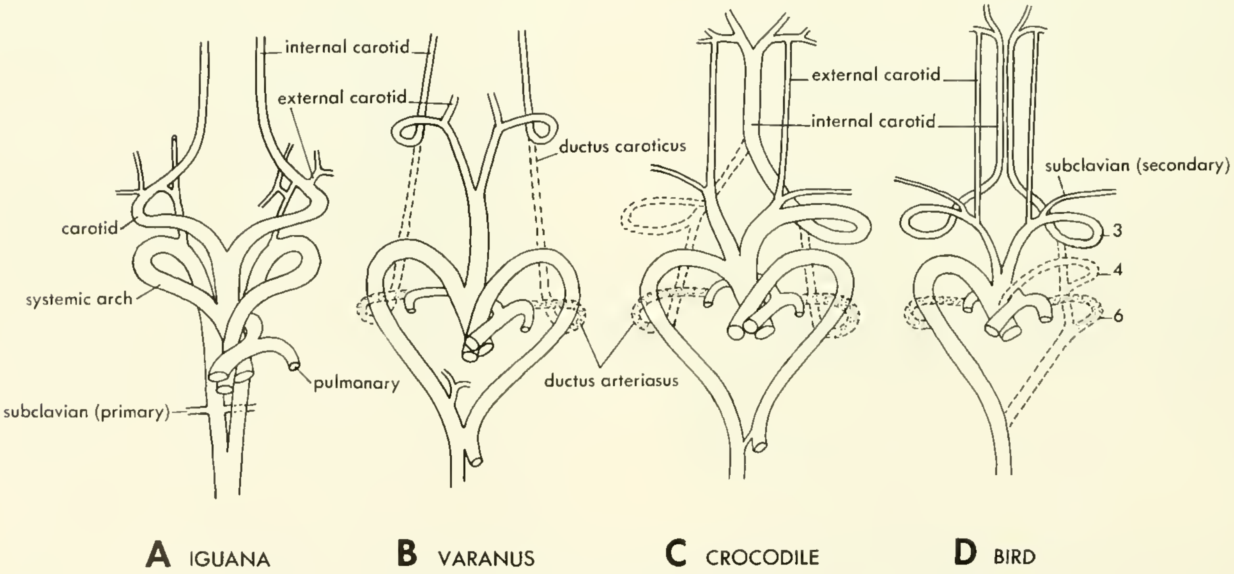


Figure 11-11. Aortic arches of reptiles and the bird. (B, C, D after Goodrich, 1930)

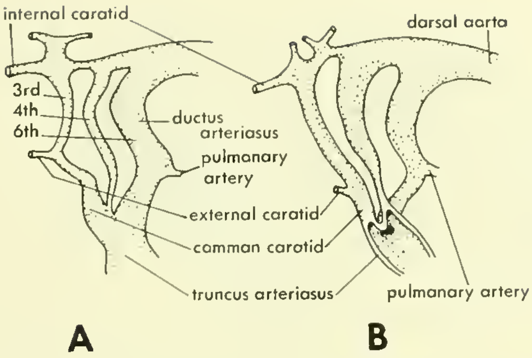
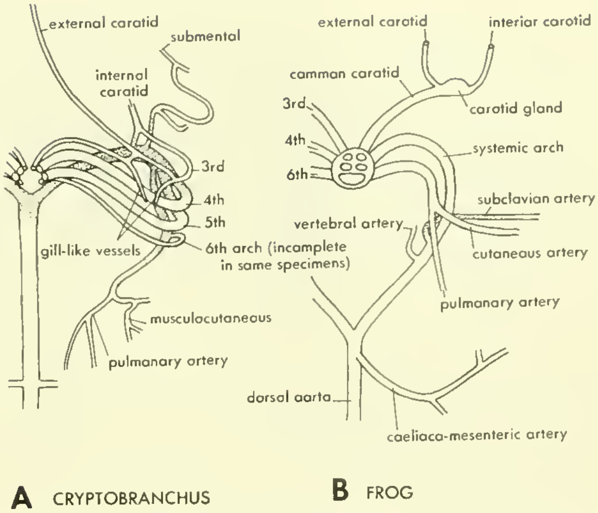


Figure 11-12. Lateral views of two stages of aortic arch development in the chick. (After Lillie, 1919)



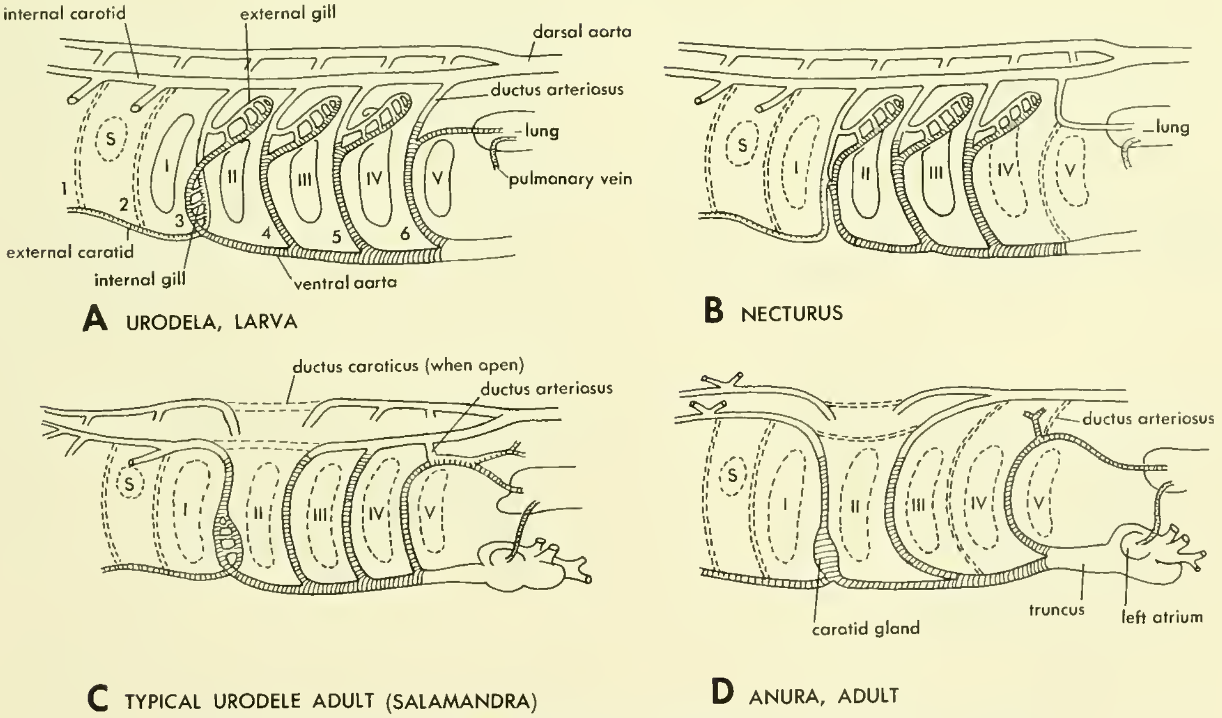
A CRYPTOBRANCHUS **B** FROG

Figure 11-13. Aortic arches of *Cryptobranchus*, A, and Rana, B, as seen in semidiagrammatic ventral view.

the carotid arch (Figure 11-11 D). The limb lies somewhat anterior to the heart in the adult bird. Again the crocodilian parallels this change.

Amphibians

Among the amphibians bilateral arches are retained. A well-developed fifth arch is observed in *Cryptobranchus* (Figure 11-13). Ventrally the sixth arch is small. It gives rise to the pulmonary artery, then, in most urodeles but not in the frogs, continues to the dorsal stem as the ductus arteriosus. The pulmonary artery bears a **musculocutaneous** branch. In *Necturus* the first external gill is served by the third afferent arch; the efferent arch extends down and forward from the gill as the external carotid (Figure 11-14). *Cryptobranchus* is similar even though an external gill is lacking. Neither has a **carotid body.** The base of the sixth arch is lost in *Necturus;* the



A URODELA, LARVA

B NECTURUS

C TYPICAL URODELE ADULT (SALAMANDRA)

D ANURA, ADULT

Figure 11-14. Fate of aortic arches in different amphibians. A, larval urodele; B, *Necturus;* C, typical adult urodele (*Salamandra*); D, adult anuran. (After Goodrich, 1930)

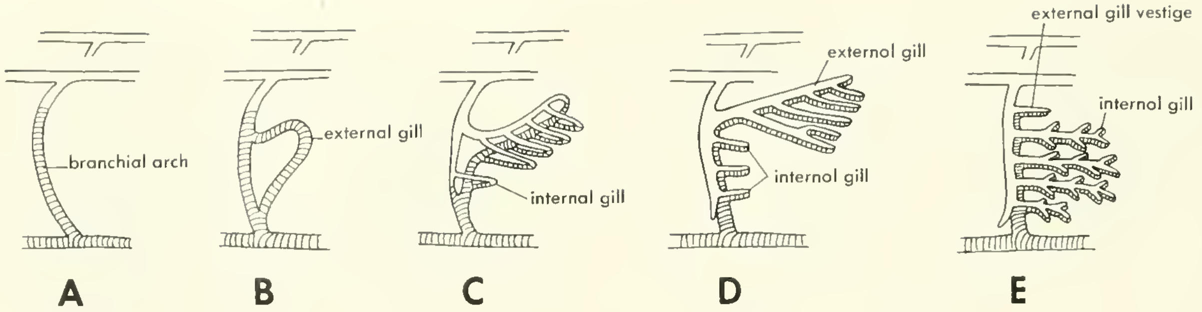


Figure 11-15. Five early stages in the development of an aortic arch in a larval anuran.

ductus arteriosus now connects the pulmonary artery with the dorsal stem. In the tadpole the development of the aortic arch, in terms of both external and internal gills, can be observed (Figure 11-15).

Choanate fishes

Among the dipnoans there are four or five aortic arches leading away from the heart: the second, third, fourth, fifth, and sixth in *Protopterus* (Figure 11-16). The arches bearing gill filaments are fish-like with afferent and efferent divisions (Figure 11-17). The artery to the lung arises dorsally from the common efferent channel (radix aortae). The first three arches have a common ventral stem as do the fifth and sixth arches. *Neoceratodus* lacks the second efferent vessel but is otherwise similar (Figure 11-17). *Latimeria* has not been described, but, on the basis of the lungfishes, is probably like the actinopterygian.

Actinopterygian fishes

Among the actinopterygian fishes, there are four pairs of branchial arches arising from a ventral aorta. These are arches 3 to 6 of the pairs observed in the embryo of higher vertebrates (Figure 11-18). They are associated with five gill openings derived from pharyngeal pouches. Each arch is broken into an afferent division taking blood to the filaments and an efferent division collecting blood from the filaments and carrying it to the dorsal aorta (Figure 11-19).

In the primitive fishes, *Polypterus* and *Amia,* there is a pulmonary artery leading from the sixth efferent vessel on either side back to the swim bladder. This pulmonary artery has the same association observed in the choanate fishes. In most actinopterygians, the dorsal aorta supplies the swim bladder (Figures 9-31, 9-32).

In *Acipenser* or *Lepisosteus,* the second afferent arch is present and serves the hyoid hemibranch (Figure 9-35). The spiracular, or mandibular hemibranch, is served by the efferent vessel of the hyoid hemibranch and the efferent vessel of the first branchial arch (3). In the more advanced fishes, with the loss of the hyoid hemibranch, the second (hyoid) afferent has been lost or replaced by connection with the efferent vessel of the first branchial arch. The pseudobranchial circulation is variable, but generally only oxygenated blood reaches this gill. The **efferent pseudobranchial artery** supplies the eye.

Chondrichthyes

In the sharks there are six pairs of aortic arches or more depending upon the number of branchial arches (Figure

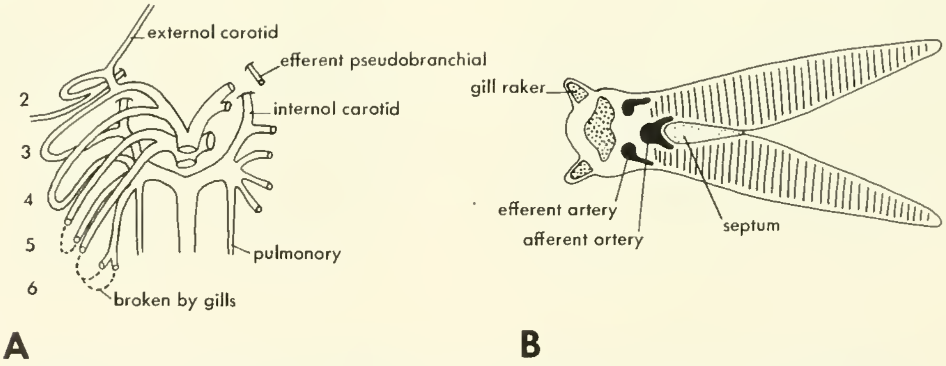
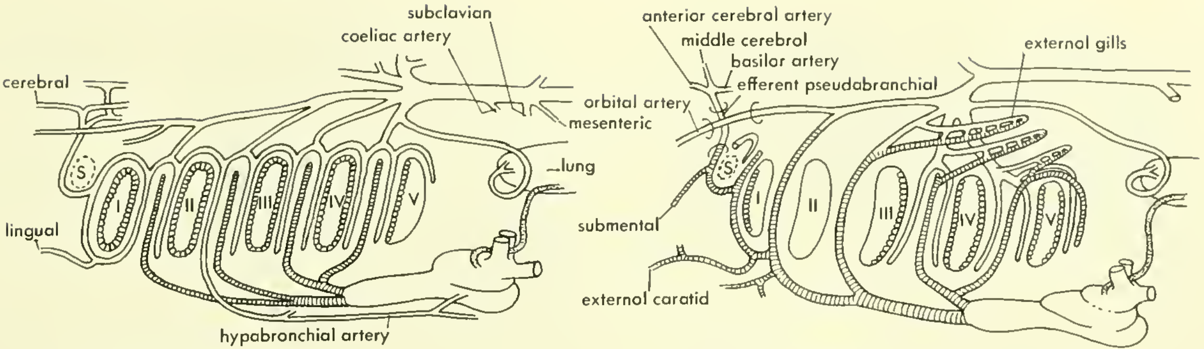


Figure 11-16. Aortic arches of *Protopterus* as seen from below, A, and a cross section of a gill showing interrelationships of main parts, B.



A NEOCERATODUS **B** PROTOPTERUS

Figure 11-17. Aortic arches of *Neoceratodus*, A, and *Protopterus*, B, as seen in lateral view (semi-diagrammatic). (In part after Goodrich, 1930)

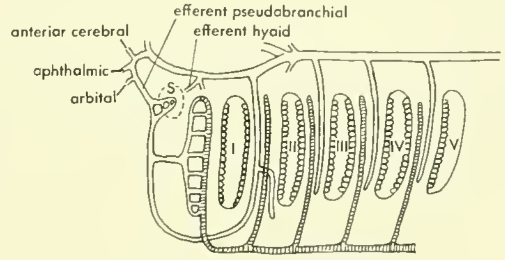
11-20 E). The efferent vessels differ somewhat from those observed in the actinopterygian in that there are two per arch and the stem vessels drain adjacent gill bars (Figure 11-21). This style of drainage is suggested in *Amia* and *Neoceratodus*. *Chlamydoselachus* resembles the teleost in having the mandibular arch connected with the hypobranchial efferent of the hyoid arch. It is distinctive in having the first six arches represented and a seventh as well. In *Squalus* or *Mustelus* the mandibular afferent reaches only to the angle of the mouth; the afferent pseudobranchial comes from the efferent hyoid. The pseudobranch thus receives oxygenated blood.

The development of the arches in *Squalus* has been studied (Figure 11-20). Six arches appear and for a time all are present. With the separation of afferent and efferent divisions, the mandibular arch becomes connected, below the level of the gill pouches, with the first branchial efferent. With this connective now supplying blood to the mandibular arch, the mandibular afferent stem atrophies. Presence of a single efferent in each arch in the young shark suggests that this is the primitive condition; the two efferents of the adult represent a modified state.

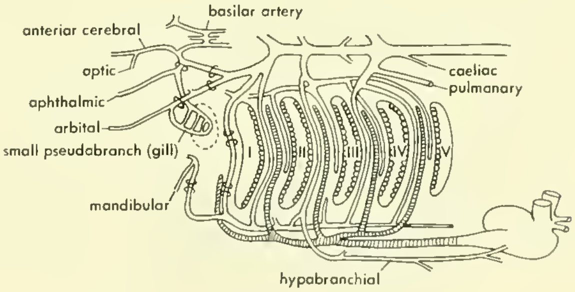
Hydrolagus agrees with the actinopterygian fish in having four complete arches which serve the four gill openings (Figure 11-22). There is a hyoid hemibranch in front and a fifth hemibranch behind. The hyoid hemibranch is supplied by the second afferent arch. The efferent vessel joins the efferent mandibular stem or the efferent hypobranchial of the first branchial arch to supply the mandibular and throat areas. *Hydrolagus* has only a single afferent and efferent artery in each bar, and the efferent arteries are not joined above the gill pouches as in the shark (Figure 11-22).

Cyclostome fishes

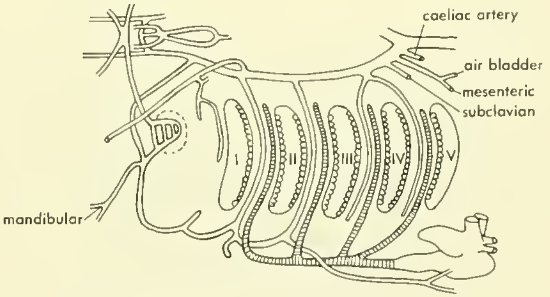
The most anterior aortic arch of the lamprey is the hyoid (2), the second is the first branchial (3), and there is a gill pouch between these (Figure 11-23). There are eight aortic arches in all. The afferent and efferent arteries branch at



A LEPISOSTEUS AND ACIPENSER



B AMIA



C GADUS OR ESOX

Figure 11-18. Semidiagrammatic lateral views of aortic arches of actinopterygian fishes. A, *Lepisosteus* or *Acipenser*; B, *Amia*; C, *Gadus* or *Esox*. (After Goodrich, 1930)

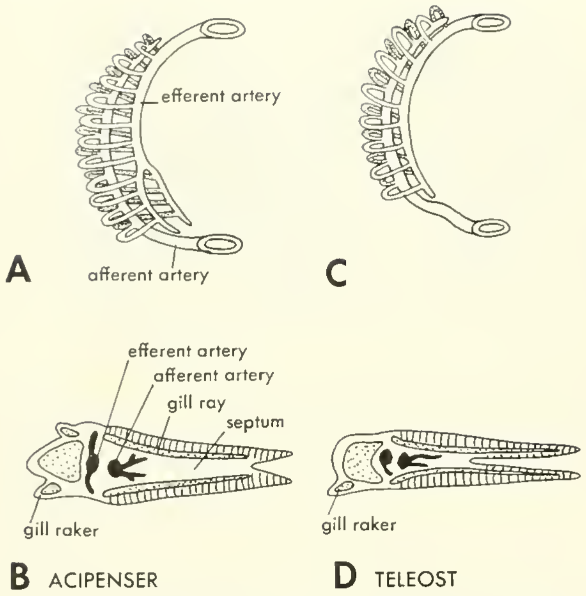


Figure 11-19. Interrelationships of vessels in the gill and as seen in semidiagrammatic anterior view, A and C, and in cross section, B and D. (After Goodrich, 1930)

the interior opening of the gill pouches, and send vessels to the posterior and anterior hemibranchs of adjacent pouches. The efferent arteries draining adjacent hemibranchs are interconnected.

The hyoid afferent serves only a posterior hemibranch. The hyoid efferent extends dorsally to the region of the hypophyses where it joins the carotid stem. The external carotid arises directly from the efferent of the second branchial arch but receives contributions from the efferents of the first branchial arch.

In development, the first aortic arch is the mandibular which appears at a stage of 40 somites. By 70 somites the mandibular arch is reduced in size and three other arches have appeared. The mandibular arch has lost its connection with the ventral aorta in an embryo of 4.5 mm; this velar artery persists into the adult but along with its large postorbital branch forms a part of the external carotid system. By 6 mm the arches have divided into an outer afferent and an inner efferent division. This relationship is not found in the adult, where both afferent and efferent vessels lie medial to the pouch. These vessels extend to the region of the internal branchial opening and there divide into dorsally, laterally, and ventrally extending branches. Their branches

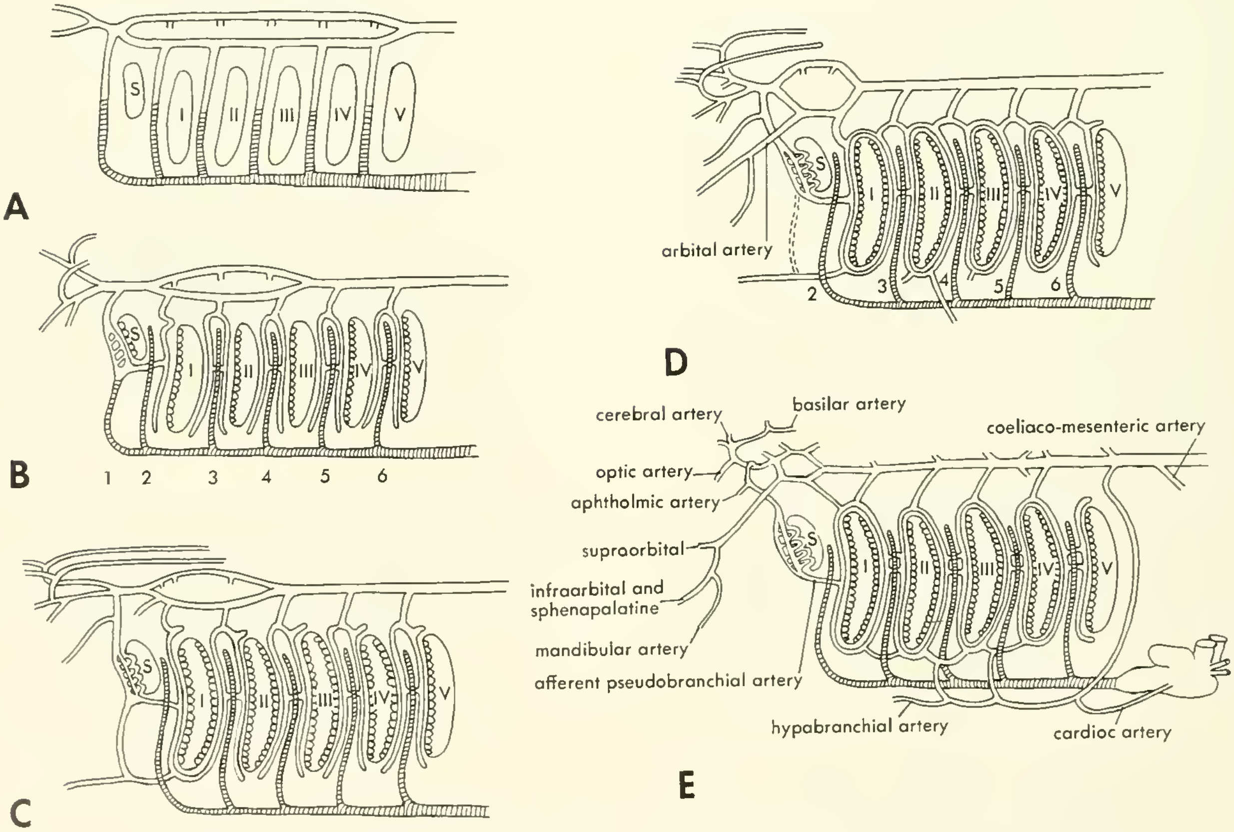


Figure 11-20. Five stages in the development of the aortic arches of the shark. (After Goodrich, 1930)

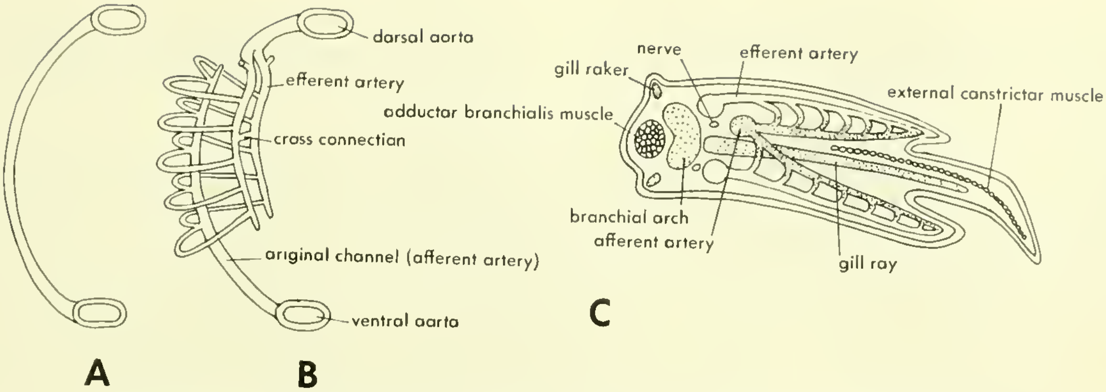


Figure 11-21. Interrelationships of vessels in the arch of a shark. A and B, semidiagrammatic anterior view of two stages (A and D of Figure 11-20) of arch development; C, cross section of arch. (After Goodrich, 1930)

extend outward in the gill filaments: one afferent and two efferent vessels in each filament.

In *Myxine* the aortic arches are similar to those of the lamprey with the exception that each aortic arch serves the hemibranchs of a single pouch, a unique situation. The afferent artery is associated with the outer opening of the pouch, the efferent with the inner. There are interconnections between the arteries of a series, and it is quite possible that the pouch relationship is secondary, resembling that observed in the efferent system of the shark. The pouches are difficult to homologize with those of the lamprey or the other vertebrates because the arches cannot be numbered.

General observations on aortic arches

There appears to be a consistent plan of arch formation among both agnaths and gnathostomes. This constancy is a reflection of the similarity of having branchial bars which primitively bore gills. There is no fixed number of aortic arches, no fixed type of ventral aorta or of dorsal vessel or vessels. The lack of a premaxillary arch in any vertebrate casts doubt on the existence of such a segment. The loss of the first (mandibular) arch as a simple entity in all vertebrates is of interest, and it might be significant in terms of the original presence of jaws even in the agnaths.

The usual discussion of the evolution of the aortic arches in tetrapods implies that the observed adult conditions are retentions of phylogenetic stages suggesting an amphibian to reptile to mammal sequence. Actually parallel modifications are indicated in the loss of the second and, usually, the fifth arches and in various asymmetries. The living amphibians have maintained symmetry in the reduction of arches, while shortening the ventral aorta. The living reptiles have lost the truncus and have developed separate outlets (4) for the carotid, pulmonary, and right and left systemic arches. The reptile pattern may have been derived from that observed in the salamander. The bird has carried the reptile pattern one step further with the loss of the left systemic arch. The mammal has separate openings (2) for the joined carotid and systemic arches, and the pulmonary stems, and has re-

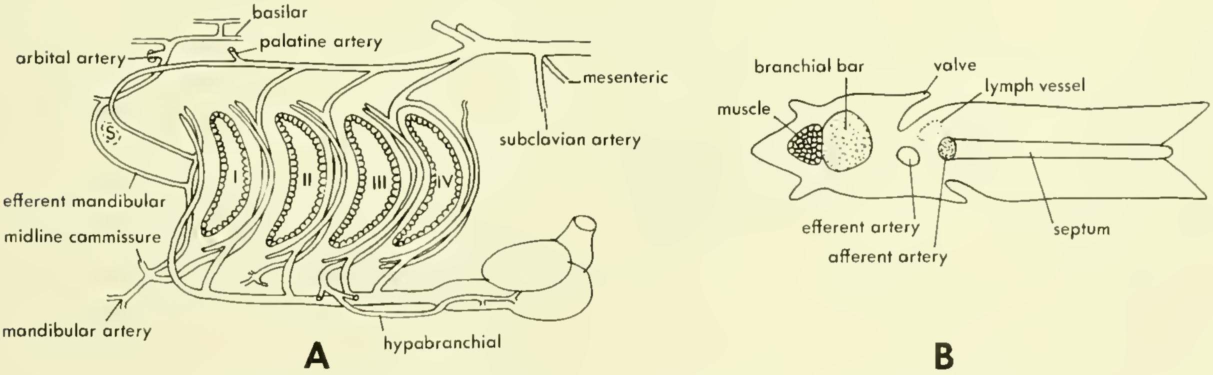
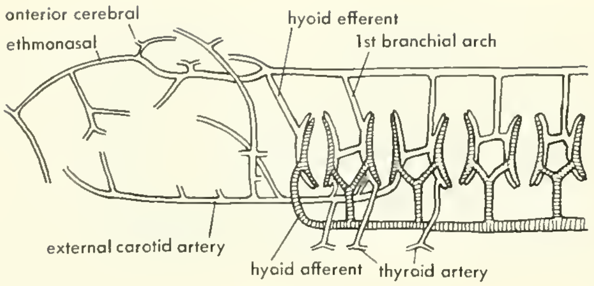
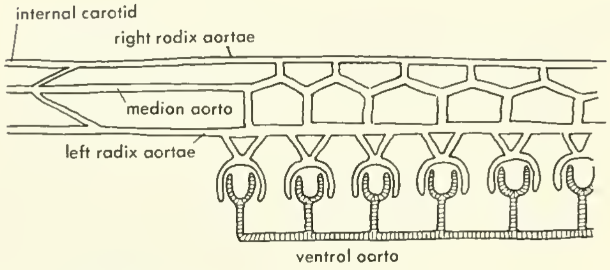


Figure 11-22. Semidiagrammatic lateral view of aortic arches of a chimaerid, *Hydrolagus*, A, and a cross section through an arch, B.



A PETROMYZON



B EPTATRETUS

Figure 11-23. Semidiagrammatic lateral views of aortic arches of lamprey, A, and *Eptatretus*, B. (B, after Müller, 1839, and Goodrich, 1909)

duced the right systemic arch to a subclavian stem. The mammal pattern may have been derived from the amphibian but not from the pattern observed in living reptiles.

A discussion of the aortic arches of fishes is best considered as a part of a more general discussion of the arteries of the head.

CIRCULATION IN THE HEAD

Arteries

Mammals The main arteries of the head can be described in terms of the human (Figure 11-24). The **common carotid** branches in the neck to form **internal and external carotids.** The external carotid sends branches to the **thyroid** area, a **lingual artery** to the tongue, and **external maxillary** artery up over the outside of the jaw, an **occipital** artery to the back of the skull, a **posterior auricular** to the region behind the ear, an **internal maxillary** to the inside of the jaws, and a **superficial temporal artery** up over the side of the head between the ear and eye. From the internal maxillary come two **deep temporals** serving the jaw musculature. The external carotid also sends a **pharyngeal artery** up along the internal carotid.

The internal carotid passes just behind the external and enters the skull through the **carotid canal.** It turns forward to either side of the **sella turcica,** where it expands as a **cavernous portion** (enclosed in a venous sinus), gives off the **ophthalmic artery** to the orbit, and divides to form the **middle** and **anterior cerebrals.** Where it divides, a connective from the **vertebral** and **spinal arteries** joins the internal carotid.

Examination of other mammals indicates a rather similar pattern. The usual main trunks are an external carotid, an internal maxillary, and an internal carotid. In the rat, there is also a **stapedial artery.** This enters the tympanic bulla through its own foramen, perforates the stapes, passes through a small canal in the periotic bone, and then exits from the bulla. From here it passes forward through the alar canal to the orbit, where it becomes the internal maxillary stem. The internal carotid is also developed in the rat. The external carotid differs in not supplying the internal maxillary division.

The cat differs in that the internal carotid stem is present in the young but eliminated in the adult; the pharyngeal artery replaces the carotid stem. The pharyngeal artery enters the skull at the anterior carotid foramen to join the **circle of Willis** at the base of the brain. The external carotid bears the internal maxillary as a branch, which has much the same division as in the human.

Of particular interest is the **carotid rete** which is observed in most mammals. In the human the carotid stem expands as the carotid sinus. This is enclosed by a cavernous venous sinus to either edge of the sella turcica. In the cat the internal maxillary stem forms a rete, in the orbit just outside the skull. This is enclosed by a venous rete from the ophthalmic veins. From the arterial rete several channels lead into the carotid portion of the circle of Willis, and a small internal rete is associated with these connections. A second connective, the **middle meningeal,** also forms a rete where it joins the circle of Willis. Most animals have some sort of close arterial and venous relationship, with the vein enclosing the artery, in the orbit or inside the skull at the side of the sella turcica.

EMBRYOLOGICAL DEVELOPMENT In the earliest stage of development, there is a network of small vessels permeating the tissues of the head into which the arteries feed and from which the veins arise (Figure 11-25). With the appearance of the aortic arches, there is an anterior extension from the ventral aorta, the external carotid, and another from the dorsal aorta, the internal carotid. The internal carotid has branches to the region of the eye and to the brain, the middle cerebral (Figure 11-26).

Behind the level of the aortic arches, a number of segmental arteries extend up toward the nerve tube, and from these a vessel develops forward through the capillary net. This vessel is the vertebral artery. It passes below and medial to the ear region giving off branches to the cerebellar region of the brain. The vessels of either side now join and form the basilar artery, which gives off additional branches to the cerebellar region of the brain. The anterior end of this vessel forks as the posterior communicating branches of

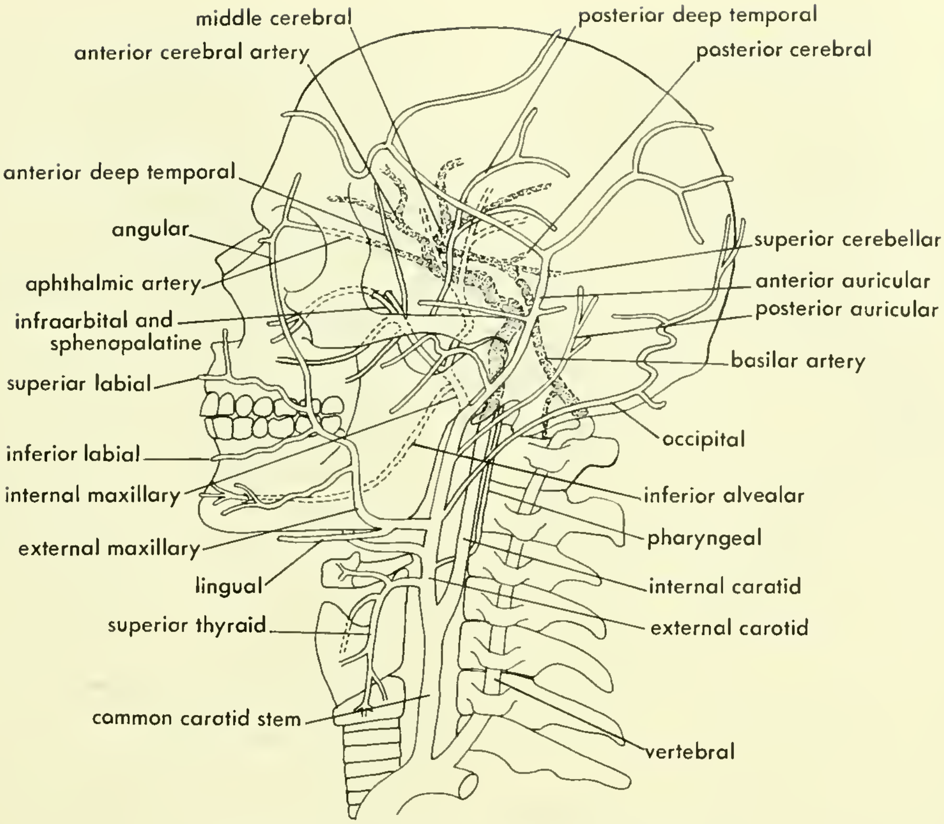


Figure 11-24. Arteries of head in man. (After Tandler)

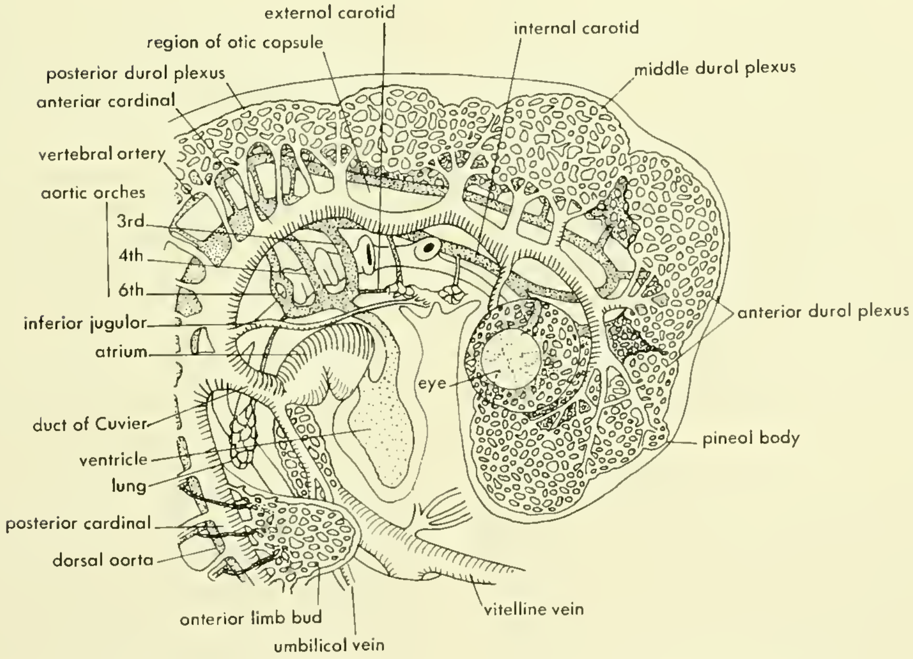


Figure 11-25. Vascular system of head end of 4-day-old chick. (After Patten, 1958)

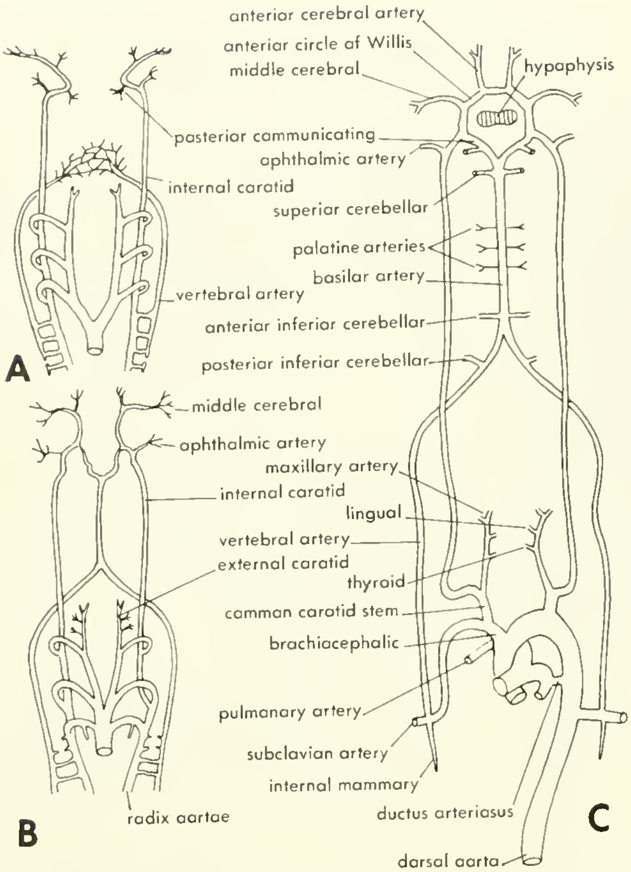


Figure 11-26. Three stages of anterior arterial development in man. (After Patten, 1946)

the circle of Willis; these join the internal carotids. The anterior cerebrals now appear, and there is a small communicating branch between them which completes the anterior half of the circle of Willis. The anterior cerebrals extend forward and upward on the inner surface of the two cerebral lobes.

The spinal artery arises as a posterior midline development from the basilar artery, and it extends back inside of the vertebral canal. The ophthalmic artery arises as a branch of the internal carotid just before it is joined by the posterior communicating division of the basilar artery.

Meanwhile the external carotid, the anterior extension of each of the paired ventral aortae, has given rise to the external maxillary, the lingual, and the thyroid arteries.

Reptiles In the reptile (Figure 11-27) the external carotid is represented by the lingual (or **mental**) branch of the common carotid. The carotid stem branches to form the internal carotid and the **stapedial artery**. The internal carotid passes ventromedially into the parabasal canal. Here it gives rise to a palatine artery, which emerges above the palatine bone, then enters the sella to supply the middle and anterior cerebral arteries. In Sphenodon a parabasal canal is lacking; the palatine branch arises before the internal carotid enters the basis cranii. An ophthalmic artery, from the internal carotid, accompanies the optic nerve.

The stapedial artery passes upward and outward in front of the stapes or columella and gives rise to two branches. One is a mandibular branch, which extends down inside the quadrate to the mandible and enters the bone by way of the mandibular fossa and foramen. The other, the internal maxillary stem, passes forward through the **cranioquadrate passage** and gives rise to a superior orbital artery, then continues down and forward to serve the upper jaw and snout area.

The above description applies to *Sphenodon* or to *Iguana*. In the turtle the picture is much the same, one difference being that a second stem passes outward from the internal carotid to join the lingual (the external carotid). This new stem now replaces the old, more proximal to the heart, stem of the lingual artery. In the crocodile a similar situation occurs; the internal carotid is connected with the mandibular and lingual arteries by way of a vessel similar to that of the turtle. There is no common carotid vessel.

In the bird the external and internal carotids arise as in the other groups, but, as a result of the elongation of the neck, the external becomes a branch of the internal. The external carotid stem may be preserved as the superficial cervical, as in the crocodile.

The pattern observed in the reptiles is quite comparable to that of the mammals. In mammals the external carotid has become a larger stem and has taken over the distribution of blood to much of the surface of the head including the usual maxillary and mandibular branches. This ascendancy of the external carotid is a distinctive mammalian feature, even though it is not found in all mammals. In the case of *Erinaceus,* a fairly reptilian distribution is observed, with the stapedial and internal carotids serving the entire head and the external carotid serving only the lingual area.

Amphibians In the amphibian we see further evidence of the evolution of the head arteries. In the case of the salamander, *Necturus,* the carotid stem has internal and external divisions which serve the head (Figure 11-28). The external carotid goes to the musculature of the throat as a lingual artery.

The internal carotid stem passes forward below the stapes and upward in front of that structure where it divides. There is a posteriorly extending temporal division passing above the stapes, a mandibular (and hyoid) division extending ventrolaterally behind the quadrate, and an internal division which enters the parabasal canal. The parabasal division gives rise to the palatine artery, then enters the cranial cavity to branch as the middle and anterior cerebral vessels and the ophthalmic vessel. The last division of the internal carotid stem passes forward through the cranioquadrate fissure, supplies the muscles in the region behind the eye, and passes down laterally to become the internal and

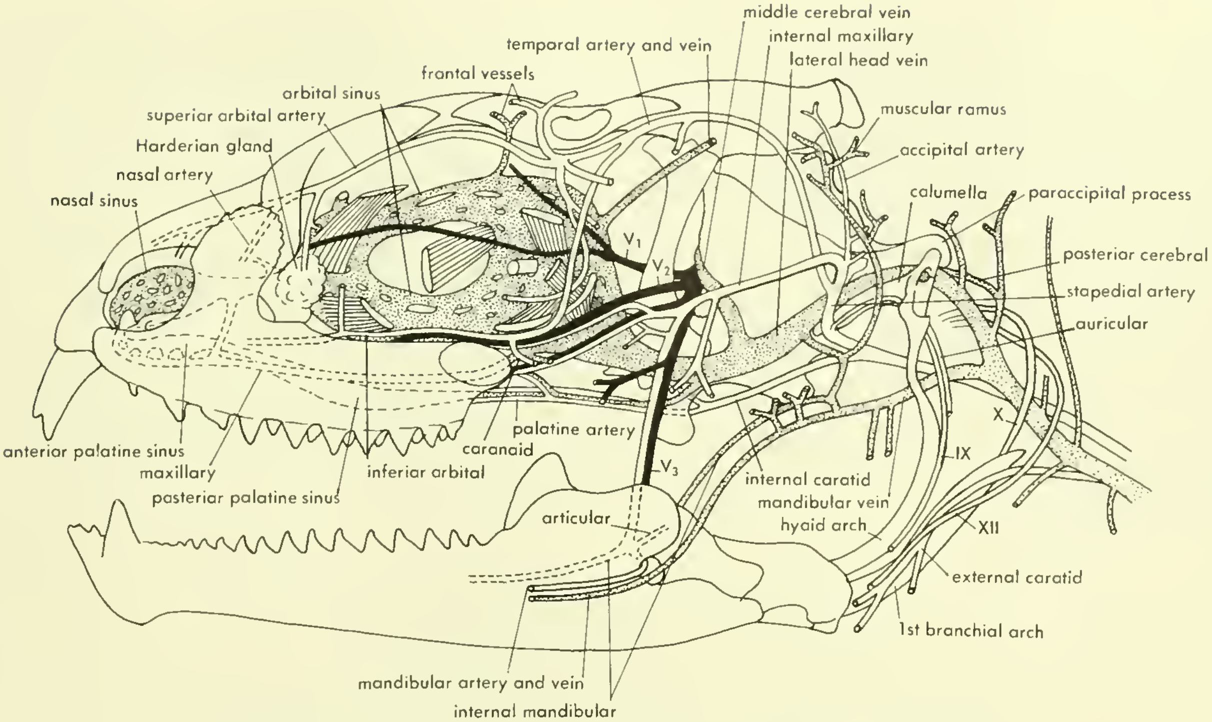


Figure 11-27. Vascular system of the head in Sphenodon. (After O'Donaghue, 1920)

external maxillary arteries. The ophthalmic division emerges with the optic nerve; it also serves the snout region of the skull.

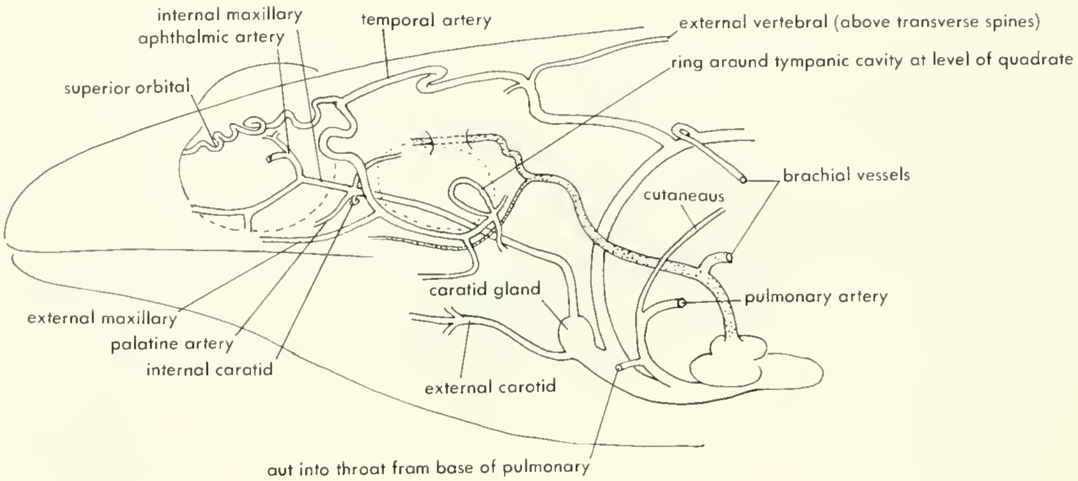
The situation in *Necturus* is not matched in the frog (Figure 11-28), although they agree in that the external carotid forms only the lingual artery. The internal carotid passes upward into the orbit, where it sends divisions upward, anteriorly, and into the cranial cavity. It serves the general region of the eye, the ethmoid area, and part of the brain. The **supraorbital,** maxillary, and mandibular divisions arise from an artery passing forward over the top of the head from the systemic stem. This artery also gives rise to branches passing into the skull and passing backward along the vertebral column above and lateral to the spines of the vertebrae.

In the frog or salamander, one observes a large swelling, the **carotid gland,** at the base of the internal and external carotids. This gland is derived from the gill and connective vessel remnants between the first branchial afferent and efferent arteries; its function is not known, but its spongy nature suggests control of blood pressure in the internal carotid.

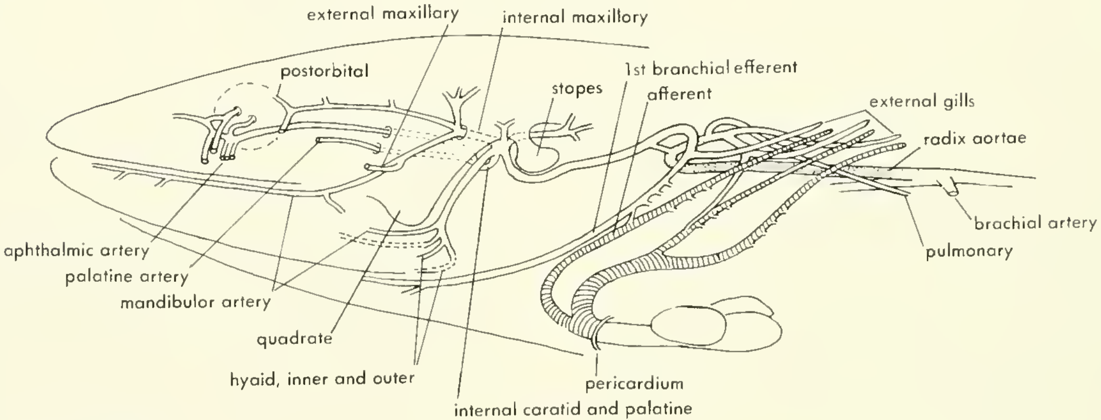
The arterial system of the frog is a modified one as determined on the basis of its embryological development. The ontogeny of this region in the tetrapods shows many interesting points. The three basic stems: stapedial, internal carotid, and external carotid are probably primitive for the mammal. In man a stapedial artery appears early but is later replaced. The internal carotid and stapedials are derivatives of a common stem as suggested in the amphibian. The external carotid is a lingual artery in the primitive type. The modified type observed in the mammal is thus derivable from the type observed in the salamander. Even in the case of the salamander, there has been a certain amount of alteration. The exact primitive pattern is not necessarily repeated in any living form.

Choanate fishes There is no readily available figure or description of the head arteries for a choanate, but examination of *Protopterus* indicates that it is more like the fish than the amphibian. The external carotid, as represented by the **hypobranchial branches** of the **hyoid efferent,** serves the hyoid arch and the throat area; it is a typical lingual artery. The internal carotid is the dorsoanterior continuation of the **hyoid afferent;** there is a broad dorsal connective between the second and third arches. From the third arch an artery extends forward through the palatoquadrate into the orbit; it supplies the snout, maxilla, and mandible.

Actinopterygian fishes Two species of actinopterygians can be compared in terms of their head arteries; these are *Ophiodon* and *Lampanyctus* (Figure 11-29). Although these two types differ greatly in detail, they agree in certain basic features. There are four branchial arches in each. The **efferent artery** of the **first branchial arch** extends forward to the hyoid arch as an external carotid; it follows the hyoid arch back to the area of the interhyal, where it joins the



A BULLFROG



B NECTURUS

Figure 11-28. Anterior arteries of *Rana* and *Necturus* as seen in semidiagrammatic lateral view.

mandibular artery. The mandibular artery continues up to the pseudobranch in *Lampanyctus* or past the pseudobranch, which is supplied by a side branch, in the case of *Ophiodon*. The mandibular arch of *Lampanyctus* has afferent and efferent parts, while that of *Ophiodon* is unbroken and enters the dorsal aorta. The **efferent pseudobranchial** artery in both extends to the eye, where it serves the chorioid coat. In *Lampanyctus* there is a transverse connective between the vessels of either side which is lacking in *Ophiodon*. An **infraorbital artery** extends downward and forward from the bilateral dorsal aortae to serve the snout and upper jaw.

In the case of the actinopterygian fish, it is apparent that parts of the hyoid arch have been done away with or modified. The mandibular arch has been partly retained but modified. The pseudobranch, or mandibular hemibranch, is drained by a special channel running forward to the eye rather than entering the dorsal aorta.

Chondrichthyes Although several species of sharks have been described, only a few are well known. Of these, *Chlamydoselachus*, is similar to the actinopterygian in that the first efferent branchial arch extends ventrally and anteriorly, along with the efferent of the hyoid arch, as a "lateral hypobranchial" or external carotid (Figure 11-30). From this a **submental artery** extends forward, while an external mandibular extends out and upward to the outer surface of the lower jaw. An **afferent mandibular artery** parallels the posterior external mandibular; this has cross connections with the anterior efferent hyoidean, and sends branches forward on the inner surface of the upper and lower jaws. The external mandibular connects by way of a postorbital stem with the dorsal aorta, while the anterior efferent hyoidean becomes the **afferent pseudobranchial.** The efferent pseudobranchial serves the eye and also connects with the dorsal arterial stem, the internal carotid.

The arterial pattern of this species seems little modified in terms of a hypothetical ancestral type. In other sharks, *Squalus* or *Mustelus*, the external carotid is only hypobranchial in distribution, and there is no connection with the postorbital stem. The shark differs from the actinopterygian or dipnoan in that the hyoid vessels are like those of the branchial arches (only *Amia* approaches this).

Hydrolagus is much like *Squalus* in that the hyoid aortic arch is retained and forms afferent and efferent divisions associated with a hemibranch. The efferent hyoid connects with the lateral dorsal aorta, and the mandibular efferent (pseudobranchial artery—there is no pseudobranch) enters the endocranium to supply the brain. An orbital artery arises from the efferent hyoid connection with the dorsal aorta. This penetrates the palatoquadrate and sends branches anterolaterally to the maxilla and snout and posteriorly to the otic region.

Cyclostomes The head arteries of the lamprey have been described but are not generally known. The external carotid arises from the efferent vessels of the first two branchial arches (Figure 11-25). It gives rise to a **thyrolaryngeal** branch and passes forward medial to the afferent stem (on either side). At the anterior margin of the branchial skeleton, a branch extends forward and inward to the roof of the mouth. A short distance anteriorly, the main stem gives off an external branch which passes up behind the muscles of the mouth. This branch gives off branchlets to the muscles in front and behind it and continues up behind the eye, where it supplies the musculature. The external carotid stem continues forward branching to the muscles of the rasping organ. There are several separate efferent branches serving the ventral wall of the branchial basket.

The internal carotids arise from the dorsal aorta in the region of the otic capsule. Each receives a hyoid efferent

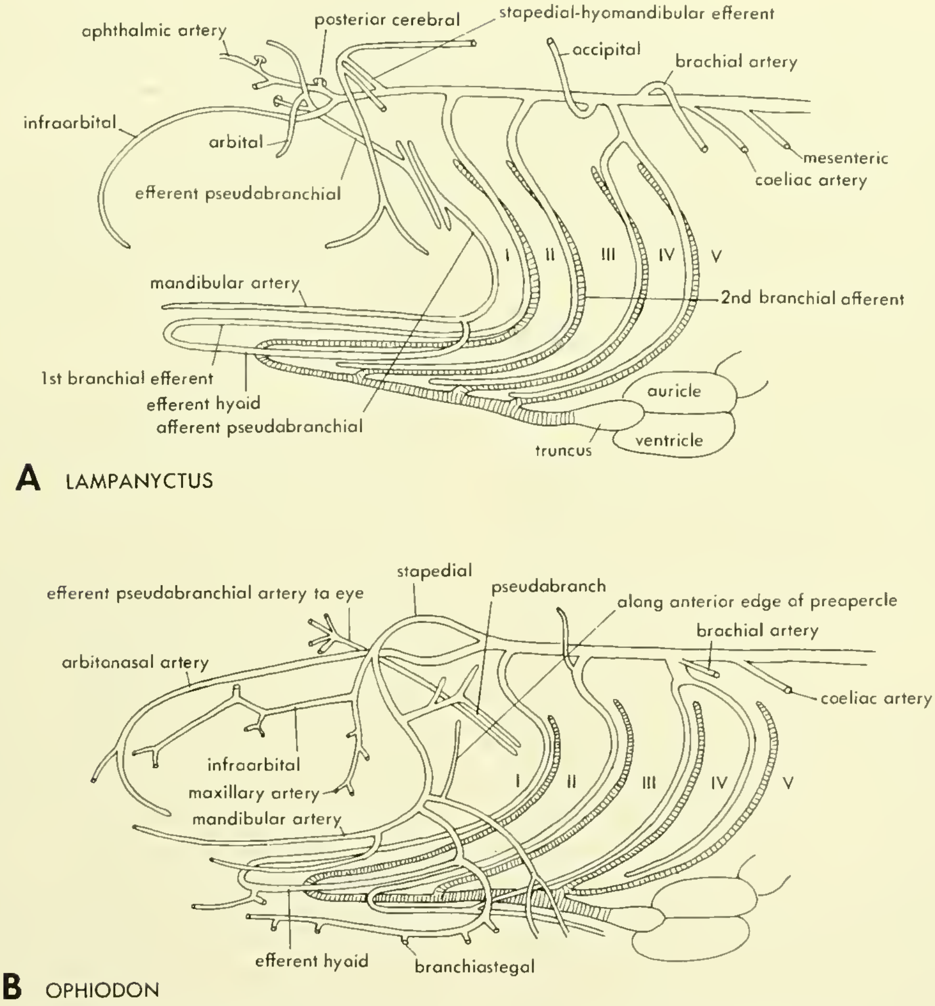


Figure 11-29. Anterior arteries of two teleosts, *Lampanyctus* and *Ophiodon elongatus*, as seen in semidiagrammatic lateral view. (B after Allen, 1905)

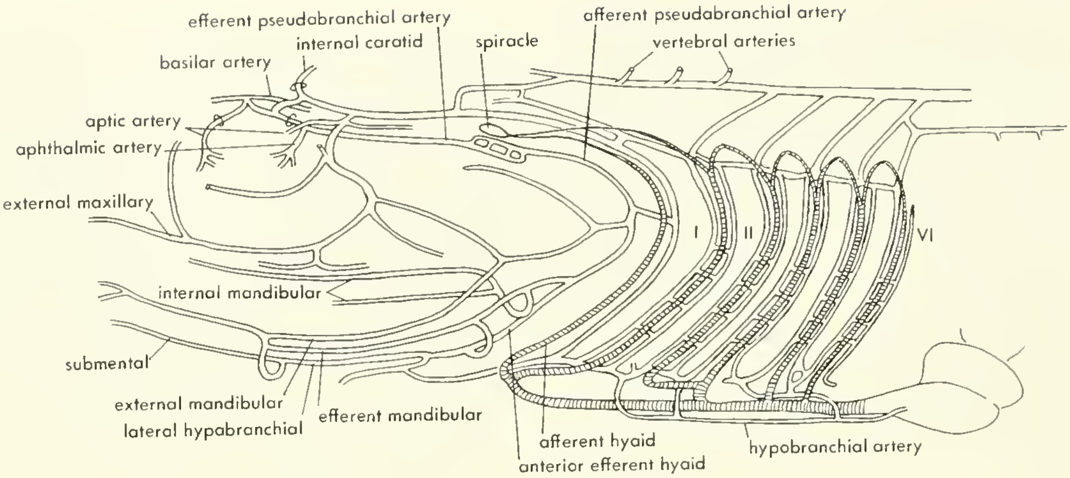


Figure 11-30. Anterior arteries of *Chlamydoselachus*. (After Allis, 1923)

lateral to the infundibulum. Here the internal carotids penetrate the cranial wall and enclose the infundibulum and pituitary in an interconnecting network of arteries. The two stems send branches to the eye muscles and also give rise to anterior and middle cerebrals.

The main stem now passes across the ventroanterior wall of the orbit and gives off a large palatine artery to the roof of the mouth cavity, the anterior end of the tongue muscles, and the ventral wall of the buccal funnel. The main stem passes out through the anterior inner margin of the orbit, along with the large supraorbital nerve trunk, and extends to the dorsal and lateral margins of the buccal funnel. This orbitonasal stem has branches to the nasal area and to the musculature anteroventral to the eye.

Myxine is much like the lamprey. The lingual artery, which may represent the external carotid, is a branch of the internal carotid. The paired internal carotids are accompanied for some distance by a median vessel: they continue forward beneath the brain capsule and out to the upper lip. Branches from these vessels serve the various parts of the head.

General observations on head arteries The pattern of head arteries in the tetrapods shows many minor variations, variations traceable to the strong specialization shown by some members, the frog for example. Among the fishes, the tetrapod pattern is scarcely recognizable although there is some similarity which is reflected in the use of common terms. The development of a pseudobranchial circulation in the shark and actinopterygian suggests that this was common to early fishes and has been lost both in the choanate and the holocephalan. Since the pattern of the agnath is quite remote, little direct comparison with other fishes is possible. Lack of a pseudobranchial circulation can be mentioned and the system might be viewed as generally less modified than in gnathostomes, or, perhaps, it might better be described as independently evolved.

Veins

Mammals The main veins of the head of the mammal can be described in terms of the human (Figure 11-31). The **anterior** (superior) **vena cava** branches to form right and left **internal jugulars** and **subclavians.** The internal jugular of either side passes up next to the vertebral centra. Behind the jaw it enters the skull at the jugular foramen to receive the veins from the brain.

The **superior sagittal sinus** lies in the base of the membranous falx which extends down between the cerebral lobes. Bilateral great cerebral veins exit from the ventricles of the cerebrum and join with the **inferior sagittal sinus,** which extends back along the ventral margin of the falx, to form the **straight sinus.** This midline channel joins posteriorly with the superior sagittal sinus (the confluence of the sinuses). The sagittal sinus now leads into bilateral transverse sinuses which follow the base of the tentorium. Then an **occipital sinus** continues along the midline to the small vessels of the region of the foramen magnum. The **transverse sinuses** laterally become the **sigmoid sinuses,** which in turn become the **internal jugulars** with passage through the jugular foramina. **Superior** and **inferior petrosal sinuses** connect the sigmoid sinus of either side with the **basilar plexus** in the region behind the sella turcica.

The internal jugular receives a number of vessels from the superficial regions of the head. An **occipital vein,** which passes up behind the skull, connects, through the skull, with the transverse sinus or the confluence of the sinuses. There is also a connective between the occipital vein and the mastoid division of the **posterior auricular vein.** From the internal jugular, below the jaw, there are several branches—**lingual, pharyngeal,** and **thyroid.**

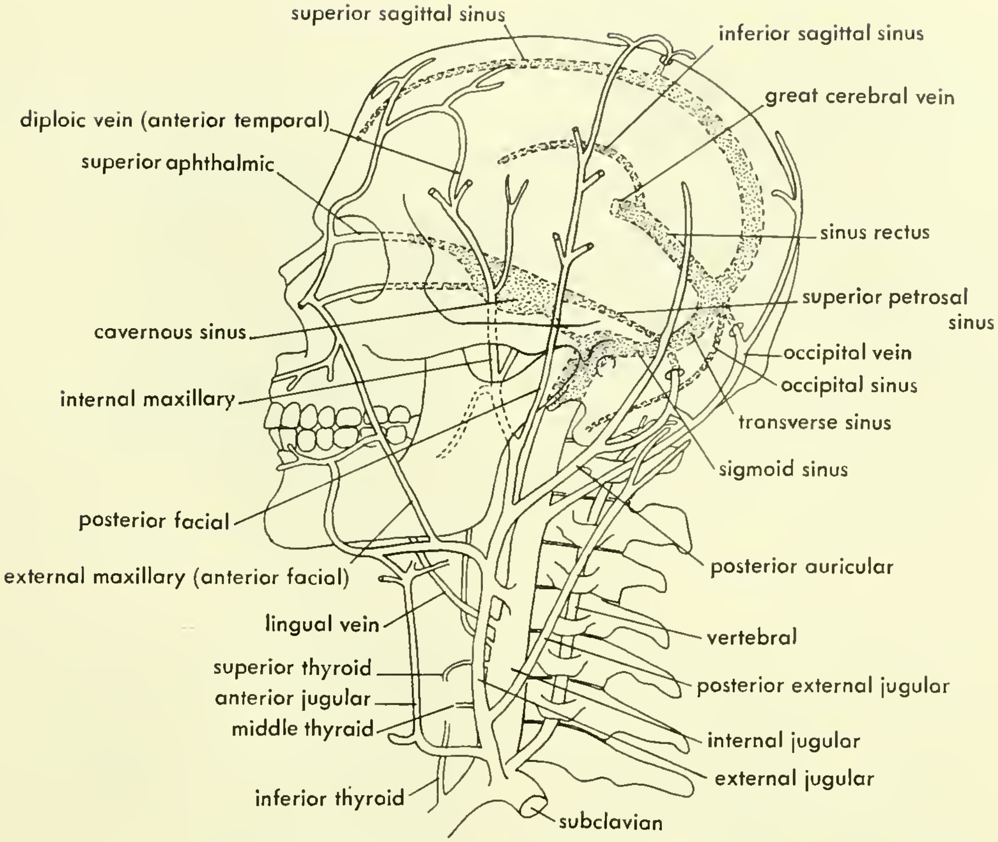


Figure 11-31. Veins of the head in man. (After Tandler)

Paralleling the internal jugular but lying superficially in the neck is the **external jugular vein.** The branches of the external jugular drain most of the outer regions of the head. A **posterior facial** division, paralleling the superficial temporal artery, receives **diploic veins** from the skull bones. A large **posterior auricular** enters the skull at the mastoid foramen to connect with the transverse or sigmoid sinus. The large **anterior facial vein,** which parallels the external maxillary artery, has **mandibular, inferior labial, superior labial,** and **orbitonasal** branches.

Draining a part of the blood of the anterior facial is an **anterior jugular** vessel, lying superficially in the neck, just lateral to the midline. The vessels of either side connect ventrally or posteriorly and are joined by a stem with the external jugular. The external jugulars join the subclavian veins, then fuse to form the superior vena cava.

In the neck is also a **vertebral vein,** a reticulum of channels enclosing the vertebral artery. This helps drain the occipital region and the internal vertebral system.

Lying within the brain cavity are bilateral channels with **cavernous sinuses** to either side of the sella turcica. **Superior** and **inferior ophthalmic veins** and their branches connect with the cavernous sinus through the orbital fissure. There is a cross connection through the floor of the sella turcica between the cavernous sinuses; this cross connection encircles the infundibular stem. There is also a cross connection behind the dorsum sella; this enters the basilar plexus which extends back through the foramen magnum into the vertebral canal. The cavernous sinuses connect on either side with the sigmoid sinuses through superior and inferior petrosal sinuses.

In the description of the skull it was pointed out that the main venous drainage channel of the brain cavity was not necessarily through the jugular foramen, for it may be through the postglenoid foramen. In the dog (Figure 11-32) the postglenoid commissural vessel drains the transverse sinus into the external jugular. The internal jugular is small as is the sigmoid sinus.

EMBRYOLOGICAL DEVELOPMENT In the development of the venous channels, at first there is a reticulum of channels passing above and below the ganglia and roots of the cranial nerves. From these channels, which can be seen in the 10-mm pig, the **anterior cardinal** forms. This extends forward above the vagus nerve, passes lateral to that nerve near its ganglion, lateral to the ninth ganglion and root,

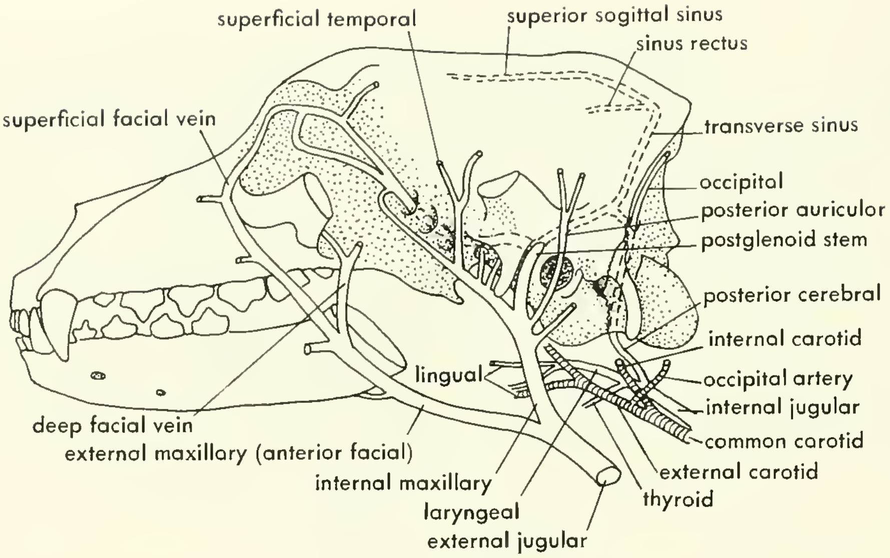


Figure 11-32. Veins of the head in the dog. (After Launay, 1896)

ventrolateral to the otic capsule, outside the ganglion of the seventh nerve, and inside (below) the ganglion and root of the fifth nerve. A vein following the course of the mandibular branch of the trigeminal enters the main channel here. This branch has maxillary and mandibular divisions. The main channel extends from here to the region behind the eye where it receives infraorbital, orbital, and supraorbital branches. The latter has a branch, the anterior cerebral vein, which passes upward alongside the diencephalon to the area above the brain, then forward over the telencephalon near the midline. Below the brain there is a small connective between the orbital sinuses of either side which passes behind the tip of the infundibulum.

In later stages, modification of the brain drainage occurs (Figure 11-33). Involved are three main plexuses of vessels enclosing the brain. The anterior plexus encloses the telen- and diencephalon; its stem is the anterior cerebral vein. Behind the ganglion of the fifth nerve is a stem for a plexus enclosing the midbrain and the metencephalon; this is the middle cerebral vein. The plexus of the myelencephalon (medulla) is drained by the posterior cerebral vein passing down, and just behind, the vagus nerve.

As development proceeds, the dorsal ends of the anterior cerebral channels join across the midline to form the sagittal sinus. The three cerebral plexuses now become connected by cross channels lying inside the cranial wall. The most posterior cross connection joins the middle and posterior stems above the otic capsule; this is the sigmoid sinus. The middle cerebral stem below this connection now becomes the superior petrosal sinus; above, it becomes the transverse sinus which joins through a connecting channel with the sagittal sinus of the anterior plexus. The anterior cerebral stem now disappears.

With the development of the cranial wall, the venous drainage is divided into interior (**vena capitis medialis**) and exterior (**vena capitis lateralis**) channels connected through the various foramina. The ophthalmic veins now enter the cranium through the orbital fissure to reach the basilar system which posteriorly drains through the internal jugular stem. The basilar system (the vena capitis medialis) involves the appearance of a new channel, the inferior petrosal sinus.

A part of the vena capitis lateralis, now the internal maxillary vein, drains the maxillary and mandibular veins through a new channel below the middle-ear cavity into the internal jugular stem; this new connective is the external jugular. This evolution of channels is indicated among the adults of mammals (Figure 11-34). The monotremes have retained the primitive vena capitis lateralis channel passing above the stapes. This channel, however, drains the cranium through the anterior lacerate fissure. Marsupials vary; in the opossum, the main cranial drainage is through the middle cerebral channel which enters an external jugular shunt passing below the middle-ear cavity to reach the internal jugular stem. In the foetus of *Trichosurus,* there is a typical vena capitis lateralis.

The inferior jugular of the embryo forms the lingual vein of the adult; sometimes this becomes quite separate as an anterior jugular.

In the region of the heart, the anterior cardinals are joined by a cross connective, the **brachioradialis vessel,** with the result that blood from the left passes through this connective to the right anterior cardinal to reach the heart. The right common cardinal stem becomes the anterior vena cava.

Among adult mammals this change in the anterior cardinal relationship can also be observed. In the monotremes and marsupials, both anterior cardinal stems are retained and enter the heart separately through their **ducts of Cuvier.** In the monotremes, an innominate connective joins these two stems. In the placental, the left duct of Cuvier (common cardinal) is retained as the **coronary sinus** of the heart.

Reptiles The head drainage pattern of the reptile is much the same as that of the mammal (Figure 11-29). The internal jugular vein gives off a branch, the **inferior jugular,** to the musculature of the throat; it then passes up behind and over the tympanic cavity. Here it receives a posterior cerebral branch which passes through the vagus (jugular) foramen. This posterior cerebral stem is connected by a sigmoid sinus with the middle cerebral vessel, which in part forms the transverse sinus. The main lateral head vein passes forward from the posterior cerebral stem, over the columella, receives the middle cerebral vein emerging from the trigeminal notch, and goes forward into the orbit and the **orbital sinus.** Between the orbital sinus and middle cerebral branch, the lateral head veins are interconnected through the basis cranii below the dorsum sellae. The orbital sinuses are also interconnected through the interorbital septum.

Branches from the orbital sinus serve the temporal region and extend into the maxilla, passing forward through the alveolar passage of that bone. There is also a pterygoid vein, which in the roof of the mouth gives off a palatine division. Anteriorly the orbital sinus connects through the orbitonasal fissure with the **nasal sinus;** the nasal sinus is connected also with the maxillary vein.

The brain is largely drained by a dorsal sagittal sinus which leads into transverse sinuses. The middle cerebral stem may exit behind the trigeminal (Sphenodon) or in front of (and over) that root (*Lacerta* and turtle). In some lizards and in crocodiles, the posterior cerebral stem is replaced by another passing out through the foramen magnum. The alligator lacks the middle cerebral connection. The turtle has all of these stems. In the reptile a vena capitis medialis is only slightly developed.

In the case of the reptile, we see a primitive venous pattern with internal vessels suggesting those which have become the primary vessels of the mammal.

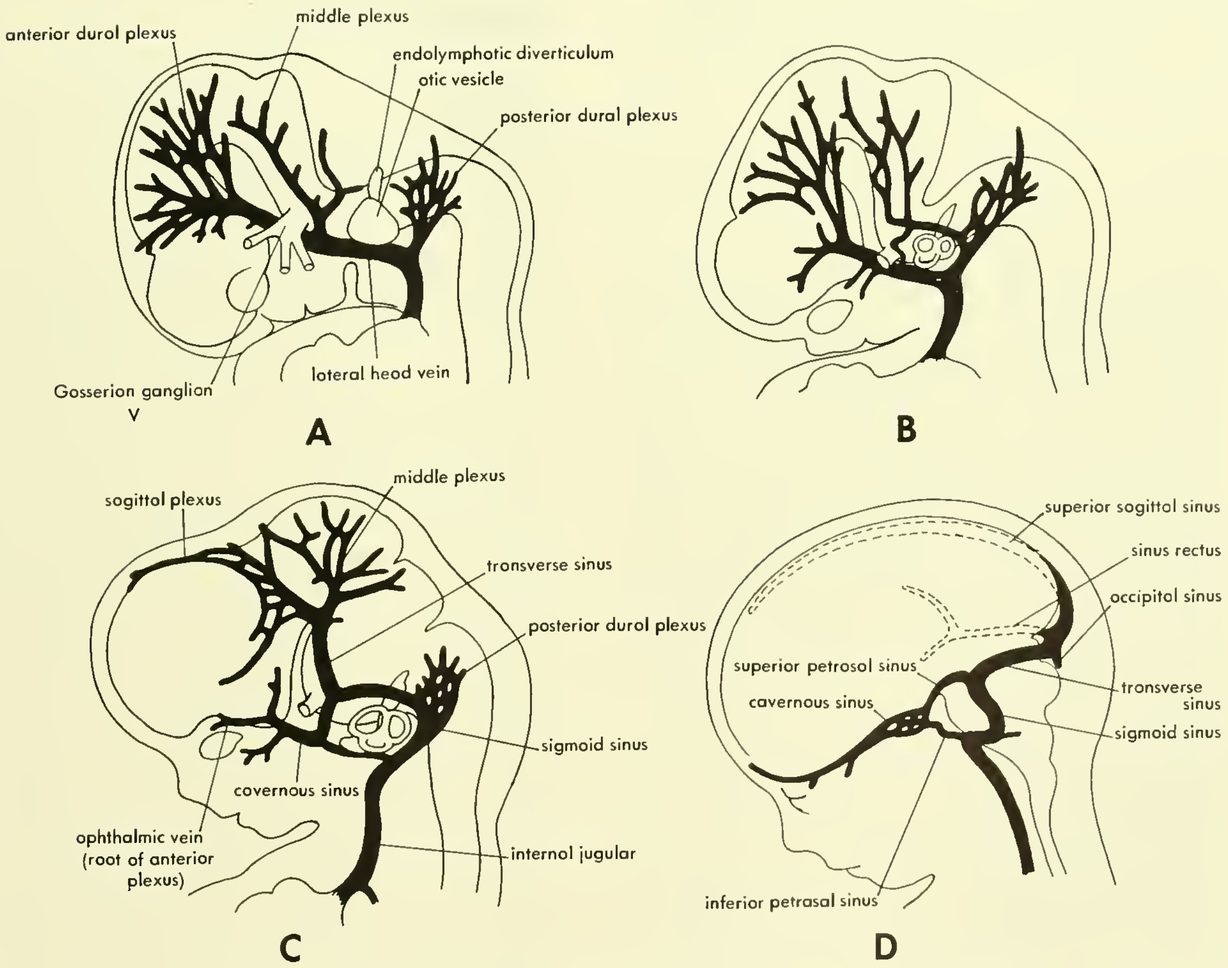


Figure 11-33. Development of venous drainage of the head in the human. (After Streeter, 1918)

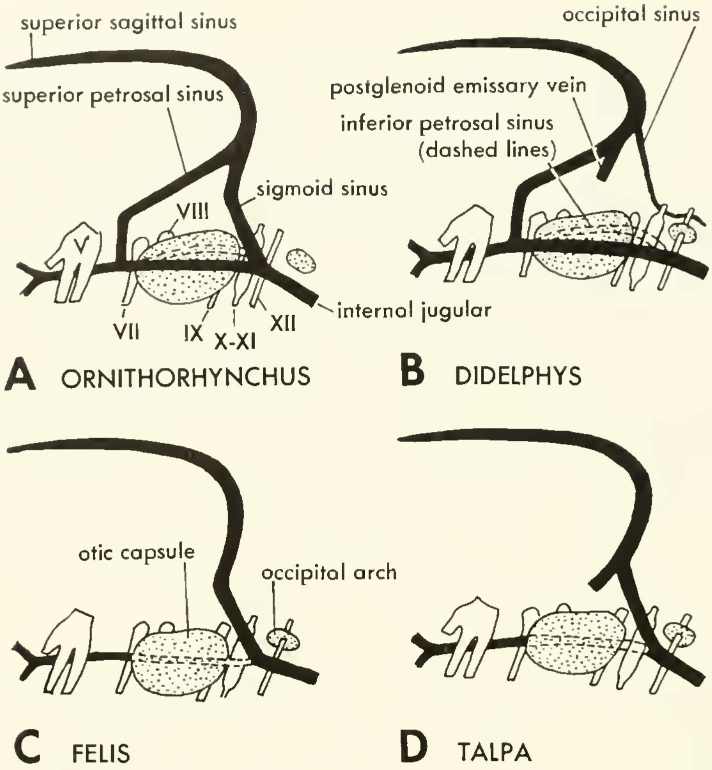


Figure 11-34. Variations in venous drainage of mammals. (After van Gelderen, 1933)

Bird The venous system of the bird is modified. Blood is shunted below the middle-ear cavity in an external jugular stem. The external jugular shunts of either side are interconnected, and the right jugular is the larger (turkey). Drainage from the brain is by way of middle and posterior cerebral channels and out through the foramen magnum as well.

The development of the venous channels can readily be observed in the chicken. The 72-hour chick has a network of channels above and below the nerve roots and the otic capsule. The dorsal channel of the otic capsule has a division passing lateral to the capsule. The 96-hour chick has a single anterior cardinal channel which passes below the vagus, lateral to the glossopharyngeal, below the otic capsule, lateral to the facial, and below the trigeminal. This channel has the same branches as the 10-mm pig.

Amphibians In the salamander or frog, the pattern of head veins is essentially that of the reptile. In the frog, there is a small inferior jugular which extends to the musculature of the throat; it has submental and shoulder branches. The anterior cardinal stem also has large subclavian and branchial divisions.This stem, as the vena capitis lateralis, extends into the head over the columella and through the cranioquadrate passage; it enters the orbit above the trigeminal root.

In the Bullfrog a posterior cerebral branch is lacking; the middle cerebral branch of the lateral head vein enters the skull and extends out on the dorsal surface of the optic lobes. The vessels of either side converge on the posterior half of the brain and are connected by a fine reticulum of vessels. These vessels pass through the foramen magnum, side by side, and back through the spinal canal on the dorsal surface of the cord.

The lateral head vein of the Bullfrog also receives an orbital vessel which has branches extending out through the ventral margin of the orbit along the maxilla anteriorly and posteriorly. The posterior maxillary follows the course of the maxillary artery to become the external mandibular vein. There is also an internal maxillary division from this orbital stem. The lateral head vein has a large palatine branch which follows the palatine artery.

In the salamander there is an inferior jugular passing below the branchial region to the throat musculature. The anterior cardinal (jugular) stem passes up behind the branchial opening, or openings, and forward above these. At the angle of the mandible, this stem receives several branches, one from the outside of the mandible, another from the maxilla. The main stem passes inward toward the jugular foramen, through which the posterior cerebral branch passes, then forward through the cranioquadrate fissure as the lateral head vein.

In the orbit it receives branches draining the palate, the walls of the orbit and adjacent skin, and the brain (the middle cerebral). *Necturus* is similar to *Cryptobranchus* in most details.

The salamanders differ from the frog in that the maxillary and mandibular veins join and enter the main stem rather than the orbital vein. They also differ in the very superficial position of the main stem. This lies in the position of an external jugular.

The development of the venous channels of the frog (anuran) has been described, and the general pattern follows that of the higher forms.

Choanate fishes The main veins of *Protopterus* are similar to the salamander; the mandibular, maxillary, and lateral head veins join to form a jugular stem which passes down through the body-wall musculature above the branchial openings. The duct of Cuvier passes down behind the gill cavity to reach the heart. The duct of Cuvier receives brachial, subclavian, and inferior jugular branches. The lateral head vein has orbital, palatine, and all three cerebral branches, anterior, medial, posterior. There is no sagittal sinus above the brain. These are paired inferior jugulars.

Actinopterygian fishes In the antinopterygian fish, the anterior cardinal (jugular) stem passes forward above the gills where it receives a brachial vessel. Anteriorly the lateral head vein passes above the spiracular pouch or medial to it. It receives a posterior cervical vein through the jugular foramen. There are vessels draining the operculum, the jaws, and orbit; these are received by the lateral head vein anterior to its passage through the lateral canal—there is no cranioquadrate fissure. The hypobranchial region is drained by paired inferior jugulars.

The development of the anterior channels is fairly direct and has been described for *Amia*. The anterior cardinals arise in a capillary network located ventrolateral to the brain and ventromedial to the cranial ganglia and nerves. In a 15-mm specimen, the channel passes below and inside the vagus nerve; the posterior cervical vein exits in front of the vagus root. The lateral head vein then passes above or below the glossopharyngeal ganglion—above and below in some cases. Above the geniculate ganglion of the facial nerve, it receives external and pharyngeal channels. The external channel extends back above the adductor hyomandibularis muscle to the body wall above the branchial chamber. From here it passes down medial to the thymus to enter the anterior cardinal at the duct of Cuvier along with a thymus vessel.

Between the geniculate and Gasserian ganglia, the lateral head vein branches. One part follows out along the trigeminal nerve, while the main channel passes forward below the Gasserian ganglion and within the lateral canal. In the orbit this trunk divides into superior and inferior orbital channels and into the hypophyseal cross connective. The course of this vein is similar in the adult.

Chondrichthyes In the shark there are large anterior cardinal sinuses. Anteriorly each becomes a lateral head vein which passes above the hyomandibula. Anteriorly this channel gives rise to the orbital sinus. The brain is drained by a posterior cerebral vessel, passing through the jugular foramen, along with the vagus nerve, and an anterior cerebral entering the orbit and orbital sinus. A dorsal **myelonal** vein from the posterior cerebral root extends down through the vertebral canal above the spinal cord. Ventral myelonal (basilar) veins may also be present. The orbital sinus is connected with a nasal sinus through the orbitonasal fissure.

The anterior cardinal has a supraorbital division supplying the top of the head. This also connects with the orbitonasal channel through the nasal capsule. There are **buccopharyngeal** vessels an either side serving the roof of the mouth. These connect anteriorly with the orbitonasal channel and posteriorly with the anterior cardinal.

The hyoid vein connects the cardinal sinus with the inferior jugular sinus. The **nutritive veins** of the branchial arches are noteworthy.

The elasmobranch fishes are somewhat peculiar in that they frequently have greatly enlarged sinuses with tendonlike strands passing from one wall to another. The anterior cardinal is such a sinus, as is the postcardinal. The orbital sinus, and cavernous sinuses of other organisms, are of similar form.

Cyclostomes The head veins of the two groups of cyclostomes deserve special attention.

LAMPREY The venous system of the lamprey is not easily described because of the relationship of veins to various venous or lymphatic sinuses. Blood is returned to the heart from the anterior part of the body through three channels; a median inferior jugular and two lateral, anterior cardinals. Both the anterior and the posterior cardinals utilize the right duct of Cuvier in reaching the sinus venosus. The single inferior jugular enters the sinus venosus independently.

The branchial sinuses associated with these veins consist of three roughly longitudinal channels. These are: a single mid-ventral, posteriorly branching sinus, the **ventral jugular sinus** (or ventral branchial sinus); bilateral **inferior branchial sinuses** lying below the gill pouches; and bilateral **superior branchial sinuses** overlying the gill pouches.

These longitudinal sinuses are interconnected through the branchial bars. The most anterior connective is the hyoidean sinus. The branchial sinuses are irregular in shape and tend to form an enclosing vascular sac for the gill pouches. The ventral jugular sinus encloses the ventral aorta.

The anterior cardinals develop from channels passing above, lateral, and below (next to the dorsal aorta) the otic capsule. These unite in the region of the second branchial arch. The relationship of the anterior cardinals to the dorsal aorta is not the same as that of the posterior cardinals; the anterior cardinals lie lateral or even dorsolateral to the notochord, while the posterior lie ventrolateral. The relationship of the superior branchial sinuses is essentially like that of the posterior cardinals. Each cardinal enters the duct of Cuvier of its side. At metamorphosis, the left and right join and enter the right duct of Cuvier; the left duct disappears.

Each branchial arch has a large irregular sinus passing through it externally. There is a **velar** (mandibular) **sinus** joining the ventral cardinal channel below the otic capsule. The large **hyoidean sinus** connects with both ventral and lateral otic channels. The **branchial sinuses** develop directly from the venous channels of the larva.

There are paired inferior jugular veins in the early larva which are later replaced by the median inferior jugular of the adult, which lies mainly below but encloses the ventral aorta and the jugular sinus. Anteriorly it connects with the hyoidean sinus of either side. There are segmental connections along the course of the inferior jugular with the inferior branchial sinus, which in turn communicates with the ventral jugular and branchial sinuses. Posteriorly the inferior jugular vein shifts to the right side to enter the sinus venosus.

In *Petromyzon*, the inferior jugular system is somewhat different. The median inferior vessel proceeds forward from the sinus venosus and at the level of the posterior (7th) gill pouch gives off two large branches which parallel it.

HAGFISH The veins of the Hagfish (*Myxine* or *Eptatretus*) are included in two systems: the general system and the hepatic portal system. From the head region, the deep cardinal veins course posteriorly alongside the pharynx, internal to the constrictor muscles. These veins pass under the first branchial arch, just posterior to the skull, but over the second. About 2 to 3 cm behind the second arch, each deep vessel is joined by a superficial one to form the anterior cardinal vein. This passes back next to the pharynx, just external to the corresponding lateral aorta and internal to the vagus nerve.

Posterior to the vertical of the posterior end of the lingual muscles, the courses of the two cardinals differ. The left anterior cardinal continues back beside the vagus, above the gills, between the left pronephros, from which it receives a twig, and the alimentary canal, and empties into the anterolateral angle of the dilated posterior portion of the sinus venosus.

The right anterior cardinal, near the posterior end of the jaw muscles mass, leaves the pharyngeal wall, passes downward toward the posterior end of the "tongue muscle" and the median line, and empties into the median inferior jugular vein. The posterior portion of the original right anterior cardinal becomes the anterior portal vessel. This arises in the right branchial region, a little in front of the posterior end of the "tongue-muscle," just below and to the right of the notochord. It continues backward into the fold (portal septum) separating the inner and outer chambers of the right pericardial cavity. It passes between the alimentary canal and the right pronephros, opens into the roof of the **portal heart** (the modified right duct of Cuvier) near the anterior end of that structure. Just before entering the portal heart, it receives a branch from the pronephros. Two or three somatic veins lie opposite and posterior to the portal heart.

The median inferior jugular vein arises in the posterior end of the "tongue-muscles," from which it emerges ventrally. It passes backward a little to the left of the median line, immediately inside the body wall. After receiving the right anterior cardinal vein, it continues back a little below and to the left of the median ventral aorta. Finally it empties into the anterior end of the sinus venosus (Figure 9-28).

There is some question as to the relationship between the veins and the lymphatics in cyclostomes; it has been suggested that the lymphatics are but venous sinuses.

General observations Because the anterior cardinal system is derived from a reticulum of channels, its comparison from one group to another is rather difficult. In the head this reticulum tends to be divided into an inner vena capitis medialis and an outer vena capitis lateralis.

The vena capitis lateralis is the primary channel in cyclostomes, gnathostome fishes, amphibians, reptiles, monotremes, and marsupials. It runs outside the auditory capsule alongside the hyomandibular branch of the facial nerve, through the cranioquadrate passage, and dorsal to the spiracular gill pouch. In selachians, it passes dorsal to the hyomandibular cartilage; in actinopterygians, below and inside the hyomandibula; in tetrapods, dorsal to the columella auris or stapes. A new venous loop occurs in some teleosts which passes outside of the hyomandibula. Occasionally in cyclostomes, selachians, *Polypterus*, and anurans, the vena capitis lateralis passes outside the trigeminal nerve, but usually this vessel passes below and inside the nerve.

In the neck region the cardinal system is aided by the formation of an external jugular channel. A pair of inferior jugulars is also present for draining the throat region (anterior jugulars).

The venous system of the head suggests that the various groups have each developed a few modifications of a basic plan. Just as in the head arteries there is evidence of a common ancestor of the several groups of tetrapods, an ancestor much like the choanate fish and less like the ray-finned fishes or sharks. Common ancestry of the gnathostomes is suggested by agreement in many details. The cyclostome pattern shows only the most general resemblance to that of the gnathostome.

CIRCULATION IN THE BODY

Arteries

Mammals The dorsal aorta in the mammal sends branches ventrally through the mesentery to the various parts of the gut. The first branch is the **coeliac.** It has divisions going to the liver, stomach, spleen, and to the underside of the duodenum. These arteries form loops in some instances: a branch of the **lienal** (splenic) swings around on the greater curvature of the stomach and joins the **gastroduodenal branch** of the **hepatic.** A second branch of the gastro-duodenal curves along the underside of the duodenum and connects with the **superior mesenteric artery.**

The second main division of the dorsal aorta is the superior mesenteric. This artery extends out through the mesentery where it fans out into a large number of branches serving the small and much of the large intestine.

The third stem from the dorsal aorta is the **inferior mesenteric;** this is interconnected with the superior mesenteric, a loop supplying the transverse and descending parts of the colon. The inferior mesenteric also supplies the sigmoid colon and rectum. Feeding into the inferior mesenteric stem are the **middle** and **inferior hemorrhoidals** which arise from the **hypogastric artery.** The kidneys and gonads also receive branches from the dorsal aorta, and there are vertebral branches extending into the body-wall musculature.

Posteriorly the dorsal aorta divides to form two large, **common iliac arteries,** between which a small middle sacral **artery** continues posteriorly below the vertebral column. The common iliac artery passes laterally and downward, giving off the **hypogastric artery** medially and continuing as the **external iliac artery** into the lower limb. The external iliac artery becomes the **femoral artery** in the base of the limb. The femoral sends branches to the hip area and to the various parts of the lower limb. Among the mammals there is much variation in the exact arrangement of the various branches but a general pattern is evident.

EMBRYOLOGICAL DEVELOPMENT The dorsal aorta is formed by the fusion of bilateral channels. From it, segmentals extend upward between the myotomes and outward over the yolk sac as the vitelline arteries. Of the several vitellines, a single channel finally develops and later becomes the superior mesenteric. The coeliac and inferior mesenteric condense from a number of segmental mesenteric vessels. The umbilical arteries follow the allantois outward and supply the placenta. The intraembryonic umbilical becomes the common iliac and the hypogastric stem of the adult which connects with the body wall through the lateral umbilical ligament.

The functional nature of the origin of the definitive vessels is well shown by the development of a limb stem (Figure 11-35). At first there are several segmental vessels involved. The number decreases until one remains. This vessel is lost distally in a reticulum of channels from which a final channel or channels is selected.

Reptiles The reptile pattern is comparable to the mammal. The dorsal aorta may give rise to a small gastric branch, passing to the dorsal wall of the stomach, and then a large coeliac stem which serves the spleen (lien), a part of the greater and the lesser curvature of the stomach as well as the anterior part of the duodenum. The coeliac stem may include a part of the superior mesenteric, which serves the small intestine and the anterior part of the large intestine. In Sphenodon, the superior mesenteric is separate from the coeliac stem but is continuous with the inferior mesenteric which springs from the dorsal aorta posterior to the renal arteries. In *Lacerta* there are several small mesenteric stems arising from the dorsal aorta. Among lizards there is a large number of patterns representing the basic stem as well as some of the large branches of these stems.

Amphibians In the Amphibia the pattern of main arteries is like that already described, and the nature of the development of this system is apparent. In a series of forms, the

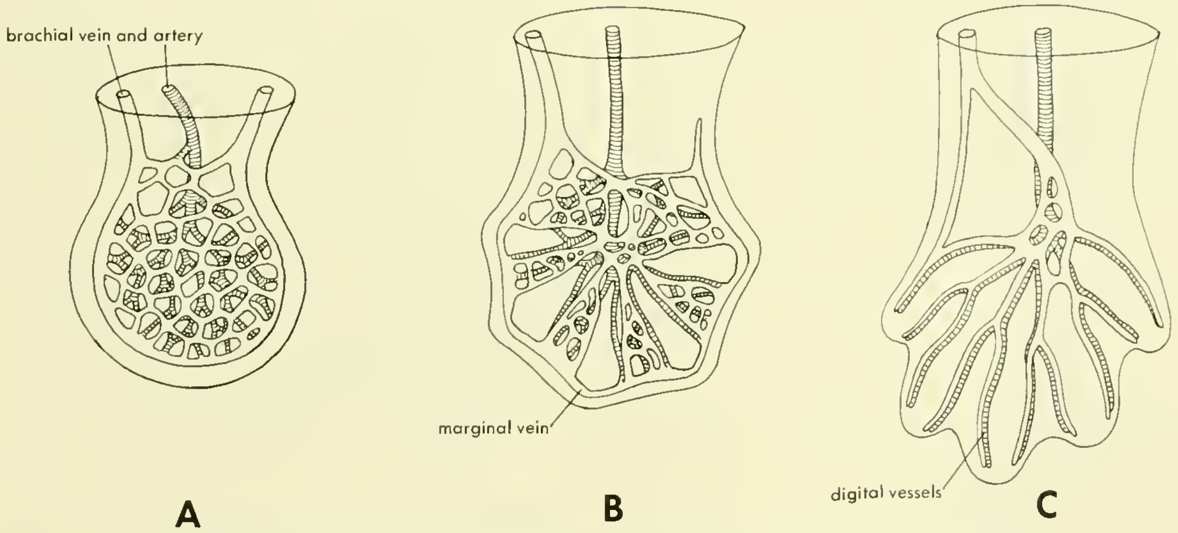


Figure 11-35. Three stages in the formation of the arteries and veins of the forelimb of a tetrapod. (After Gradzinski, 1933)

gradual condensation of the coeliac and superior mesenteric stems from segmental vessels can be observed.

Fishes The arterial pattern of the fishes, whether dipnoan, actinopterygian, or shark does not suggest anything beyond that which is seen in the more advanced forms.

In the cyclostomes there is marked contrast between the lamprey and the hagfish. In the lamprey there is a large coeliacomesenteric artery which comes off the dorsal aorta near the duct of Cuvier and, passing down to the left of the gut along with the bile duct, enters the typlosole. It extends most of the length of the intestine. Far posteriorly are two or three mesenteric arteries, each enclosed by a venous channel, which also serve the gut wall.

In the hagfish the **coeliacomesenteric** passes down to the left of the gut, to the right of the bile duct, and posteriorly a short distance next to the hepatogastric mesentery. Most of the length of the intestine is served by numerous mesenteric arteries—the primitive style as suggested in the Amphibia.

Veins

Mammals In the human, blood is returned to the heart through a large **postcaval vein** or **posterior vena cava** which parallels the course of the dorsal aorta but lies beneath that vessel. The posterior vena cava receives blood from the various **hepatic** vessels and, more posteriorly, a pair of **renal veins** and several **vertebral branches;** it is formed posteriorly by the union of two common **iliac veins** and a middle sacral vein. Each iliac has **femoral** and **hypogastric** branches. The pattern of the postcava and its branches is much the same as the pattern of the main arteries.

The difference between these two systems lies in the fact that the veins draining the digestive tract form an **hepatic portal vein.** This enters the liver and branches to all parts of that structure in order to supply the small sinusoids. Blood is collected from these sinusoids by the hepatic veins and drained into the postcava.

EMBRYOLOGICAL DEVELOPMENT The earliest vessels to appear are the **vitelline veins.** These are soon augmented by and functionally replaced by the umbilical veins which extend back to the allantois and out along the allantois to the placenta. The umbilical and vitelline veins join the ducts of Cuvier (common cardinals) to form the sinus venosus. The development of the circulation within the liver involves formation of hepatic veins and the hepatic portal stem from the vitelline veins; the right umbilical disappears, while the left connects the embryo with the placenta and continues through the liver as the **ductus venosus.** Behind the liver, the vitelline veins unite above and below the gut. As a result of these anastomoses, an hepatic portal channel extends up on the left side of the gut, over the gut, and down on the right side where it comes to drain the channels in the supporting mesenteries of the digestive tract.

The development of the postcava is a complex story (Figure 11-36). The **posterior cardinals** (or postcardinals) at first are the main drainage of the body wall. With development of the mesonephric kidney, there is a rearrangement

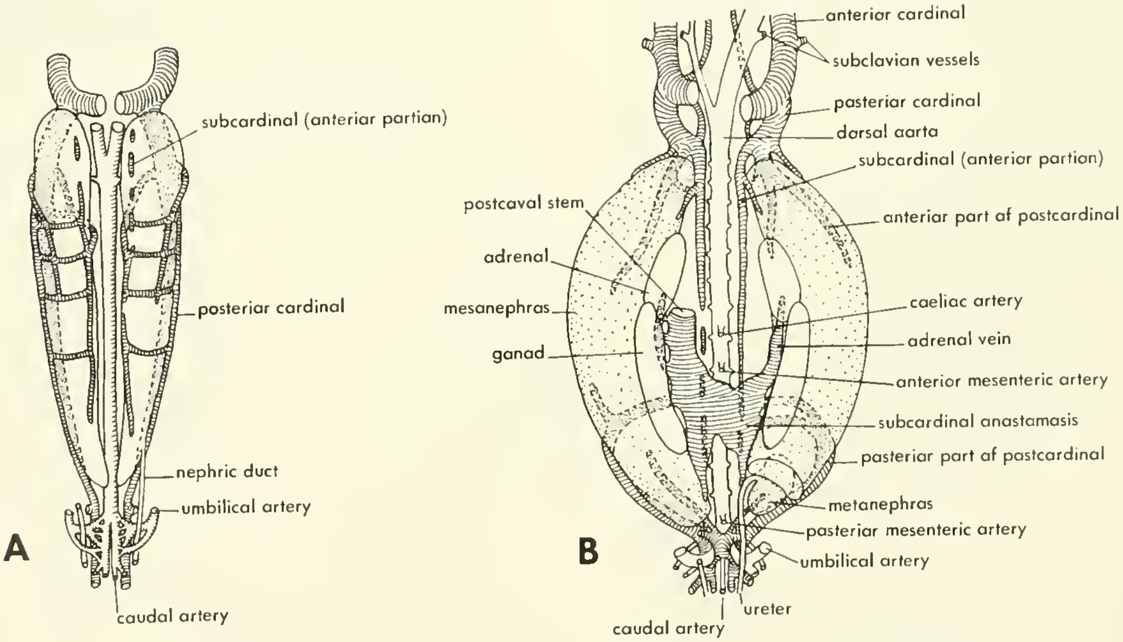


Figure 11-36. Two stages in the development of the renal circulation of the cow. (After Grau, 1933)

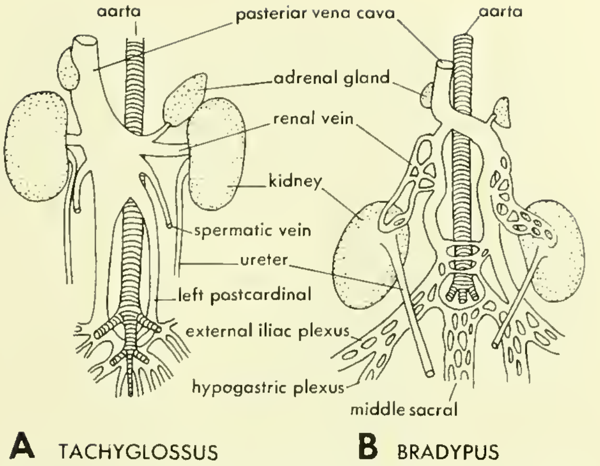


Figure 11-37. The adult renal circulation in specimens of *Tachyglossus* and the sloth, *Bradypus*. (After van Gelderen, 1933)

of the blood flow involving use of the posterior cardinal channel as a renal portal vein and appearance of a new drainage, the **subcardinal,** lying in the medioventral part of each kidney. **Supracardinals** may also appear in the dorsomedial part of the kidney.

The result of these new channels is that blood return involves cross flow through the sinuses of the kidney from posterior cardinal to subcardinal. From the latter the blood passes down through the mesentery to reach the heart by a new channel, the **postcaval stem.** The development of this new channel short circuits the blood which normally returns through the posterior and common cardinals to the heart.

Loss of most of the mesonephric mass and development and movement of the metanephros results in a new type of circulation for the kidney: arterial from the aorta, and venous into the posterior vena cava. The postcava now extends back, by way of the right supracardinal and postcardinal channels, to the hind limbs, where it receives the common iliac and middle sacral veins. In the monotremes both cardinal channels are retained, with anastomoses above the dorsal aorta (Figure 11-37). In the sloth a pair of reticulate channels lies in the position of the paired cardinals of the monotreme. treme.

The anterior ends of the posterior cardinal channels remain as the highly variable **azygous vessels.** That of the right side connects with the anterior or superior vena cava to drain into the heart, and that of the left side has a cross connection with the right. The left vessel is called the **hemiazygous.** The left duct of Cuvier forms the coronary sinus of the heart.

Reptiles In the reptile the same general picture is observed. In *Lacerta* the postcardinal stems appear first and later subcardinal vessels develop. As development continues, the anterior and posterior segments of the postcardinals become separated. The renal portal portion lies on the middle of the undersurface of the kidney and its blood flows into the renal sinuses. From the sinuses the blood is collected into the medial subcardinal channels, which more anteriorly drain into the anterior parts of the postcardinals.

The changes in this area were described somewhat differently by Hochstetter (1893). The subcardinals at first carry the blood from the caudal vein forward, and the flow through the kidney is toward the postcardinal channels. Later, flow from the caudal vein shifts into the "renal portal" part of the postcardinal, and the blood moves medially through the kidney to the subcardinal channel, which now connects by way of the postcaval stem with the sinus venosus. This same history is also observed in the shark.

The postcaval stem of the reptile extends down from the right subcardinal, anterior to the gonads, through the mesentery to the sinus venosus. This channel does away with the flow through the postcardinals anterior to the kidney.

The posterior part of the postcardinals, the renal portal vessels, also drain into a ventral abdominal vein passing forward on the inner surface of the body wall. This vessel anteriorly enters the liver and feeds directly into the hepatic portal system, as in Sphenodon.

In the crocodile the posterior vena cava extends back between the kidneys, from which it receives branches, and is joined by the ischiac, caudal, and inferior mesenteric veins. The midline stem continues posteriorly beyond these as the vertebral sinus. The posterior cardinals remain as renal portals leading into the kidney tissues. There is a pair of ventral abdominal veins partly draining the caudal, ischiac, and femoral stems into the liver. The ventral abdominal arises in the embryo as paired channels in all reptiles.

In the bird the iliac (the ischiac in some) stem drains the leg into a renal portal channel which connects with hypogastric and caudal veins (Figure 11-38). The caudal has a **coccygeomesenteric** branch which brings blood into the renal portal system from the gut. Although there is direct connection between the renal portal and postcaval stems, valves direct the blood into **afferent renal channels.** Parallel **efferent vessels** collect it from the kidney tissue. The postcaval stem extends back to the subcardinal anastomosis. The development of the venous channels in birds is like that of the reptiles. The postcardinal channel appears before the subcardinal (see sections of the 72-hr chick).

The hepatic portal channels of birds and reptiles are similar to those of the mammal.

Amphibians In the amphibian the posterior ends of the postcardinals function as renal portal vessels connecting with the caudal vein and the ventral abdominal vein. The iliac vein also enters the renal portal vessel of the same side. The ventral abdominal vessel connects with the hepatic portal system. Subcardinal vessels collect from the kidney and lead into the azygous portions of the postcardinals and

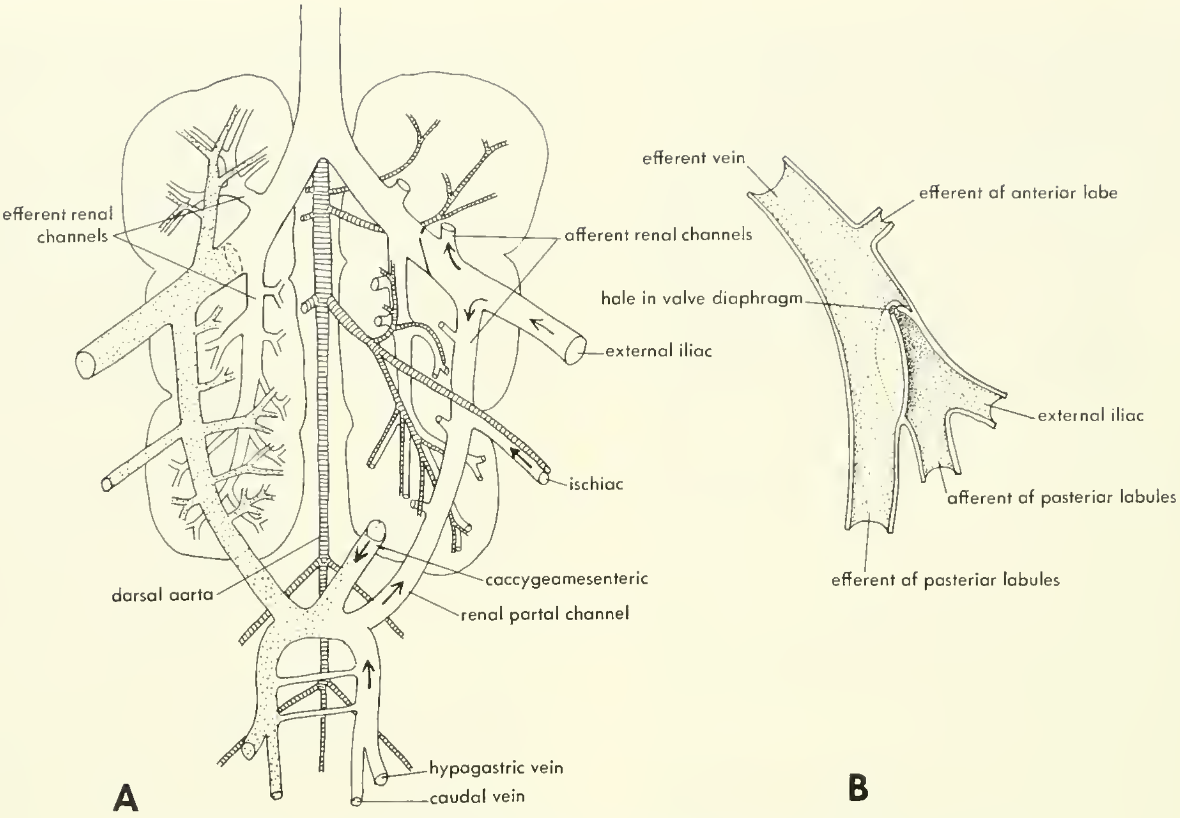


Figure 11-38. The renal portal system of the bird, A, with details of the valve between the external iliac and the efferent renal channel. The arrows in A indicate the direction of flow. (After Spanner, 1925)

the posterior vena caval stem. In the frog, only the postcaval stem is involved in this drainage.

In the development of the postcardinal drainage of the anuran (Figure 11-39), lateral (postcardinal) and medial (subcardinal) channels of a reticulum enclosing the nephric duct are seen. The medial (subcardinal) channel appears first (10-mm frog). The postcaval stem connects with the right postcardinal. Both postcardinals flow through pronephric sinuses to reach the duct of Cuvier (Figure 11-39); these sinuses are eliminated with the loss of the pronephros. The same general pattern appears to hold for the salamanders.

Choanate fishes *Protopterus*, described by Parker, has lost the right connection with the duct of Cuvier; this is replaced by a postcaval stem. The posterior parts of both postcardinals form renal portal vessels which drain the pelvic and caudal veins. Subcardinal channels, interconnected by cross channels, drain the kidneys. The postcava enters the liver and receives the hepatic veins along its course. The hepatic portal system drains the intestine by way of **intraintestinal** and **subintestinal** channels.

In *Neoceratodus* the picture differs in that the caudal vein flows into the postcava rather than the renal portal veins. In addition, there are both **ventral abdominal** and **lateral cutaneous veins,** connected with the renal portal and caudal veins respectively.

The development of the circulatory channels of *Neoceratodus* has been described by Kellicott (1905) and the very early stages of *Lepidosiren* by Robertson (1913). In the early embryo, the duct of Cuvier extends down over the yolk sac to reach the heart. Numerous segmentals, of which the duct of Cuvier is one, form a reticulum of channels in the pronephric area and over the yolk. These drain into the bilateral vitelline veins, which unite posteriorly below the gut as a subintestinal. The subintestinal connects to either side of the anus with the posterior cardinal channels, which, posteriorly, unite to form the caudal vein.

Neoceratodus follows a similar pattern. The left vitelline becomes the stem for the subintestinal vein, which is retained in the adult and forms part of the hepatic portal.

Actinopterygian fishes In the actinopterygian fishes there is a great deal of variation in the posterior cardinal drainage. The caudal vein enters the kidney by way of the subcardinal channels; these may be fused at the midline.

Anteriorly the postcardinal channel is involved. The renal portal blood is also received from the segmentals of the body wall. In some teleosts, the left subcardinal is much reduced and the right is more strongly developed. This resembles the situation in the dipnoan, but it differs in that a postcaval stem does not develop.

Development within the actinopterygian group shows extreme variation, but the general pattern is that seen in the higher groups. There are paired subcardinal stems, lying medial to the nephric ducts which lead from the caudal vein. The latter connects to either side of the anus with a subintestinal channel (of bilateral origin) which bifurcates

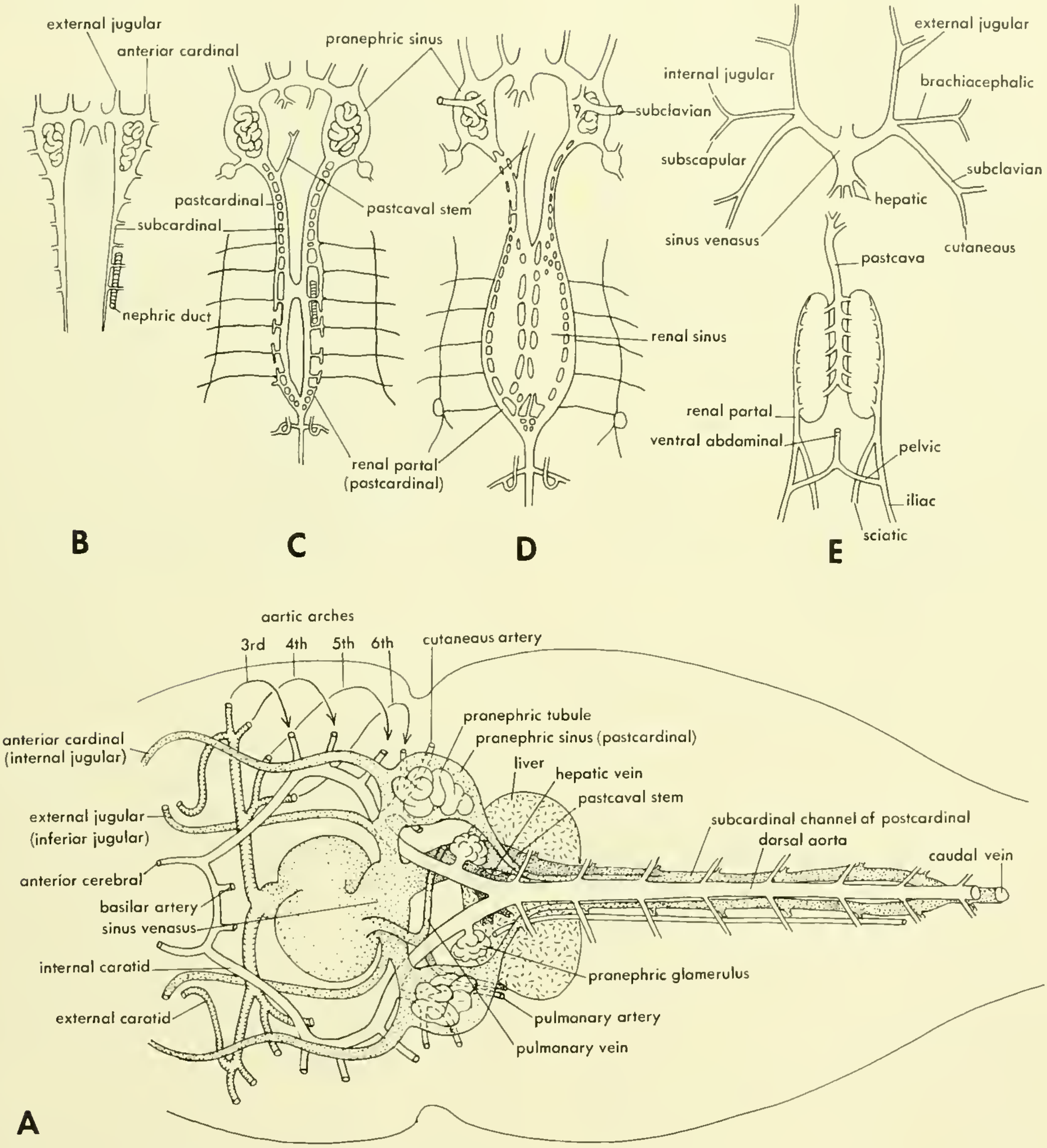


Figure 11-39. Development of the posterior venous pattern of an anuran. A, the circulatory system of an early larval frog (about 4.6 mm); B to E, four stages in the development of the veins in *Bufo*. (A after Adamstone and Shumway, 1947)

to pass around the yolk mass as the vitelline veins. The vitellines may become separated from the subintestinal by a network of fine channels (*Acipenser*), or they may form a ring sinus (salmon) for draining such a vascular net, or they may fuse to form a midline sinus, often identified as part of the sinus venosus. The ducts of Cuvier may extend out around the yolk sac to enter the sinus venosus or they too may form a network of fine channels. The reticulum of vessels on the yolk sac serves for the respiratory as well as for the nutritive needs.

Amia in its development seems typical in most respects of the ray-finned fishes. The caudal vein arises in a plexus of three or four small vessels ventral to and irregularly connected with the caudal artery. The posterior cardinals connect with this caudal channel, and each is formed of a reticulum of vessels around the nephric duct. Of these channels the medial one, the subcardinal, is the larger. The subcardinals of either side are interconnected at intervals. Anteriorly each postcardinal forms a pronephric sinus emptying into the duct of Cuvier. The ducts of Cuvier extend ventrolaterally around the yolk sac, receiving many of the channels of the yolk sac; they enter the sinus venosus ventrally.

From the caudal vein, connectives pass to either side of the **postanal gut.** These are interconnected above and below the gut. In the anal region a large channel passes down medial to the nephric duct of either side to form the subintestinal vein and the plexus of vessels enclosing the gut. This plexus is drained by dorsal mesenteric vessels joining the postcardinals as well as by way of the subintestinal which leads into the yolk-sac reticulum. The capillaries of the liver are continuous with the vessels of the yolk sac to the left of the anterior intestinal portal.

Later the left postcardinal is reduced and the right becomes the sole channel of the posterior part of the kidney. The subintestinal connects around the left side of the gut with the posterior cardinal and with dorsal sinuses leading to the yolk sac and liver on the right. The definitive hepatic portal stem follows the same course as in other vertebrates: up on the left side and over the gut into the liver.

In actinopterygians the yolk sac is usually attached to the gut by a narrow stalk, and the subintestinal channel may be almost entirely associated with the yolk sac. In the salmon the yolk mass lies far forward. The subintestinal passes up to the left of the gut and over the gut to reach the liver. From the liver the hepatic channels extend out to the yolk sac reticulum which is drained by the vitelline veins. Earlier stages of the salmon have the subintestinal feeding directly into the yolk-sac circulation.

Acipenser is the exception in yolk sac-gut relationships. In this the yolk lies in the foregut, the liver diverticulum arises behind the yolk mass (Figure 9-17). In later stages the stomach is much expanded but there is yolk throughout much of the gut. The vascular relationships appear to be similar to *Salmo* or *Amia*—there are more or less separate but interconnected yolk-sac and liver circulations.

Chondrichthyes In the shark the same general pattern of vessels is observed as in the other fishes. The posterior cardinals are broken into a renal portal vessel and a subcardinal channel which anteriorly leads into the outer postcardinal channel. In place of a ventral abdominal vein there are **lateral abdominal veins** draining the body wall. Such veins are represented in the amphibia by the musculocutaneous veins. Posteriorly there is a caudal vein, and there are fin veins that enter the interconnected system of renal portal and lateral veins.

EMBRYOLOGICAL DEVELOPMENT The development of the yolk-sac circulation and the hepatic portal stem in this group illustrate the functional plasticity of this system. The most complete account of the very early stages is that of *Torpedo* (Figure 11-40). As in other vertebrates, the first indications of the blood system are the "blood islands" formed in the area opaca of the blastodisc at the two-somite stage. These increase in number and anastomose as the embryo begins to rise up from the blastodisc. The blood islands fuse to form two sinuses, an outer terminal sinus around the outer edge of the expanding blastodisc and an inner ring sinus surrounding the mesoderm-free area of the blastodisc anterior to the head region of the embryo, the proamnion.

The first vessels to appear (the exact sequence is doubtful) are the anterior vitelline veins which fuse to form the heart. These veins drain the inner ring sinus. The development of blood vessels in the body begins with the formation of the ventral aorta, a pair of aortic arches, and paired dorsal aortae. In the posterior part of the embryo, which has now separated partially from the yolk sac, appear two caudal veins, closely underlying the aortae and receiving blood from them through connectives. These caudal veins proceed anteriorly and at the yolk stalk curve downward as the posterior vitelline veins to enter the terminal sinus. The terminal and ring sinuses are connected by the yolk-sac channels, thus completing the circulation.

At this early period of development, the yolk sac serves as a respiratory organ and in viviparous forms, such as *Torpedo,* continues to do so until birth. With the yolk-sac circulation completed, changes begin to take place. A small vessel draining the right pronephric sinus into the right anterior vitelline vein becomes connected with the dorsal aorta. The influx of arterial blood enlarges this vessel and reverses the flow of blood in the right anterior vitelline vessel. As a result of this, the anterior connection of the right anterior vitelline vein with the sinus venosus atrophies and is lost. The blood now flows down through the pronephric artery into the right vitelline and through it into the ring sinus and into the heart by way of the left anterior vitelline vein.

Meanwhile the caudal veins have elongated by the process of constriction of the yolk stalk and the outgrowth of the tail region and hindgut. In the region of the cloaca, the caudal veins bypass the gut to either side and continue anteriorly, as the subintestinal veins, to the yolk stalk where they descend onto the blastodisc to enter the terminal sinus. The left subintestinal is much the larger, and at the yolk stalk a branch appears which circles the yolk duct on the left and connects with the left anterior vitelline vein. This vessel can be identified as the yolk-stalk shunt.

As the hindgut develops, the cloaca contacts the proctodeal area between the anterior continuations of the now single (fused) caudal vein. A short, anteriorly projecting, right yolk-stalk shunt develops to balance partially the now well-formed left shunt.

As the yolk stalk becomes more constricted, the two an-

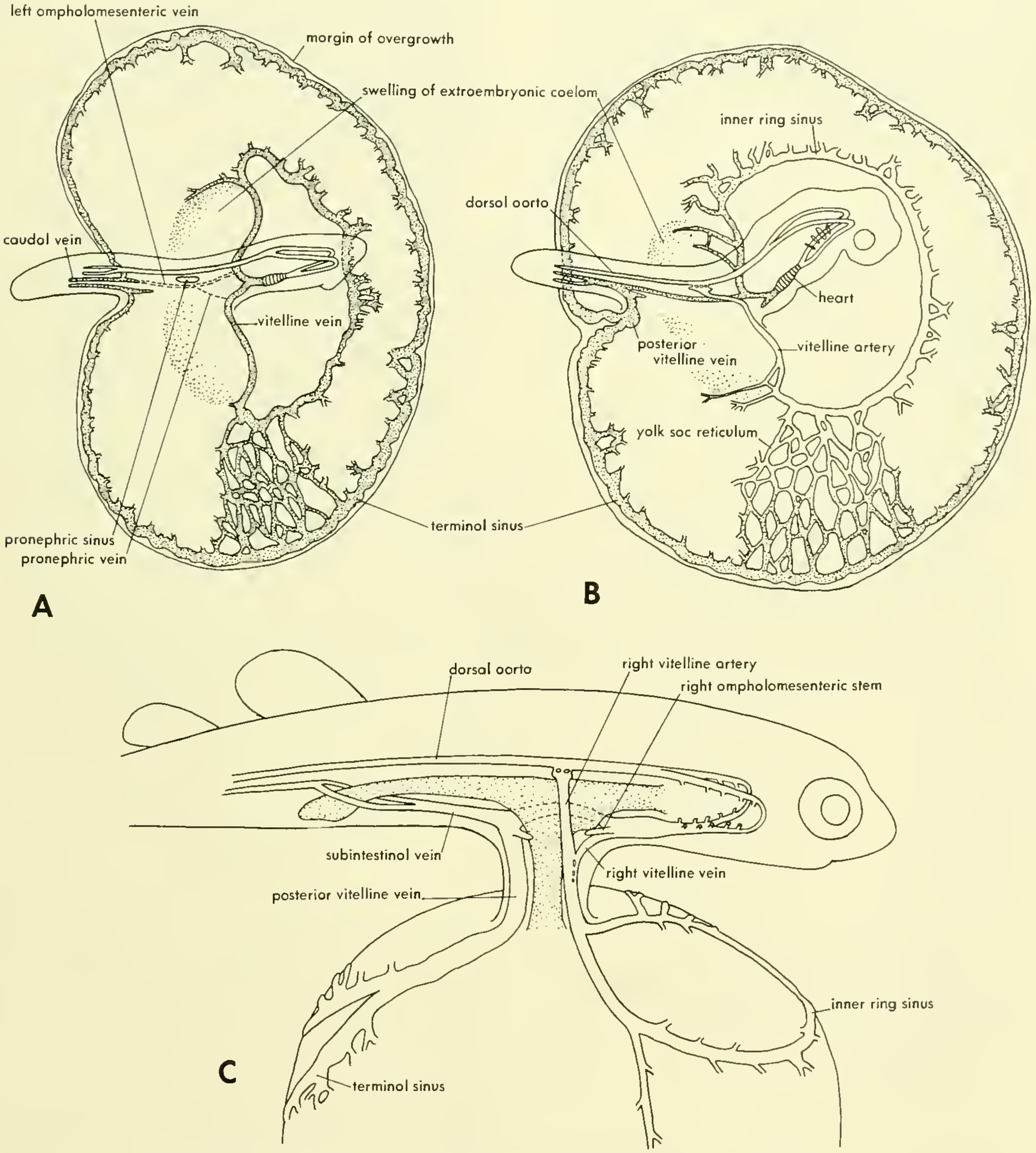


Figure 11-40. Three stages in the development of the circulatory pattern of *Torpedo*. (A and B after O. Hertwig, 1906; C after Hertwig and Mayer, 1886)

terior vitelline vessels are pressed together and fuse to form a single vitelline artery, similarly the two posterior vitellines fuse to form a single median vein. The fusion of the anterior vessels, a right arterial with a left venous, sees the final conversion of these primitively venous channels into an arterial one. Connection of this now arterial stem with the sinus venosus and the left yolk-stalk shunt is lost. The inner ring sinus contains only arterial blood which traverses the channels of the yolk sac to the outer terminal sinus, re-enters the body by way of the posterior vitelline vein, and passes forward to the heart through the yolk-stalk shunt. The flow of blood is thus reversed in the entire yolk-sac circulation.

Development of the venous system of *Squalus* and selachians in general appears to follow a similar course (Figure 11-41). The vitelline artery appears to have captured the inner ring sinus almost as soon as circulation begins.

The sharks can be identified as having an arterial-venous yolk-sac circulation as compared with the completely venous pattern of the other fishes. The posterior vitelline channel, which corresponds to the subintestinal of other groups, has the blood flowing in toward the body rather than out onto the yolk sac. The yolk-stalk shunt is unique but produces an hepatic portal stem similar to that of the other groups. This vessel passes up on the left, over the gut, and into the liver on the right through the stub of the shunt (Figure 11-41).

The cardinal system develops as in other groups. The channel medial to the nephric duct appears first; then the

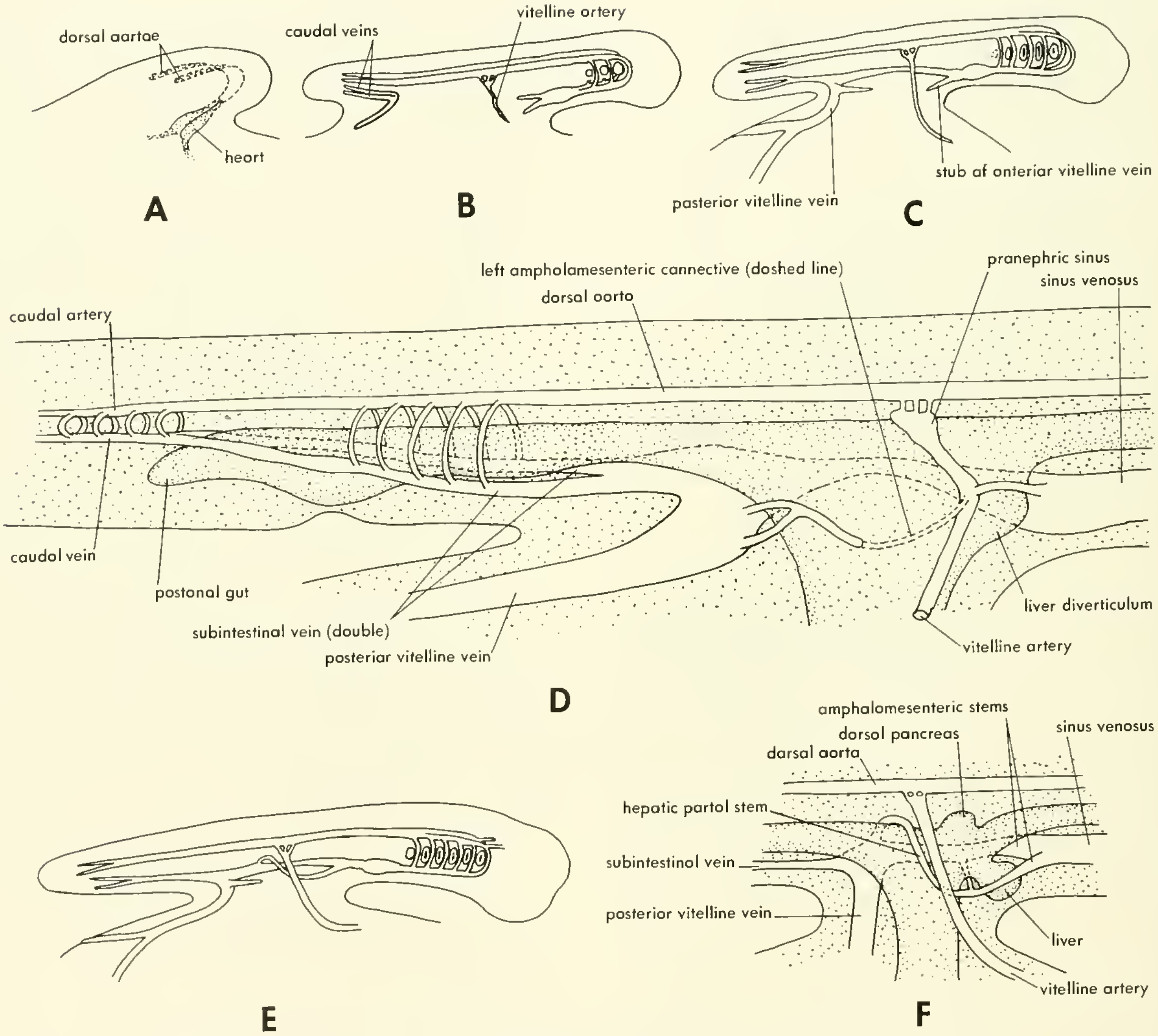


Figure 11-41. Several stages in the development of the circulatory system of sharks. (After Hoffman, 1893, and Mayer, 1867–87)

duct is enclosed in a network of channels. Blood at first flows from the caudal-subcardinal channel laterally to the postcardinal channel. Later, when a caudal-renal portal channel forms, the flow is reversed.

Cyclostomes

LAMPREY The posterior cardinals of the lamprey arise from the caudal vein, which in turn is formed from two lateral caudal twigs from the lateral caudal hearts. These "hearts" are contractile and communicate with the subdermal spaces of the tail region. The posterior cardinals are joined by numerous cross anastomoses along their length, and receive various asymmetrical twigs from the gonads, kidneys, and somatic regions (not from the digestive tract). The right posterior cardinal is larger than the left. The left cardinal joins the right just posterior to the level of the heart, and both cardinals drain into the sinus venosus through the right duct of Cuvier.

The **suprarenal sinus** lies just below the cardinals through out the entire length of the kidney. The sinus is connected by narrow channels with the posterior cardinals. These openings pass through a loose tissue lying along the ventromedial wall of either postcardinal. Several venous channels pass upward from the posterior end of the gut into the suprarenal sinus. These are peculiar in that they enclose arteries passing down to the gut. One of these arteries connects with the intraintestinal artery of the typhlosole, while the enclosing venous channel connects with the intraintestinal vein. Anteriorly the suprarenal connects with the hepatic channels as well as with the right posterior cardinal.

Blood from the intestine (from the coeliacomesenteric artery and posterior viscerals) is drained by a single mesenteric vein coursing along the right dorsal aspect of the gut. At the anterior end of the intestine, the mesenteric vein swings to the right and enters the substance of the liver, which in the breeding adult has undergone fatty degeneration with the loss of the gall bladder and bile duct. The blood from the liver is picked up by a single median vein which carries it to the sinus venosus.

The intraintestinal vein is omitted in most descriptions. It courses through the typhlosole of the gut, emerging to form the anterior intestinal at the region where it leaves the gut to enter the liver. Posteriorly the vein connects dorsally with the suprarenal sinus.

In the early larva of *Lampetra* the posterior cardinals (subcardinal channels) enter paired ducts of Cuvier. The caudal vein passes to either side of the anus to enter the subintestinal drainage. The subintestinal vein connects anterolaterally with bilateral vitelline stems to enter the heart (Figure 11-42). The vitelline stems become the hepatic veins; the left stem loses its connection with the subintestinal. At this stage the gut begins to rotate counterclockwise, making nearly one full turn so that the bile duct now extends from the gall bladder to the left above the gut, and down around the left side to nearly the ventral midline where it enters the gut.

As this rotation takes place, the mesenteric artery is growing back along the course of the invaginating intestinal fold, the typhlosole. The subintestinal vein has also been rotated to a new position on the right aspect of the gut, draining directly into the right posterior lobe of the liver. The caudal vein now connects both with the posterior cardinal and the subintestinal (mesenteric) channel. The mesenteric artery lies in the midst of mass of myeloid tissue filling the typhlosole; this myeloid tissue is the main embryonic site of blood-cell production. Blood from this artery passes through the reticulum of vessels enclosing the gut and enters the mesenteric vein.

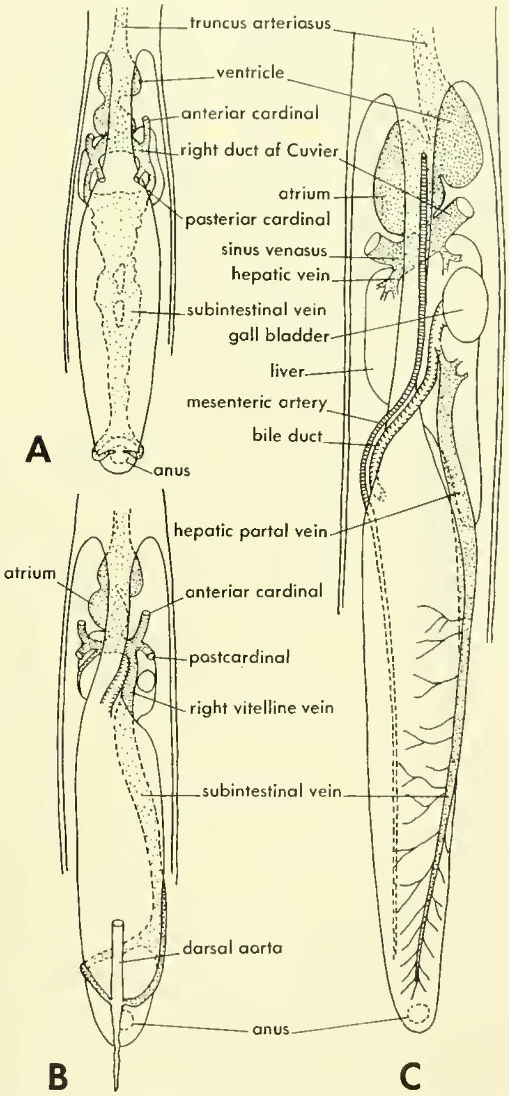


Figure 11-42. Development of intestinal drainage of the lamprey. (After Goette, 1900)

At metamorphosis the left and right posterior cardinals join anteriorly and drain through the right duct of Cuvier into the sinus venosus.

HAGFISH In the tail, small twigs enter lateral vessels arising from two caudal venous hearts. The hearts are elongated tubes which in section are pyramidal, the apex pointing upward. Usually both are filled with red corpuscles, but ordinarily one is distended more than the other; from this it is assumed that they contract alternately.

The lateral veins accompany arteries on either side of the cartilaginous median ventral plate in the caudal region. They unite to form the median caudal vein, which runs forward immediately beneath the caudal artery. In the cloacal region, the caudal vein divides into the right and left posterior cardinal veins. These vessels run just below and on each side of the dorsal aorta, internal to the mesonephros (i.e. subcardinal channels). The right posterior cardinal is much smaller than the left. The posterior cardinals are joined by a large number of commissural vessels.

The posterior cardinals receive no veins from the intestine, but they do receive renal and somatic branches. Anteriorly, a short distance behind the heart, the right and left posterior cardinals unite, and the left becomes the main channel to the sinus venosus.

The "subintestinal" vein arises from the ventral wall of the intestine toward the anterior end. It passes forward along the median ventral line of the intestinal wall and, on reaching the hepatic ligament, passes down along its posterior margin to the posterior lobe of the liver. In some specimens it passes through the tissue of the liver for a considerable distance, but in others it runs forward on the ventral and external aspect. It receives branches from the posterior lobe of the liver, and becomes the "posterior hepatic vein." As such it passes upward, parallel to and near the bile duct of the posterior lobe, and empties into the posterior end of the sinus venosus.

The veins of the anterior lobe of the liver converge to form the anterior hepatic vein, which lies on the dorsal surface of the lobe. This vein runs forward and upward and empties into the left side of the sinus venosus, a little behind the sinoatrial opening.

The portal system of the myxinid presents several interesting features. The anterior cardinal division of it has already been described (Figure 9-27). The intestinal vein receives the blood from the entire intestinal wall, except the ventroanterior region drained by the subintestinal; it runs forward just above the intestine a little to the right of the median line, within the mesentery. It lies to the right of the vagus nerve and the mesenteric arteries. In the region of the reproductive organs, this vein receives several genital veins which descend through the mesentery. These veins are formed by the plexus of small venous twigs in the special genital fold of the mesentery.

On reaching the pericardial region, the "intestinal" vein turns to the right side of the intestine, where it receives the cystic vein from the gall bladder. It then passes through the pericardio-peritoneal foramen, beside the intestine and below the right mesonephros, crosses the roof of the outer chamber of the right pericardial cavity, just below the right vagus nerve, and enters the roof of the portal heart posteriorly.

The portal heart lies in the pericardial fold which forms the septum in the right pericardial cavity. It is an elongated sac, somewhat irregular in shape and variable in size. It stretches diagonally across the pericardial cavity, and lies nearly opposite the ventricle. The points of entrance of the anterior portal vein and the intestinal vein are dorsal and are guarded by semilunar valves. At its posterior (ventral) extremity, the portal heart empties into its efferent vessel, the common portal vein. The opening into the common portal vein is guarded by a pair of semilunar valves.

The common portal vein extends backward and inward toward the median line passing above the anterior lobe of the liver, to which it gives off ventrally a large branch. This branch is the anterior hepatic portal vein, and it descends almost vertically alongside the hepatic duct of the anterior lobe. The common portal vein then crosses the median line to the left side and continues backward and downward alongside the hepatic duct of the posterior lobe as the posterior hepatic portal vein. It enters the posterior lobe about the center of the dorsal surface. Blood is pumped to the liver by the portal heart and drains into the sinus venosus from the liver lobes by way of the anterior and posterior hepatic veins. The latter also drains the subintestinal channel.

GENERAL OBSERVATIONS

In examining the circulatory system and its development, one comes to the conclusion that it is derived from an indifferent "capillary" or intercellular space network which permeates the body. The final channels are in most cases the result more of functional circulatory needs (hydrodynamics) than they are of an inherently fixed pattern. The fixation of pattern that does exist is explainable on the basis of the similarity in general body form and of functional problems of the early stages of all vertebrates. In cases where vessels follow circuitous routes, these routes have been produced by modification at stages after the establishment of the basic pattern which becomes fixed with the development of the vessel walls. Once the connective tissue walls of the blood vessels begin to develop, blood no longer has the choice of seeking the most expedient channel.

The development of the arterial system presents several interesting points. The first of these is that a premandibular arch is never present, although it has been assumed that the external carotid and other structures such as the choroid gland of the eye are remnants of such an arch. The lack of such an aortic arch has been one of the strong points used in arguing against the existence of such a somite. Even in the lamprey, the mandibular aortic arch is the most anterior; it is associated with the velum which marks the extreme anterior end of the pharynx. In terms of the gut, there is no room for a more anterior arch.

On the basis of its development, the arterial system of the cyclostome fish is quite modified. It does not appear to represent a stage from which the gnathostome system was derived. Again as in some other features, the cyclostome appears to be a parallel development to the gnathostome.

The general agreement of aortic arches among the gnathostomes does support the supposition of common ancestry. The exceptions to this picture are some of the sharks where additional posterior arches develop. The increase in the number of arches reflects the number of pharyngeal pouches. It is generally assumed that pouches may be added posteriorly by a simple process of serial replication just as the number of vertebrae, or any of the serial homologs, can be altered.

The venous system shows parallel tendencies in the several groups of vertebrates. Again the cyclostomes have apparently solved circulation problems in a fashion distinct from the gnathostomes. The great differences between the lamprey and hagfish—differences that are perhaps greater than the extremes of the gnathostomes—suggest their origin from quite divergent stocks followed by convergent evolution which has produced end forms that are not particularly different in life habit and appearance.

Among the gnathostomes, there appears to be a general tendency toward the development of a postcaval stem and for the establishment of a renal portal system. The conversion of the kidney from an arterial-renal portal to a purely arterial supply in the mammal is probably related to the form of the metanephric kidney. The pattern of circulatory change associated with kidney change appears rather early and permits the view that the reptiles could have had several parallel evolutionary lines, one of which gave rise to the mammal. In terms of the whole circulatory system, the mammal is not far removed from the general reptile pattern, nor for that matter is any tetrapod or even gnathostome.

The yolk-sac circulation of the various fishes and tetrapods is of interest. The subintestinal vein is a functional product of the movement of blood from the posterior end of the animal—from the caudal vein out on the yolk sac and into the terminal sinus, then forward through this sinus to the vitelline veins, or ring sinus, and the heart. This venous yolk-sac circulation is probably the basal type for vertebrates. In the shark the ring sinus becomes arterial, and the blood flow in the yolk sac is reversed. In the amniotes the yolk-sac channels receive arterial blood from the dorsal aorta through segmental (body wall) arteries situated far back in the body (region of posterior limb).

Here, as elsewhere, there is some question as to the use of terms. For example, the cardinal veins of the embryo are shown to be the precursors of a complex and frequently subdivided drainage. Should the whole drainage be described by this term or should it be restricted to a specific channel within the drainage? Restrictive terms would make discussion extremely difficult and perhaps meaningless. Certainly it is reasonable to associate the terms anterior and posterior cardinals with the everchanging embryonic channels or the similar channels in the adult. However, one cannot effectively discuss internal and external jugulars as the anterior cardinal even though the former is a fairly direct derivative. A certain amount of judgment appears to be necessary.

BLOOD

Comparative hematology

Blood, a liquid tissue, circulates through the channels already described. There are two aspects of blood cells which can be examined: first the various types and secondly their sites of origin in the embryo and the adult.

The comparative anatomy of blood cells has not been thoroughly investigated. As a generality, there are four types of cells present: **erythrocytes, granulocytes, agranulocytes,** and **thrombocytes.** The erythrocytes or red corpuscles are usually flattened, ovoid cells. They contain hemoglobin which acts in the transport of oxygen. In the mammal the erythrocytes are round, biconcava, and **enucleate** (without a nucleus). In the camels they are enucleate but ovoid. In a few frogs and salamanders, some erythrocytes fragment, producing anucleate pieces which continue to function for a time. Erythrocytes are characteristic of vertebrates and are not found even in Amphioxus. They vary in different vertebrates mainly in size.

The white cells or leukocytes are of two types, with and without granules in the cytoplasm—the nuclei of most blood cells are granular. Mammalian granulocytes are of three kinds based on the staining of their granules: neutral (**neutrophile** or **heterophile**), acid (**eosinophile**), or basic (**basophile.** These are usually polymorphonucleate, that is, having irregularly lobed nuclei. The agranulocytes have compact nuclei, a homogeneous cytoplasm, and stain basically. There are two types, **lymphocytes** and **monocytes,** differing in size, shape, and function; the former frequently show **pseudopodial extensions.**

The agranular leukocytes are not far removed from connective tissue cells of the **reticuloendothelial system,** a system which includes all phagocytic cells except those of the blood. Phagocytosis refers to the engulfing and digestion of damaged cells or bacteria. The agranular leukocytes are particularly like the amoeboid (moving around like an amoeba) **macrophages** of connective tissues. It is thought that these leukocytes can become fixed in position and changed in form for tissue repair or modification.

The leukocytes of other vertebrates cannot be directly compared with those of the mammal. For example, frogs have a **polymorphonuclear cell** (with a nucleus irregularly lobate) resembling the mammalian neutrophile, but without granules.

Thrombocytes are associated with clotting. In most vertebrates these are spindle cells resembling the lymphocytes; in mammals cell fragments or **platelets** serve this function.

In the mammal, **hemopoietic** (blood-cell producing) **tissue** is of two types, **myeloid** and **lymphatic.** The myeloid tissue produces erythrocytes, granular leukocytes, and platelets. Lymphatic tissue produces nongranular leukocytes. Myeloid tissue is confined to the bone marrow in the mammal; lymphoid tissue occurs as lymph nodes in the visceral connective tissue or gut wall, hemal nodes, the tonsils, thymus, and spleen.

In the embryo, there is change in the area of origin of blood cells. The first cells are those derived from the blood islands of the yolk sac. Here clumps of mesenchyme cells differentiate to form vesicles containing a fluid and suspended cells. Some of these cells contain hemoglobin but are nucleated, resembling early stages of the erythrocytes of the adult (see 10-mm pig, serial sections). The differentiation of the blood islets has been viewed in two ways, as described above and as a **syncytium** which becomes **cellular.**

The vesicles formed by the blood islands tend to join and form channels. In this way the reticulum of the yolk sac develops and enters the body as the vitelline veins from which the heart and the first aortic arch form.

The venous channels of the body appear to arise *in situ* from clumps of mesenchyme cells which form into channels for the return flow of fluid to the yolk sac or heart. At first the arterial and venous channels are directly connected. With the beating of the heart, the fluid is put under pressure and given a direction of flow. This circulation movement determines the development of outgoing channels as well as return channels. Direct connection between arteries and veins is discouraged by the outgrowth of their walls into the tissues as a branching system of vessels. The vessels are connected at all times through the tissue spaces until the final connection through lined capillaries is achieved.

As the embryo differentiates, blood cells are derived from mesenchyme clumps along the blood channels throughout the body. Many new cells arise by division of circulating cells. As the embryo gets older new types of cells appear. With the formation of the liver, spleen, and lymphoid tissue of the throat, cell production shifts to these sites. In the mammal these early areas, along with the lymph nodes, retain only the capacity to produce nongranular leukocytes. The bone marrow takes over the production of erythrocytes and granulocytes (third month and later in human). All of these areas are active in the phagocytosis of damaged blood cells.

In the reptile and bird, the pattern of blood-cell production parallels somewhat that of the mammal, but the kidney is an important embryonic source. The adult bone marrow produces all kinds of cells including the nongranular leukocytes. Lymph nodes are absent although a lymphatic system is present. In the amphibians the red cells are formed mainly in the kidney and destroyed in the liver and spleen (endothelioreticular tissue). The bone marrow may be an important red-cell forming center of the adult, and it may be only a seasonal source (males in breeding season). The spleen is a source of lymphocytes, although there is little white pulp in it.

In the fishes there is a variety of hemopoietic tissues. The first cells arise from the yolk sac, followed by cells derived from the mesenchyme of the body vessels. An intermediate cell mass, along the notochord in the kidney region, produces blood cells. These areas are followed by the development of the liver and spleen, but primarily the kidney. Lymphoid tissue is scattered in the intestinal wall, in the mesentery supporting the gut, and the thymus.

In many teleosts the kidneys appear to be the most important blood-cell producing structures, and in some the spleen becomes an organ functioning in the removal of blood cells. In the sturgeons there is a large pericardial mass of hemopoietic tissue, while in *Amia* and *Lepisosteus* the cover of the fourth ventricle appears to be involved in this function.

In the lamprey and myxinid, blood-cell production seems to be limited to the intestinal wall and mesenteries. In the lamprey the kidney of the adult and the typhlosole in the gut of the larva are important centers.

General observations

Although blood-cell production is of interest to the embryologists and the shifting of sites of blood-cell production indicates an evolutionary history, this area of information has not supplied any usable clews to the study of phylogeny.

THE LYMPHATICS

A part of the functional circulatory system is the lymphatic. The intercellular spaces are drained by thin-walled channels which eventually drain into the blood circulatory system. In the mammal the vessels of this system are associated with lymph and hemal nodes, and there is an extensive system of vessels permeating the tissues. Similar systems are observed in all vertebrates, but the difficulties of observation do not encourage comparative study.

12

The Endocrine Glands

The endocrine glands of vertebrates are several in number, and of these the pituitary is perhaps the most complex and important in function.

THE PITUITARY

The pituitary of the mammal arises as a product of an invaginated pouch from the **stomodeum, Rathke's pouch,** which meets and fuses with a pouch, the **infundibulum,** growing down from the diencephalon. These two components give rise to the **adenohypophysis** and **neurohypophysis,** respectively. As development proceeds, Rathke's pouch loses connection with the stomodeum and becomes fused to the neurohypophysis (the **pars nervosa**). The adult pituitary has several types of tissues in it, each identified by histological features.

The **anterior lobe** is differentiated into **pars anterior, intermedia, and tuberalis.** The anterior and tuberalis parts represent the front half of the adenohypophyseal sac; the intermediate lobe is the posterior half in contact with the pars nervosa. In man the pars tuberalis develops as an outgrowth around the stalk connecting the pars nervosa to the brain.

The pituitary is generally considered the master gland of the body, extremely important in the coordination of internal affairs. In the pituitary there is an interesting combination of nerve tissue and glandular tissue. In the supraoptic and paraventricular nuclei of the brain there are neurosecretory cells, whose axons pass down into the neurohypophysis. Secretory granules form in the cell body and pass down along the axons. It is assumed that capillary clusters pick up the secretions from the axon endings. The capillaries unite to form venules which pass into the pars anterior where they break up into a plexus of sinusoids. The transport of these secretions thus involves a portal system. The secretions are important in determining events in the adenohypophysis, whose secretions regulate many events. This relationship between the central nervous system and the endocrine system makes possible responses to various environmental conditions.

Within the other classes of vertebrates, essentially the same story of pituitary development is encountered. The adult gland is very similar to that of the mammal. In the reptiles or amphibians, a pars tuberalis as such is not identifiable. It can be assumed to be included in the anterior part. In the fishes there is an extreme anterior part of unknown endocrine function which may represent the pars tuberalis. The middle portion, in terms of its endocrine product, appears to be the homolog of the pars anterior; behind this is a pars intermedia which is closely associated with the tissue of the pars nervosa.

Comparative study of the endocrines produced has been responsible for the indentifications of these areas which histologically do not present a uniform picture. Among the fishes the shark is the most aberrant, in that the adenohypophysis remains a vesicle with or without differentiation. The sharks, actinopterygians, and *Latimeria* also have a **saccus vasculosa** associated with, or as an outgrowth of, the pars nervosa. It has been suggested that this is a sensory organ functioning in depth perception; it is more likely of endocrine function. A saccus vasculosa is present in the lamprey as well as a pituitary formed of pars intermedia and pars anterior (plus tuberalis?). In *Myxine* there is only a pars intermedia and the saccus is rudimentary.

The development of the pituitary in the fishes appears to be the same as that in the higher forms; a Rathke's pouch and infundibular pocket rise to the definitive gland. The exception to this picture is observed in the lamprey (Figure 12-1). Here the nasohypophyseal pouch extends back underneath the brain to contact the only slightly evaginated infundibulum. This posterior pouch forms a dense mass of tissue, without an internal lumen, connected by a strand of tissue with the nasal pouch. At the time of metamorphosis a new sac-like outgrowth from the nasal pouch extends posteriorly below the adenohypophysis to give rise to the adult "hypophyseal" sac. The **subhypophyseal sac** is thus a secondary structure, not a part of the original Rathke's pouch.

THE THYROID

The **thyroid** develops in the lamprey from the **subpharyngeal gland,** which seems to be the homolog of the **endostyle**

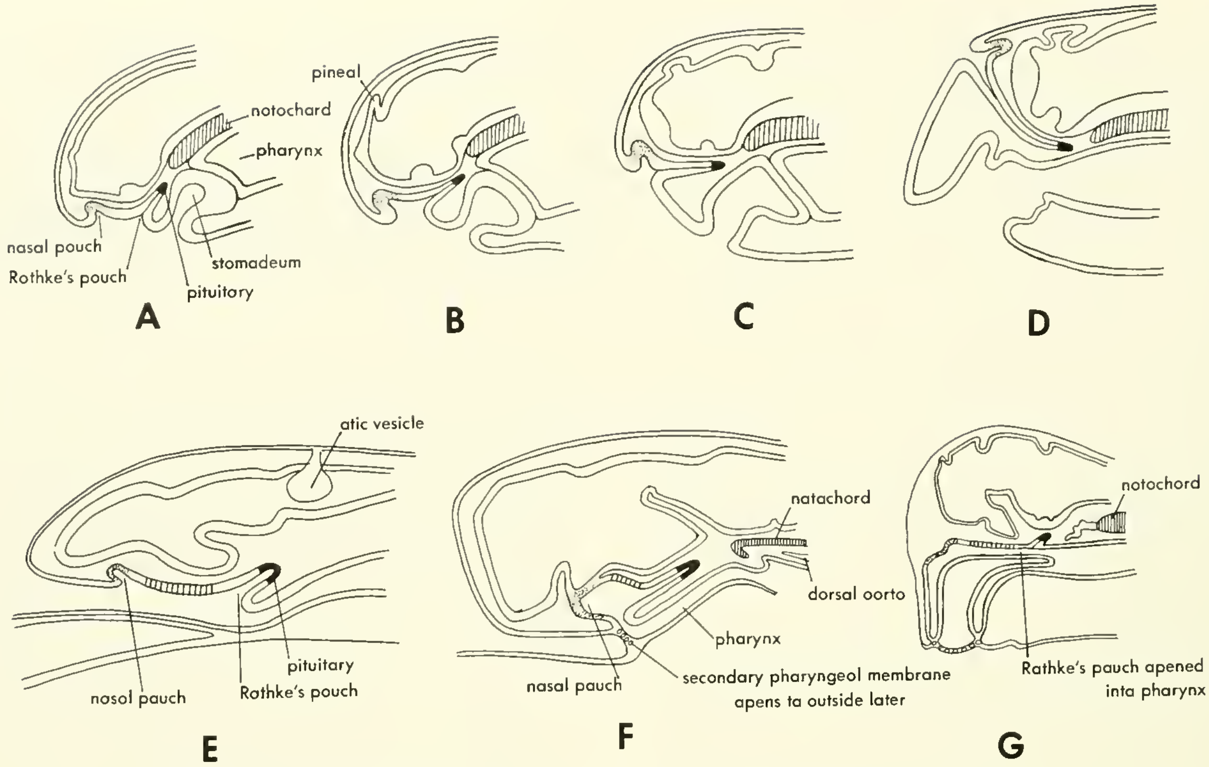


Figure 12-1. Stages in the development of Rathke's pouch in the lamprey and *Eptatretus*. (After Dohrn, and Kupper, 1900)

of the protochordate as in Amphioxus. In Amphioxus the bilobed nature of the endostyle when it first appears suggests a pair of pharyngeal pouches (Van Wijhe).

The endostyle evaginates early in the lamprey and soon differentiates into a complex and apparently mucoid secretory organ. Some of the cells of this organ take up iodine very much in the way of the thyroid tissue, which develops later. With the onset of metamorphosis, the endostylar gland loses connection with the pharynx and a part of its tissue forms thyroid-like follicles. In the hagfish the thyroid arises as a groove extending the length of the floor of the pharynx.

In the actinopterygian fishes the thyroid arises, along a line, from the floor of the pharynx. From this groove, clumps of cells come to lie along the course of the ventral aorta. Each clump forms a follicle or groups of follicles of a typical thyroid structure. Experimental evidence indicates that their secretion is of a thyroid nature. A few teleosts have a massive thyroid like that of a shark.

In the sharks the thyroid tissue is rather gelatinous, but formed of typical follicles, and encapsulated by connective tissue. This mass lies far forward, behind or below the basihyal cartilage, anterior to the forking of the ventral aorta. It may be crescentic in shape or irregular.

In the shark the gland arises as an evagination from the floor of the pharyngeal cavity with or without a central lumen. As it sinks deeper it loses connection with the pharynx. In *Chlamydoselachus* the duct retains its connection with the pharynx even in the adult. This duct enters the pharynx through a perforation in the basihyal cartilage. In the lining of the duct, numerous scale-like structures are present, perhaps remnants of stomodeal denticles.

In amphibians the gland arises as a midline element but divides into two parts which lie close below the basihyal in the frog or well out to either side in the salamander. *Latimeria*, the coelacanth, has a compact midline thyroid lying

THE THYMUS, PARATHYROID, AND ULTIMOBRANCHIAL BODY

In the mammal the **thymus** arises from evaginations from the dorsal wall of **pharyngeal pouches** III and IV, while the **parathyroid** arises from anterior outpocketings from these same pouches (Figure 12-2). From the fifth pouch a pair of evaginations produce the **ultimobranchial body.** In man the thymus evaginations of the third arch form the definitive gland. The evagination of the fourth arch remains rudimentary and becomes embedded in the thyroid. In some mammals these elements may remain as distinct thymus masses. During development this gland is moved back into the upper chest or base of the neck as a result of the constricted nature of the neck.

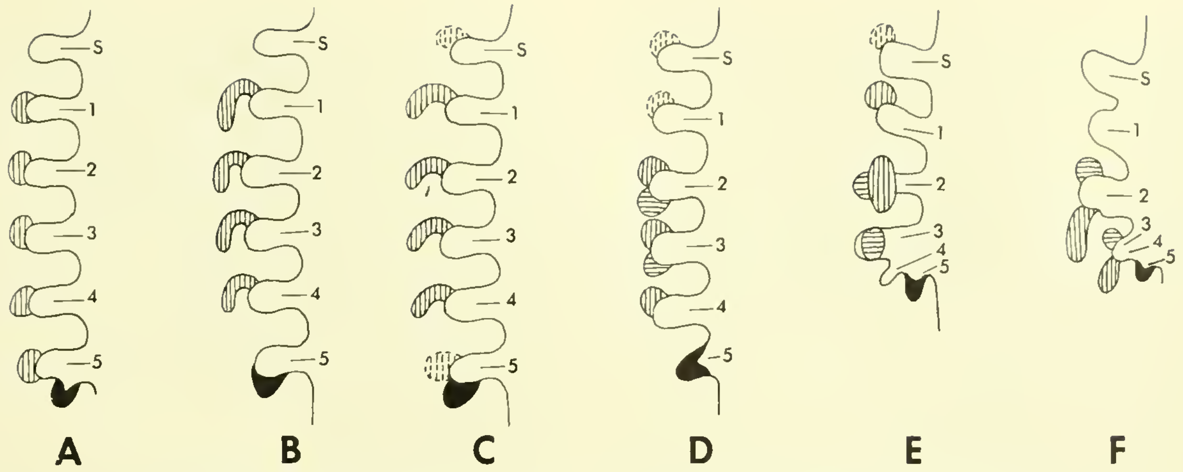


Figure 12-2. Endocrine derivatives of the pharyngeal pouches of different vertebrates. (After Bertmar, 1961)

The parathyroid masses become associated with the thyroid gland and generally are embedded in that gland. The ultimobranchial body also becomes embedded in the thyroid.

The thymus gland is of unknown function in the mammal. Appearing to be lymphoid in nature, it is large in the young and regresses in the adult.

In the reptiles these lobular glands lie in the neck; in the amphibians the thymus is small and lies behind the angle of the jaw. In the sharks the thymus appears as a series of nodules connected into a chain which lies above the gill pockets, and it arises as thickenings of the branchial pouch linings. There are six sets of nodules in *Heptanchus,* four in most sharks. These thickenings may occur in the spiracular and in the most posterior pouch of Spinax. In *Heptanchus* the thymus nodules have the form of a bunch of grapes with a duct opening into the pharyngeal pouch.

In the actinopterygian fishes a rather massive thymus is observed in the medial wall of the branchial cavity. This thymus apparently arises from contributions of several of the branchial pouches. The thymus of *Latimeria* is comparable to that of the actinopterygian but is lobular. In the cyclostomes all of the gill pouches give rise to thymus tissue dorsally. The anterior pouches also have ventral anlagen. In the adult only the dorsal parts remain.

There are no parathyroid glands in the sharks or in the actinopterygian fishes. Unquestionable parathyroids appear first in the amphibians, and this may be correlated with the loss of gills. It should be remarked here that a secretory or endocrine function is assumed for the pseudobranch of fishes, especially those buried in the tissue. In addition the gills of marine teleosts have "chloride secreting" cells which help in maintaining the internal osmotic state. Such secretory cells could be the forerunners of endocrines.

An ultimobranchial body is said to be present in the sharks, holocephalans, and some ray-finned fishes. It some of the teleosts, there is a flat discoidal mass lying in the connective tissue between the floor of the esophagus and the sinus venosus. Experimental work with extracts of this tissue suggests that it is parathyroid in function. It has also been viewed as an accessory thyroid. The embryological source of this tissue is in question but has been attributed to the last gill pouches or the wall of the gut in the region of this pair of pouches. In a few teleosts (characids), there are accessory branchial organs, diverticula of the fifth branchial pouch, which appears to be endocrine in function. Paired or unilateral ultimobranchial bodies lie in the connective tissue dorsolateral to the anterior end of the pericardial cavity of the salamander. The position of these bodies in the mammal has been described.

THE ADRENAL GLAND

The adrenal gland of the mammal is compound, formed from chromaffin cells of neural-crest origin and enclosed by a capsule of splanchnopleure. The chromaffin cells form the medulla. The secretion of this mass is similar to the adrenalin (epinephrin) secreted by the sympathetic part of the autonomic nervous system. The cortex of the gland is differentiated into several layers and produces a number of steroid secretions which are important in the functioning of the body.

In reptiles this may be a single organ on either side (crocodiles and turtles) or each may be separated into suprarenal (chromaffin) and interrenal (epithelial) components. In birds and amphibians a single pair of adrenal glands is present. In the lungfish *Protopterus,* interrenal and chromaffin tissues are intermingled and are located along the venous channels of the ventral side of the kidney.

In actinopterygian fishes there is a range from a fairly compact adrenal gland in *Cottus,* where chromaffin cells are massed within the interrenal tissue, through *Pleuronectes,* in which the two components are more or less closely associated, to the typical teleost, where they are scattered along the postcardinals (Figure 10-26). The interrenal, or cortical tissue, of the teleost forms a sheath of acidophylic cells around the posterior cardinal veins in the cranial region of the kidney.

In the shark or holocephalan the chromaffin or suprarenal tissue is completely separated from the interrenal. The former lies anterior to the interrenal as masses associated with the sympathetic ganglia. The interrenal tissue forms a compact mass between the opisthonephric kidneys which is distinct enough to be removed. Experimental work indicated that the secretions of these two parts are suggestive of those of the adrenal of higher forms. However, there is considerable variation in details of function.

In cyclostomes the suprarenal and interrenal tissues are separated. The latter is represented by clusters of cells along the posterior cardinals throughout the length of the body cavity. The suprarenal tissue is arranged as strands along the dorsal aorta (Figure 10-26).

THE GONADS

The gonads of all of the vertebrates are secondarily endocrines; they contain interstitial cells which secrete steroid compounds. These interstitial cells may be of splanchnopleure origin like those of the adrenal cortex, which are also capable of secreting sex hormones. The sex hormones function not only in the production and maintenance of sex cells but also in the appearance and continuance of secondary sex features which are necessary for reproductive success. Sex reversals, sometimes functional and involving many morphological changes, can be produced by use of the hormone of the opposite sex early in development.

ISLETS OF LANGERHANS

Within the pancreas of higher forms and sharks, islets of Langerhans develop from the tubules of this otherwise digestive gland. Islet tissue in the actinopterygian fishes tends to be concentrated. There is usually one islet or sometimes two large islets in the region of the bile duct (Figure 9-13). In the agnath fishes pancreatic islets have been observed in the lamprey (Figure 9-26) but not the hagfish. In the lamprey there are three masses of cells in the wall of the gut just behind the junction of the pharynx and the midgut. These masses have been shown experimentally to affect the sugar concentration of the blood. Whether or not they actually produce insulin is another thing.

CORPUSCLES OF STANNIUS

The corpuscles of Stannius, which occur in the kidney of many actinopterygian fishes, have often been viewed as potentially endocrine. These arise as many (40 or more) diverticula from the nephric ducts in the anterior part of the opisthonephros (segments 9 to 12) of *Amia* (Figure 10-23) and *Lepisosteus* or, in teleosts, as a few or even a single pair of diverticula in the posterior region of the kidney.

These corpuscles have not been observed in other vertebrates and are thus assumed to have evolved within the actinopterygian group. They are not observed in the chondrosteans (*Acipenser*). It has been suggested that they are homologous with the Müllerian ducts, but such an homology is unlikely. Furthermore, these corpuscles are not a part of the adrenal system. Experimental work has revealed no function for them. They appear to be only modified kidney tubules, perhaps related to the Leydig's glands of chondrichthians. The number of these appears to have undergone reduction in the teleosts. There are none in some.

THE PINEAL ORGAN

The pineal organ, an outgrowth from the roof of the brain (Figure 12-1, see next chapter), is recognized as a photoreceptor in fishes (it is vestigial in the hagfish), but its glandular structure suggests endocrine activity. Removal of the pineal organ of the guppy (*Lebistes*) is followed by reduced growth rate, skeletal abnormalities, and marked stimulation of both pituitary and thyroid glands. Increased activity was also noted in the corpuscles of Stannius and in remnants of the pronephric tissue. It is suggested that the action of the pineal is secretory and its action is mediated through the pituitary and thyroid glands. The presence of a pineal nerve also indicates a more direct (nervous) association.

In the mammal the pineal is glandular and richly supplied with blood. There are no nervous elements in it although the parenchymal cells have processes. No endocrine function has been demonstrated and the structure is looked upon as rudimentary and, in the adult, degenerate.

GENERAL OBSERVATIONS

The presence of a system of distinct endocrine glands characterizes the vertebrates, but does not subdivide this array. Presumbably these glands can be followed back to some stage in phylogeny at which they disappear as discrete structures. It can be assumed that like the mammals the lower vertebrates have endocrine-producing cells or tissues, similar to those producing secretin (doudenal wall) and rennin (kidney), which are not organized into distinct, separate glands.

The protochordates lack apparent endocrines. Hatschek's fossa of Amphioxus and the stomochord of the hemichordates may be divergent developments of the Rathke's pouch of the vertebrate. The urinary vesicles and solenocytes of Amphioxus may represent the thymus diverticula of the vertebrate, while the endostyle and thyroid are definitely divergent products of a single structure. The aggregation of specialized secretory cells into endocrine glands is but another of the evidences of the increasing complexity of the vertebrates as contrasted to invertebrates.

13

The Nervous System

The nervous system of the vertebrate consists not only of the brain, spinal cord, peripheral nerves, and autonomic system but also of the various sensory structures: nose, eye, ear, lateral line, etc. This system is composed then of sensory cells of one sort or another and conducting cells or neurons. A good part of the substance of the nervous system is made up of supporting tissue which is formed of glial cells and matrix (secreted material). Some scientists have accorded an important role to glial cells in the integration and control of central nervous system function, but generally they are viewed as a kind of "insulation."

The central nervous system is enclosed in connective tissue envelopes collectively identified as the meninges; these are highly vascular and share with the central system the spinomeningeal fluid. This fluid fills the central cavity of the brain and spinal cord and also the spaces between these and the meninges.

THE CONDUCTING AND INTEGRATING SYSTEM

The nervous system is extremely complex and necessitates an approach from the simple to the more detailed in order to bring the myriad details together in a meaningful way. To achieve this it seems desirable to describe first the development of the brain in the mammal, as exemplified by the human, and then to consider the variations of this structure in other forms.

Mammal

Embryological development of the brain The invagination of the neural tube has already been described. The brain begins to differentiate by the appearance of three vesicles separated by two constrictions. These divisions are the **prosencephalon, mesencephalon,** and **rhombencephalon.** The third vesicle tapers to the spinal tube (Figure 7-7).

From the prosencephalon, **optic vesicles** grow out to either side and these invaginate distally to form **optic cups.** While the optic cups are forming, bilateral lobes begin to grow out from the anterior end of the prosencephalon. These are the beginnings of the **cerebral lobes,** the beginnings of the **telencephalon** (Owen, 1868—used prosencephalon for telencephalon). The prosencephalon has now divided into a **telencephalon** and a **diencephalon;** the optic cups are attached to the latter. From the roof of the diencephalon a small **epiphyseal evagination** arises.

While these events are going on, a flexure has developed in the region of the mesencephalon; this is the **cephalic flexure.** Somewhat later, as the **rhombencephalon** divides into an anterior **metencephalon** and a posterior **myelencephalon,** a **ponteen flexure** develops; the apex of this flexure lies in the region that will become the pons of the adult brain. Between the brain and spinal cord is the **cervical,** or nuchal, **flexure.**

The tubular brain is now five-parted and folded at three points. The walls begin to differentiate, thickening in some spots, thinning in others. The cerebral lobes become proportionally very large. Outgrowth of these lobes leaves behind a part of the original anterior wall of the prosencephalon marked by the **anterior commissure** and above this the **pallial commissure.**

The roof of the diencephalon becomes membranous and in turn highly vascular as a **chorioid plexus.** The third ventricle is constricted posteriorly as the **aqueduct of Sylvius.** Behind this aqueduct, the fourth ventricle lies within the metencephalon.

The roof of the myelencephalon is membranous and developed into a chorioid plexus which extends into the fourth ventricle.

Anatomy of the adult mammal brain From this beginning the anatomy of the adult mammal brain can be considered in more detail (Figure 13-1). The **cerebral lobes** are large and fill much of the cranial cavity in the case of the human, considerably less in some of the lower mammals. The surfaces of the cerebral lobes are folded into an intricate pattern of ridges in some mammals (man) or remain smooth (*Ornithorhynchus*). Each cerebral lobe (or hemisphere) has a **ventricle** (cavity) which connects with the **prosencoel,** or third ventricle, by a **foramen of Monroe.** These cerebral ventricles extend forward and down into the **olfactory bulbs.**

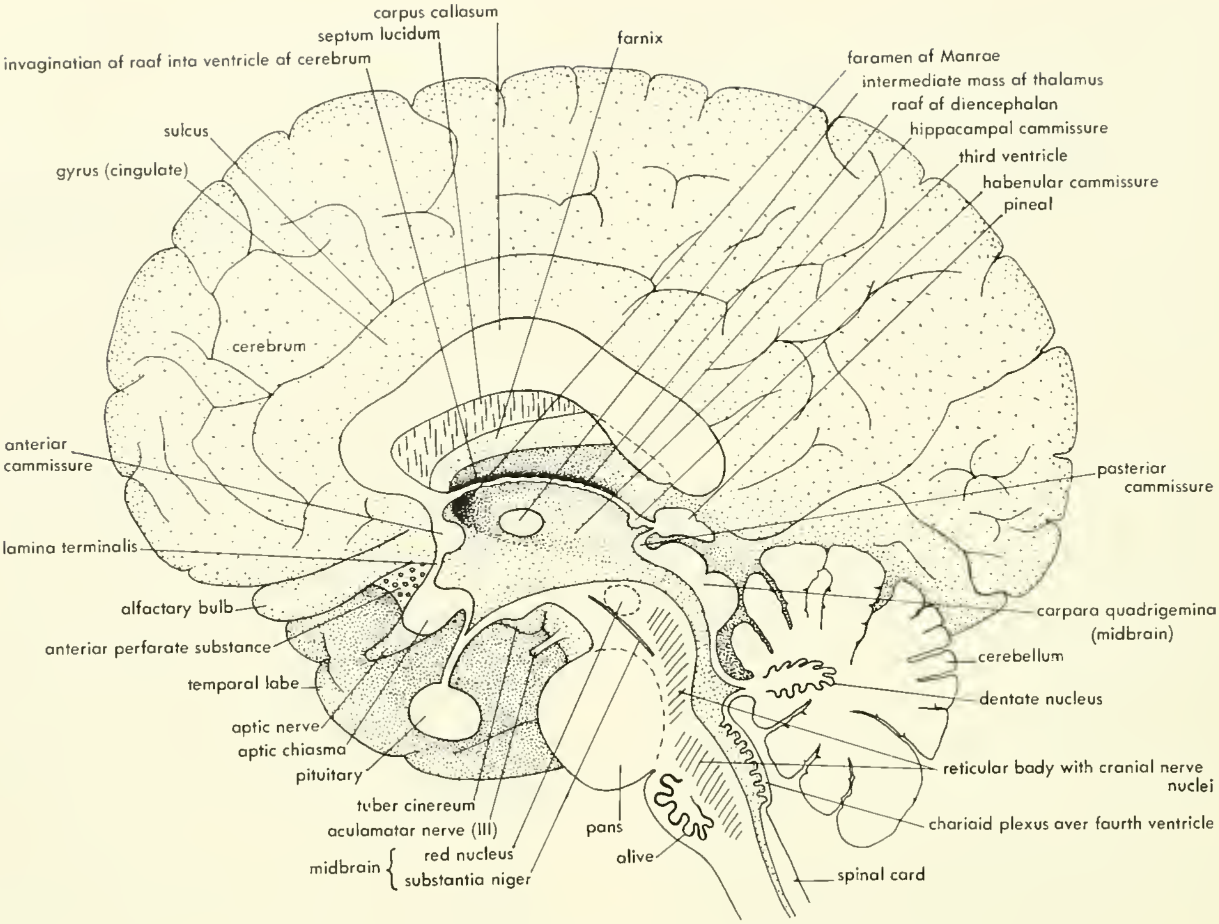


Figure 13-1. Semidiagrammatic medial aspect of right half of a human brain.

The two **hemispheres** are joined across the midline above the level of the diencephalon by a **corpus callosum** formed of transverse fibers. This structure is characteristic of the placental brain and is derived from the **pallial commissure** of the opossum, the monotreme, or the reptile (Figures 13-2, 13-4). Hanging down from the corpus callosum are bilateral tracts identified as the **fornix.** These are suspended by a **septum lucidum.** Below the corpus callosum, in the anterior wall of the brain (the lamina terminalis) is the **anterior commissure.** Below this and anterior to it are the olfactory bulbs and nerve.

The posterior limit of the **telencephalon** is marked ventrally by the **preoptic recess,** a thinning of the floor just anterior to the **optic chiasma.** Dorsally there is no marker, but the ingrowing chorioid tissue probably represents the **velum transversum** which separates the telencephalon and diencephalon of the embryo.

The roof of the **diencephalon** is modified into a chorioid plexus which extends down into the third ventricle and through the foramina of Monroe into the lateral ventricles of the cerebral lobes. Behind this membranous roof is a **pineal organ.** This organ is derived from the epiphyseal diverticulum. Ventrally and anteriorly is the **optic chiasma** where part of the fibers of the optic nerves decussate (cross). Behind this and suspended by a thin stalk is the **pituitary body** or hypophysis. In the posterior wall of the infundibulum, or **hypothalamus,** are a **tuber cinereum** and above this paired **mammillary bodies.** Connecting across the cavity of the diencephalon is the **intermediate mass** which develops from bilateral ingrowth of the thickened walls, the **thalami.** The intermediate mass does not contain cross-connecting fibers. The supraoptic and paraventricular nuclei, mentioned in relation to the pituitary gland, lie in the diencephalon.

The **mesencephalon** consists of the **corpora quadrigemina** above. These are two pairs of lumps: the anterior pair, the **superior** or anterior **colliculi,** are visual relay centers; the posterior pair, or **inferior colliculi,** are auditory reflex centers. The side walls and floor of the mesencephalon, the **tegmentum,** contain the nuclei for the third and fourth nerves which serve the eye muscles. Nucleus here refers to a clump of nerve-cell bodies, or ganglion, within the brain giving rise to nerve fibers. Also located in the floor of the mesencephalon is the functionally important **red nucleus.** Here the brain stem also contains fiber tracts connecting higher and lower parts of the brain. These tracts are described as the **peduncles.**

The **metencephalon** has a dorsal **cerebellum** and a ventral **pons** as well as the usual ascending and descending fiber tracts of the brain stem. The **myelencephalon** has a membranous roof, a chorioid plexus, and a thick basal portion consisting of bilateral **reticular bodies, olivary nuclei,** and fiber tracts.

Cranial nerves of the mammal A description of the brain is quite incomplete without the cranial nerves which stem from it. These are ten to fifteen in number depending on how and in what animal one approaches them. Mammals

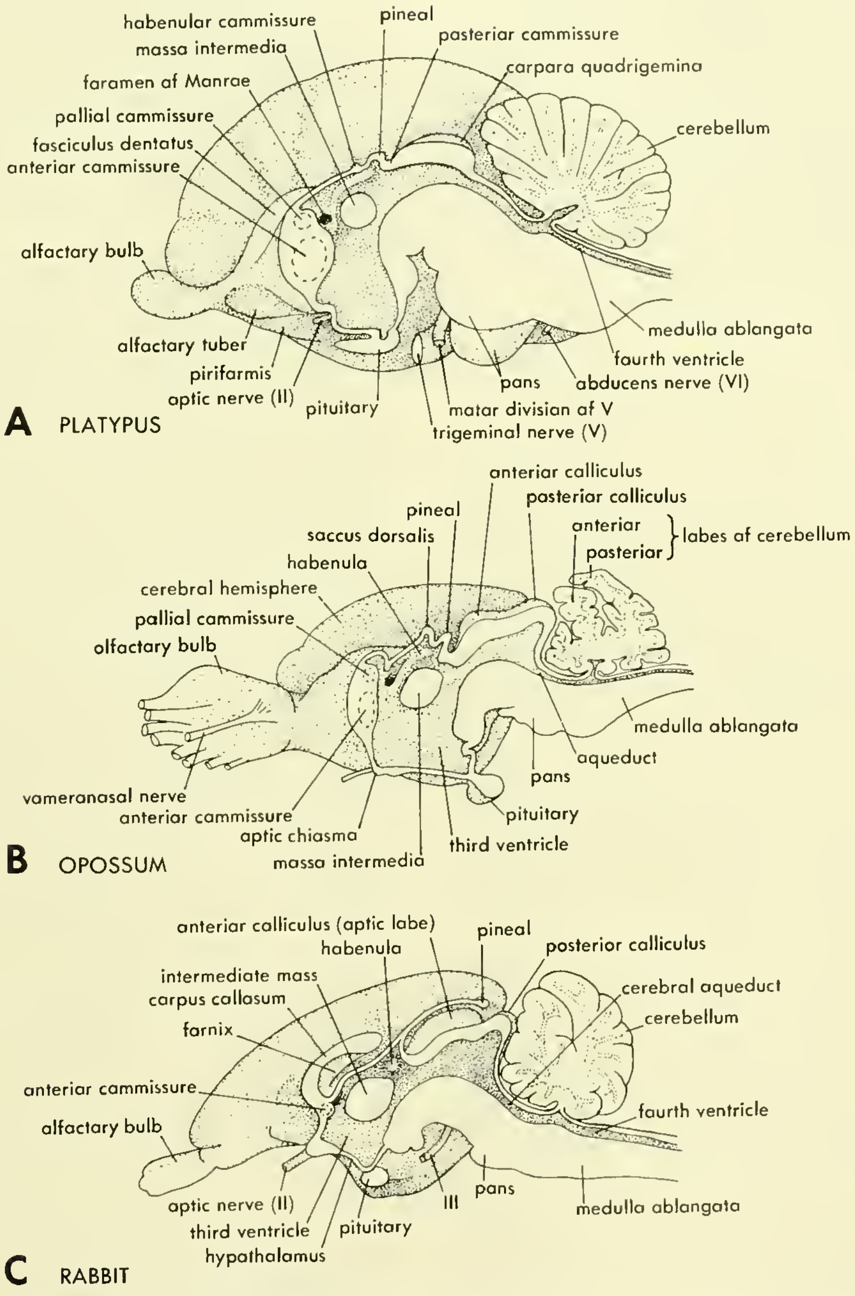


Figure 13-2. Semidiagrammatic medial views of right brain halves of three mammals. (A after Neal and Rand, 1936; B after Romer, 1955; and C after Young, 1957)

are said to have twelve, each assigned a roman numeral (Figure 13-3).

The **terminal nerve** (0) was described, after the other cranial nerves had been numbered, by F. Pinkus in 1895 from the dipnoan, *Protopterus*. This nerve is closely associated with the olfactory nerve and should not be confused with the **vomeronasal division** of that nerve. The fibers are distributed to the nasal septum and the area around the external naris. The nervus terminalis is presumed to be a **sensory nerve** (general cutaneous), with a ganglion near or at its base, but it may be a part of the autonomic system (Figure 13-3). This nerve is not apparent in the mammal.

The **olfactory nerve** (I) arises from the sensory cells of the **olfactory epithelium** in the **olfactory chamber** or capsule. Its vomeronasal division arises from the separate area of sensory cells of Jacobson's organ. The olfactory nerve enters the olfactory bulb, the anterior part of the telencephalon, where its fibers **synapse** with those of the cells forming the **olfactory tract** which leads back to the **olfactory lobe** (nucleus) and other areas of the brain.

The **optic nerve** (II) is a brain tract rather than a nerve since the retina of the eye is a part of an evagination of the wall of the diencephalon (see below under eye). The fibers of the optic nerve arise from a ganglionic layer in the surface of the retina—there are two other layers of neurons between these ganglion cells and the sensory cells. The fibers pass over the inner surface of the retina to the **blind spot** where they form the optic nerve which passes out through the wall of the eyeball to the brain. At the **optic chiasma** these fibers **decussate** (cross to the opposite side of the brain) or not, according to their area of origin, and pass up through the **optic tracts** to the **lateral geniculate nuclei** of the thalamus. A few of the fibers continue on to the superior colliculi. Synapse in the lateral geniculate nuclei switches the optic sensory area from the mesencephalon to a part of the cerebral cortex.

In mammals the fibers from the medial half of the retina of each eye cross over, or decussate, and accompany the fibers from the lateral half of the retina of the opposite eye into the brain. Decussation of the optic nerve fibers is complete in lower forms—all fibers pass to the opposite side. As a generality one can say that the left side of the brain serves the right side of the body.

The **oculomotor nerve** (III) supplies the superior, inferior, and internal rectus muscles of the eyeball. This **motor** nerve arises from a small **nucleus** in the mesencephalic brain stem. This nerve also contains **proprioceptive fibers** from the eye muscles to the central nervous system. These sensory fibers are employed in the tonal (tension) reflexes of these muscles. There are also preganglionic fibers emerging from the eyeball to join the oculomotor nerve. These fibers lead to the ciliary ganglion and are involved in the operation of the smooth muscles of the ciliary body of the lens and the iris.

The **trochlear nerve** (IV) arises in the posterior part of the floor of the mesencephalon near the ventral commissure. The fibers extend dorsally and somewhat posteriorly from their nucleus, within the walls of the mesencephalon until they reach the mid-dorsal line. Here they emerge and decussate. Each now passes down and forward to the eye region. This nerve innervates the superior oblique muscle, and contains somatic sensory fibers involved in the proprioceptive reflexes of that muscle.

The **trigeminal nerve** (V) is a large complex unit involving sensory and motor fibers. It derives its name from its three branches. The **ophthalmicus** or **profundus branch** (V_1) arises from the **Gasserian** (or semilunar) **ganglion;** it extends through the orbit to the snout region. The **maxillary branch** (V_2) arises from the same ganglion and is composed of sensory elements like the profundus. It passes down beneath the orbit and forward into the maxilla. The **mandibular branch** (V_3) extends down from the Gasserian ganglion behind the orbit and into the mandible through the mandibular foramen.

Primarily the trigeminal is a sensory nerve but it has a **visceral motor component.** The motor portion arises from a nucleus in the floor of the metencephalon and extends out to the jaw muscles. The interrelationships between motor and sensory components in the mandibular branch are secondary ones. The **general visceral fibers** (proprioceptive) of this nerve pass to a nucleus in the roof of the mesencephalon. A sensory nucleus within the brain is unique but not uncommon in invertebrates and Amphioxus.

The **abducens nerve** (VI) arises in the caudoventral part of the pons. The nerve passes out then forward from its nucleus to innervate the lateral rectus muscle of the eyeball. This nerve, although primarily motor, contains some proprioceptive sensory fibers.

The **facial nerve** (VII) is primarily motor with some sensory fibers having their cell bodies in the **geniculate ganglion.** This nerve innervates the muscles derived from the hyoid arch, and the dermal muscles of the face and scalp. The **special visceral sensory fibers** are from the **taste buds** of the anterior two-thirds of the tongue; these pass through the **chorda tympani division** of the nerve. **General visceral sensory fibers** from the submaxillary and sublingual **salivary glands** pass through the hyoid division of this nerve to reach the brain. Motor fibers of the facial nerve also activate the salivary glands.

The **auditory,** or acoustic, **nerve** (VIII) has a **special somatic sensory** nature. The large ganglion of this nerve lies between the otic capsule and the brain; it has vestibular and cochlear divisions. The ganglion receives nerves from the various parts of the inner ear. The neurons of the ganglion are unique in being bipolar, like those of the retina, the nasal epithelium, or the early stages of spinal sensory ganglion.

The **glossopharyngeal nerve** (IX) is associated with the third arch, the first branchial arch. It has motor and sensory components. The sensory fibers are from the posterior part of the tongue and the pharyngeal area; the root ganglion is the **petrosal.** The motor component serves the muscu-

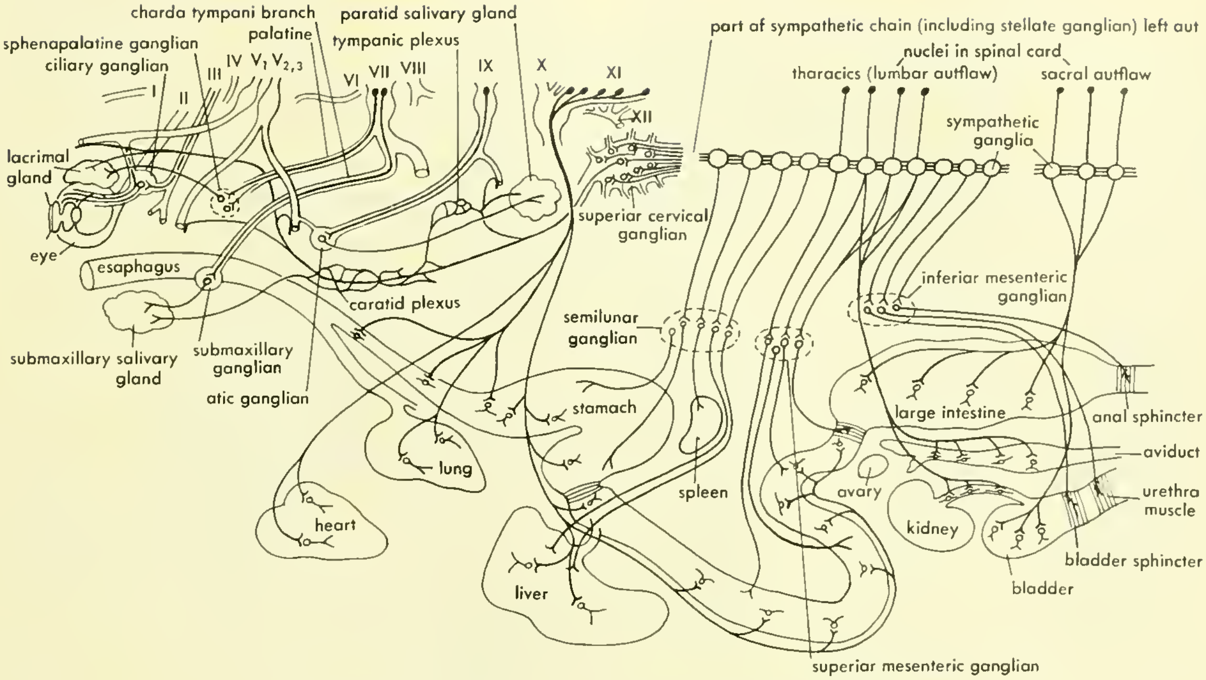


Figure 13-3. Autonomic system of the tetrapod. (After Goodrich, 1930)

lature of the third arch (hyoid), and the parotid salivary gland.

The **vagus nerve** (X) is composed of several components which appear to be comparable to the spinal nerves behind the brain area. This nerve like the facial is largely sensory and, in lower forms, related to the **lateral-line** system, which will be described later. It also has motor components serving the arch muscles of the branchial region. It extends into the body cavity as an element of the **parasympathetic** system supplying most of the visceral organs. The root of this nerve is associated with two large ganglia, a proximal **jugular** and a more distal **nodose** ganglion.

The **spinal accessory nerve** (XI) arises in association with the vagus, and is composed primarily of motor fibers distributed to the muscles of the pharynx and larynx (also the sternocleidomastoid and trapezius muscles). The more posterior roots enter the skull through the foramen magnum. The separation of an eleventh nerve from the tenth appears to be a characteristic of the amniotes.

The **hypoglossal nerve** (XII) arises from a large number of roots of spinal origin. The fibers arise from motor neurons in the myelencephalon and the anterior part of the spinal cord, ventral to the roots of the vagus. The trunk leaves the skull with the vagus and innervates the hypoglossal muscles of the tongue.

The peripheral and autonomic systems The typical segmental nerve is that of the spinal cord. Each has a dorsal root (with a sensory ganglion) and a ventral root. The sensory ganglion is derived from neural crest cells. Processes from these cells grow into the spinal cord, where they synapse, and outward along with fibers from motor neurons of the ventral horn to form the spinal nerve and its branches.

The cranial nerves develop similarly. The motor elements grow out from their nuclei; the sensory ganglia arise from neural-crest cells along with contributions from epibranchial placodes (ectodermal thickenings which sink into the underlying tissues) in the cases of V, VII (including VIII), IX, and X.

The **autonomic** system plays a role in the vegetative functioning (internal maintenance) of the body. It is made up of two basic divisions: **parasympathetic** and **sympathetic** which reciprocally innervate each visceral organ (Figure 13-3). Where one stimulates, the other inhibits. The autonomic system has both sensory and motor elements but primarily consists of the latter. The segmental sympathetic ganglia (housing motor neurons) and the plexuses associated with the gut (cardiac, coeliac, hypogastric) are of neural-crest origin; the crest cells migrate out along the developing spinal nerves. Some of motor elements and the sensory components are of spinal origin. The plexuses of the gut wall (**Meissner's** and **Auerbach's**) arise from cells migrating along the path of the vagus nerve and along other visceral nerves.

Reptiles

The brain of the lizard is quite similar to that of the mammal but has a smooth cerebral surface (Figure 13-4). Histologically the cerebrum is different. The **neopallium**

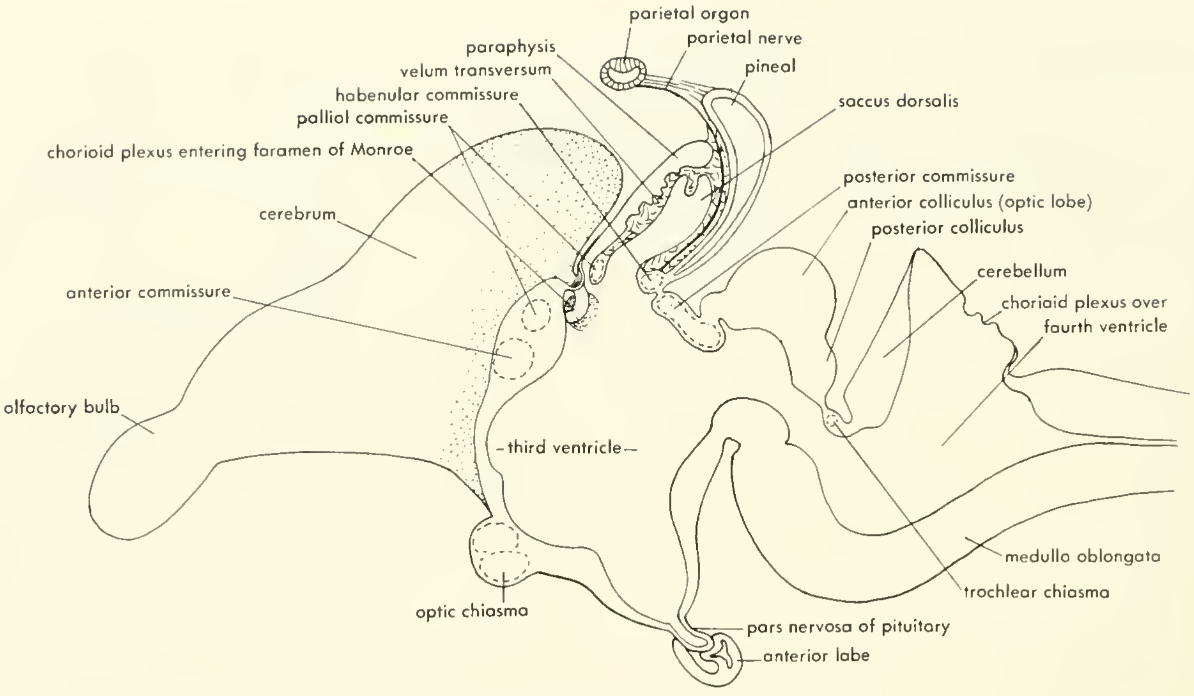


Figure 13-4. Medial view of the right half of the brain of *Lacerta vivipara*. (After von Kupffer)

covering most of the surface of the cerebrum of the mammal is only a dorsolateral band in the reptile (Figure 13-5). The **archipallium** (hippocampal cortex) covers the dorsal and medial aspects, while ventrolaterally there is an extensive **paleopallium** (olfactory area). The pallial commissure is not developed as a corpus callosum. The cerebral lobes are proportionally smaller than in the mammal and the olfactory bulbs project anteriorly from them.

From the extreme posterior part of the roof of the telencephalon, a chorioid invagination occurs which enters the cerebral ventricles and a **preparaphysis** extends upward; behind this is a hippocampal commissure in the **velum transversum.** Behind the velum is an irregularly digitated **dorsal sac,** a **parietal** (parapineal) **eye** on a long stalk, and a **pineal evagination** (epiphysis). The pineal structure is sometimes partly glandular. Both parietal and pineal organs are lacking in the crocodilian but a dorsal sac is present; only a well-developed pineal is present in the bird.

In some lizards and Sphenodon the parietal organ is developed as a light sensitive "eye." There are clear lens cells above, and below are sensory cells which connect through ganglion cells with cells of an external ganglion. The fibers of the external ganglion form a parietal nerve which extends down to the **left habenular ganglion.** The parietal eye is enclosed ventrally by pigment cells and lies in the parietal foramen of the skull, close beneath translucent scales of the skin. In early fossil reptiles the skull has a parietal foramen suggesting that this eye was well developed.

The remainder of the diencephalon is generally like the mammal. The optic nerves decussate completely (only half in the mammal). There is a lateral geniculate nucleus at which a part of the optic nerve fibers synapse with cells connecting with the posterior part of the cerebral cortex (visual area). There is a **massa intermedia** in the turtle but not in the other reptiles or birds.

Behind the diencephalon, nearly in contact with the cerebral lobes, are large **optic lobes.** Behind the optic lobes is a fairly large cerebellum and behind this a medulla with a chorioid plexus in its roof. A pons is present in the bird, and suggested in the turtle.

The cranial nerves of the reptile are like those of the mammal. The **vomeronasal division** of the olfactory, which innervates the **Jacobson's organ,** is distinct in the turtle or lizard, absent in the alligator or bird. Jacobson's organ is an accessory olfactory and taste organ. In addition, there is a **parietal nerve** which, like the optic, represents a brain tract. In some lizards (*Iguana*) there is a pair of parietal nerves entering the right and left habenular nuclei and a pineal nerve entering the posterior commissure on the right. The remainder of the nervous system agrees with the mammalian plan both in its structure and development.

Amphibians

The brain of the amphibian differs from that of the reptile only in the general reduction of the cerebral lobes and cerebellum (Figure 13-6). There are large olfactory bulbs be-

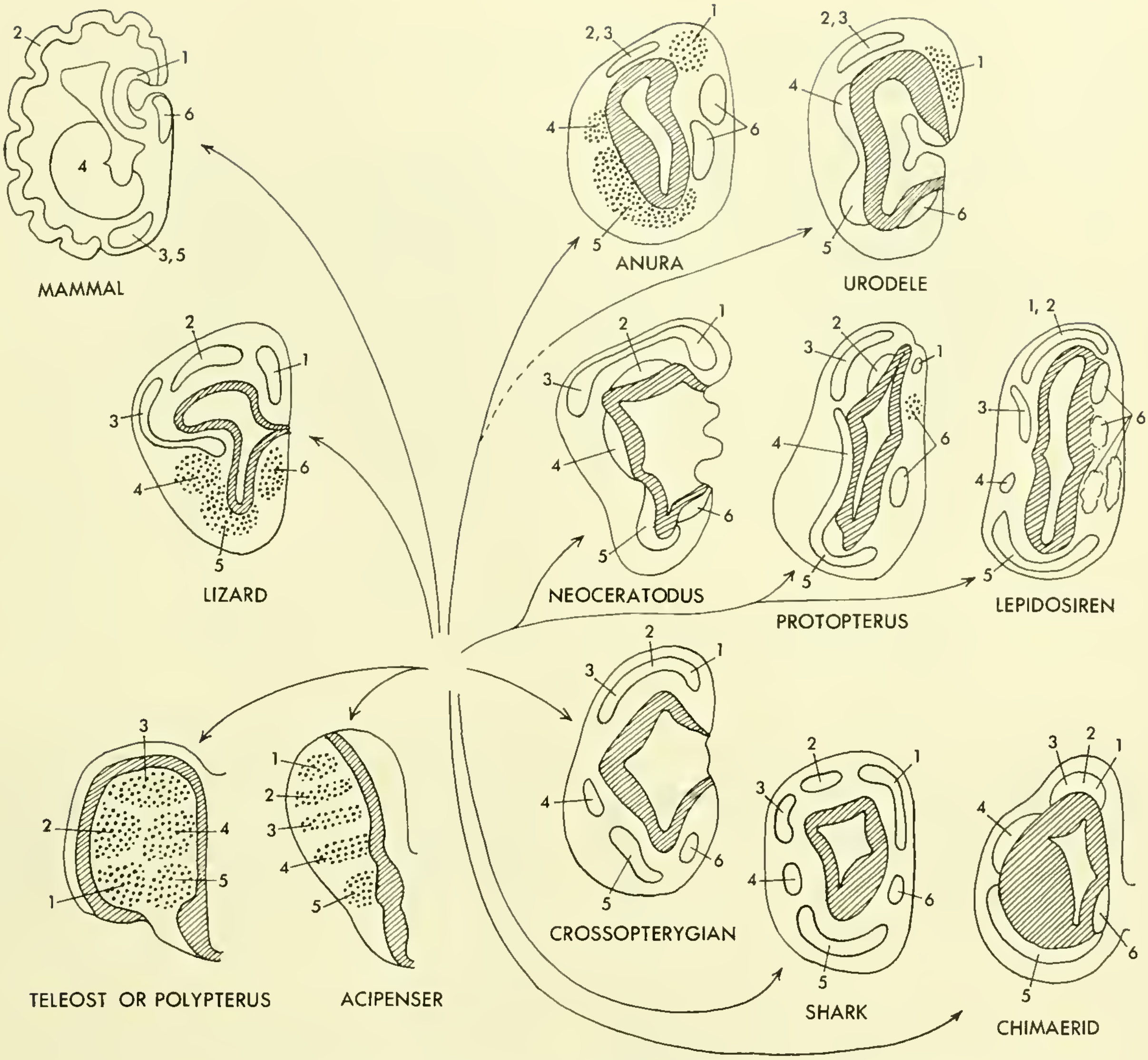


Figure 13-5. Cross sections of cerebral hemispheres of different vertebrates with suggested pathways of evolution. 1, hippocampus; 2, general pallium (neopallium); 3, pyriformis; 4, lateral olfactory nucleus (striate body); 5 tuberculum olfactorium (palaeopallium); 6, septal nuclei; ventricular layer of nuclei cross hatched. (Mainly after Rudebeck, 1945)

fore the cerebral lobes. Basically the cerebral lobes are olfactory lobes, but have incipient higher centers.

The diencephalon has a pineal evagination which generally lacks an eye at its tip; a pineal nerve is lacking. In the frog a pineal eye is present and the pineal sac has in part lost connection with the brain (Figure 13-7). Anterior to the posterior commissure is a saccus dorsalis which in front culminates in a paraphysis. Paraphysis and roof are much thickened as a chorioid plexus from which fingers of tissue extend down into the third ventricle and through the foramina of Monroe into the telencoels. A distinct velum transversum is lacking.

The optic nerves decussate in entering the brain and some fibers of each optic tract synapse at a lateral geniculate nucleus with neurons leading to the cerebrum. The reduced eyes of *Necturus* are reflected by the relatively smaller optic lobes, as compared with the frog.

The amphibian brain is peculiar in having a greatly reduced cerebellum which is no more than a transverse band of tissue anterior to the chorioid plexus in the roof of the medulla.

The cranial nerves of the amphibian resemble those of the preceding groups (Figure 13-8). The seventh has a **superficial ophthalmic branch** in salamanders but not in anu-

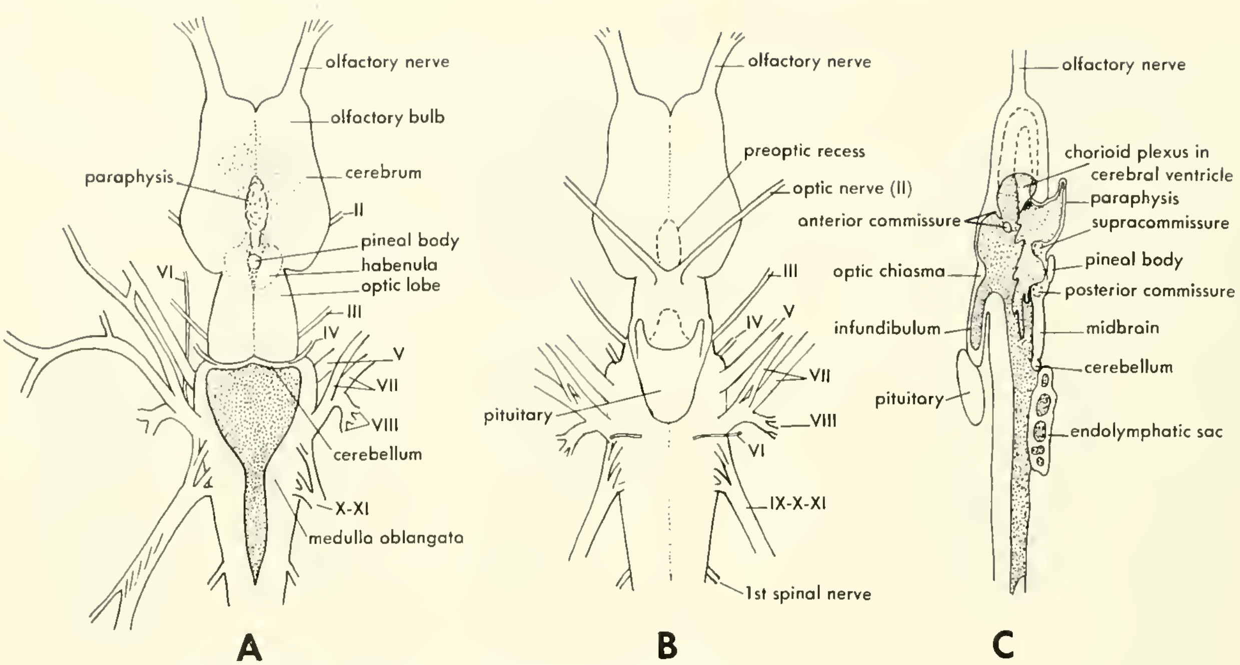


Figure 13-6. The brain and cranial nerve roots of *Necturus*. A, dorsal view; B, ventral view; C, medial view of right half. (In part after McKibbin, 1913)

rans. This branch, along with **buccal** and **mental** branches, serve the sensory lines. The superficial ophthalmic branch of the trigeminal is small or lacking. These branches are comparable to those observed in the fishes and are lacking in the amniotes. Sensory-line branches of the ninth and tenth nerves are also present.

In the mammals, birds, reptiles, and anurans, the trunk of the seventh nerve passes back above the stapes and then down behind that bone. The internal mandibular branch, the **chorda tympani,** passes forward above the stapes (or columella) and then down to the mandible in all of these except the anurans in which it passes forward below this bone. In the urodeles the seventh nerve root passes below the stapes in most salamanders and *Cryptobranchus* (Figure

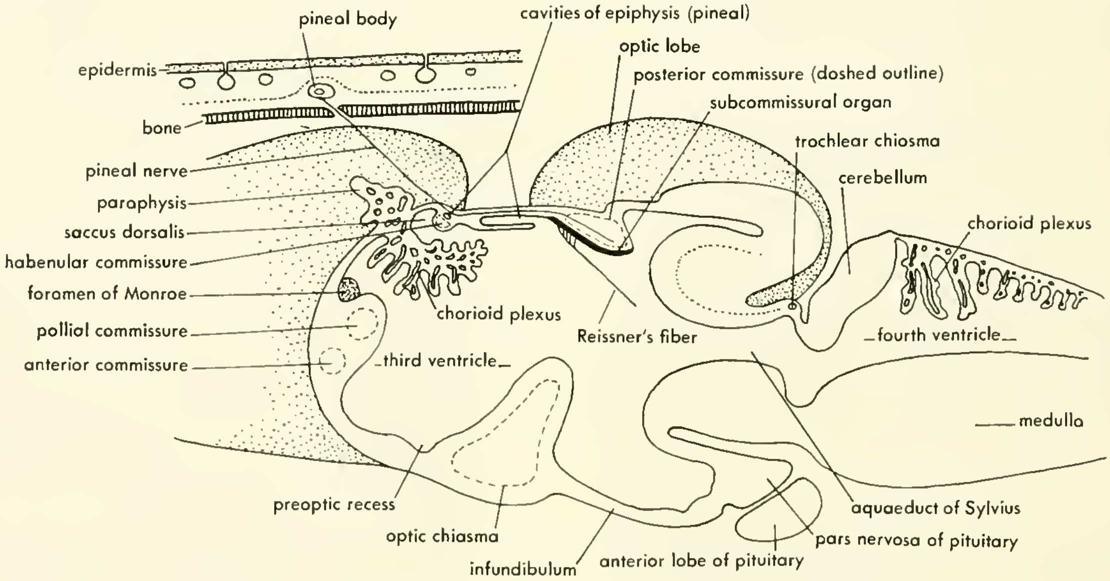


Figure 13-7. Medial view of right half of frog's brain. (In part after Oksche, 1960)

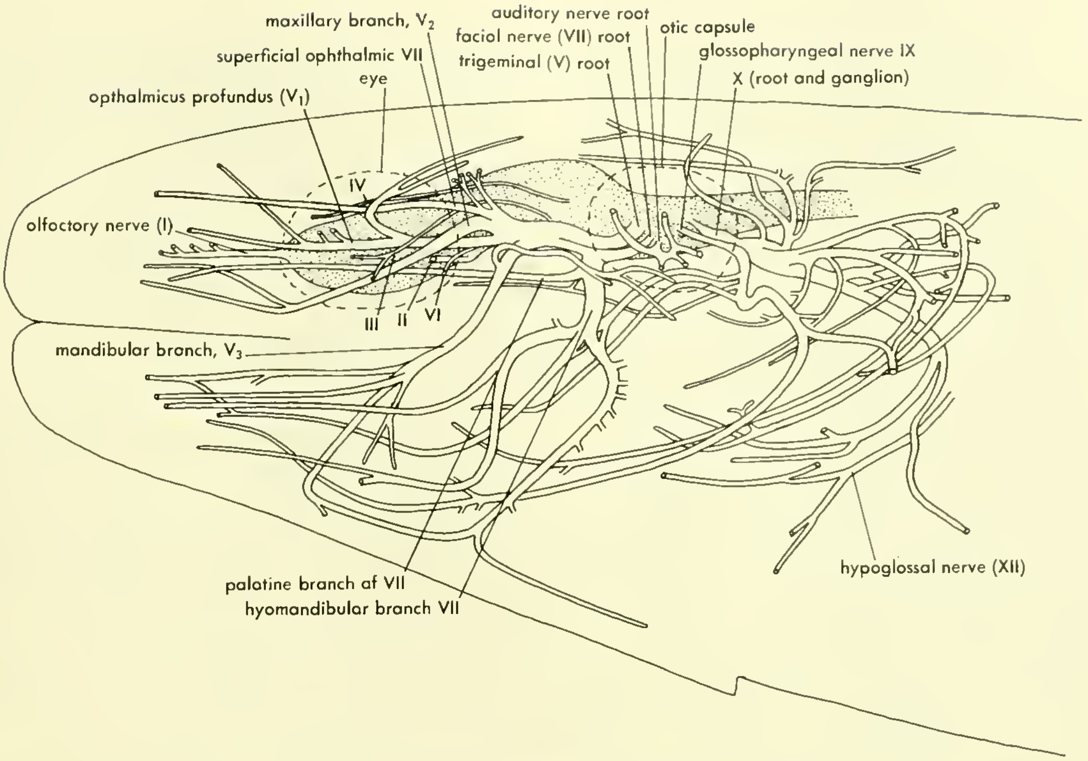


Figure 13-8. Distribution of the cranial nerves of Ambystoma. (In part after Strang, 1895)

4-20) but above the stapes in *Necturus*. The chordae tympani separates anterior to the stapes in *Necturus* and passes below that bone. In the others it separates behind the stapes and passes forward and downward well below the stapes. Explanations of these relationships can be based on changes in position of the tympanic membrane and the middle-ear cavity and on the development of different processes extending outward from the footplate. In the amniotes the middle-ear cavity is not strictly the spiracular pouch but rather a posteroventral diverticulum of that pouch. In salamanders the process of the footplate might be equated with the dorsal process of the columella of reptiles, but it could also be a neomorph in this group.

The first, or the first and second, spinal nerves give rise to the hypoglossal nerve (XII). The spinal accessory is a part of the tenth nerve. However, there is a problem of terminology here; the "vagus" of the amphibian could be identified as the vagoaccessory.

In its development, the brain of the amphibian follows the pattern of the mammal with the exception that only a cerebral flexure develops (the pontine and cervical flexures are only temporary in the mammal).

Choanate fishes

Dipnoan The brain of the dipnoan *Protopterus* is not unlike the amphibian (Figure 13-9). The telencephalon of this group is peculiar in that the olfactory bulbs lie dorsal to the anterior ends of the elongate cerebral lobes. A "preparaphysis" arises from the roof anterior to the velum transversum.

The diencephalon is relatively small with a large saccus dorsalis of chorioid tissue forming its roof. On this is a pineal body, whose stem extends down and back toward the posterior commissure. The habenular nuclei are prominent and lie to either side of the pineal stem. The habenulae are joined by a (superior) commissure. The hypothalamus has slight inferior lobes. The optic lobes are fused to form a single midline mass. The cerebellum is a narrow transverse ridge as in the amphibian.

Neoceratodus is somewhat different in that the cerebral hemispheres are smaller and with membranous dorsal and medial walls. This membranous part forms a thick, folded, glandular chorioid plexus which continues as the roof of the diencephalon. In the young, the dorsal and medial walls of the lobes are nervous, the adult condition is achieved by an eversion suggesting that of the actinopterygian. The optic lobes are slightly separated.

Actinistian The brain of *Latimeria* is distinct from that of the dipnoans. It is extremely small as compared with the cranial cavity (a parallelism to the situation in *Acipenser*); except for the olfactory bulbs it lies entirely behind the dorsum sella, in the occipital part of the skull. The olfactory

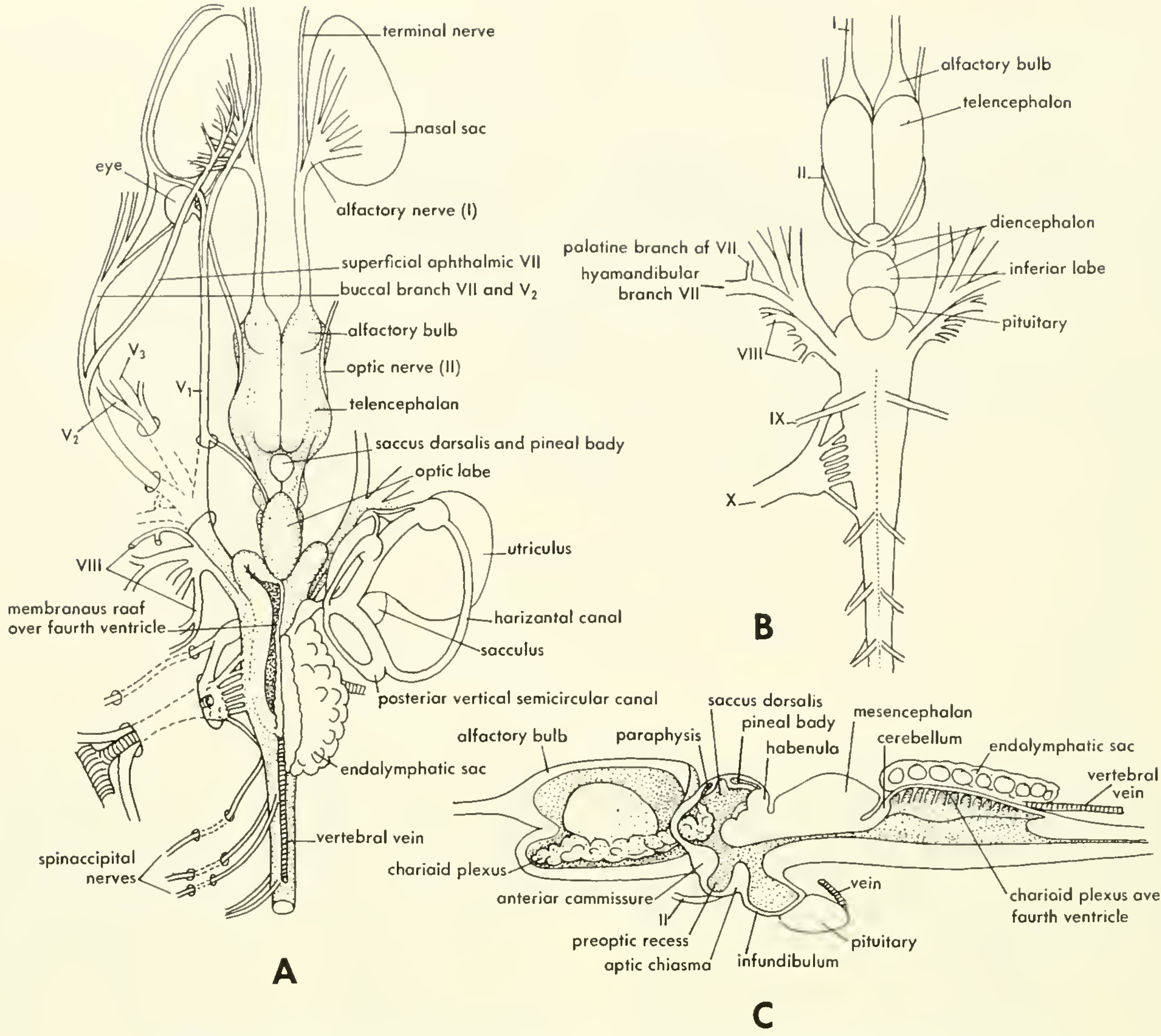


Figure 13-9. Brain and cranial nerve raats af *Protopterus.* A, darsal view with endolymphatic sac and inner ear af right side included; B, ventral view; C, medial view af right half of brain.

bulbs lie in contact with the olfactory capsules and are connected by very long stalks with the rest of the telencephalon. The cerebral lobes have a restricted ependymal septum as in the young of *Neoceratodus.* The diencephalon has a pineal organ above, and an infundibulum with bilateral inferior lobes and a saccus vasculosus ventrally.

The saccus vasculosus is an irregular evagination of the rear wall of the infundibulum above the level of the pituitary and is only slightly developed in this fish. It is perhaps represented by the posterior recess of higher forms. Such a saccus is well developed in actinopterygians and sharks.

The pituitary of *Latimeria* is drawn out anteriorly in the direction of the sella turcica. The optic lobes form a single medial mass behind which is a large cerebellum resembling that of the shark or actinopterygian (i.e. with large facial lobes). The cerebellum lacks a valvula (see under actinopterygian) but has distinct auricles (restiform bodies).

In its cranial nerves, *Latimeria* is thoroughly fish-like. The olfactory nerves are represented by many bundles of fibers. There are well-developed superficial ophthalmic as well as buccal mental and palatine branches of the seventh; the ninth and tenth have typical sensory-line branches. The hypobranchial musculature is served by branches of the first spinals.

Actinopterygians

The olfactory bulbs lie in contact with the rest of the brain in most actinopterygians, but in a few cases (Figure 13-10), they are separated by long olfactory tracts from the cerebral lobes (*Gadus, Ameiurus,* many cyprinids). The olfactory bulbs may be solid and joined at the midline or separate and contain ventricles connecting with the third ventricle (*Acipenser*). Much of the latter lies within the telencephalon. The cerebral lobes are of the everted type, that is, the membranous ependymal plate has been expanded to cover the dorsal and lateral aspects of the large basal nuclei (Figure 13-5). These nuclei are joined by the anterior commissure, which includes the pallial commissure. A small preparaphysis may project upward from the telencephalic roof just anterior to the velum transversum. A velum is not always present.

The diencephalon is much restricted and not apparent from the outside. Dorsally there is a large pineal body joined to the posterior commissure by a pineal nerve. The roof of the diencephalon is evaginated upward as a saccus dorsalis and in part overlies the basal nuclei of the telencephalon. The thalamic walls of the diencephalon extend down and back underneath the optic lobes. The infundibular evagination ends in a large saccus vasculosus. This is a

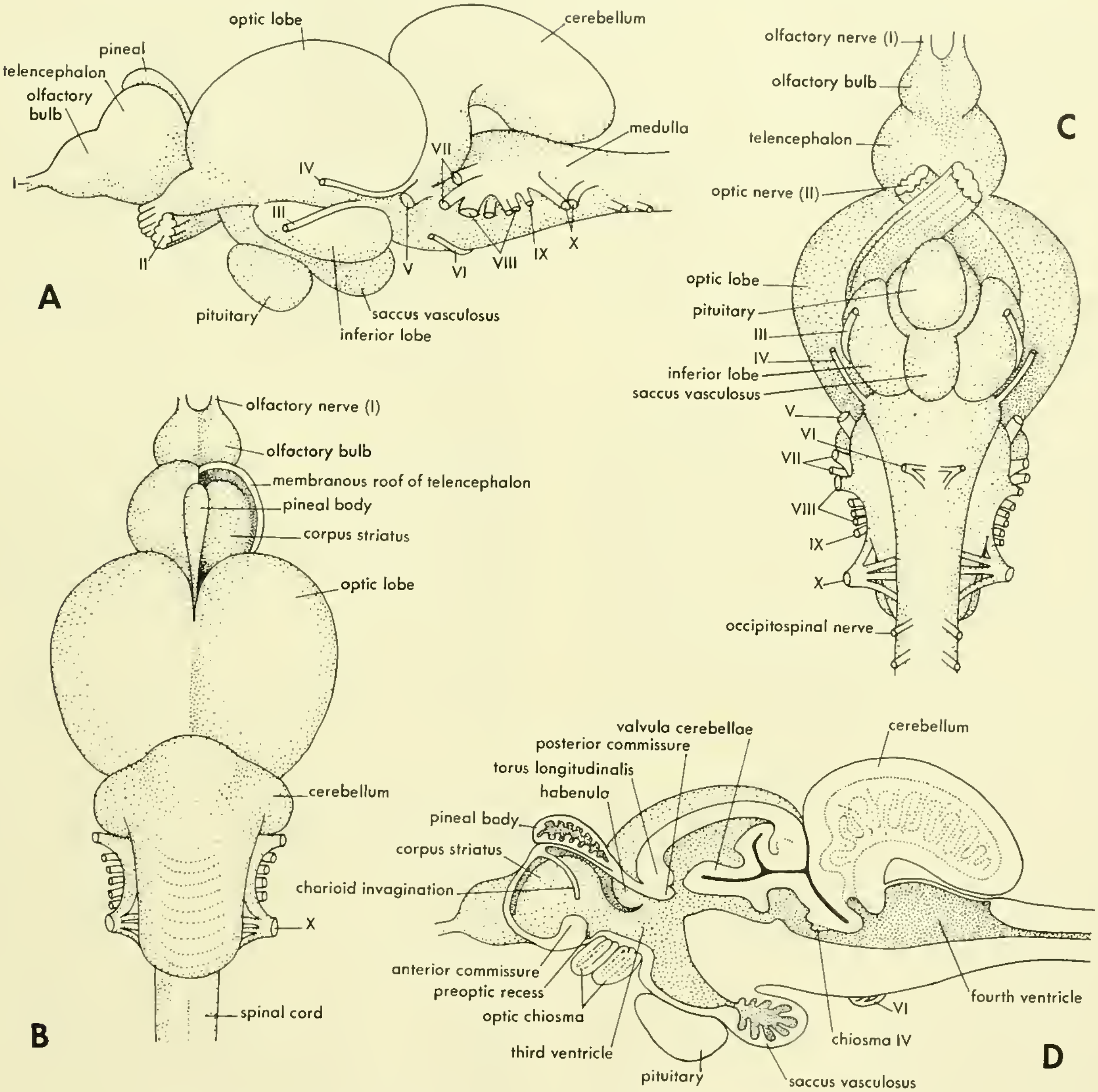


Figure 13-10. Brain and cranial nerve roots of the salmon. A, lateral view; B, dorsal view, membranous roof on right half of forebrain removed; C, ventral view; D, medial view of right half. (After Parker and Haswell)

glandular mass containing peculiar cells which were originally thought to be sensory in function. It is now assumed that they are endocrine. The pars nervosa and the anterior lobe of the pituitary form a large mass lying somewhat anterior to the saccus vasculosus. Dorsolateral to the saccus are the bilateral inferior lobes of the hypothalamus. The optic nerves form a chiasma anterior to the inferior commissure of the thalamus; in this decussation the two nerves cross one above the other: one nerve passing through the other or both nerves interlacing.

The mesencephalon is represented by large paired optic lobes, which are essentially hollow; anteriorly they touch the telencephalon and posteriorly the cerebellum. The mesencephalic brain stem is not distinguished by any particular structures from the rest of the lateral wall and floor. The oculomotor nerve emerges from this part of the stem.

The metencephalon has a large cerebellar mass dorsally. This mass is extended forward as a tongue between the optic lobes; this extension is the **valvula cerebelli.** The valvula is folded upon itself in the salmon and projected into the cavity of the mesencephalon. The decussation of the trochlear nerve passes below the posterior end of the valvula. In the mormyrid fishes the valvula is extended outward above the optic lobes as folded bilateral lobes. These cover much of the brain. The stem portion of the metencephalon is not marked from the rest of the brain stem, but from it arises the fourth and perhaps a part of the fifth nerve.

The membranous roof of the myelencephalon is modified into a chorioid plexus. The vagal lobes are highly developed in some teleosts and may meet above the fourth ventricle, forming a tuberculum impar (*Lampanyctus*). From the sides and ventral wall of the medulla arise nerves V to X. The seventh and eighth nerves are represented by a common group of roots. The tenth has two main roots: one lateral-line sensory root the other a sensory and motor root serving the branchial arches and the viscera. The sixth nerve arises ventrally from the motor part of the myelencephalon. Posterior to these, the spino-occipital nerves and finally the spinal nerves arise. The spino-occipital nerves exit through the cranial wall. The first spinal nerve lies between the skull and the first vertebra.

In the medulla there is a pair of giant neurons called Mauthner's cells. The cell bodies lie at the vertical of the roots of the seventh and eighth nerves near the midline; the axons cross and descend through the spinal cord just below the central canal. These giant fibers are observed in the larvae of salamanders as well as actinopterygians. They function in the coordination of swimming. In the adult of some teleosts these cells are lacking.

It would be difficult to describe all of the many variations of brain pattern observed among the actinopterygians. The most diagnostic feature appears to be the everted telencephalic lobes. Other features are the usual lack of evaginated olfactory bulbs and the occurrence of a valvula projected into the roof or cavity of the mesencephalon. The highly developed cerebellum and medulla is related to the development of the lateral-line system in this group.

The cranial nerves of the actinopterygian are similar to those already observed (Figure 13-11). As in the dipnoans, coelacanths, or the larval amphibians, there is a well-developed lateral-line system. The seventh nerve gives rise to a superficial ophthalmic, buccal, and mental divisions. In the catfish a branch of the seventh extends back on the body to serve the "taste" buds which are scattered over much of the surface of the anterior half of the body. The ninth and tenth nerves have large sensory components. The tenth nerve. which includes the spinal accessory nerve of the higher forms, is here two-parted: one a lateral-line nerve and the other a more typical vagoaccessory nerve. The "hypoglossal nerve" arises from the branchial plexus formed from the first two or three spinal nerves.

It is interesting to note the common origin in development of the seventh and eighth nerves. It is usually assumed that they are parts of a single nerve. In some actinopterygians the profundus division of the fifth is separated from the V_2 and V_3 division (*Amia, Lepisosteus,* and *Polypterus*), suggesting that it is not a part of the trigeminal. A problem of terminology is thus encountered regarding the Gasserian ganglion. Should one refer to Gasserian profundus and Gasserian maxillaris and mandibularis or should both parts receive new names?

Chondrichthyes

Shark The nervous system of the shark, *Squalus,* is typical of this group (Figure 13-12). The olfactory bulbs lie close to the olfactory capsules; the olfactory nerve is made up of many small bundles of fibers entering the bulb directly. The bulb is connected with the cerebral hemispheres by a long olfactory tract. The length of the tract is determined by the elongation of the head.

The cerebral hemispheres are relatively larger than those of teleosts and have thick walls. The third ventricle extends forward for half the length of the telencephalon. Anteriorly the cerebral lobes are joined across the midline, and the lateral ventricles extend anterolaterally into the olfactory bulbs. Within each hemisphere the lateral ventricle expands as a distinct chamber. Posteriorly the roof between the cerebral lobes is membranous and is extended outward as a distinct paraphysis. The posterior end of the telencephalon is marked by a transverse velum above and by the preoptic recess below.

The diencephalon has a membranous roof which is developed as a dorsal sac; the velum transversum gives rise to a chorioid plexus. There is a long, thin epiphysis extending upward from the posterior end of this roof. The epiphysis is attached in the region of the habenulae, which lie just anterior to the posterior commissure. Ventrally there is an optic chiasma and the hypothalamus is drawn out and back as a distinct infundibulum ending in a saccus vasculosus.

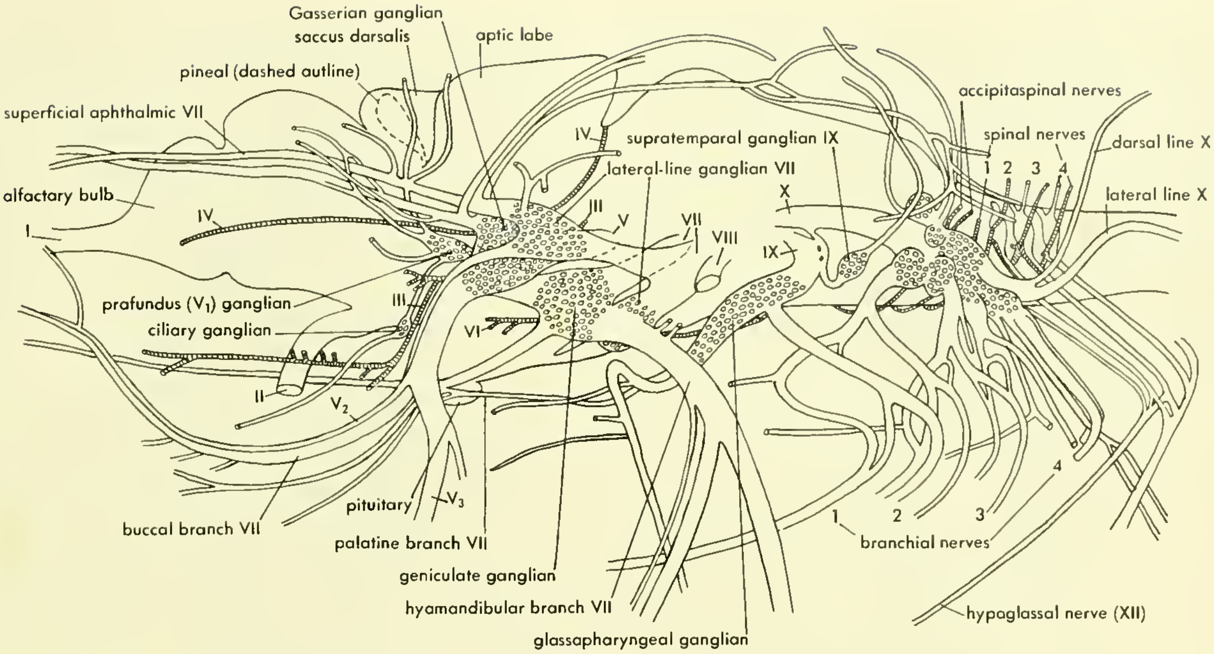


Figure 13-11. Roots of cranial nerves of *Amia*. (After Norris, 1925)

The infundibulum is attached below to the pituitary. In the region just above the saccus vasculosus there are distinct, bilateral inferior lobes.

Behind the diencephalon the optic lobes are large bilateral structures. The floor and the sidewalls of the mesencephalon are thick as in the other groups. The cerebellum is large and has a small cavity (metencoel) extending upward into it and into its various lobes. Posterolaterally there are folded **restiform bodies** which project forward. There is no valvula cerebellae in this group.

The myelencephalon has a large chorioid plexus in its roof with digitations extending down into the fourth ventricle; the lateral walls and floor are not as well developed as in the teleosts.

Holocephalan The brain of *Hydrolagus* agrees in detail with that of *Squalus* differing in that the diencephalon (and part of the telencephalon) is much elongated (Figure 13-13). This modification of the brain is related to the large eyes, whose sockets are separated only by an interorbital septum. The optic lobes are small and the cerebellum is not distinctly divided into bilateral halves. The lateral-line lobes are larger and extend further back. The saccus vasculosus is comparable.

The chimaerid, like the shark (Figure 13-14), has the usual ten cranial nerves, and the number of branches of these is less than in the actinopterygian. The general distribution of these nerves is similar to that in other fishes with the seventh, ninth, and tenth supplying the lateral-line organs. The autonomic system is like that observed in the mammal.

Cyclostomes

Lamprey In the lamprey (Figure 13-15) the olfactory nerves are paired and relatively short. They extend back from the walls of the midline nasal capsule to enter the medial anterior aspect of the olfactory bulbs. These bulbs are the larger part of the telencephalon. Behind each is a small cerebral lobe. The olfactory bulbs and cerebral lobes have small ventricles which connect with the medial third ventricle, a good part of which lies in the telencephalon.

The diencephalon has a membranous roof which is evaginated outward as a large saccus dorsalis. Anteriorly to the saccus is a small paraphysis; on top of the saccus rests a parietal organ and above this a pineal organ. Both of these organs are developed as photoreceptors. The parietal organ has a nerve extending down to the left habenula; the nerve of the pineal organ extends down and back on the right side to the posterior commissure. The anterior end of the diencephalon is not marked by a velum transversum.

Ventrally the optic nerves cross without exchange or interlacing of fibers. The hypothalamus has small inferior lobes and an indistinctly differentiated "saccus vasculosus." The floor of the infundibulum, the pars nervosa, is attached to the underlying anterior lobe of the pituitary.

The mesencephalon has bilateral optic lobes between which is a membranous, evaginated chorioid plexus. This plexus is fused to the plexus overlying the fourth ventricle in the myelencephalon. A small transverse cerebellum and a tapered myelencephalon, much like those of the amphibian, lie behind the optic lobes.

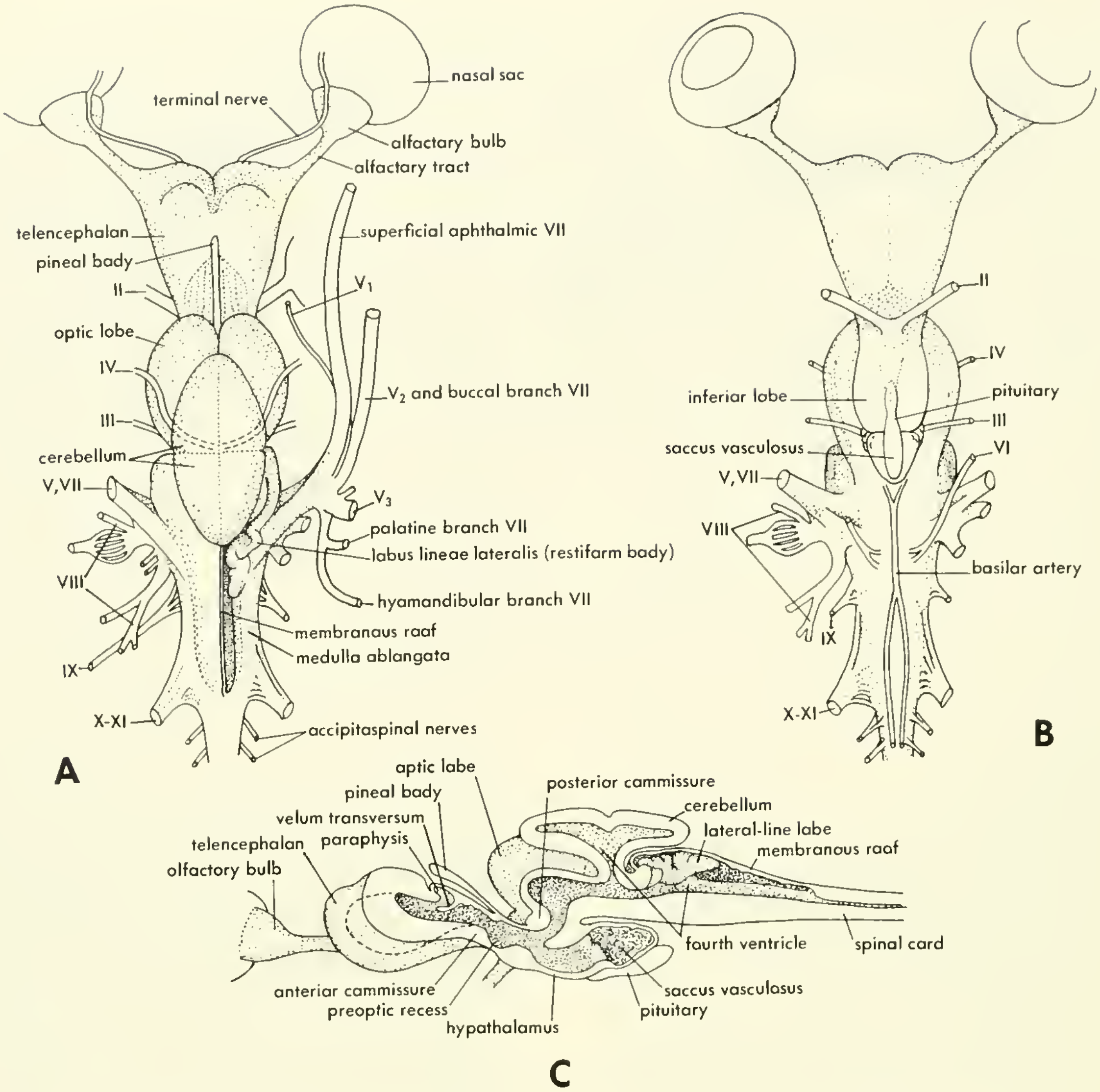


Figure 13-12. Brain and cranial nerve roots of *Squalus*. A, dorsal; B, ventral; C, medial view of right half.

The cranial nerves of the lamprey are in general comparable to those of the gnathostomes (Figure 13-16). The olfactory consists of many fibers. The optic nerves cross without complication; the oculomotor is comparable to that of the higher forms, but the trochlear does not decussate; the nerve of either side goes to the superior oblique muscle of the same side. There is doubt as to whether there is a sixth nerve since the nerve in question comes out along with the fifth and is said to contain at least some oculomotor fibers. The profundus division of the fifth arises from the brain wall independent of the combined maxillary and mandibular branch. Their ganglia are in part separate.

Unlike the other fishes, the lamprey lacks a superficial ophthalmic division of the fifth and seventh nerves, but the lateral-line sensory system is only poorly developed. The fifth and seventh nerves are closely associated, making it difficult to identify distinct lateral-line branches similar to those of other fishes. The seventh and eighth nerve roots are close together and both perforate the otic capsule, the eighth entering the capsule, the seventh passing down through the anterior capsule wall. The glossopharyngeal and vagus are similar to those of other fishes with lateral-line and branchial arch divisions. Each branchial nerve has typical pre- and post-trematic divisions. The vagus also continues into the body as the visceral component of the parasympathetic system.

The hypoglossal nerve is a derivative of the more anterior spinal nerves and as such is like that in other fishes.

The lamprey is of particular interest in the origin of the vagus since there is no indication of missing segments; each somite which appears in the embryo is retained and served by a segmental nerve. The vagus is not developed by the collection of segmental nerves into a single bundle but as a single outgrowth which branches and extends back to all of the branchial arches, behind the hyoid, and back into the body cavity to the gut. The lateralis division grows outward in a similar fashion. The development of the tenth cranial nerve is thus like that of the fifth and seventh. The seventh and tenth roots are joined by a connective outside the octic capsule.

Myxinid The brain of the myxinid is quite unlike that of the lamprey (Figure 13-17). It lacks any chorioid plexus or extensive membranous roofs. This lack is apparently due to late changes in development and is not primitive. The posterior part of the brain (myelencephalon) is large, while the anterior three segments are relatively reduced. From front to back there are paired olfactory bulbs, cephalic enlargements, diencephalic and mesencephalic lobes. The metencephalon cannot be distinguished or is lacking. There is a swelling above the midline groove of the diencephalon formed by the fused anterior and habenular commissures. Behind these is a small epiphyseal evagination. Ventrally

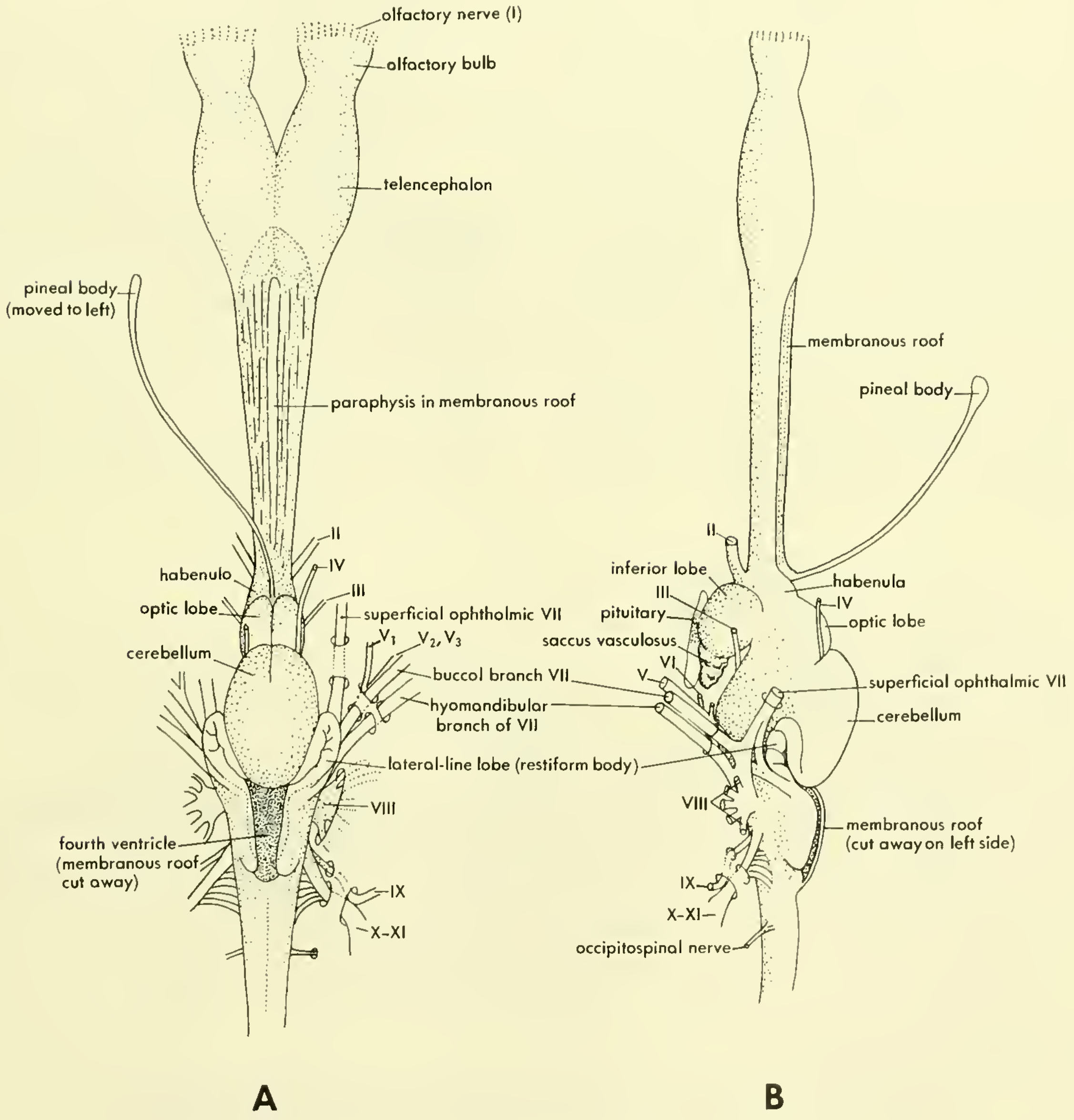


Figure 13-13. Brain and cranial nerve roots of *Hydrolagus*. A, dorsal; B, lateral view.

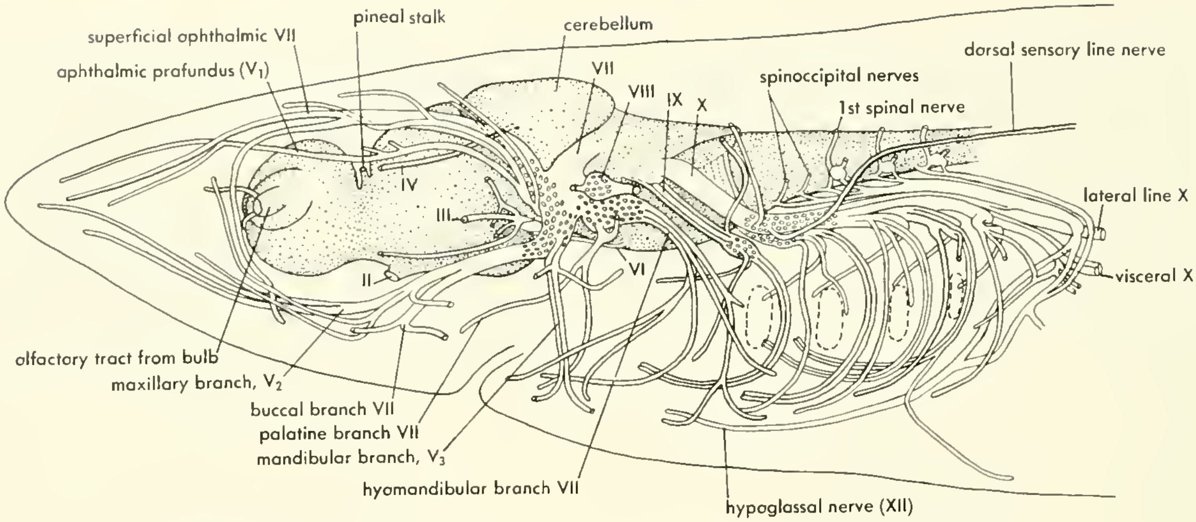


Figure 13-14. Cranial nerve distribution in *Squalus acanthias*. (After Norris and Hughes, 1920)

there is a small infundibulum ending in an undifferentiated saccus vasculosus. There are small bilateral lobi inferiores. The anterior lobe of the pituitary is small and inconspicuous. The pars nervosa of the infundibulum is undifferentiated.

The cranial nerves are like those of other groups with the exception that the three eye-muscle nerves are lacking (the oculomotor, the trochlear, and the abducens) along with the muscles of the vestigial eye (Figure 13-18). The olfactory nerve is represented by a large number of bundles passing directly from the wall of the nasal capsule into the olfactory bulb. The olfactory bulbs and cerebral lobes have narrow ventricles connected by equally narrow passages (foramina of Monroe) with the restricted third ventricle. The optic nerves are very small and cross within the substance of the diencephalon, which appears to extend forward beneath the telencephalic lobes to touch the olfactory bulbs.

The fifth nerve has a number of branches which correspond only partly to the branches observed in the gnathostomes. The seventh nerve is small and quite separate from the fifth; it can be presumed that fibers from the seventh pass out through the divisions of the fifth nerve. The eighth

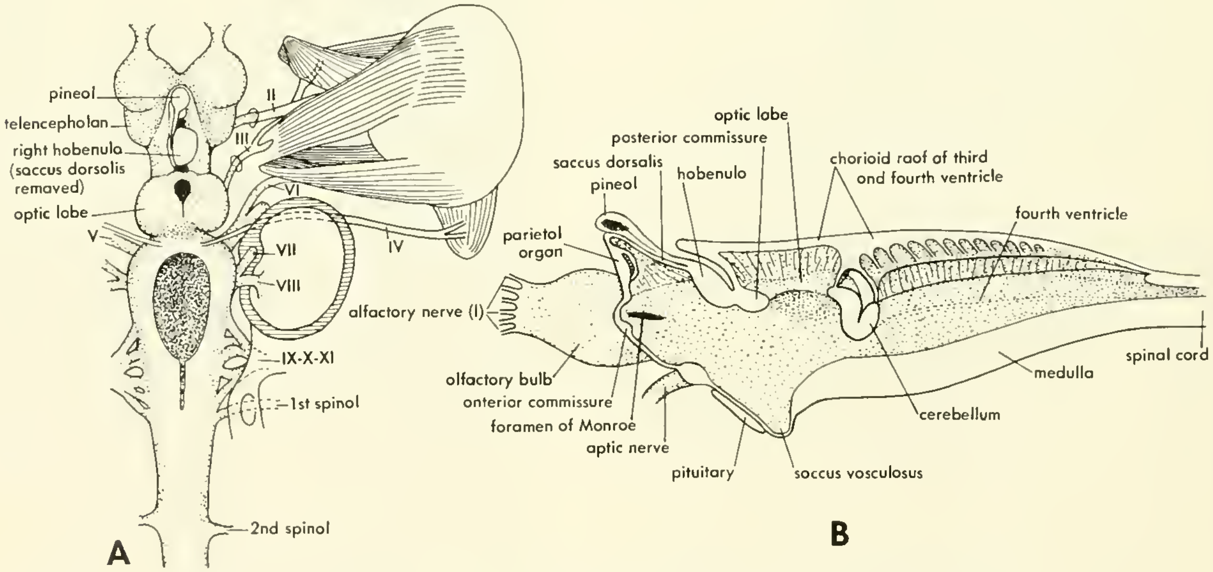


Figure 13-15. Brain and cranial nerve roots of the lamprey. A, dorsal view including, on the right, the eye and its musculature and the ear capsule; B, medial view of right half of the brain.

nerve comes out of the brain stem as two distinct parts below the root of the seventh. The ninth and tenth have a common root but soon branch.

The spinal nerves each have dorsal and ventral roots in contrast to the lamprey where a dorsal root nerve is separate from a ventral root nerve. The decision as to which of these situations is the more primitive is based on the condition in Amphioxus, where there are separate dorsal and ventral root nerves which alternate with each other. The spinal nerves of the lamprey have visceral motor fibers in the dorsal root nerve. Presumably this is also the case in the myxinid and in most fishes.

General observations

Since the head shows a certain amount of segmentation in having muscular somites, it has been assumed that the cranial nerves are in fact only highly modified nerves similar to the spinal nerves. The separation of motor and sensory divisions is not unlike the primitive spinal condition.

Various attempts have been made to count the number of segments in the head and to associate with these parts of the cranial nervous system. These attempts are summarized in Table 31-1. Opinions vary as to the number of preotic segments: ranging from three segments in the case of Young

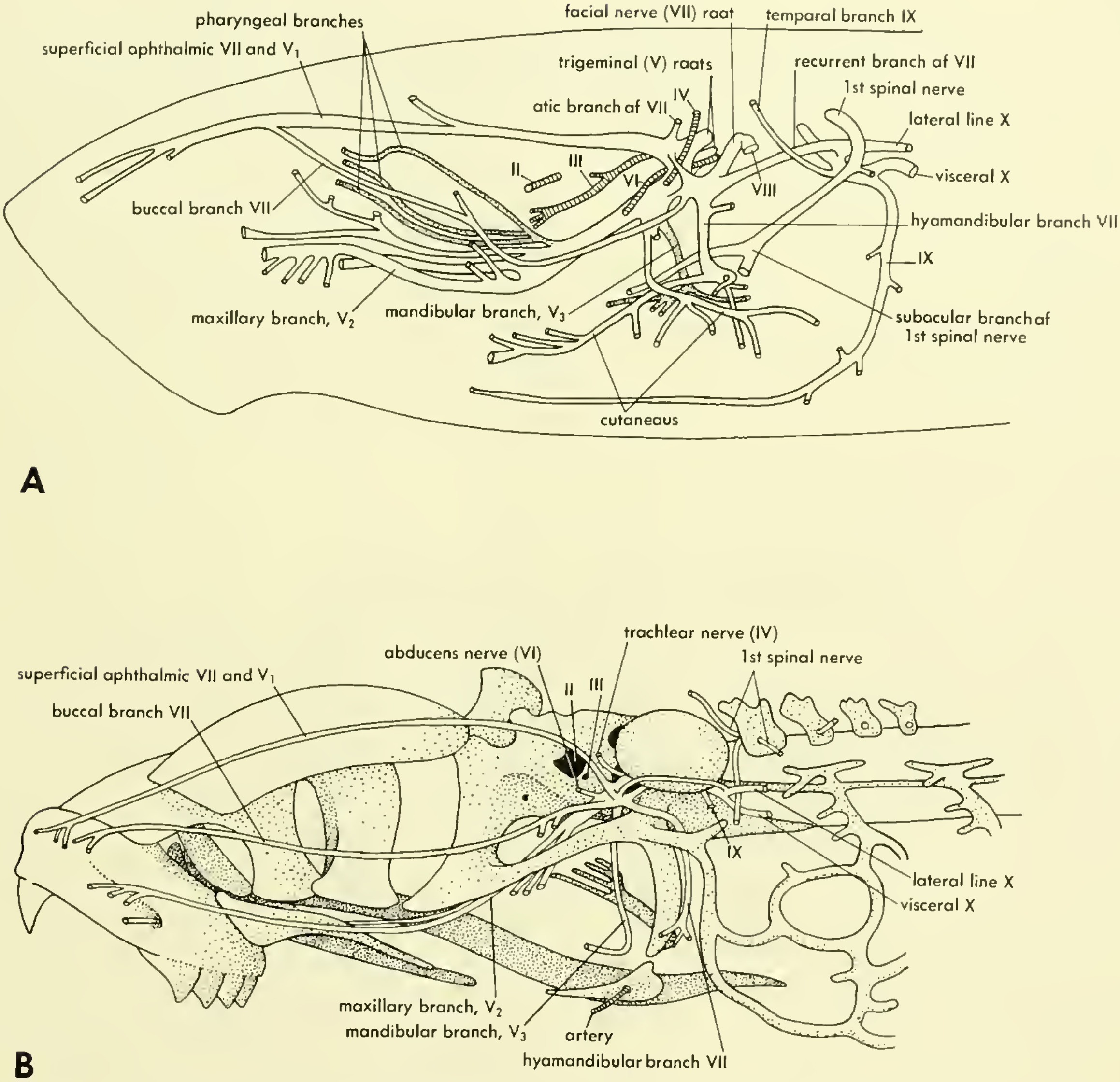


Figure 13-16. Cranial nerve distribution in the lamprey. A, nerves; B, nerves in relation to head skeleton. (A after Lindström, 1949; B After Marinelli and Strenger, 1954) (For skeletal elements see Figure 5-24 B, p. 129)

TABLE 13-1 THE NUMBER OF SEGMENTS IN THE HEAD AS INDICATED BY ARCHES, NERVES, AND MYOTOMES*

		Gegenbaur (1871)		Marshall (1881)			van Wijhe (1882)		
		Arch	Nerve	Somite	Eye Muscles	Nerve	Somite	Nerve	Eye Muscles
preotic segments	5								
	4	labial 1				I	1	V_1–III	rectus superior rectus inferior rectus internus obliquus inferior
	3	labial 2	V_2	1	(4 eye muscles)	III, IV	2	V_2, V_3–IV	superior oblique
	2	mandibular	V_3	2		V	3	VII, VIII–VI	rectus externus
	1	hyoid	VII	3	(rectus externus)	VII–VI	4	VII, VIII	
POSITION OF OTIC CAPSULE									
postotic segments		1st branchial	IX			IX	5	IX	
		2nd branchial	X			X	6	X–XII	
		3rd branchial	X			X	7	X–XII	
		4th branchial	X			X	8	X	
		5th branchial	X			X	9	X	

* Dorsal nerve roots lie to the left of the hyphen, ventral roots to the right.

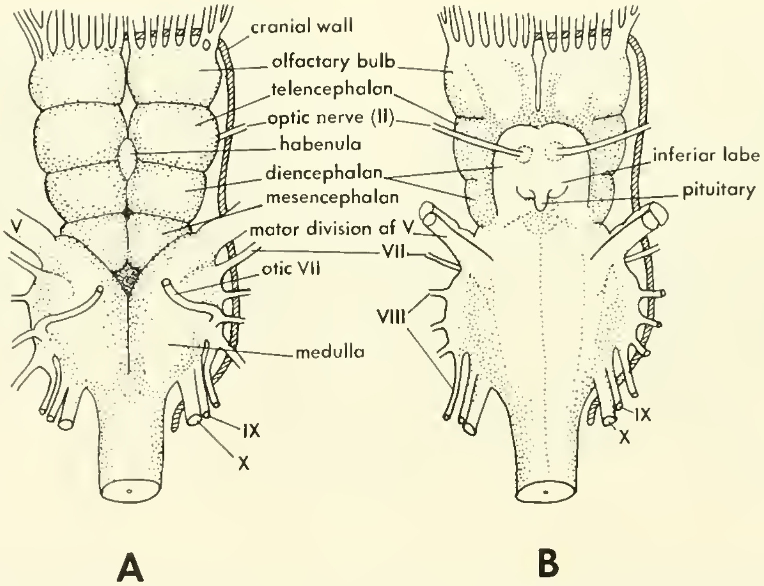


Figure 13-17. Brain and cranial nerve roots of *Eptatretus*. A, dorsal view; B, ventral view. (After Worthington, 1905)

TABLE 13-1 (continued)

Beard (1885) Nerve	Young (1950) and Others Arch	Nerve	Eye Muscles		
I				5	preotic segments
-III				4	
V–IV	premandibular	V_1–III	rectus superior, inferior, internus, obliquus inferior	3	
VII–VI	mandibular	V_2, V_3–IV	superior oblique	2	
VII	hyoid	VII, VIII–VI	rectus externus	1	
VIII	POSITION OF OTIC CAPSULE				
IX	1st branchial	IX			postotic segments
X	2nd branchial	X, XI–XII			
X	3rd branchial	X, XI–XII			
X	4th branchial	X, XI–XII			
X	5th branchial	X, XI–XII			

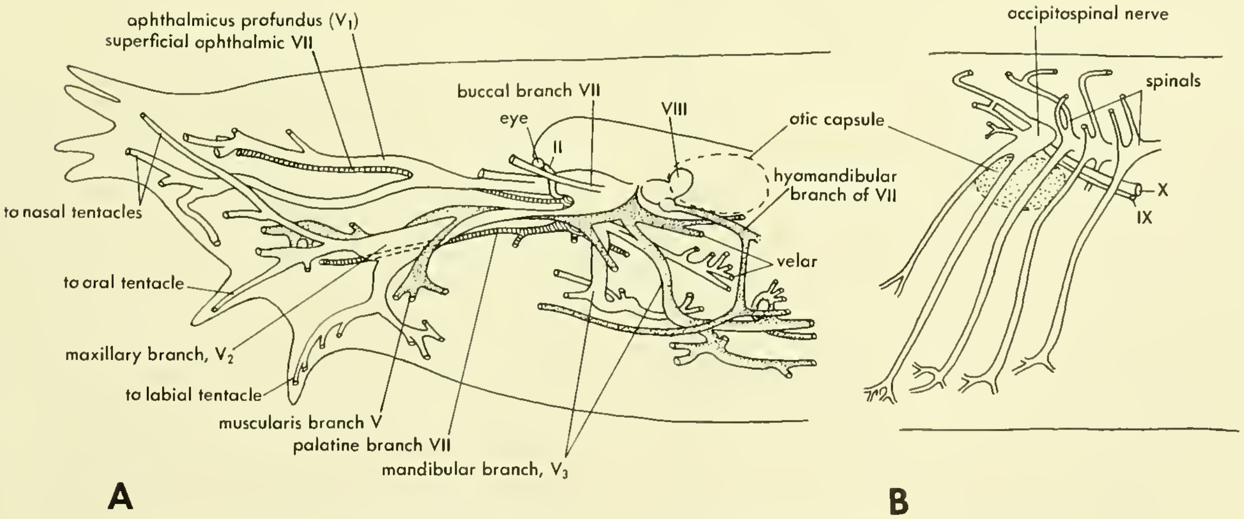


Figure 13-18. Distribution of cranial nerves in *Myxine*. (The spinoccipital and anterior spinal nerves are shown in B to reduce crowding in the otic capsule region.) (After Lindström, 1949)

to five in the case of Beard. The current view is that there are three corresponding to the three somites.

The neuromeres observed in the development of the brain have been used in this connection; their number is presumed to equal the number of somites. However, the cranial nerves do not have a simple one-to-one relationship with these (for example, the abducens of the shark has its nucleus in neuromeres 5 to 7). Further, neuromeres are more conspicuous in the higher forms than in the lower forms. At best it is difficult to associate these with other structures.

In reviewing the materials on the conducting portion of the nervous system, agreement among the gnathostomes is marked while the variation between the two cyclostomes is exceptional. The case of the agnaths can be accounted for on the basis of the great length of time assumed to separate these two branches of the agnath fishes, a period of separation which may exceed the total length of time involved in the radiation of the gnathostome fishes. On the basis of agreement of agnath and gnathostome types of brains, we can assume that five divisions, or six if one choses to identify the olfactory bulbs as a separate one, were established before separation of these two lines. Similarily the formation of the multisegmental fifth, seventh, and tenth nerves preceded this separation.

SENSORY ORGANS

The nervous system is associated with a number of highly developed organs of which the nose, eye, and ear are the most obvious. Less obvious are the Jacobson's organ associated with the nose, the lateral-line system of the fishes which is closely related in function to the ear, and the various chemical senses, which may be related to the nose. Organs capable of temperature evaluation are present in some animals. Within the body are other sensory structures used in proprioception. These usually involve single cells or aggregations of cells around a sensory ending.

Nasal structure in tetrapods

Bilateral nasal structures are developed in all of the vertebrates. In the cyclostome fishes there is a single midline nasal sac in the adult. This arises from a single placode in which bilateral invaginations appear and then join. Two olfactory nerves, as areas of fibers, also indicate the bilateral nature of this structure.

The nasal organ arises in embryology from an epidermal placode on either side which invaginates into the snout to form a vesicle. This has a single opening to the exterior. The single opening to the exterior is variously divided into external and in some cases internal nasal openings.

It has been suggested that the reptile represents the more primitive style of nasal passage observed in living forms of tetrapods. In this group the nasal sac becomes elongated to form a groove, one end of which opens on the outside of the mouth margin and the other on the inside of the mouth (Figure 13-19). The margins of this groove meet in the middle section to form the jaw margin and separate an external and an internal nares.

In the mammal the course of events is somewhat different; the groove closes throughout its posteroinner half, leaving only an external naris. This closure produces a bucconasal (oro-nasal) membrane in the position of the internal naris which later ruptures. In the Echidna, development is reported to be as in the reptile.

In certain amphibians the posterointernal half of the groove closes and becomes a strand of tissue, with or without a lumen. If the lumen is present, it secondarily comes to open into the mouth as the internal naris; if the lumen is not present, a cavity develops from the outer end of the strand into the mouth, thus secondarily producing the internal naris. Whether the development is direct from a groove or whether it involves secondary opening into the mouth does not seem to be particularly important, although it may be interpreted as two quite different ways of development.

The origin of the lacrimal duct in tetrapods appears to be much alike in the different groups. A nasoptic furrow extends from the nasal opening to the eye, but the nasolacrimal duct is not formed directly from this structure. In man it appears first at the eye and extends along the course of the furrow to the nasal capsule. In the frog the middle part of the duct appears first as a solid strand which extends and tubulates in either direction. It is probable that originally the nasoptic groove gave rise directly to the lacrimal duct.

It has been suggested that the dipnoans are basically different from the amphibians in their nasal development. Their nasal openings have been compared with the two external openings of the osteolepiform crossopterygian rather than the external and internal openings of the tetrapods. The entire question of the evolution of the upper jaw of the dipnoan must be more thoroughly understood before its nasal development can be properly assessed.

In the actinopterygian the opening of the vesicle is divided into anterior and posterior outer openings. The anterior one is valved so that water flows into it, through the chamber and across the olfactory organ, then out the posterior opening. Water flow is produced by forward motion of the fish, by action of the ciliated lining of the capsule, or by compression of the nasal chamber with respiratory movements.

In the shark there is a single opening partly divided by a flap into anterior and posterior openings. In the rays and *Chimaera* the flap leads from the nasal opening back to the mouth (Figure 13-29).

In the wall of the nasal passage of the mammals, turbinals develop and there is a restricted area of olfactory epithelium dorsally. The cells of the sensory epithelium give rise to fibers which extend into the olfactory bulb of the brain where they synapse with olfactory tract neurons. This general picture applies to amniotes generally. The Amphibia

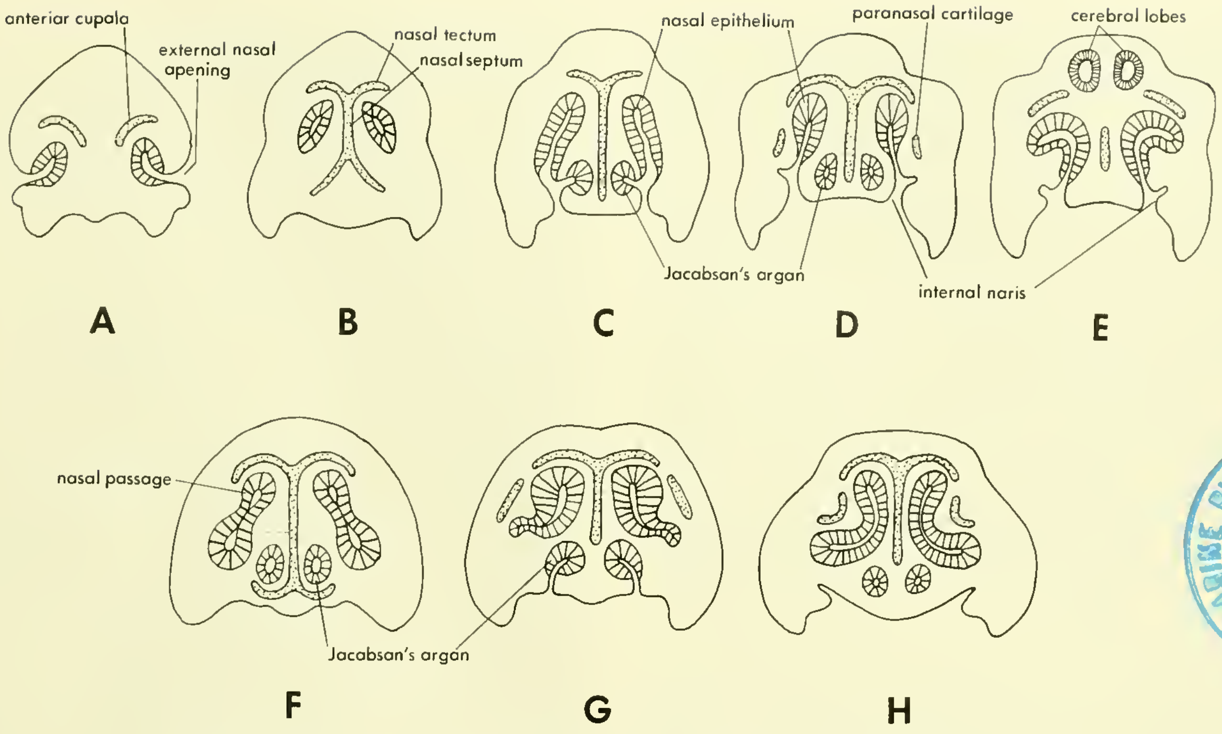


Figure 13-19. Two stages in the development of the nasal passage and Jacobson's organ in the lizard. A to E, serial sections through embryo of 4-mm head length; F to H, serial sections of embryo of 4.5-mm head length. (After Bellairs, 1950)

lack turbinals. In the fishes including the dipnoans and *Latimeria,* there is a highly developed olfactory organ—usually a rosette of folds extending into the nasal chamber.

The development of the olfactory sense varies; some animals have it highly developed, while others do not.

Jacobson's organ

Tetrapods Jacobson's organ is found in all tetrapods and is associated with a distinct **vomeronasal nerve,** a division of the olfactory nerve, and an **accessory olfactory bulb** within the olfactory bulb.

In the amphibians a groove or pocket, the **lower blind sac,** in the lateral or anterolateral wall of the nasal chamber has an area of sensory epithelium which is identified as the Jacobson's organ. Typically Jacobson's organ, and its pouch, lies medially (Figure 13-19); the position in the amphibian appears to be the results of rotation of the nasal chamber during development. The olfactory sensory epithelium lines much of the dorsal, medial, and ventral walls of the nasal passage. Throughout this sensory area there are many flask-shaped **Bowman's glands,** or glandulae olfactoriae. The sensory epithelium of the Jacobson's organ lacks these glands.

An accessory olfactory bulb is present in amphibians, but this lies dorsolaterally (*Hypogeophis*) or ventrolaterally (*Rana*) to the posterior end of the bulb, whereas in amniotes it is usually located posteromedially—dorsally in turtles and most mammals, dorsolaterally in two shrews (*Blarina* and *Scalopus*). Among the Amphibia, a distinct vomeronasal nerve has been reported only in *Rana.*

In the turtle the ventral or anteroventral part of the nasal passage, ventral to the olfactory chamber, has areas of sensory epithelium served by a vomeronasal (medial) division of the olfactory nerve. In other reptiles a pocket forms in the ventromedial wall of the nasal pit well before the nasal processes separate the external naris from the internal choana.

The anlage of this organ disappears in the crocodilian, and in birds, but in Sphenodon and the squamates (lizards and snakes) it enlarges to form a tubular or spherical pocket in the medial nasal wall. In squamates the duct of this pocket moves down and eventually comes to open separately into the mouth; it retains its embryonic relationship in Sphenodon.

In mammals this organ is always present in the embryo but may be lacking in the adult (man, bats, and whales); when present it is associated with the **nasopalatine duct** (incisive or Steno's duct). In rodents and rabbits this organ opens into the nasal passage, not into the mouth. Bowman's glands are present in the olfactory epithelium but absent in Jacobson's organ—this is always the case in amniotes.

Dipnoans and other fishes A rudimentary accessory olfactory bulb is seen in the dipnoan *Protopterus,* but is apparently lacking in the shark or actinopterygian. A lateral diverticulum from the nasal sac has been observed in *Lepidosiren* and *Protopterus* which resembles the structure of the urodele. This diverticulum lies dorsolaterally. In *Protopterus* there is a medial diverticulum which appears early and is innervated by a distinct division of the olfactory nerve. Later both lateral and medial walls have become folded. The olfactory nerve has a bundle of fibers which might represent the vomeronasal nerve.

It has been suggested that the ventromedial recess of the nasal cavity of *Eusthenopteron,* and the osteolepiform crossopterygians in general, corresponds to the Jacobson's organ of the frog. Such a recess is lacking in the porolepiform crossopterygians which have been assumed to be forerunners of the urodeles.

The nasal sac of *Salmo* arises from two parts, the medial area of which may correspond to the organ of Jacobson. In the fishes the olfactory epithelium lacks Bowman's glands but has mucous cells.

Taste buds

The sensory cells of the taste buds are similar to those of olfaction. Taste buds occur in fishes not only in the mouth but on the lips and even over the surface of the head. In some of the teleost fishes, taste buds occur over much of the anterior part of the body (*Ameiurus*). These organs do not show any particularly useful feature for comparative study. They present one interesting facet, that of entodermal origin in the pharynx and ectodermal origin outside of the mouth.

The eye

The eye of the vertebrate shows a basic plan in its structure and in its development. The main variations are related to method of accommodation or focusing.

The mammal eye In its development the eye begins as an outgrowth of the brain wall. This invagination forms an optic vesicle and then a cup which is notched ventrally as a chorioid fissure. The cup induces the formation of an ectodermal lens placode which invaginates and cuts off from the overlying ectoderm. The development of the optic cup induces the condensation of mesenchyme around it to form the outer coats. Mesenchyme enters its inner cavity to give rise to the vitreous body.

In the fully formed eye the lens is a solid, relatively transparent structure composed of fibrous cells; their long axis is roughly parallel to the line of light transmission. The lens is suspended by ligaments from a ciliary apparatus formed mainly of mesodermal tissue. The iris is formed from the margin of the optic cup which extends in front of the lens. Mesoderm is attached to its outer surface and gives rise to the smooth radial and circular muscle fibers.

A fluid chamber forms in front of the lens, and the iris extends into this. The vitreous body, which has a few cells associated with the fibrous material, fills the eye behind the lens. This posterior chamber is lined behind by the retina, the inner layer of the optic cup. Outside the retina is the chorioid coat formed from the outer layer of the cup. The whole eye is enclosed by sclera derived from the mesenchyme or mesoderm surrounding the cup.

The optic nerve is formed from the fibers of the inner ganglion cells of the retina; these fibers converge toward the area of the chorioid fissure and follow the underside of the optic stalk to the brain.

Early in the development of the eye there is a hyaloid artery supplying the vascular tunic of the lens. The hyaloid artery passes through the chorioid fissure along with the optic nerve. Later it sends branches to the retina, becoming the central retinal artery; the vessel to the lens disappears leaving the hyaloid canal through the vitreous body. The chorioid fissure closes except for the area of penetration of the nerve and artery. Later the optic stalk disintegrates forming glial cells associated with the optic nerve.

Mechanisms of accommodation vary. The ciliary body of most mammals has circular as well as radially arranged muscle fibers. Accommodation may involve contraction of the ring and radial muscles by pulling in the direction of the lens, thus reducing the tension in the suspensory ligaments and allowing the lens to round up through its own elasticity. Thickening of the lens focuses near objects. In the horse, movement of the head or the eye in its socket shifts the image to different parts of the retina, which, because of the shape of the eyeball, are nearer or farther from the lens.

The eye of other vertebrates Within the vertebrates there are variations in eye structure but not eye origin. In the myxinid the eye is degenerate and buried beneath several layers of muscle. The eye consists of little more than a retina enclosed by some chorioid cells, and there is no lens. The optic nerve is very small. The muscles of the eye are lacking as are their nerves.

In the lamprey, the eye is much the same as in the other vertebrates; it lies in a socket formed of blood and lymph spaces and has well-developed muscles. The eye is firmly attached to the rim of the orbit but not to the overlying skin, the conjunctiva. Focusing is effected by a body-wall muscle, lying behind the eye, which inserts on the hind margin of the cornea. The pull of this muscle flattens the normal curvature of the cornea and pushes the lens inward.

In the fishes there are other devices for accommodation which are quite distinct from the ciliary apparatus of the mammal. In teleosts a **falciform process** extends upward from the floor of the retinal chamber. This has a small **retractor lentis muscle** extending from its outer end which pulls the lens backward to focus far objects. The lens is supported by a **dorsal suspensory ligament.** In the sharks the lens is pulled forward to focus near objects by a small ventral muscle in the position of the ciliary body. Amphibians are generally like the shark; the frog has both dorsal and ventral muscles for moving the lens forward.

In reptiles and birds accommodation is peculiar in that the muscles of the ciliary body are only radially disposed and appear to act, in conjunction with the scleral ring of bones, in changing the shape of the eyeball and thus its accommodation. In the bird the ciliary muscles are cross striated and are divided into a main portion, **Crampton's muscle,** extending from the margin of the cornea back to the middle of the inner surface of the sclerotic ring of bones, and into **Brücke's muscle,** arising outside the Crampton's fibers and extending back to the outer rim of the fibrous ciliary zone. Contraction of Brücke's fibers releases the tension on the ciliary body (replaces circular muscles of mammal), while contraction of Crampton's muscle acting on the sclera at either end changes the shape of the eyeball, thus increasing the focal distance behind the lens, moving the lens forward, and causing the cornea to be more rounded (forced out medially and drawn in marginally). These changes focus near objects. In most birds the lens is firm and inelastic, and it is enclosed marginally by a soft annular ring of tissue. There is no way that the shape of the lens can be changed by action of the ciliary muscles. In the cormorant the lens is soft and elastic, and its shape is altered by constriction of the iris. This constriction supplements the accommodation effects of the ciliary muscles.

The eye of the bird has an elaborate **pecten,** a comb-shaped vascular fold of tissue, extending into the vitreous body from the area of the chorioid fissure. This appears to help in detection of moving objects and in orientation in reference to the sun. The retina also has one or two **foveas** for detailed vision. A fovea and conical pecten are present in some lizards.

The variations in accommodation suggest that no intrinsic device was present in the primitive eye. In some specialized forms the eye may be degenerate or lost. In the process the eye muscles with their nerves disappear first and then finally the eyeball itself.

Median eyes

It has been assumed that there are anterior and posterior "epiphyseal" outgrowths of the diencephalic roof with eye-like or glandular tips. In the lamprey the sensory tip of the dorsal, ("posterior") vesicle, the **pineal,** has a nerve which enters the **posterior commissure;** the lower ("anterior") vesicle, the **parapineal** or **parietal,** has a nerve which enters the **left habenula** (Figure 13-15). In the Australian lamprey *Geotria,* the vesicles are side by side and the nerves enter the right and left habenulae. In the Australian species *Mordacia mordax,* the parapineal is missing. Both vesicles are lacking in the myxinid.

The embryology of these vesicles in the lamprey shows that the pineal arises in association with the right **habenular ganglion** (10-mm stage); its connection with the posterior commissure at the midline is secondary. The parapineal has a similar relationship to the left habenula, which it retains.

In teleosts the nerve of the sensory organ enters the posterior commissure, and therefore the vesicle is assumed to be a posterior one. This is supported by the observation that in the course of development an anterior diverticulum appears briefly.

In the Anura there is a "pineal eye" (Figure 13-7), whose nerve enters the posterior commissure. In the salamander an eye is lacking.

Right and left nerves for the "parietal eye" were observed in three embryos of *Iguana* 18 days old—the left nerve was smaller than the right in two cases. In this genus the organ is ordinarily served by the nerve of the right habenula. *Iguana* and other lizards have a "pineal" organ whose nerve goes to the posterior commissure. Both structures appear to arise from a single diverticulum.

Contrasting parietal and pineal organs suggests a fundamental gap between living amphibians (and fishes) and the amniotes. Such a gap is not indicated by other anatomical features. In the embryology of each of these groups, an epiphyseal or pineal evagination appears which in the frog or reptile divides into an eye and an epiphyseal sac. The difference lies in the courses of the nerves. The association of "parietal eye" and right habenula in the lizard suggests that this is in fact only a pineal organ. The association of the nerve of this organ with the posterior commissure in the frog is probably a secondary relationship, as in the lamprey. The complicated explanations usually resorted to can be abandoned in favor of a more simple one, i.e. that there is but a single diverticulum divided into right and left halves in the lamprey, or, in the frog or lizard, into distal and proximal divisions from which nerves can grow along several paths. The epiphysis may not produce an eye as in the salamander, lungfish, or mammal.

General observations

The origin of the vertebrate eye is shrouded in antiquity, but it evidently arose within this group and is not a part of the chordate heritage. In the cephalochordate, Amphioxus, there are only pigment-enclosed photosensory cells in the wall of the nerve tube through most of the length of that tube. It seems probable that the paired eyes arose as diverticula from the brain wall in the fashion observed in the embryo. These outgrowths functioned to bring the photosensory cells concentrated on their outer aspect nearer to the surface of the head. This need arose as the animal increased in size and pigmentation and as the cranial skeleton developed. The lens was induced by the eye diverticulum through the same mechanics observed in many invertebrates. This is a reaction which cannot as yet be explained.

The development of a median eye from the epiphyseal outgrowth of the diencephalon was the result of parallel events or interactions of brain tissue with light when brought close to the skin. In this case the "lens" is of neural origin rather than ectodermal. Whether the median organ (or organs) ever was an eye is doubtful since it finds its highest development in the reptile not in the fishes. As a photosensory organ (not image forming) it is useful in diurnal rhythm responses and in chromatophore control (color changes). On the basis of the presence of a parietal foramen, an organ was developed in the most primitive vertebrates, the ancestors of both agnath and gnathostome.

The ear

The ear serves two basic functions: equilibrium and hearing. Equilibrium involves responses to gravity as well as angular acceleration produced by movement. The term hearing is difficult to define. Vibrations in the earth or in solid structures can be detected by the organs of touch, and in effect this is hearing. Hearing is generally reserved for vibrations of higher frequency and lesser magnitudes. Because of the low energy levels involved, special mechanisms are necessary. In the tetrapods, the inner ear is associated with a middle-ear cavity and tympanum. Connecting the inner ear and tympanum, across the cavity, is a compound columella (bird, reptile, amphibian) or a series of three bony ossicles (mammals).

The tetrapod ear The inner ear arises from a thickened ectodermal area, the **auditory placode**, which invaginates to form the **otic vesicle.** The development of this vesicle varies somewhat, but a general pattern applies to most vertebrates. In the Bullfrog, the vesicle, or **otocyst**, is divided by ridges into a medioventral **endolymphatic duct** and the **inner ear** proper. The latter develops evaginated folds for the three **semicircular canals;** ventrally an outpocketing forms the **sacculus.** With completion of separation of the middle parts of the semicircular canals, the **utriculus** is defined. Three lesser diverticula, the **basilar** and **amphibian** papillae and the **lagena,** separate from the **sacculus** (Figure 13-20). All of these become more sharply defined in the older larva.

Internally, sensory **cristae** ("crests") develop in each of the **ampullae** of the semicircular canals, and patches of sensory cells form the maculae ("spot") in the utriculus, sacculus, and lagena. Sensory membranes develop in the amphibian and basilar papillae. These membranes are formed of sensory and **supporting cells** projecting halfway across the lumen of the papilla. Each sensory cell has groups of hairs forming a conical projection which is embedded in a gelatinous and fibrous tectorial membrane. Fibers radiate from the ends of the supporting cells into the tectorial membrane, and these interlace distally to form a support for the margin of the membrane.

A **perilymphatic space** forms in the mesenchyme between the membranous labyrinth and the capsule wall, first in the area of the fenestra vestibulae. From here it extends dorsoposteriorly around the sacculus in contact with the amphibian papilla, then around behind to the inner wall of the otic capsule. It passes through the **perilymphatic fenestra** and expands as a **perilymphatic** sac lying ventrolateral to the medulla.

Up to this point the development of the ear of the Bullfrog is representative. The following description of the **bronchial columella** applies only to the Bullfrog (Figure 13-20 A) and is important only as an example of the plasticity of this area. A branch of the perilymphatic sac extends outward, through the metotic foramen, in contact, above and internally, with the basilar papilla, and below with the dorsal aorta.

In the larval frog the contact with the dorsal aorta is related to a band of connective tissue which develops in the dorsal aorta. This appears first on the medial wall and later comes to span the aorta from top to bottom. This band, the bronchial columella, is continued below the aorta to the top surface of the lung. It acts in transmitting vibrations from the lung through the aorta to the perilymphatic space and directly up through this to the basilar papilla. In the course of metamorphosis, the bronchial columella atrophies and is lost.

The loss of the bronchial columella in the Bullfrog is related to the development of the tympanic **columella** and the **middle-ear cavity,** which forms from the first branchial pouch. This cavity when formed is separated from the exterior by a **tympanic membrane;** and it is connected with the pharynx by the **eustachian tube.** The columella is formed of the **stapes** and **extracolumella;** it spans the tympanic cavity and conducts vibrations to the perilymphatic fluid at the **fenestra vestibuli.**

Xenopus, another anuran, is more typical of the tetrapod (Figure 13-20 B). The perilymphatic canal passes between the amphibian papilla, above, and the lagena, below. Beyond these it expands into a chamber which contacts the basilar papilla. From here it constricts to pass through the perilymphatic foramen to enter the metotic foramen and reach the cranial cavity.

In the salamander both the amphibian and basilar papillae are usually developed, at least in the larva. The basilar papilla is not found in neotenic forms such as *Proteus* and *Necturus.*

The endolymphatic duct enters the cranial cavity and forms a midline **endolymphatic sac** in the salamander (Figure 13-21). This is partly subdivided by septa and heavily pigmented in *Necturus* (Figure 13-6). In the frog, bilateral sacs develop which extend forward and posteriorly. These join and extend down through the spinal canal with a pouch evaginating from the spinal column with each spinal nerve.

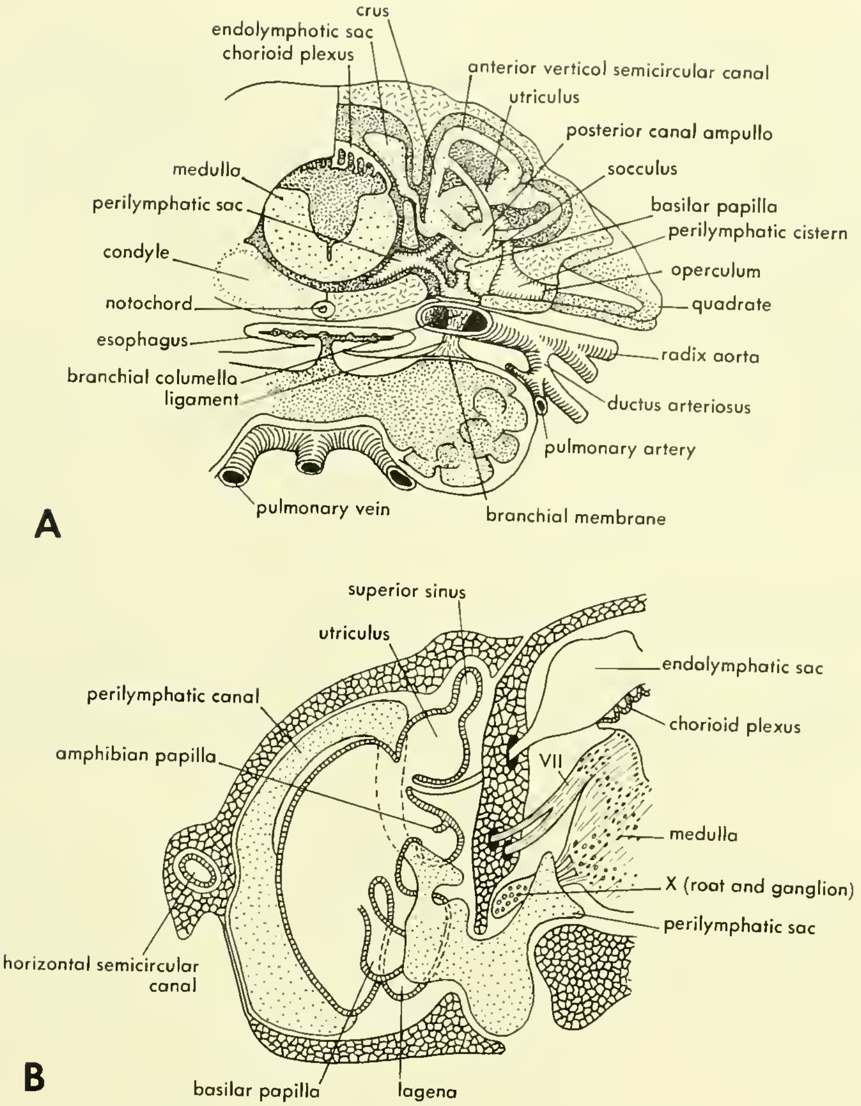


Figure 13-20. Semidiagrammatic cross section of the otic region of the Bullfrog, *Rana catesbiana*, A, and the Clawed Toad, *Xenopus laevis*, B. (A after Witschi, 1956; B after Paterson, 1949)

There is a large amount of calcified material in this endolymphatic system.

In the amphibian there is much modification in the auditory system. In the Bullfrog larva the lungs are used to receive vibrations which are transferred through the bronchial columella to the inner ear; in the adult the tympanic membrane and columella are utilized. In various amphibians different devices appear; some use the lower jaw, which rests against the ground to transmit vibrations to the inner ear; others use the forelimb, which is attached by means of an opercular muscle or ligament to the ear capsule. Among salamanders a tympanic membrane is lacking, but this is better explained as loss than as a retention of the primitive state.

Fossil forms dating back to the earliest known reptiles and amphibians have a tympanic notch for a tympanic membrane. The spiracle of the fish is high on the side of the head in somewhat the same position as the otic notch of fossil forms. In amniotes, the drum lies more posteriorly and ventrally; because of this, there is a question whether it is the same membrane in both positions. Primitively the drum was nearly flush with the surface of the head, while in amniotes, with the exception of the turtles, it is sunk into the head at the inner end of an external auditory meatus.

It can be assumed that there has been a continuum in function from the original large "columella" (stapes), associated with the otic notch in the primitive amphibian, to

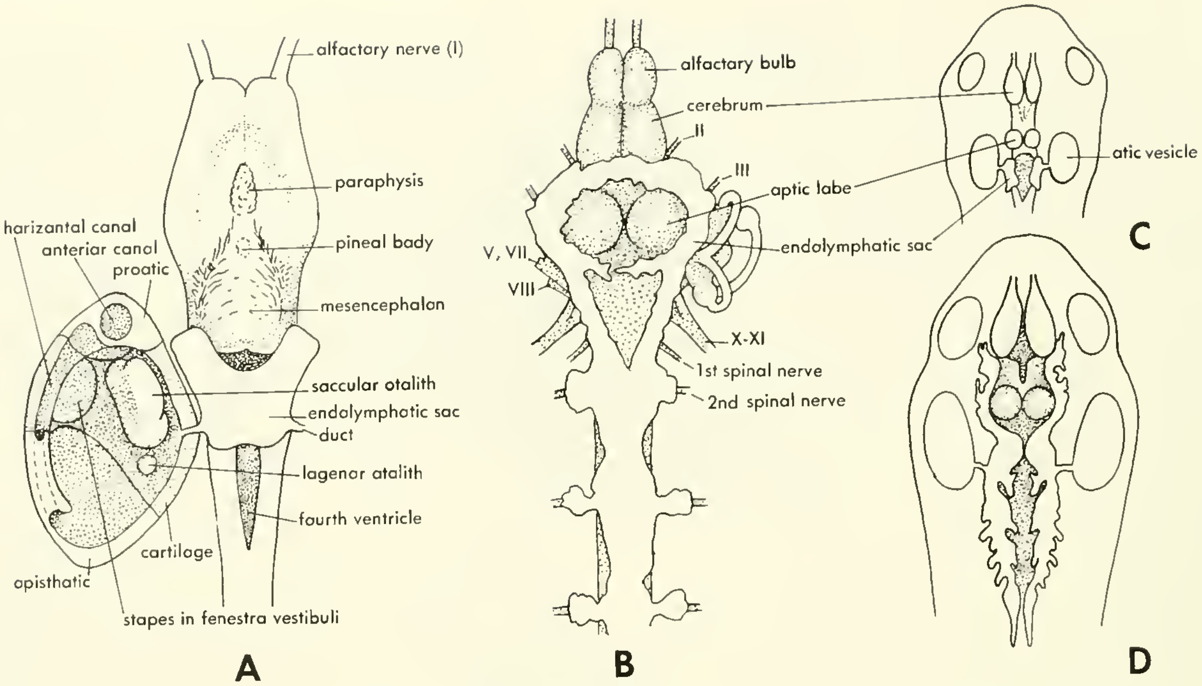


Figure 13-21. Endolymphatic sac development in amphibians. A, dorsal view of brain and endolymphatic sac of *Necturus*, with the ear capsule shown on the left side; B, dorsal view of brain, with endolymphatic sacs and inner ear of right side of the Bullfrog; C to D, two stages in the development of the endolymphatic sac of *Xenopus*. (B after Witschi, 1956; C to D after Paterson, 1949)

the delicate columella, associated with the more posterior and ventral tympanum seen in the later reptiles or the chain of bones associated with the tympanum in the mammal. The assumption that rapid changes or extensive mutations are required does not seem to fit the case. The ear has been functional at all times as a hearing device, using one or another mechanism.

In the development of the middle-ear cavity, a diverticulum of this space is observed to expand around the columella or chain of ossicles. It also penetrates adjacent skull bones, particularly in birds. The connection of this cavity to the pharynx may be wide as in the lizard or a long narrow tube as in the mammal.

The inner ear of the reptile and mammal is like that of the amphibian, but the lagena and its associated basilar papilla are drawn out into the **cochlea** (Figure 13-22). This is slightly curved in the reptile and bird and spiraled in the mammal. The amphibian papilla is not observed in these groups. The lagenar macula disappears, while the sensory membrane of the basilar papilla becomes the **organ of Corti.** The lagena is associated with a perilymphatic space which forms the scala **vestibulae** and **scala tympani.** These are associated with the oval and round windows respectively.

The ear of fishes Among the fish a tympanum and a middle-ear apparatus are lacking; transmission of vibrations into the inner ear presents no difficulties in a liquid medium. The inner ears of the myxinid and lamprey differ markedly. In the myxinid it consists of a ring-like structure, a part of which is a semicircular canal lying at an angle between the horizontal and vertical canals of other forms. There is an endolymphatic duct which comes off from the inside of this donut-like structure or dorsomedially. This duct extends into the cranial cavity and enters the meninges, where it forms a slim endolymphatic sac. Internally the inner ear has two cristae in anterior and posterior ampullae, or only one, the posterior ampulla. There are several sensory areas (maculae) in what might be called the vestibule. These probably correspond to the utricular, saccular, and lagenar organs.

In the lamprey there are two semicircular canals corresponding to the anterior and posterior vertical canals of higher forms. The **crus communis,** where these join, opens into the top of the vestibule. The vestibule is divided into anterior and posterior utricular chambers by a fold of the medial wall. The ampullae of the canals open into these. Below these divisions of the utriculus is a small (anterior) sacculus, and a larger (posterior) lagena. The utricular chambers are partly subdivided by ridges along the course of the semicircular canals. Long cilia on the medial walls of these chambers produce currents in the endolymph.

In the vestibule of the lamprey are utricular, saccular,

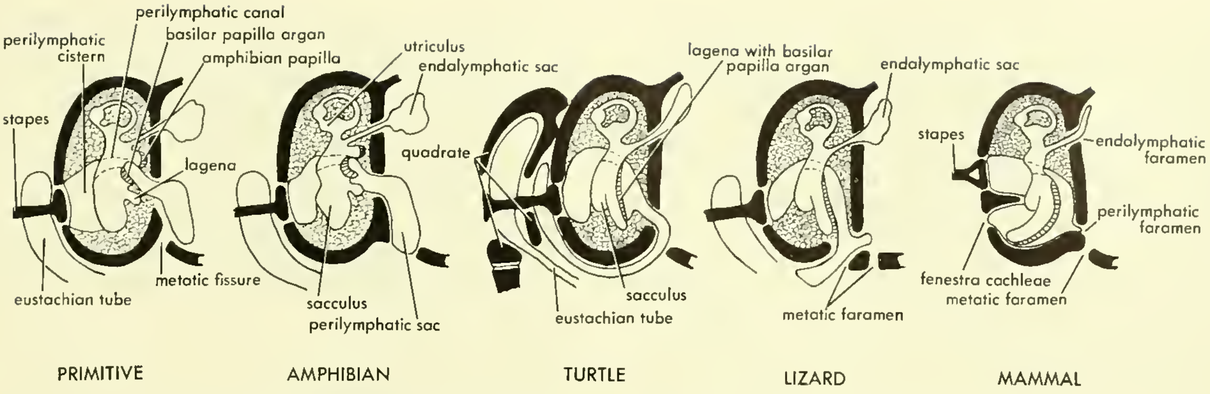


Figure 13-22. Diagrammatic cross section through the otic capsules of several tetrapods showing the variations of inner ear and perilymphatic sac development. (After Cardier and Dalcq, 1945, and Romer, 1955)

and lagenar maculae (sensory areas) as well as a **macula neglecta** (Figure 13-23). There are no otoliths or granules; the currents within the utricular chambers appear to replace these. The endolymphatic duct is a short, closed tube. In fossil osteostracans and heterostracans the inner ear has two semicircular canals as in the lamprey.

In the osteostracans the inner ear is associated with radiating canals which extend out to dorsal and lateral fields. Stensiö viewed these fields as filled with electric muscle tissue and the canals as occupied by the nerves for these muscles. It has been pointed out that the fields are too small to hold enough muscle to produce an effective shock, therefore, it has been suggested that they were sensory fields for reception of vibratory stimulae and that the canals were

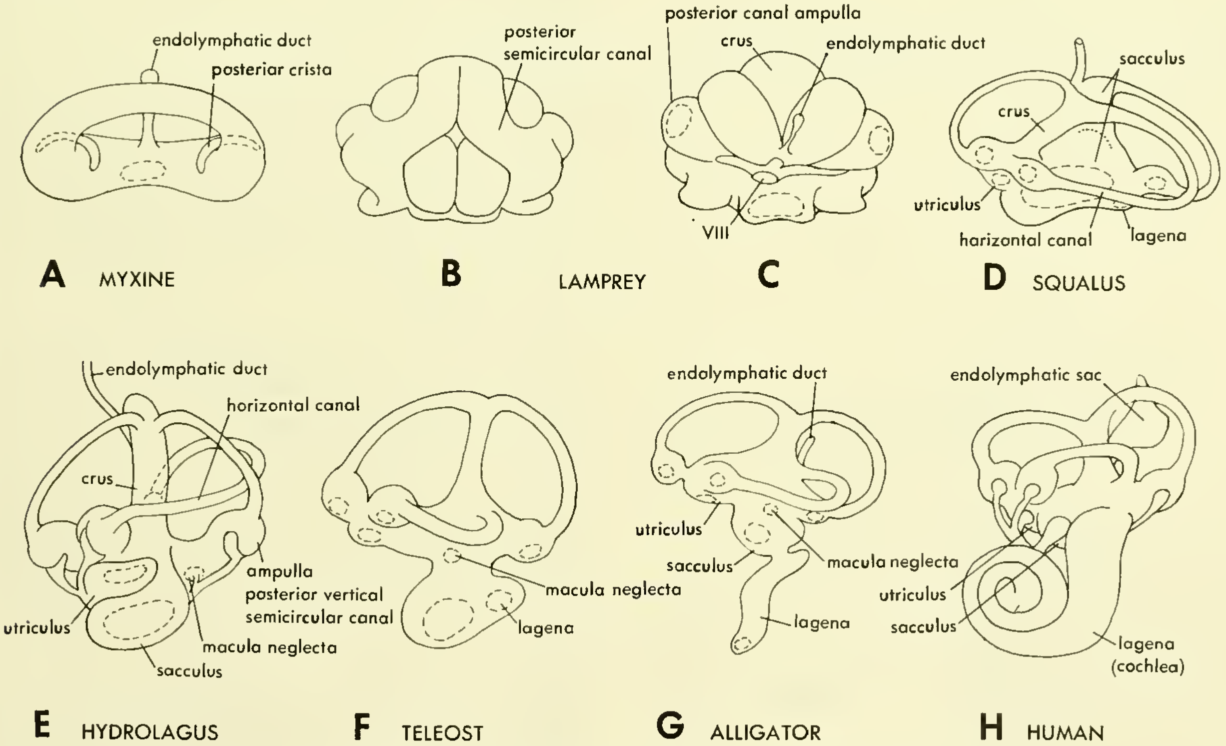


Figure 13-23. Semidiagrammatic views of the left inner ear of several types of vertebrates. C is a medial view; the others, lateral views. (In part after Neal and Rand, 1936)

occupied by perilymphatic or endolymphatic tubes. Certainly the canals to the dorsal field suggest the endolymphatic ducts of gnathostomes; however, what appear to be external openings of endolymphatic ducts are also present in some of these fossil agnaths. The presence of canalicular extensions of the inner ear would agree with the theory that the ear is a derivative of an **accustico-lateralis** system. The fields and canals of the fossil cephalaspids represent a specialization characteristic of that group.

In sharks the anterior vertical canal joins with the horizontal canal to form a crus, thus differing from other fishes including *Hydrolagus.* In the latter the vertical canals form a crus into the base of which the horizontal canal enters. The endolymphatic duct of the shark exits from the capsule directly into a fossa below the skin. There is an endolymphatic sac opening to the outside at a pore. There are granules associated with the maculae in this group. *Hydrolagus* has external pores for the endolymphatic ducts.

In actinopterygians the inner ear has distinct utricular, saccular, and lagenar sacs and usually each has a stony otolith. There is a macula neglecta on the outer wall of the constriction between utriculus and sacculus. In detail of parts in this group, there is much variation. In some, the sacculi are joined across the midline and are associated with a perilymphatic sac which extends out on either side of the anterior vertebrae. This perilymphatic sac lies in contact with a series of four Weberian ossicles, detached and modified processes of the vertebrae—Figure 13-24, which are articulated as a conducting chain. The most posterior of these lies in contact with the air bladder. Vibration of the bladder or, more probably, pressure changes (expansion and contraction) are thus transmitted through these bones and the perilymphatic fluid to the inner ear. Fishes with this structure are identified as the **Ostariophyses.** In the clupeoid fishes, paired anterior diverticula extend forward from the swim bladder to contact the inner ear directly (Figure 9-32).

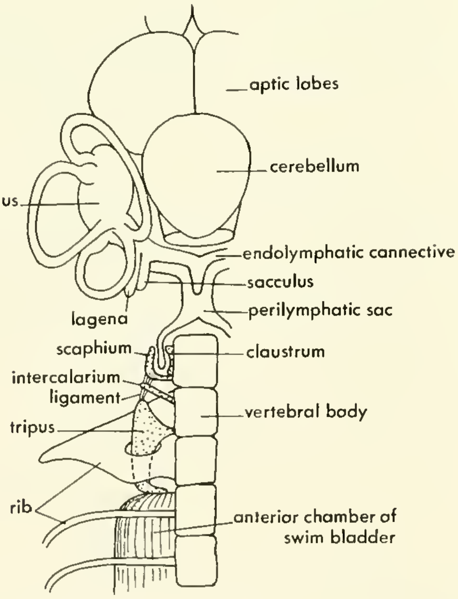


Figure 13-24. Webberian ossicles of *Catostomus commersoni* as seen in dorsal view, semidiagrammatic. (After Martin, 1961)

The endolymphatic duct is a short closed tube in teleosts. It is missing in *Salmo* and *Lampanyctus.* The latter genus is peculiar in having the sacculus (and lagena) separated from the rest of the middle ear—the macula neglecta is in the floor of the utriculus.

The lateral-line system

The lateral-line system is an integral part of the acustico-lateralis system which includes the ear. It consists of **sensory lines** radiating over the head and body, **pit organs,** and the **ampullae of Lorenzini.** The basic lines (Figure 13-25) are as follows: one above the eye, the **supraorbital;** another behind and below the eye, the **infraorbital;** one paralleling the mandibular arch and having **jugal** and **oral** parts; one passing down over the hyoid arch and on to the lower jaw and having **preopercular** and **mandibular** segments; a **temporal** division, which continues posteriorly as the main **lateral line,** and a **supraoccipital connective** joining the temporal lines. In addition to these, there are **anterior, middle,** and **posterior pit lines** on the top of the head. On the body, there are **dorsal** and **ventral body lines** in some fishes in addition to the lateral line.

The sensory lines of living forms have organs called **neuromasts** or maculae formed of clumps of cells. The cells of a neuromast have hair-like projections enclosed in a cupola of gelatinous material. Movement of the cupola, acting through the hairs, stimulates the cells. These cells, in different areas, are innervated by the seventh, ninth, and tenth cranial nerves. Whether these sensory structures are on the surface, in pits, or in a canal does not seem to be important except as a functional modification.

This system functions in the detection and location of disturbances in the water. Such a sense aids in finding food, in social behavior, in avoiding enemies, and in echo location. It functions also as an accessory rheotactic sense (orientation in flowing water). In actinopterygians this system is best developed in free-swimming forms, those living in rapidly flowing water, or surf forms (Figure 13-30). Having the organs located in closed canals is assumed to represent a high development, while surface organs are presumed to precede loss of this system.

The morphology of this system will be reviewed beginning with the agnaths.

Agnath This system in fossil agnaths (Figure 5-28 to 5-32) appears to involve a "mucous-canal" reticulum as well as sensory canals. The system is assumed to be one of epidermal. canals forming a reticular pattern over the head and trunk.

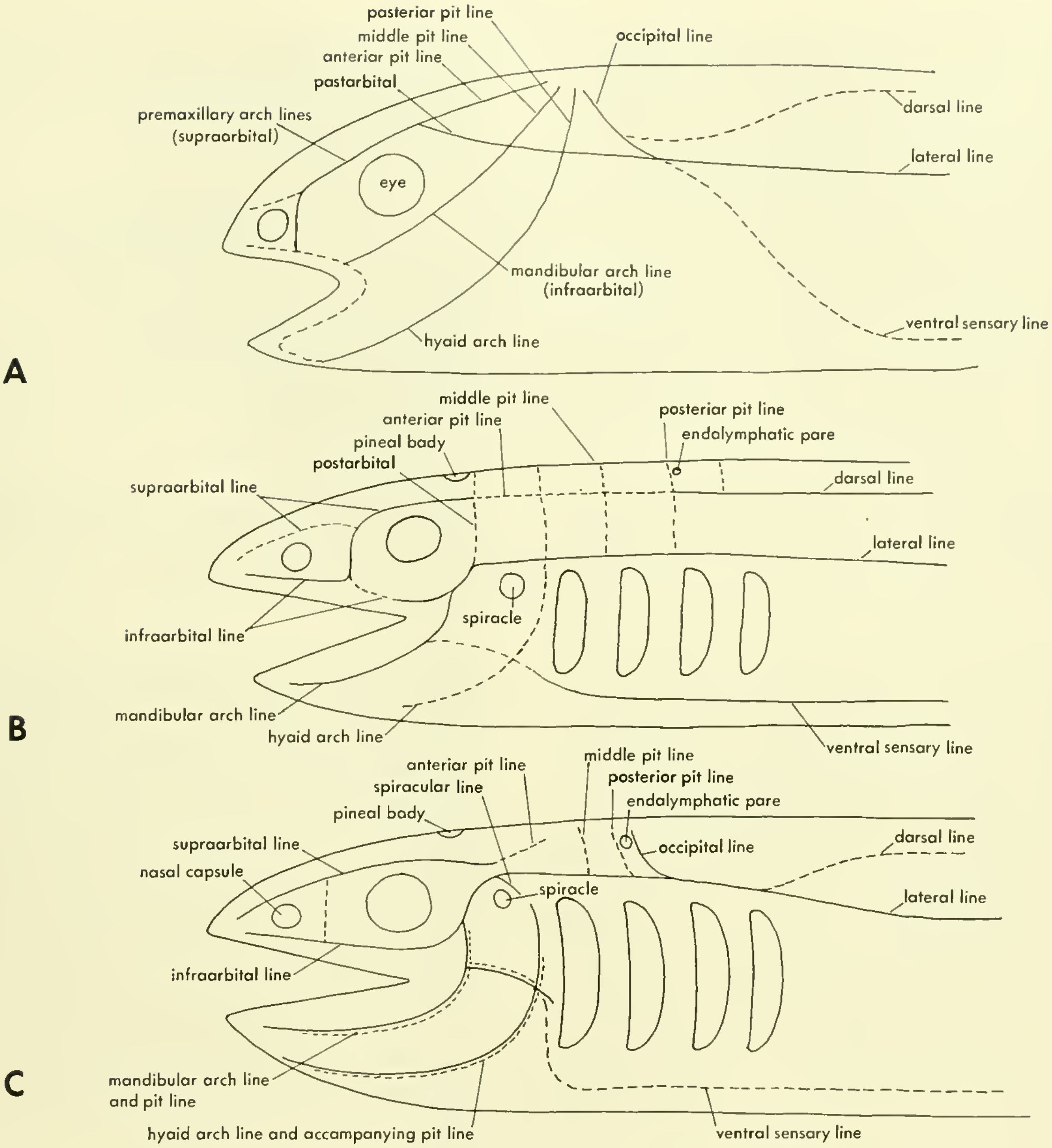


Figure 13-25. A, arthrodire; B, primitive vertebrate; C, Chondrichthyes, and Osteichthyes.

In the heavily armored forms these canals grooved the surface of the bone (interareal grooves) or were buried in the bone as in the case of *Tremataspis.*

It was early noted that there were connections between the reticular and sensory-line canal systems, and in fact one is unable to distinguish between "mucous" and sensory canals in *Tremataspis,* as they are seen in section, for they appear to be parts of a single system. The canals in this genus are divided into outer and inner parts by a thin perforated bony septum (Figure 8-26).

Among the agnaths there is a great deal of variation in this system ranging from *Irregulariaspis* and *Tremataspis,* having a network of canals in which the sensory lines are straighter and have slit-like openings to the surface of the bone, to most forms having only the sensory lines. In many of the Heterostraci, only the sensory canals are embedded in the bone, but a pattern of **interareal grooves** suggests the presence of a more superficial reticular system. In some of the heterostracans, the astraspids and amphiaspids, only the sensory canals are indicated by superficial grooves in the bone. In *Drepanaspis* these canals are represented partly by grooves and partly by canals. In most Osteostraci, except *Tremataspis* and closely related genera, the reticular canals are indicated by interareal grooves, and the sensory lines by short canal segments as well as grooves.

The pattern of sensory lines as seen in *Tremataspis* can be taken as representative of this group. The supraorbital line is reduced to a small segment behind the eye. The infraorbital canal is separated by a gap from the main or ventral lateral lines. There is a postorbital canal and a supraoccipital canal extending dorsally to the endolymphatic pore and ventrally to the ventral lateral line, which is divided into parts above and below the ventrolateral fold. Two lines occurring below the branchial openings can be viewed as continuations of the postorbital line and ventral lateral lines. There is a short section of dorsal lateral line to either side of the dorsal spine of the trunk.

The canal system of the heterostracan is much less modified since the eyes are lateral and the branchial chambers are not crowded below the cranium (Figure 13-25 B). A supraorbital canal extends forward on the snout and back to a point behind the pineal organ. There are dorsal, lateral, and ventral body lines. The postorbital canal joins the lateral and ventral lines behind the eye and continues on the throat, behind the mouth, as the oral canal. The ventral line continues forward beyond the postorbital line as the infraorbital line. There is no hyoid line. There are several connectives on the trunk, behind the level of the ear, between the dorsal and main lines. The most anterior of these probably represents the dorsal end of the hyoid line. The next is the dorsal end of the first branchial line, the middle pit line of higher forms. The posterior one appears to be the occipital canal.

Of the living agnaths, the cyclostomes, only the lamprey has an evident lateral-line system (Figure 13-26). There are superficial sensory organs (neuromasts) forming a temporal line, a supraorbital line represented by two organs, an infraorbital line not continuous with a line on the snout, and a line below the branchial chambers. There is also a vertical line passing downward parallel to the margin of the mouth. These lines are innervated by the seventh nerve. There are indistinct dorsal, lateral, and ventral body lines as well as organs behind and above the branchial openings. In some specimens there is a small hyoid clump of organs. The pattern observed in the lamprey agrees with that of the fossil forms.

From the agnaths one could conclude that the ancestral vertebrate lacked a sensory-canal system or that it had an extensive reticular system in which certain channels came to be the primary sensory lines. Either of these diametrically opposite views is reasonable, as is the possibility that the primitive state was somewhere in between. The reticular and sensory-line systems may have originally been separate (as in the crossopterygian fishes?), the former functioning in mucous production, protecting the body both from abrasion and from water penetration.

In a well-developed sensory canal system, in terms of primary lines distinct from the reticular system, three primary pairs of longitudinal lines can be distinguished. These are connected by a single canal, the postorbital. This pattern can only in part be compared with that of the gnathostome groups.

Shark Of the sharks the most primitive representative is thought to be *Chlamydoselachus,* which closely resembles the hypothetical ancestral gnathostome pattern (Figure 13-25 C). Here the main lateral line joins the temporal canal, and the dorsal line is interrupted on the cranial roof. The supraorbital line loops forward on the snout and connects with the infraorbital behind the nasal capsule. The infraorbital line continues forward beneath the nasal capsule; the lines of either side touch below the tip of the snout and are reflexed back a short distance to end blindly. The jugal portion of the mandibular arch line passes back to the angle of the mouth, where it turns down and forward as the oral line. This line extends nearly to the tip of the lower jaw, where it ends blindly or occasionally joins the canal of the opposite side. The jugal line has an extension which continues back nearly to the hyoid arch line; this is probably a section of the ventral line. The cheek portion of the hyoid arch line,

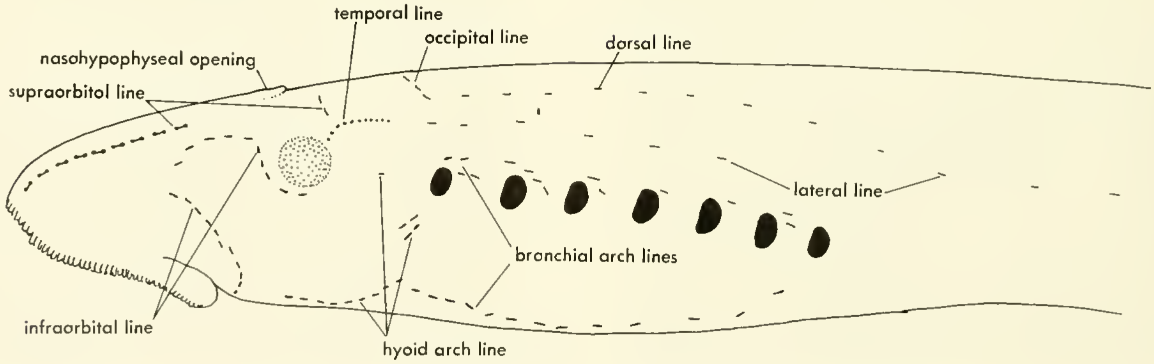


Figure 13-26. Distribution of sensory-line organs and grooves in the lamprey.

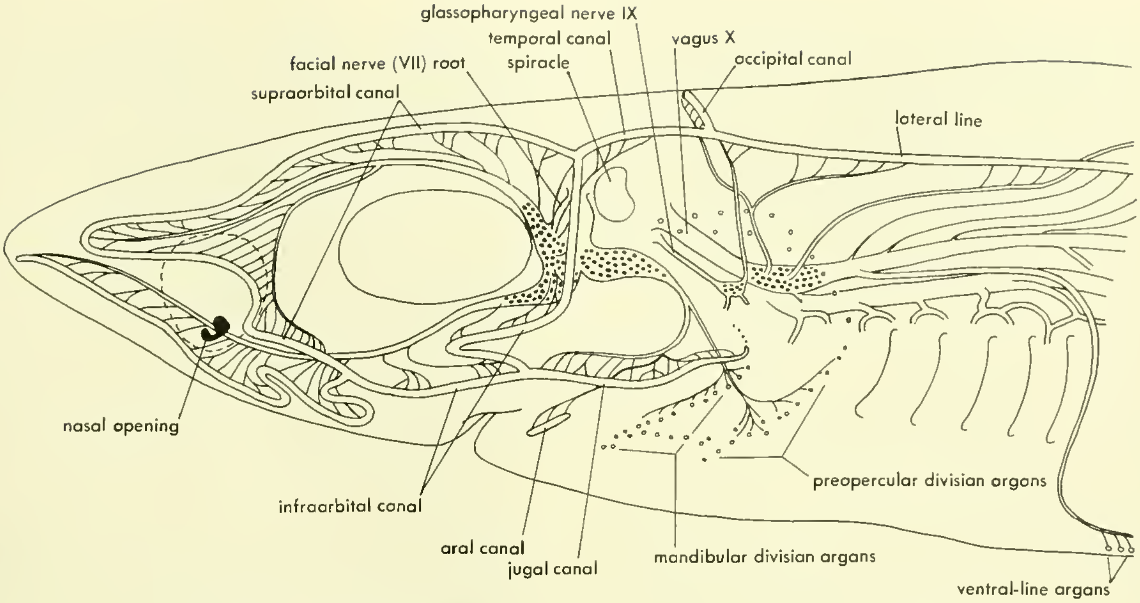


Figure 13-27. Sensory-line system of *Squalus acanthias.* (After Norris and Hughes, 1920)

the preopercular division, extends down and forward to become the mandibular division on the lower jaw. The terminology here is confusing. The mandibular segment of the hyoid arch line anteriorly joins the oral segment of the mandibular arch line. The preopercular division ends behind and below the spiracle without connecting with the temporal portion of the main lateral line. The posterior pit line, single or double, extends toward but not to the midline in front of the endolymphatic pores. Some of the lines are open grooves; these include the entire hyoid arch line, the oral portion of the mandibular arch line, the posterior tip of the jugal extension, and the lateral line posterior to the spiracle. The others are closed canals opening to the surface through irregularly spaced pores.

There is a pit line from the spiracle down toward the junction of the jugal and oral lines. The significance of this pit line is not known, but it may be the satellite of the postorbital section of the mandibular arch line. Pit lines such as this are not constant in position nor relationships, while others, as remnants of canals, are more fixed in position.

In most selachians, such as the dogfish (Figure 13-27), the canal pattern is suggestive of that observed in *Chlamydoselachus;* however, the mouth is far back below a strongly developed rostrum. Development of the rostrum has apparently distorted the proportions of the canals. The infraorbital canal ends below the tip of the snout. (The canals of either side meet and join for a short distance in *Laemargus;* this fusion occurs well back from the ends of the canals just in front of the mouth.) In *Laemargus* the supraorbital, infraorbital, and lateral lines come together at a point high on the head.

In most sharks the hyoid line is represented only by pit organs (a case of canal reduction to a pit line); the oral canal may be much reduced and without direct connection with the jugal canal, which has a strong posterior extension. The occipital canal lies behind the endolymphatic pores and the canals of either side connect. This canal is also called the supratemporal, aural, or commissural canal. A short branch of the occipital canal may pass in front of the endolymphatic pore; this is the posterior pit-line canal. The sensory lines are canals in most sharks although the posterior end of the lateral line may be a groove as in *Squalus.*

The development of the sensory system of *Squalus* has been described. In the embryo a number of ectodermal placodes give rise to separate supraorbital, infraorbital, jugo-oral, distal and proximal hyoid, temporal, posterior pit lines, and lateral line divisions (Figure 13-28). The adult pattern is thus indicated at the time of appearance of the placodes. Of interest is the fact that the jugo-oral and distal hyoid placodes arise joined by the jugal extension. In development, having the organs in a groove precedes the formation of closed canals. The pit organs of the hyoid arch line are formed by fragmentation of the placode. Each fragment sinks down into the epidermis to form an organ.

Holocephalan The pattern observed in *Hydrolagus* is distinct from that of the shark, but suggestive of it (Figure 13-29). The hyoid and mandibular arch lines join the infraorbital below the eye. The first is the better developed. The infraorbital line has a break in it and passes above (behind) the nasal capsule. Assuming that this lower line represents the infraorbital, the upper could correspond to the reflexed

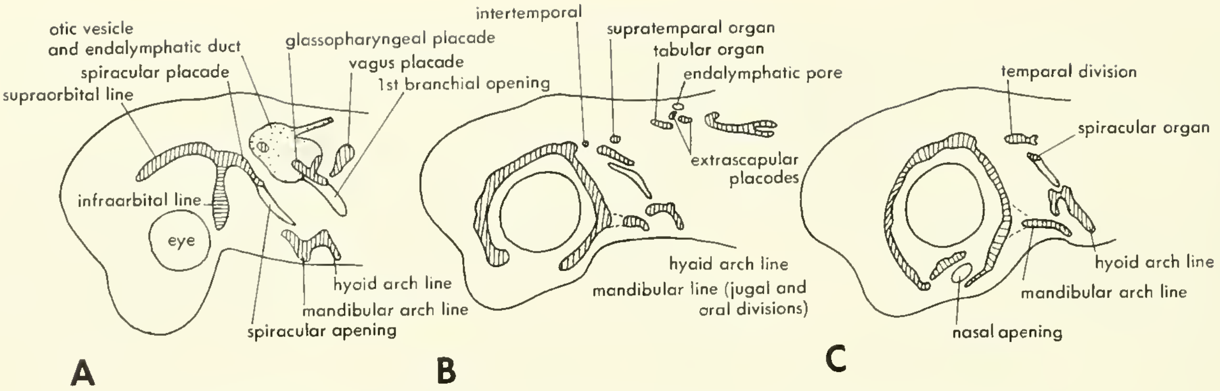


Figure 13-28. Three stages in the development of the sensory-line system of *Squalus acanthias*. (After Holmgren and Pehrson, 1949)

end of the supraorbital line of the shark. The infraorbital is then peculiar because of its relationship to the olfactory capsule and also its forking (only in *Hydrolagus*); both parts connect across the midline, and the upper also connects along the midline with the supraorbital connective.

The modifications of these lines may be related to the jaw changes and the development of the snout. The chimaerid differs from the shark in terms of the position of its nasal capsule much as the dipnoan differs from the other choanates.

Fossil gnathostome fishes In the arthrodires and acanthodians, the same general canal pattern is seen. In the acanthodian the canals lie in the scales covering the head. In one genus, *Poracanthodes*, there is a reticular canal system embedded in the scales. There are distinct mandibular and hyoid arch lines which join at the angle of the mouth, and there is a pit line of the cheek which joins the jugal section with the preopercular section. The preopercular section lies far forward of the spiracle and does not connect with the temporal line. The position of this line indicates that these

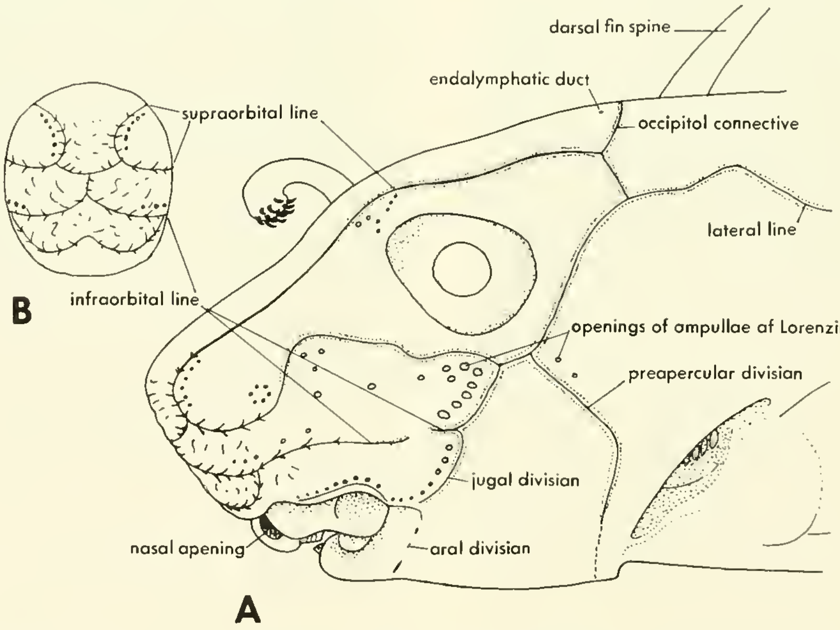


Figure 13-29. Sensory-line grooves on the head of *Hydrolagus*. A, lateral view; B, interconnections on snout.

fishes did not have a complete mandibular cleft (the canal could not have been displaced forward on the cheek if such a cleft were present). In some acanthodians a dorsal hyoid section extends from the spiracle to the temporal canal.

The supraorbital canal of the acanthodian may be connected with the lateral line or may be separate. Occipital and posterior pit-line canals are indicated in this group. The snout situation is not known.

In the arthrodires the canal system is indicated by grooves in the dermal bones (Figure 5-22, 13-25 A); this system is peculiar because of the radiating nature of the supraorbital, infraorbital, and lateral lines. This is also observed in the shark *Laemargus*. Unlike any other gnathstomes, there are also middle and posterior pit lines in this radiation. The posterior pit line is a canal in this group; the occipital canal, passing behind the endolymphatic pore, is lacking or poorly developed. The temporal line loops down toward the cheek and the preopercular canal is indicated only dorsally. A jugal connection between mandibular and hyoid arch lines is perhaps present in *Homosteus*. Like the shark the supraorbital canal extends down behind the nasal capsule, but it does not join the temporal line posteriorly. It is unlikely that the infraorbital canal passed below the nasal capsule.

Actinopterygian fishes The sensory-canal system of the actinopterygian fishes is difficult to compare with the hypothetical pattern or the patterns seen in other groups (Figure 13-30). As in the chondrichthyes, most acanthodians, and arthrodires, there is no evidence of a reticular canal system in any of the living or extinct forms. The supraorbital canal may or may not connect with the temporal division of the lateral-line canal. The infraorbital canal passes forward below the nasal capsule; anterior connection between the supraorbital and infraorbital canals is lacking with the exception of *Polypterus*. The hyoid arch canal attaches to the temporal canal behind the spiracle or ends on a line passing behind the spiracle. The mandibular arch line is poorly developed; it is suggested only by horizontal and vertical pit lines on the cheek. There is an occipital canal, and anterior, middle, and posterior pit lines on the top of the head. The anterior pit line is a continuation of the supraorbital canal behind the point of connection with the temporal canal. This suggests that it is a part of the dorsal line as seen in the agnath fish or the basic model.

Not all actinopterygians agree in detail. In the palaeoniscoids, *Pteroniscuius* or *Boreosomus* as examples, the supraorbital canal does not join the temporal canal. This state is observed in all lines of palaeoniscoid fishes. The living chondrosteans, holosteans, and teleosts in contrast have these lines joined. Although the preopercular line invariably extends up behind the spiracle, *Polyodon* is the exception. In this chondrostean it connects with the infraorbital line below the spiracle. In the haplolepid palaeoniscoids, dorsal and ventral body lines as well as a main lateral line are observed.

In the actinopterygian the sensory lines are usually embedded in the dermal bones with pores to the surface. The dermal bones may be reduced to tubes enclosing the canal. In some the canals lie superficial to the bone or are lost.

The development of this system in *Amia* has been reported (Figure 13-31). Here again are seen supraorbital, infraorbital, joined mandibular and hyoid, and temporal placodes.

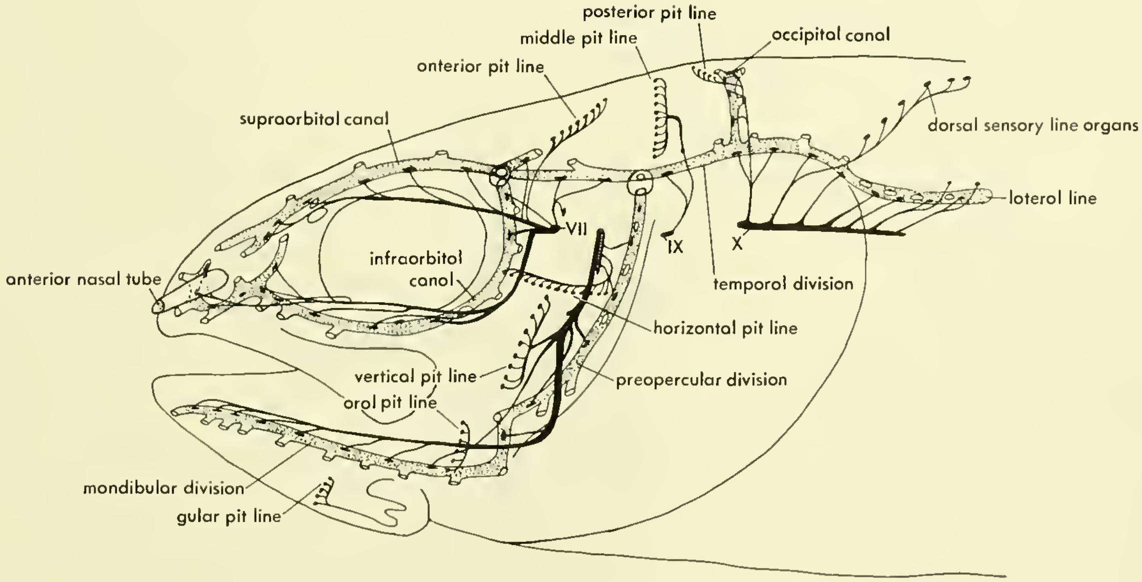


Figure 13-30. Sensory lines, organs, and innervation of organs in *Amia*. (After Allis, 1888–89)

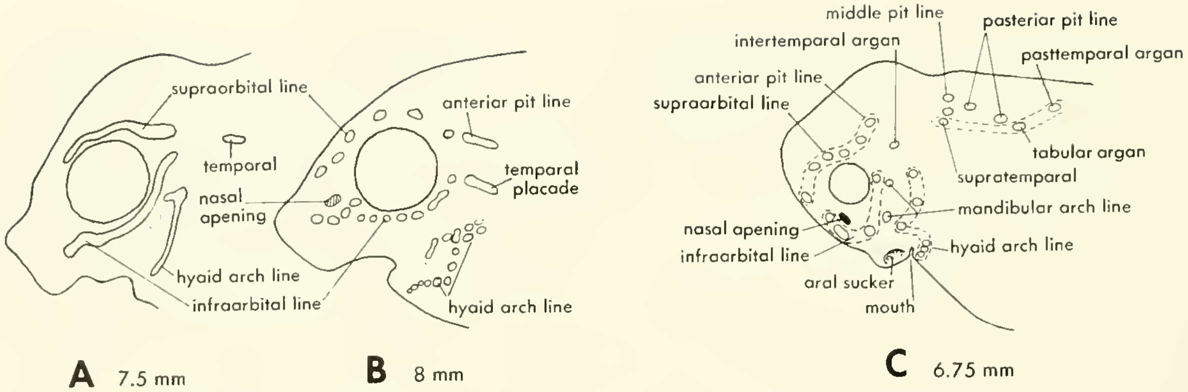


Figure 13-31. Development of the sensory-canal system of the head in actinopterygians. A and B, two stages in *Amia;* C, an early stage of *Polypterus.* (A and B after Halmgren and Pehrson, 1949; C after Pehrson, 1958)

Choanates

CROSSOPTERYGIAN In the early crossopterygians and dipnoans both reticular and sensory-line canals were present and enclosed in the dermal bones (*Porolepis, Osteolepis*). In the later forms (*Holoptychius, Eusthenopteron*) the reticular system is lacking.

Of the porolepiforms, the canal system of *Holoptychius* is best known (Figure 4-32). In this genus there is a typical crossopterygian pattern of embedded canals. The supraorbital canal is connected with the temporal line and also joins the infraorbital in front of the nasal capsule. The infraorbital canals connect from one side to the other on the snout. On the cheek a jugal canal may enter the quadratojugal, or this line may be reduced to pit organs. There may be a vertical connection between jugal and preopercular lines. The oral part of the mandibular arch line is made up of pit organs. A separate dorsal piece of the hyoid arch line may extend forward from the spiracle. There are several small pit lines on the roof along the temporal canal—anterior, middle, and posterior pit lines.

The osteolepiform type is well known from both *Osteolepis* and *Eusthenopteron* (Figures 4-28, 4-29). The latter retains a part of the reticular system as branched and radiating canals extending to the surface of the bones from the sensory line canals. The pattern of the main canals is much like the porolepid, but the mandibular arch line is represented only by horizontal and vertical pit lines. There is also an oral pit line. On the cranial roof are anterior, middle, and posterior pit lines.

The Actinistia (coelacanths) have a similar sensory-line pattern, and none has reticular canals (Figure 4-33). There has been some modification of the snout canals involving a commissure between supraorbital and infraorbital canals passing behind the nasal openings. A similar commissure is observed in some specimens of *Eusthenopteron.*

The crossopterygian can be characterized as having the mandibular arch line represented by irregularly disposed pit lines, by having the hyoid arch line connecting with the postorbital line well down on the cheek, and in having the supraorbital line connecting with the infraorbital in front of the nasal capsule.

DIPNOAN The primitive dipnoan had an embedded sensory line similar to that of the crossopterygian and, in the case of *Dipterus,* a reticular system (Figure 4-36), which was lost early in this group. The dipnoan differs in that the infraorbital line did not pass forward below the opening of the nasal capsule, or between the internal and external nares, as in the amphibian.

In living dipnoans a pattern similar to that of larval amphibians is observed (Figure 13-32). The sensory organs are located primarily in grooves in *Protopterus* but in canals in *Neoceratodus;* these lie in the skin, not in the bones. *Protopterus* differs from *Neoceratodus* in having a connecting line between the mandibular and hyoid arch lines. This groove could represent the jugal extension, turned down rather than up as in the crossopterygian. Whereas the infraorbital line of *Neoceratodus* is reflexed upward above the nasal capsule, that of *Protopterus* is bent down and back as if to enter the mouth to pass between the nares. *Protopterus* has a ventral line on the body as well as a lateral line.

The development of this system has been described for *Neoceratodus* (Figure 13-33). The pattern appears to be the same in the other lungfishes and is much like that observed in the shark or *Amia.*

Amphibians The amphibians, as derivatives of the choanate fishes, have the same general pattern of sensory lines; there is no evidence of a reticular system. The lines are present in the aquatic forms, including the living species, and they are lost in the more terrestrial forms. In the ichthyostegids (Figure 4-25) a part of the canal system is embedded in the

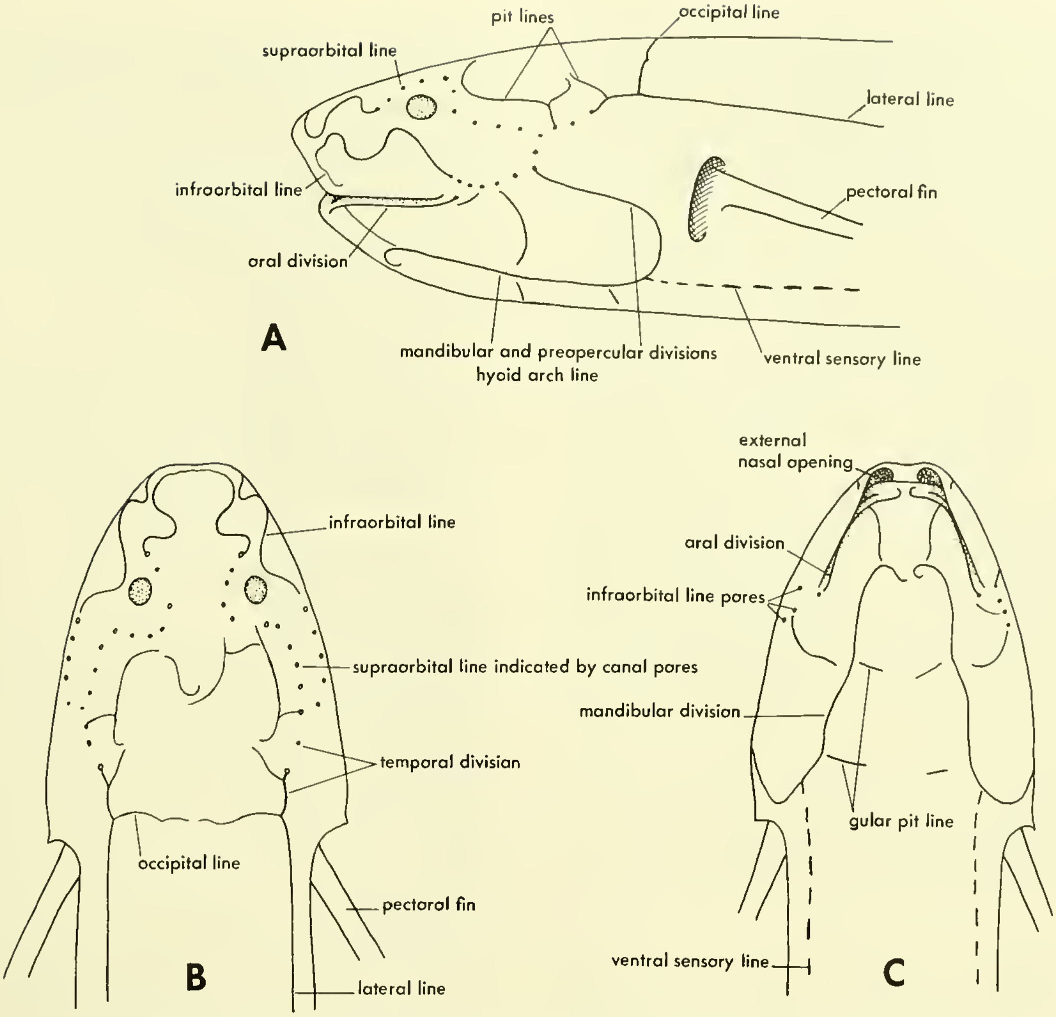


Figure 13-32. Sensory canal grooves and tubes on the head of *Protopterus*. A, lateral view; B, dorsal view; C, ventral view.

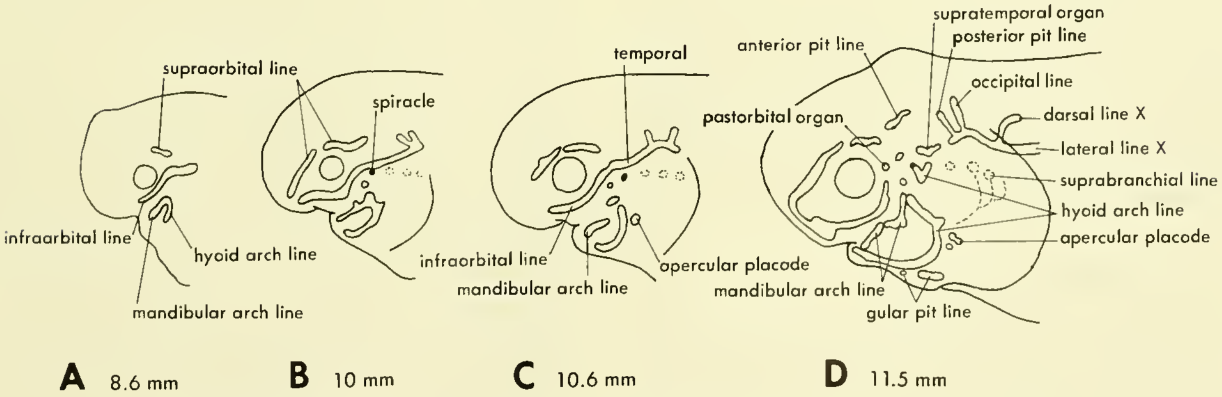


Figure 13-33. Four stages in the development of the sensory-line system in *Neoceratodus*. (After Pehrson, 1949)

bones and a part of it is indicated by grooves. The sensory lines of primitive amphibia generally lay in the skin over the bones, but grooved the bones in some areas.

The pattern of the sensory lines in the ichthyostegid, or other early amphibians, is like that of the osteolepid crossopterygian. No occipital canal is evident, although it is usually indicated in illustrations of *Ichthyostega;* in later amphibians a groove for this canal is sometimes observed on the posterior margins of the postparietals and tabulars. In some amphibians a loop is observed on the squamosal and quadratojugal (Figure 4-24), indicating perhaps that the jugal extension leads into the proximal end of the oral canal. Modification of the canals in the early Amphibia, as indicated by their looping, makes interpretation difficult.

In living amphibians, the more aquatic salamanders (*Necturus* and *Cryptobranchus*) have many neuromasts on the surface of the skin. These neuromasts, arranged as lines, are raised on elevations and are not pigmented. The lines can be identified as the supraorbital, infraorbital, mandibular and hyoid arch. There is a jugal extension connecting the last two. The temporal section is undeveloped; there is a middle pit line and an occipital connective. On the body are dorsal, lateral, and ventral lines. These lines diffuse in some areas, suggesting multiplication and spreading out of the neuromasts over the skin. In the larvae of anurans (*Rana*) these same lines are observed.

A sensory-line system is lacking in reptiles, even in those of aquatic adaptation. However, sensory organs, the prototrichs, are present and have much the same distribution on the body as those of adult anurans. Whether these were derived from lateral-line organs is not known.

General observations On the basis of the lateral-line system, the amphibian is like the crossopterygian or dipnoan in that the infraorbital and hyoid lines meet below the eye. The equal development of mandibular and hyoid arch lines in aquatic salamanders may be explained as due to retention of the mandibular as surface organs, while the hyoid was reduced from a canal to similar surface organs.

Although several elaborate schemes have been suggested to account for the various patterns of lines, it is best to apply the law of parsimony and use the simplest possible explanation. The basic pattern suggested in Figure 13-25 B appears to meet all tests; however, it is hypothetical. Again it seems that the agnath agrees no better with the hypothetical ancestral type than the gnathostome; that is, it is modified and not ancestral.

Other acustico-lateralis organs

Ampullae of Lorenzini are observed in clusters on the heads of sharks (vesicles of Savi in *Torpedo*), holocephalans, sturgeons, and one marine teleost, *Plotozus anguillaris,* a siluroid. These organs are mucous-filled tubes opening at one end through the skin. Sensory and secretory cells lining the tube are innervated by the seventh nerve. The blind end of the tube may be subdivided into several ampullae. These organs are thermosensory and are perhaps also pressure receptors.

The rostral sac of *Latimeria* can be described here although it may not be related to the ampullae of Lorenzini. The rostral sac, or internasal organ, is a large cavity in the snout which opens anteriorly through paired tubes and posterolaterally by two pairs of tubes (Figure 4-33). The cavity is largely filled by a vascular (venous) mass which is attached dorso and ventroposteriorly; its vascular connections are ventral. The lining of the sac is a mucous membrane except at the openings into the tubes where it is irregularly thickened and pitted. These pitted areas are richly supplied by fibers of the ophthalmic profundus nerve (V_1). The lumen of the sac and its tubes are filled with mucous. The role of this organ is unknown but it may be a thermoreceptor.

GENERAL OBSERVATIONS ON THE NERVOUS SYSTEM

Here, as in other areas of their anatomy, the vertebrates show a remarkable homogeneity in general plan and even in many details. The tetrapods differ one from the other only in minor details, and there is scarcely a structural gap between them and the fishes. The agnaths are most distinct but the differences are seldom clear or really impressive. The differences between the two living agnaths are nearly, or actually, as great as those between agnath and gnathostome.

Several points develop from a consideration of the differences. Since the eye is degenerate in living cyclostomes, would it follow that the ear is also retrogressive, i.e. that three canals preceded two? There is no evidence to support the conclusion that an inner ear with two canals gave rise to one with three. Also it is unlikely that the myxinid type, with one canal, is the most primitive; it is more probable that it is a regression from the two-canal condition. Thus the conclusion is reached that the otic vesicles underwent change, involving canal formation, in two separate lines of vertebrates, agnath and gnathostome.

Paired nasal capsules, as observed in the gnathostome, appear to be primitive, while the fusion of these in the agnath is probably a modified condition. The sensory-canal pattern of the agnath could be more primitive, but any attempt to superimpose it on the gnathostome results in difficulties. Parallelisms are more strongly suggested here than elsewhere; this involves the derivation of agnath and gnathostome patterns from that of a common ancestor, quite distinct from either. As a last point, if the common ancestor had a trigeminal nerve with three main divisions, would not this suggest that the jawed condition, or a situation leading to the development of jaws, preceded that of the agnaths as we know them?

It would appear that the common ancestor of agnath and gnathostome was already a complex organism with a well-defined and many-parted brain; three pairs of main sensory structures—nose, eye, ear; at least ten pairs of cranial nerves, plus a pineal structure and nerve; complex trigeminal, facial, and vagus nerves; and numerous other details. In the evolution of the vertebrates each part of the nervous system has shown some, or even marked, change, and these changes appear to be largely adaptive specializations peculiar to the group possessing them. As a possible exception, there has been a trend toward increasing size and complexity of the brain in the tetrapods which suggests a phylogenetic series, but the details of this evolution are yet to be worked out.

14

The Muscular System

INTRODUCTION

There are several kinds of muscles in the vertebrate body. These can be described as being of two basic morphological types: **smooth** and **striated.** The transition between these is observed in the striated nature of the **ciliary** muscles of the bird. In most vertebrates these muscles are smooth. The striated muscles are of two kinds: the **cardiac** muscle of the heart and the **skeletal muscles** of the body. Skeletal muscle is derived from three embryological sources. In the head region of fishes there is a combination of ectodermally derived **neural crest** tissue and **mesenchyme,** which gives rise to the skeleton of the branchial arches and to its intrinsic muscles. The mammals and higher forms lack such branchial muscles. Visceral mesoderm in this region gives rise to the masticatory, facial, pharyngeal, and laryngeal muscles as well as the heart. The **hypobranchial muscles** associated with the branchial skeleton and the skeletal muscles of the rest of the body are of somatic (myotome) origin (Figure 14-3).

Embryologically the locomotor muscles of the body arise from the **somites.** The somites are segmental condensations of mesenchyme, primarily **myotome,** enclosing a transient part of the body cavity, the **myocoel.** The myotome arises from that part of the somite next to the neural tube and notochord. The adjacent outer wall of this part of the coelom is the **dermatome.** Between the somite and the definitive coelom is the **nephrotome,** and between the myotome and the visceral part of the nephrotome is the sclerotome (Figure 10-15). Cells of the sclerotome move out of their area of origin to enclose the neural tube and notochord. Mesenchyme cells of the other parts of the coelomic wall, except the myotome, give rise to the smooth musculature of the body. The origin of the somites and coelomic divisions in Amphioxus resembles events in the vertebrate (Figure 14-1).

To produce the waves of contraction characteristic of swimming, the myotomes tend to become V-shaped or W-shaped (Figure 14-2). This is the first specialization displayed. In gnathostomes the myotome is divided by a horizontal septum into **epaxial** and **hypaxial** divisions; the latter extends down lateral to the coelom.

The myotomes of fishes have become somewhat more modified. In higher forms the myotomes have been variously fused, subdivided, and resubdivided into a complex pattern of vertebral and body-wall muscles; only the intercostal and some of the muscles of the spinal column retain the segmental form, lying as they do between the ribs and vertebrae.

With the origin of fins, a part of the myotomic musculature has migrated into the fins. This can be observed in the shark where small buds from a large number of somites grow into the base of the fin (Figure 14-3). The limb muscles of tetrapods and the fin muscles of fishes differentiate from simple dorsal and ventral masses. The ontogenetic course of this subdivision will be described for the tetrapods. In the tetrapods the limb musculature is not of apparent myotomal origin but is derived from mesenchyme condensations whose cells may be of myotomal origin.

A modification of skeletal musculature occurs in the formation of electric organs. Such organs are observed in the Torpedo, a ray-like elasmobranch, and several families of teleosts: the Mormyridae, Gymnotidae, Electrophoridae, Uranoscopidae, and Malapteruridae. Generally the electric organ is developed from the muscle of the tail, but in the Stargazer, *Astroscopus* (Family Uranoscopidae), the muscles moving the eye are modified. In *Malapterurus* the subcutaneous (smooth) musculature covering the body behind the head appears to have been transformed into this organ.

The smooth musculature of the body is much like that seen in the invertebrates. It lies in the skin and the walls of the tubular organs; physiologically it is different from the locomotor muscles. The circular and longitudinal body-wall muscles, so characteristic of invertebrates, are lacking in the vertebrate.

SKELETAL MUSCULATURE

Discussion of the skeletal musculature of vertebrates is difficult because of the large number of separate elements in this system, and the variations which these show. Muscles range from separate entities with easily determined **origins** and **insertions** to those which are partly joined onto

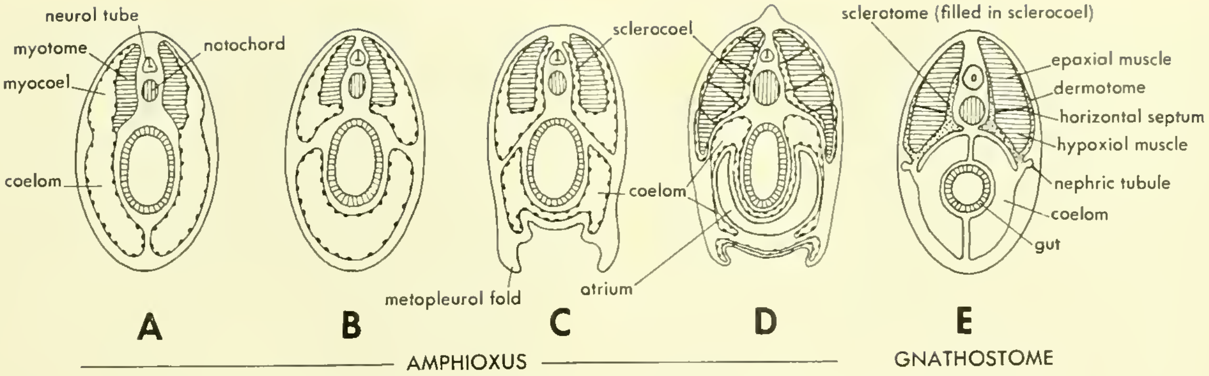


Figure 14-1. Four stages (A-D) of coelomic pouch differentiation in Amphioxus as compared with mesodermal differentiation in a gnathostome (see also Figure 10-15). (A to C after Prenant, 1936)

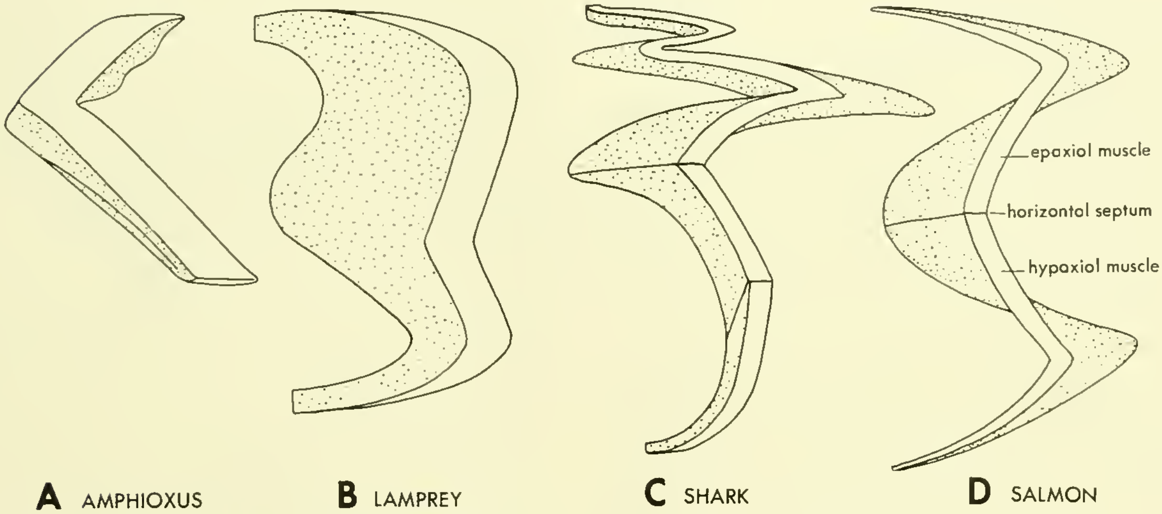


Figure 14-2. Shape of an individual myomere in four chordates. (A after Nishi, 1938; C after Coles; D after Greene and Greene, 1913)

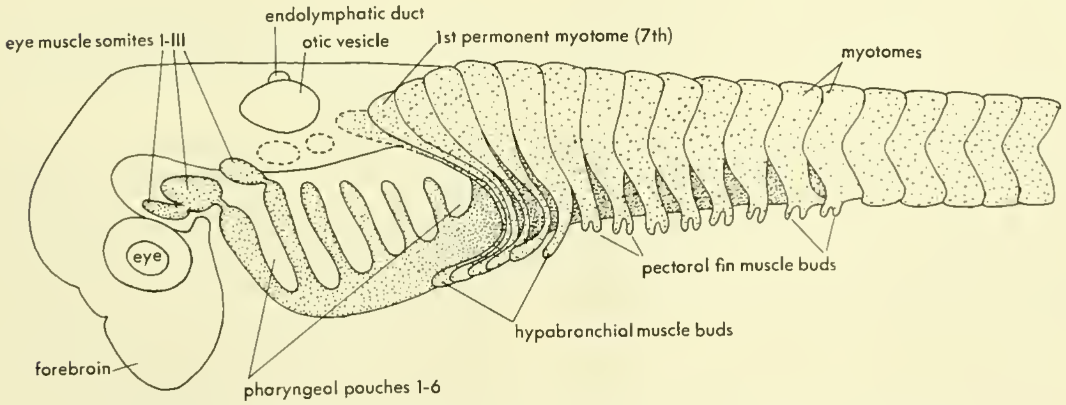


Figure 14-3. Origin of the hypobranchial musculature in a shark (gnathostome). (After Romer, 1955)

another and have variable or complex origins and insertions. The origin is the point of anchorage and the insertion is the point moved by the contraction of the muscle. Sometimes these points are purely arbitrary; in a limb the proximal point is always identified as the origin, while in the body the more anterior point is so identified.

The problems of determining muscle homologies have produced a large literature, and many bulky works such as those of Fürbringer are used to identify and discuss these problems. One result of the pioneer work in this field was the conclusion that the musculature of one class could not effectively be compared (i.e. homologized) with that of another. Therefore, it was agreed that muscles of doubtful homology should bear descriptive names derived from their origins and insertions. Muscles that could be homologized between classes would bear the name of the human homolog.

The view adopted in this text is that the complexity of the existing schemes of muscle nomenclature makes comparative discussion impossible. It is believed that a single system of names applicable to all classes of tetrapods is desirable, and that such a system can be based on the fact that the primitive pre-mammalian line of reptiles (the pelycosaurs), the primitive ancestors of the living reptiles, and the primitive ancestors of the amphibians were all very much alike: they were creeping animals with a pentadactyl (five digits) hand and foot and a nearly common system of musculature. From this starting point each line evolved separately and independently but retained much of the basic pattern.

It must be assumed that all muscles in these groups cannot be compared since homologies are not all of the same grade but range from very close, as in the comparison between the closely related species, to rather remote when comparing species at the extremes of a class or when comparing species of two classes. Within the mammals there is almost as much, or more, variation as there is between selected members of different classes. If a single system of names can be used for the mammal, then this system can be extrapolated to other tetrapods. Such a system has the value of indicating the general position and the associations of each muscle. This tends to emphasize any differences, and thus facilitates comparisons.

Extrinsic muscles of the eye

The extrinsic muscles of the eye, which rotate the eyeball in its socket, are generally described as six in number. These are innervated by three nerves, the oculomotor, trochlear, and abducens. The oculomotor innervates the **inferior oblique**, and the **internal, superior,** and **inferior rectus** muscles. The **superior oblique** is innervated by the trochlear nerve, while the abducens innervates the **external rectus.**

The variations of eye muscles are interesting particularly in comparing the cyclostomes with the gnathostomes (Figure 14-4). In the cyclostomes the superior oblique lies behind the eye and tends to rotate the eye counterclockwise in its socket. The recti are not identifiable as superior, internal, and inferior; instead there are two muscles of oculomotor innervation, one of which is in the position of the inferior oblique. The abducens, assuming that this is the homolog of the sixth nerve of gnathostomes, innervates two muscles in the position of external and inferior recti. There is a question as to whether the inferior rectus is properly named; it has been stated that oculomotor fibers extend out through the abducens to this muscle or that a branch of the oculomotor sometimes extends to it.

The condition seen in the lamprey is quite different from that of the usual gnathostome as represented by the shark, *Squalus.* Noteworthy is the fact that the rectus muscles arise around the optic pedicel not the optic foramen. In *Chlamydoselachus* the external rectus is divided into two slips, one of which partly overlaps the superior rectus insertion. In the sawfish a part of the inferior oblique inserts on the orbit margin below the normal insertion. In the rays the entire muscle inserts here. In *Carcharias* and *Mustelus* a part of the temporal muscle mass lying behind the eye inserts on the rear margin of a **nictitating membrane.** The muscle draws this transparent membrane up and back to cover the eye; another part of the muscle mass pulls the upper eyelid down.

In the actinopterygian fishes the basic pattern of six muscles is retained. There is some variation in the course of the oculomotor nerve and its branches to these muscles. The eye muscles of the salmon extend well beyond the margins of the orbit, and their origins lie inside the anterior and posterior myodomes (Figures 5-6, 5-7). A posterior myodome is characteristic of most actinopterygians.

In the dipnoan *Protopterus* there are the usual six muscles. The inferior rectus and internal rectus are close together and only partly differentiated. The external, inferior, and internal rectus arise together below the optic nerve, while the superior rectus arises more posteriorly on the connective tissue overlying the optic nerve. *Latimeria* also has the inferior and internal recti closely joined.

In the Amphibia the pattern is the same as in the fish, but the external rectus has divided to form a **retractor bulbi** and an external rectus. The name external rectus is thus used in two senses.

In the reptile (lizard) the pattern is comparable. The retractor bulbi is now divided into several sips. There are usually two of these: an upper **bursalis** and a lower "retractor bulbi." Both of these take origin inside of a posterior myodome in Sphenodon and squamates. In *Varanus* there are three retractors: two dorsal bursalis muscles and a single ventral retractor bulbi.

The bird is quite distinct as compared with the reptile. The basic pattern of six muscles is the same but the retractor bulbi has been modified into a **quadratus** and a **pyramidalis.** The pyramidalis has a long tendon circling

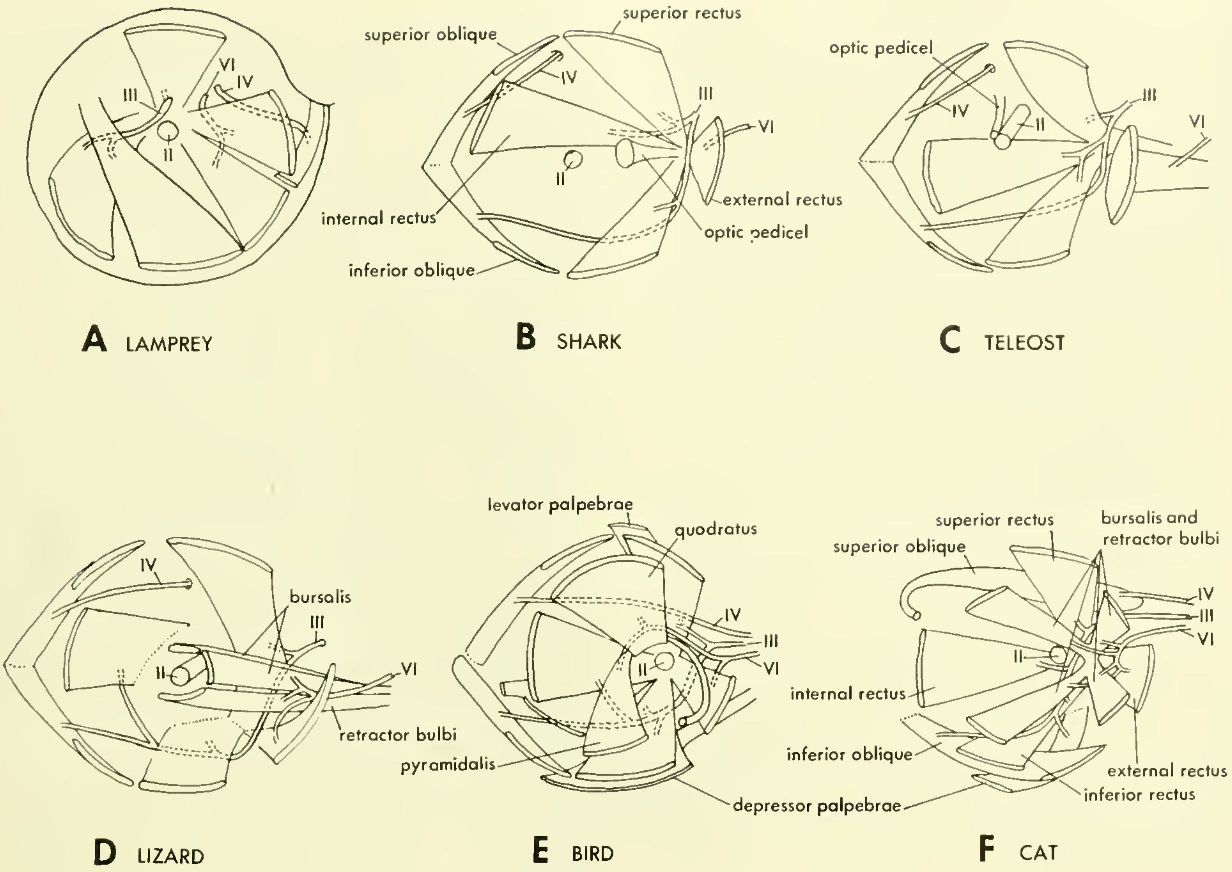


Figure 14-4. Eye muscles of vertebrates and their innervation.

around behind the eye and through the lower lid to the nictitating membrane. Contraction of this muscle pulls the nictitating membrane across the surface of the eye from front to back. The inferior rectus has been modified into two parts; a superficial **depressor palpebrae,** which pulls down the lower eyelid, and the inferior rectus proper. Again there is a problem of terminology: should one use **pars depressor palpebrae** and **pars rectus** for these two divisions or identify them as distinct muscles? The superior rectus also may be subdivided into a **levator palpebrae** and rectus proper.

The crocodilian eye musculature is like that of the bird but is not as highly modified.

In the mammal there is a marked peculiarity in the form of the superior oblique. It arises from the eye-socket wall above the origin of the rectus muscles, which as usual arise around the optic foramen. The superior oblique passes forward and upward over the eyeball through a pully of ligamentous tissue and from here backward and downward to insert on the eyeball. The action of the superior oblique is the same as the action in other vertebrates but the form is quite distinctive. The occurrence of a pully suggests that the origin had shifted backward to this new position. The superior rectus may also be divided into a levator palpebrae and a superior rectus. The retractor bulbi of the mammal is highly variable. There may be several parts paralleling the optic nerve. The retractor bulbi is innervated along with the external rectus by the abducens nerve.

The six basic extrinsic eye muscles develop from the three pairs of preotic somites of the head or from three pairs of mesenchymatous condensations. In the shark there are three distinct mesodermal vesicles from whose parts these muscles condense (Figure 14-3). There is some disagreement about the exact details for the shark. Head cavities occur in many groups: shark, *Amia, Lepisosteus,* alligator, turtle, and some birds. In some fish (salmon), the chick, and cat, head cavities as such do not appear, only mesenchymal condensations.

The evolution of eye muscles of vertebrates suggests a basic pattern, at least among gnathostomes, which has undergone some modifications in accordance with the use of the eyes and changes of the orbit area. The retractor bulbi appearing in the Amphibia was probably developed to protect the eye by retracting it into the orbit at the same time the eyelids are closed.

The limb muscles of the mammal

A study of the musculature of the mammal is generally considered an important part of a student's training in comparative anatomy because of its dissection interest, the terminology involved, and its value as an introduction to human myology. Any comparative discussion of myology must be based upon a knowledge of the musculature of at least one animal. For this purpose, the cat will be described.

The musculature of the limbs can be divided into extrinsic and intrinsic divisions. Extrinsic refers to those muscles anchoring the limb to the body; intrinsic identifies the muscles within the limb. These are arbitrary divisions which are hard to differentiate in the actual specimen.

The muscles of the pectoral appendage After drawing the skin off the shoulder region and exposing the upper part of the forelimb, the dorsal extrinsic muscles can be observed. Arising from the dorsal midline (the tips of the neural spines of the vertebrae—Figure 14-5) are a series of sheet-like muscles which taper toward and insert over the shoulder region. The first of these, the **levator scapulae,** arises in the occipital region and extends posterolaterally, below a part of the second muscle, to insert on the spine of the scapula. The next posterior muscle, the **trapezius,** is divided into three parts: the **pars clavotrapezius,** the **pars spinotrapezius anterior,** and the **pars spinotrapezius posterior.** The last two parts insert along the spine of the scapula, and the first inserts on the clavicle. The broad **aponeurosis,** or tendon, of origin of the pars spinotrapezius anterior is transparent, and through it can be seen a part of the supracoracoideus muscle, whose fibers run forward and laterally. The trapezius extends beyond the clavicle, to the forearm, as the **pars clavobrachialis.** This could be considered an intrinsic muscle. The **latissimus dorsi,** the most posterior muscle, arises over a wide arc of the body wall. The belly tapers anteriorly and inserts on the underside of the proximal end of the humerus. The latissimus is partly overlaid with a sheet of muscle which tapers to its origin in the axilla of the forelimb. This sheet is a part of the **cutaneous maximum,** which twitches the skin (a **cutaneous muscle**). An intrinsic part of the latissimus, the extensor antibrachialis, is described below.

The several parts of the trapezius can now be cut, across the middle of their bellies, and the cut ends reflexed. The rhomboideus muscle is now exposed. It arises from the body wall, along the neural spines; its fibers extend posteriorly and then laterally, as numerous separate bundles, to insert on the posteroventral margin and angle of the scapula. This same area serves for the insertion of a second muscle, the **serratus anterior** and **posterior.** The two parts of the serratus are not distinct; the fibers of the anterior are posteriorly directed from their slips of origin, off the rib basket, to their insertion, while those of the posterior are dorsally directed.

Viewed ventrally (Figure 14-6), there are also several sheet-like muscles. The most anterior band, which extends outward to insert on the forearm, beyond the elbow joint, is the **pars pectoantibrachialis** anterior of the **pectoralis major** muscle. Behind this and with a similar insertion may be a small band from the pars humeralis; this second band is the **pectoantibrachialis posterior.** The **pars humeralis** may be subdivided, and behind it is the **pars xiphihumeralis.** If the pectoantibrachialis and anterior portion of the pars humeralis are separated, deeper bands of the pectoralis are exposed; these insert nearer the proximal end of the humerus (and over the surface of the biceps muscle). The most medial of these deep bands corresponds in position and function to the **pectoralis minor** muscle of the human. In mammals generally, the pectoralis is highly variable in its subdivisions. Since homologizing the subdivisions is not possible, the names used above are arbitrary.

Returning to the dorsal aspect, the "intrinsic" muscles of the upper arm can now be examined. With the trapezius muscles reflexed, the muscles of the scapula are largely exposed. The **deltoideus** has two parts: the first, the **pars acromialis,** arising from the anterior end of the spine of the scapula (the acromial process), and the second, the **pars spinalis,** further back. These areas of origin are separated by the area of insertion of the levator scapulae. Both parts of the deltoid insert together on the anterolateral ridge (**deltoid crest**) of the humerus.

The scapula is covered by the **supracoracoideus;** above the spine it is covered by the **pars supraspinatus** and below the spine by the **pars infraspinatus.** Below the infraspinatus, near its insertion on the head of the humerus, is the **teres minor.** This is observed by cutting through the middle of the deltoid bellies and reflexing the cut ends. Along the ventral margin of the scapula is the large **teres major** muscle paralleling the infraspinatus; its insertion end passes to the underside of the upper-arm muscles.

By clearing out the fascia, connective tissue, and separating the several deep bellies of the pectoralis, the medial aspect of the scapula can be observed. The fan-shaped serratus anterior and posterior arises off the body wall by a number of slips; the belly tapers to its sertion at the posterior tip of the scapula. Along the ventral margin of the scapula is the teres major which tapers to a band and inserts on the inner aspect of the anterior crest of the humerus. This insertion passes below, next to the humerus, the origin tendon of the biceps muscle. Above the teres major is the large **subscapularis** covering the inner surface of the scapula. It tapers to an insertion on the adjacent head of the humerus. Anterior to and above the insertion of the subscapularis is the **coracobrachialis** muscle. This arises by a tendon from the **coracoid process** of the scapula and expands to its fleshy insertion on the head of the humerus next to the insertion of the subscapularis.

The muscles of the dorsal aspect of the upper arm include the **clavobrachialis,** already described, which inserts with the brachialis. The brachialis lies anterior to and below the

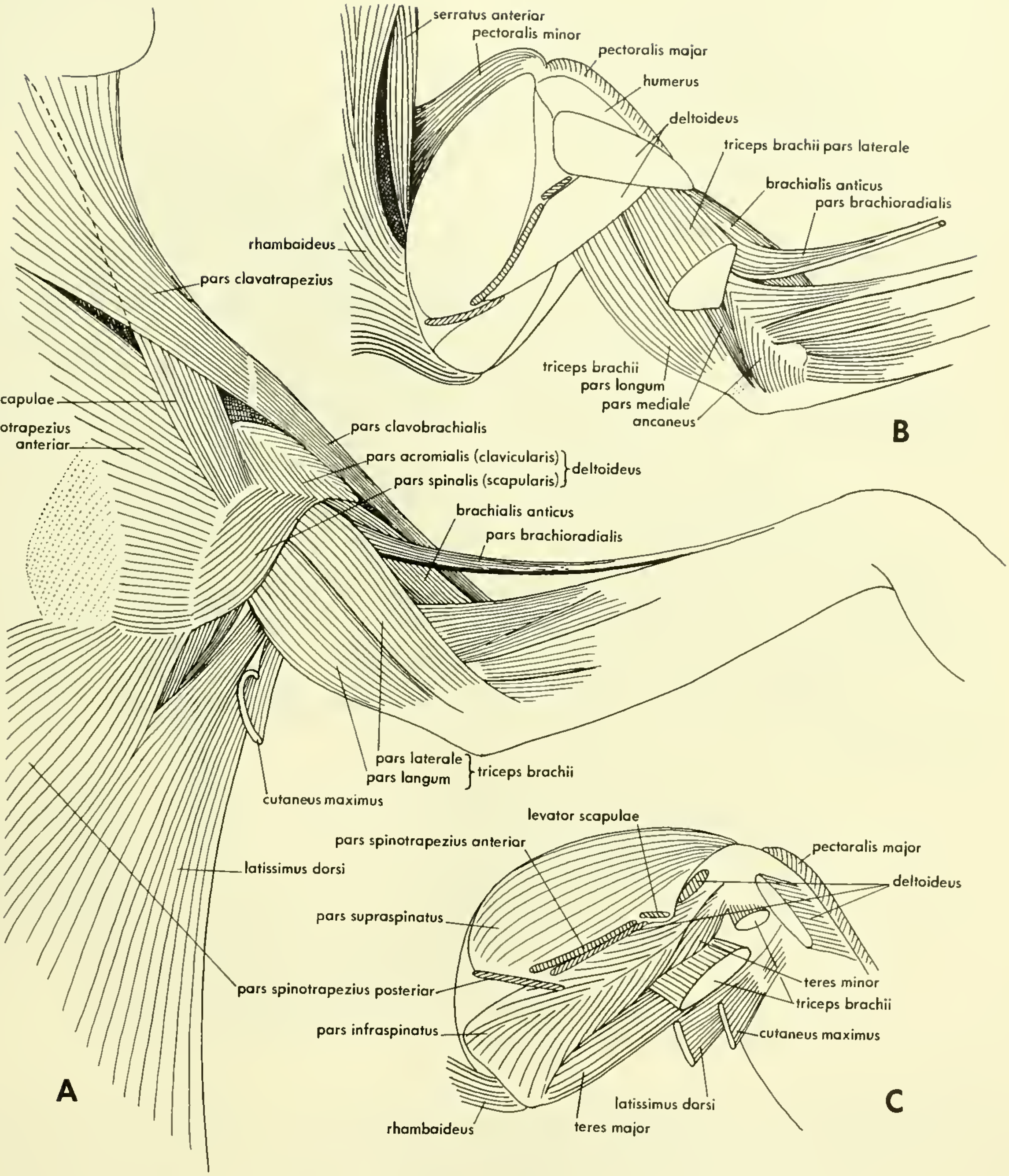


Figure 14-5. Dorsal musculature of the shoulder and upper arm of the cat. A, dorsal superficial layer; B, deeper muscles with levator scapulae, and trapezius removed; C, details of muscles associated with the scapula.

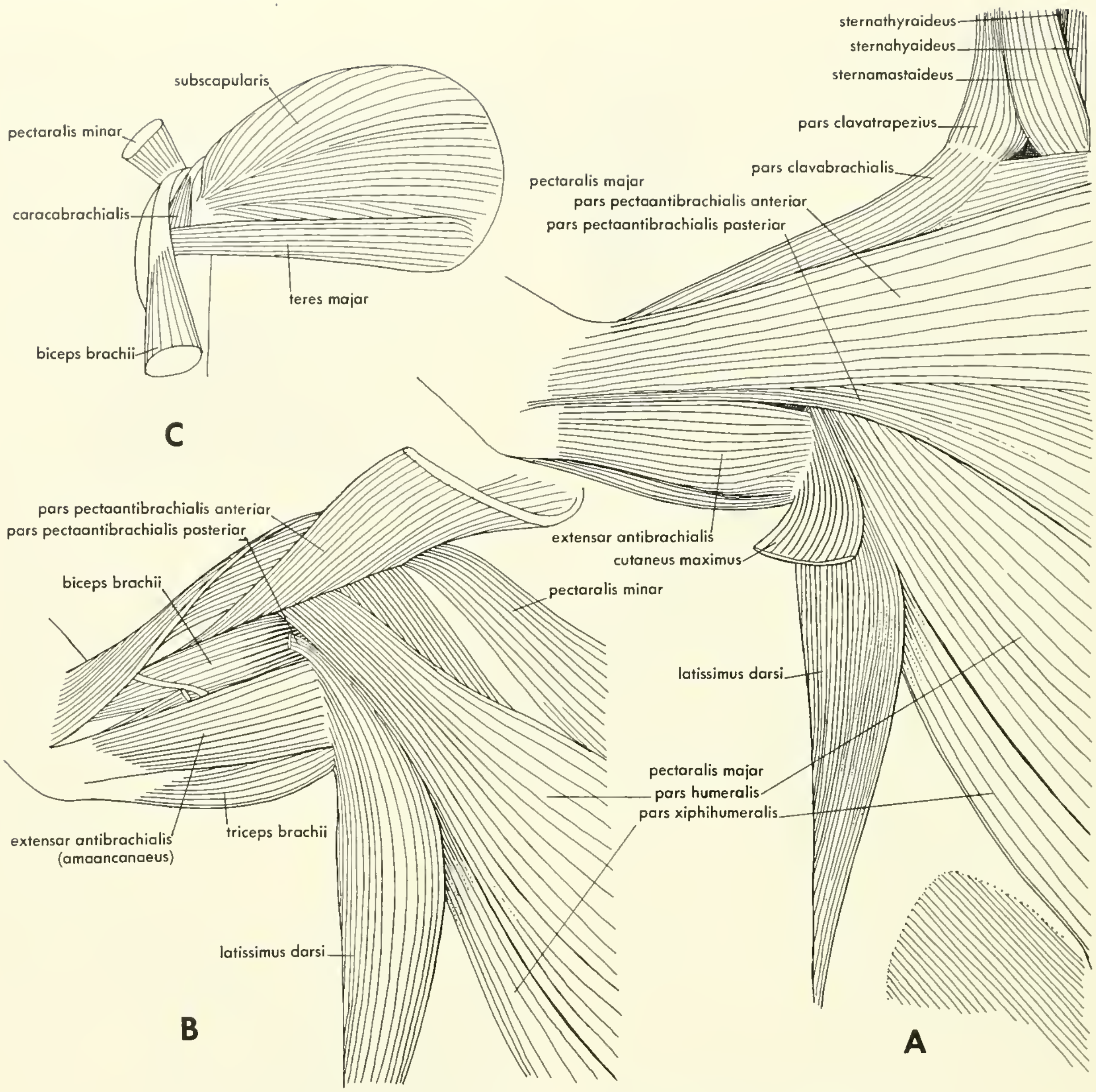


Figure 14-6. Ventral musculature of the shoulder and upper arm of the cat. A, ventral superficial layer; B, deeper layers revealed by reflexing a part of the superficial layer; C, muscles of the inner aspect of the scapula.

brachioradialis; it arises from the humerus and inserts on the radius and ulna. The brachioradialis is but a part of the brachialis, which arises from the belly of that muscle and extends as a narrow band out along the nerves and blood vessels going to the hand. Behind the brachialis is the **triceps,** two heads of which can ben seen. The **pars lateralis** and the **pars longum** are both large bellies which taper to a broad common insertion over the olecranon process of the ulna. Their origins are from the head of the humerus and the lower margin of the scapula respectively. If the lateral head of the triceps is bisected and the ends reflexed, the **medial head** and the **pars anconeus** are seen. Both of these arise along the humerus. On the ventral aspect is a muscle similar to the pars anconeus, this is the **epitrochleo-anconeus.**

On the ventral aspect of the upper arm, with the pars pectoantibrachialis raised or reflexed, is the **biceps brachii,** as distinguished from the biceps femoris of the thigh. The biceps arises from the anterior aspect of the base of the coracoid process of the scapula by a long tendon and inserts through a tapered tendon on the radius and ulna (along with the brachialis). Behind the biceps is the **extensor antibrachialis,** also called the **omoanconeus.** This muscle is a part of the latissimus dorsi extending to the **antibrachium,** or forearm, from the area of insertion of the latissimus. Along the posterior margin of the upper arm is seen the long head of the triceps.

The forearm muscles are more numerous and therefore more difficult to identify (Figure 14-7). For orientation purposes the forearm can be thought of as having anterior and posterior margins, and dorsal and ventral surfaces. On the dorsal aspect, beginning at the anterior margin, is the **brachioradialis** which inserts on the radiale bone of the

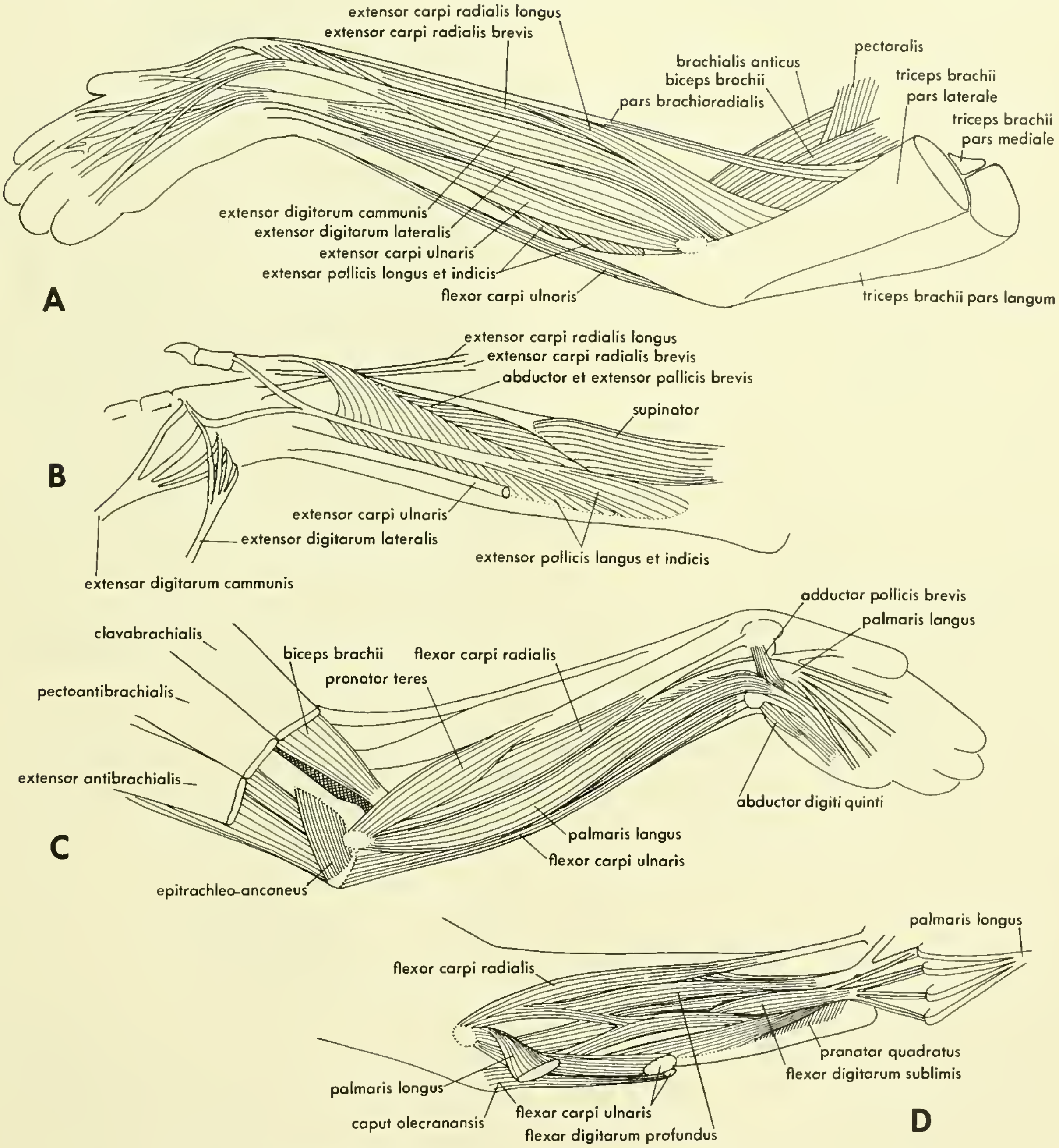


Figure 14-7. Forearm musculature af the cat. A, superficiol muscles af darsal aspect; B, deeper layer; C, superficial muscles of ventral aspect; D, intermediate and deep layers of muscles; E, deep layer.

wrist and over the surface of the insertion tendon of the extensor pollicis brevis (described below). Behind this, toward the rear margin of the forearm, and arising from the humerus by a broad flat head is the **extensor carpi radialis longus.** This muscle is closely bound to the **extensor carpi radialis brevis.** The belly of the longus tapers to a tendon after about one-third of the length of the forearm, while the brevis belly extends nearly to the wrist joint. The tendons of these muscles insert on the bases of the second and third metacarpals respectively.

Behind the extensor carpi radialis muscles are the **extensor digitorum communis** and the **extensor digitorum lateralis.** These arise from the lateral condyle of the distal end of the humerus. Their insertion tendons are subdivided into four parts which fan out and attach at the bases of digits II to V in the case of the lateralis and along the phalanges of these digits in the case of the communis. Along the posterior margin of the dorsal musculature is the **extensor carpi ulnaris.**

Beneath the superficial dorsal muscles are additional ones. The **abductor and extensor pollicis brevis** arises along and between the distal parts of the radius and ulna. Its fibers taper to a short tendon which overlies the insertion tendons of the extensor carpi radialis muscles and inserts on the proximal end of the first metacarpal. Proximal to this muscle is the **supinator** which arises from the humerus and inserts on the radius. Behind these muscles is the long, band-like **extensor pollicis longus et indicis,** which arises from the proximal part of the ulna and inserts by two tendons on the bases of the first and second phalanges.

The ventral muscle mass has the **pronator teres** along its anterior proximal margin. This muscle arises from the inner condyle of the humerus and inserts on the radius next to the supinator of the dorsal mass. Behind the pronator is the **flexor carpi radialis** and behind this a broad muscular band, the **palmaris longus.** These muscles also arise from the medial condyle. The first inserts on the radiale, the second has a complex insertion through long tendons attaching to the bases of digits II to V. At the wrist a small fleshy belly arises off the palmaris and inserts by tendons on digits IV and V, below the tendons of the palmaris. Cross-muscle fibers on the wrist joint form an **adductor pollicis brevis.** Behind the palmaris is the **flexor carpi ulnaris,** which has two heads of origin: one from the olecranon (and in part from the epitrochleo-anconeus—see Figure 14-7) and the other from much of the length of the ulna. The insertion of the flexor carpi lunaris is on the ulnare, and, through the bracing ligament of that bone, on the metacarpals. Associated with this insertion is a small **abductor digiti quinti.**

The deeper layer of flexor musculature consists of the several (and varied) bellies of the **flexor digitorum profundus.** A part of this complex can arbitrarily be identified as the **flexor digitorum sublimis.** The belly of the sublimis lies near the wrist and its slim tendons pass between those of the palmaris and the profundus proper.

The muscles of the pelvic appendage The muscles of the thigh are more difficult to identify than those of the forelimb. Since only a superficial survey of the hind limb muscles is intended, the details of origins and insertions will be largely omitted. Viewed laterally (Figure 14-8), the **sartorius** forms the anterior margin of the thigh. Behind the sartorius is an irregular-shaped **tensor fasciae latae,** which arises from the anterior end of the ilium and inserts into the **fasciae latae** covering the outer surface of the thigh. Covered by the fasciae latae and inserting on the head of the femur is the **gluteus medius** and the **gluteus maximus,** while distally, covered by the fasciae latae, is the **vastus lateralis.** Behind the line of the femur is the **coccygeofemoralis pars femoralis** and then the large **biceps femoris,** which inserts on the shank through a broad sheet-like tendon or aponeurosis. Behind the biceps femoris can be seen a part of the **semitendinosus.** With the exception of the gluteus muscles, the insertions are broadly over the knee and the lateral aspect of the proximal part of the shank. Within the aponeurosis of the knee is the **patella,** a sesamoid bone.

Exposure of the underlying muscles is difficult because of the fasciae latae. By cutting through and reflexing this layer, the gluteal muscles can be exposed. The coccygeofemoralis and biceps can be severed near their origins and the ends reflexed. Care should be taken to observe the slender band of muscle, the **pars tenuissimus** of the coccygeofemoralis. It arises just below the pars femoralis, extends distally and posteriorly on the inner surface of the biceps femoris, and inserts just inside or along the posterior margin of the biceps femoris. This part is lacking in some specimens. From the origin of the coccygeofemoralis on the transverse processes of two or three caudal vertebrae, a short belly extends down and forward to insert along the margin of the ischium; this can be identified as the **pars ischiadicus** of the coccygeofemoralis.

The gluteus medius and maximus have thick and fleshy bellies tapering to broad insertions on the margin of the outer or greater trachanter of the femur. By careful section of these muscles, a deeper layer consisting of the **gluteus minimus** and **pyriformis** is exposed. The minimus parallels the ventral margin of the medius and can be seen by lifting that margin. The pyriformis is largely fused with the medius and is difficult to expose. The sciatic nerve trunk passes below (medial to) and behind the pyriformis and separates it from another layer of muscles inserting on the margin of the greater trochanter of the humerus.

The muscles behind the sciatic nerve are not distinctly separated one from another. The most posterior muscle is the **quadratus femoris;** its thick belly tapers anteriorly to insert on the posterior margin of the greater trochanter. Above the quadratus is the **obturator internus,** only the ininsertion portion of which is seen. The obturator internus arises on the inner surface of the pelvis, from the ischium and the margins of the obturator fenestra. The belly tapers and passes over the margin of the ischium; here it forms a thick

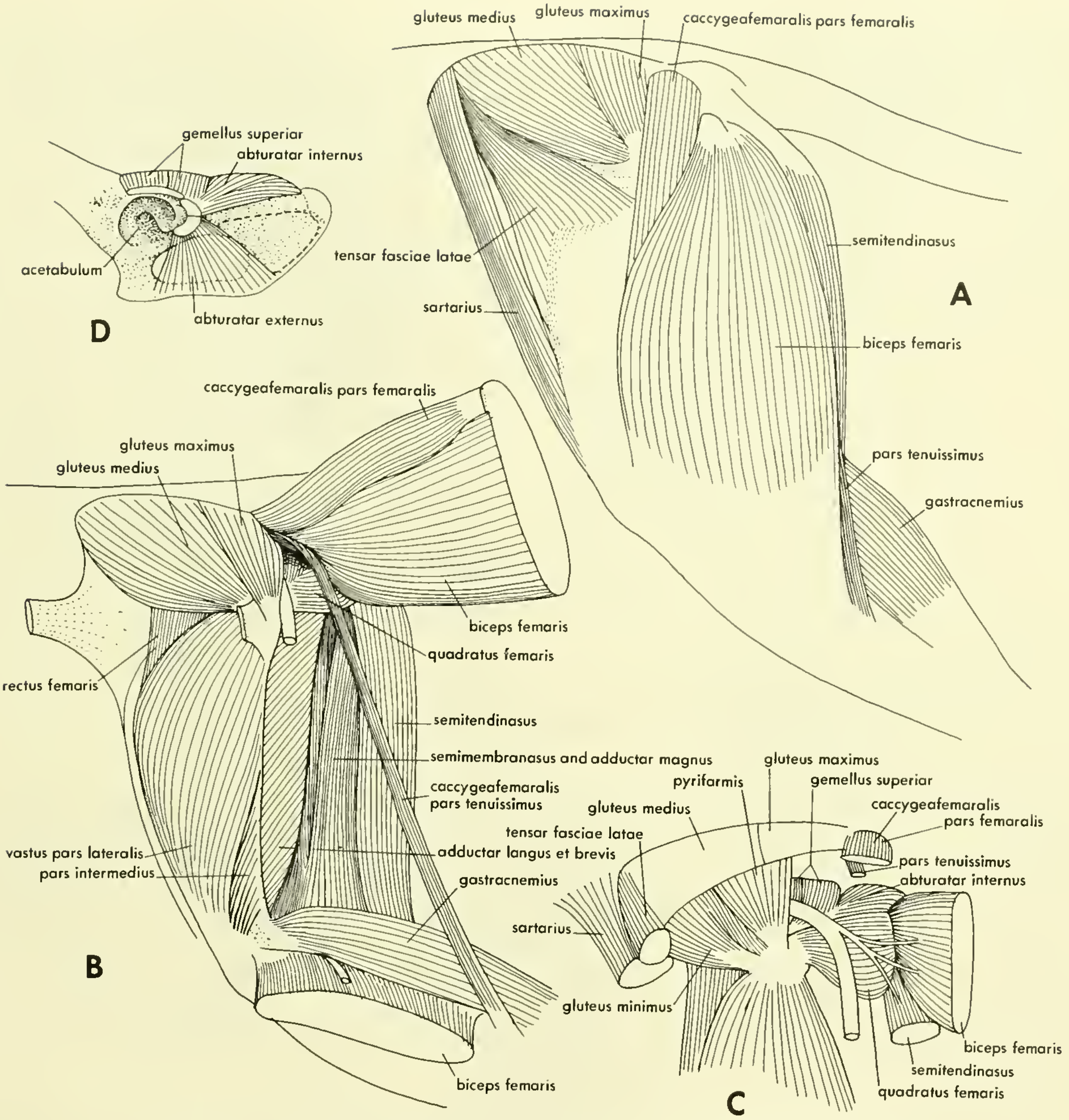


Figure 14-8. Dorsal (outer) musculature of the hip of the cat. A, hip seen in lateral view; B, lateral view with caudofemoralis and biceps femoris reflexed; C, deeper muscles of hip joint; D, relationships of obturator muscles to pelvic girdle as seen in lateral view.

tendon which inserts on the greater trochanter. Anterior to the tendon of the internus is the **gamellus inferior** which arises from the pelvis, above the acetabulum, the socket for the head of the femur. Anterior to, and below, the inferior is an indistinct **gamellus superior.**

The extrinsic muscles of the internal aspect of the thigh are several (Figure 14-9). Anteriorly there is the broad sartorius, posteriorly the sheet-like **gracilis.** Section of these two muscles reveals, from front to back, the **rectus femoris** clasped between the vastus lateralis and **vastus medialis,** the insertion end of the "iliopsoas," the **pectineus,** the **adductor longus,** the **adductor magnus** (or femoralis), the **semimembranosus,** and the **semitendinosus.**

Followed into the body cavity, the "iliopsoas" is seen to

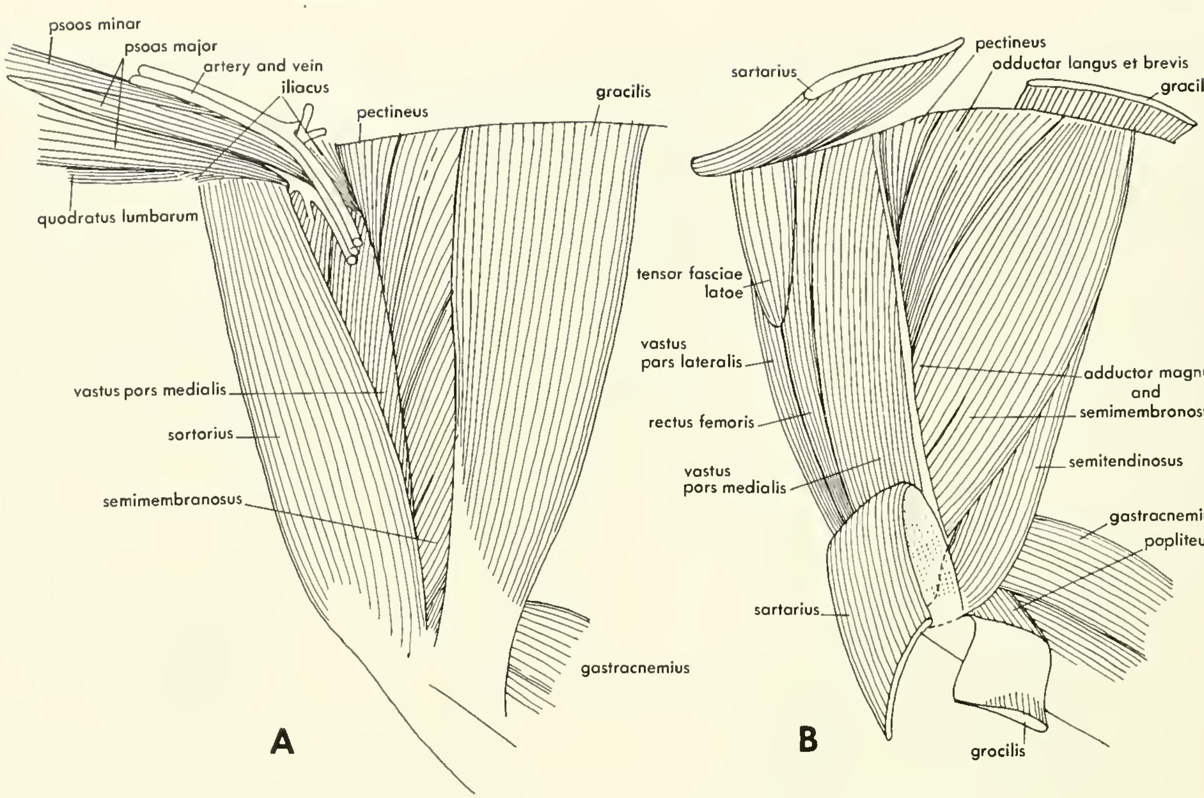


Figure 14-9. Ventral (inner) musculature of the hip of the cat. A, hip in medial view with body wall opened to expose the iliacus and psoas muscles; B, deeper layer.

be made up of a **psoas major** arising from the under side of the vertebral muscles. Medial to the major is the **psoas minor** tapering posteriorly to a long tendon which inserts on the ilium, below the head of the femur. From the margin of the pelvis behind and above the insertion of the minor, another muscle, the **iliacus** arises. Its belly extends posteriorly and laterally, wrapped partly around the psoas major, to insert in common with the psoas major. Section of the bellies of the pectineus and adductor longus reveals the **obturator externus.** This muscle arises around the margins of the obturator fenestra; its belly tapers to a tendon which inserts on the femur, behind the neck, in common with the obturator internus.

The intrinsic muscles of the thigh are the vastus lateralis, vastus medialis, and **vastus intermedius.** These arise from the surface of the femur and insert on the knee region with the extrinsic muscles.

The shank musculature is separable into an anterior (dorsal) division and a posterior (ventral) division (Figure 14-10). The superficial layer of the posterior muscles includes the two heads of the **gastrocnemius, lateral** and **medial,** and the distally separated **plantaris.** Below this outer layer is a spindle-shaped muscle, the **soleus,** which inserts with the outer muscles. Medial to the proximal end of the soleus is the **popliteus,** which inserts along the fibula. Below the soleus and lateral to the popliteus are the **flexor hallucis,** and **flexor digitorum longus,** in that order.

The anterior muscles are the outer (and medial) **tibialis anterior** and below this the **extensor digitorum longus.** On the lateral aspect of the tibia is a series of three **peronaeus muscles:** the **longus, tertius,** and **brevis** in a proximal to distal order.

The muscles of the foot and the insertions of the shank muscles, the flexors and extensors of the digits, resemble those of the hand.

General observations In describing limb muscles a number of basic terms of functional connotation are encountered. The contraction of a muscle is related to responses in antagonistic and complementary muscles and results in the movement of one, or more, skeletal unit in relation to another, or others. The resultant actions are described by the terms defined in Table 14-1.

As is apparent from the examples given and the previous description, these terms are commonly used in the naming of the muscles. The shape of a muscle (deltoides), the number of parts or heads (biceps), as well as the origin and insertion of a muscle (coccygeofemoralis), have also been utilized in forming names.

EMBRYOLOGICAL DEVELOPMENT The embryological origin of the limb muscles gives an insight into their functional differentiation. The musculature of the mammal arises as dorsal (extensor) and ventral (flexor) condensations of mesenchyme in the limb bud. Table 14-2 indicates the progressive modification of these masses in the pectoral limb into proximal, forearm, and hand segments and the separate components of the proximal mass.

The phylogeny of the scapular muscles of the placental mammal is indicated by their ontogeny in the opossum. In Echidna or the reptile the supracoracoideus muscle is a unit, just as it is in the early developmental stages of the opossum (Figure 14-11). In the latter the single muscle grows backward and upward, bifurcates at the spine of the scapula to become the supra and infraspinatus muscles. The embryology of other muscles indicates changes in shape, number of parts, and even origin and insertion. Circuitous routes of innervating nerves are observed to be the result of migration of the muscle.

INNERVATION Another aspect of myology which has been emphasized concerns innervation, the identification of the nerve serving each muscle and the constancy of this relationship in the several classes. Much of the past discussion

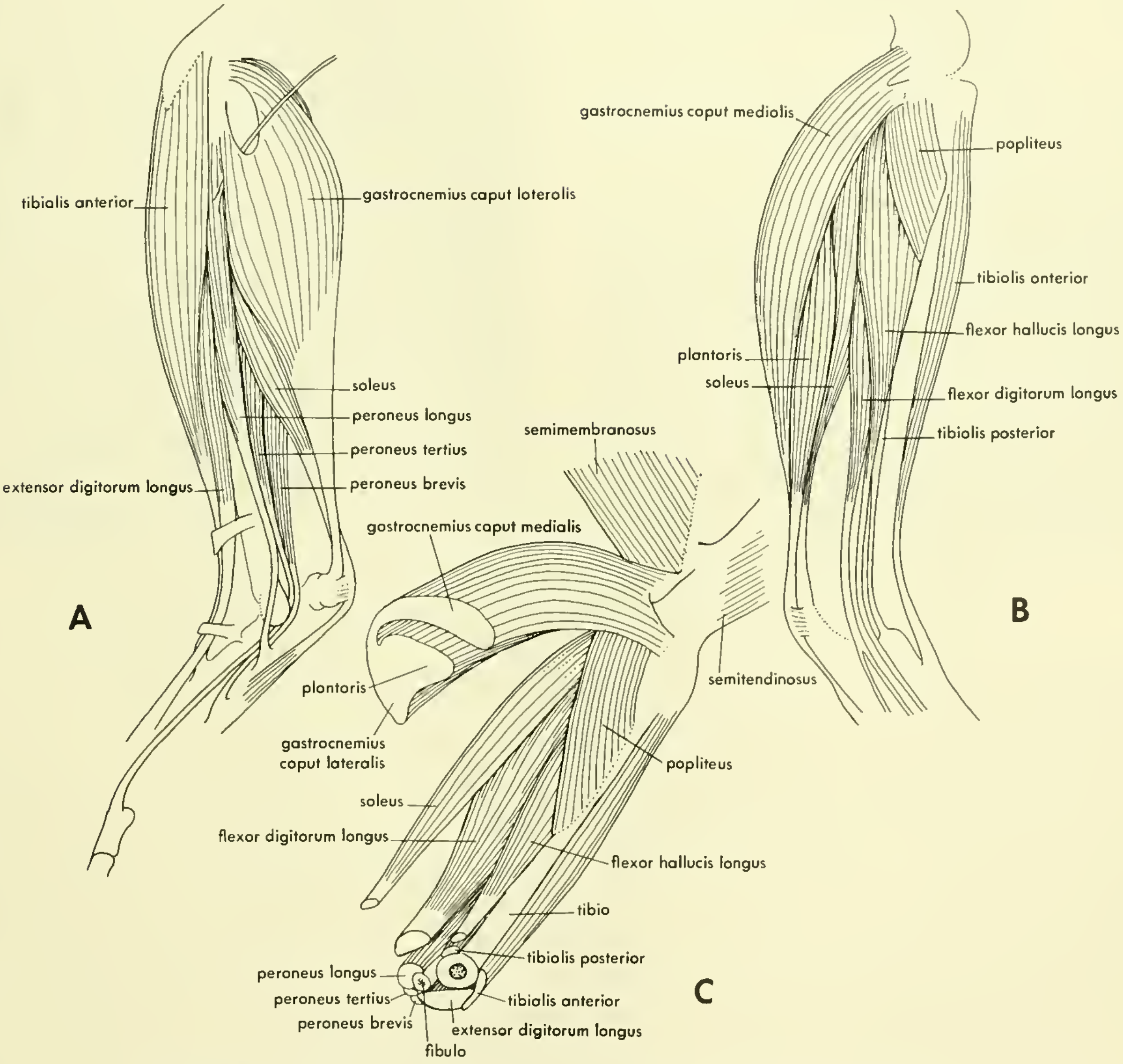


Figure 14-10. Muscles of the shank of the cat. A, outer muscles; B, inner muscles; C, deeper details of B.

of muscle homology was related to the theory that nerve and muscle have a fixed relationship and in fact are joined from the very beginning. It is now known that these structures arise separately and that the nerves grow out to reach their end structure. Experimental work shows that the innervation can be altered without loss of proper function. Comparative studies indicate that the pattern of nerves is plastic and reflects the loss, subdivision, or fusion of muscles. Peculiar innervations are the result of migration of a muscle to a new position and relationship after its nerve has reached it. In spite of this plasticity, the branchial plexus and pattern of nerves of the rabbit (Figure 14-12) can be compared readily with that of the cat or man, and more superficially with the reptile or bird.

TABLE 14-1 TERMS USED TO DESCRIBE THE ACTIONS OF MUSCLES OR THE CATEGORIES OF MUSCLES HAVING A COMMON ACTION

flexors	muscles which tend to close the angle between two bones
extensors	muscles which increase the angle between two bones
abductors	muscles which draw the bone away from the median line of the body or midline of the limb
adductors	muscles which draw the bone toward the median line of the body or limb
rotators	rotate bones around a central axis. The supinator rotates the radius in relation to the ulna so that the palm is turned up; the pronator teres rotates these bones so that the palm (the ventral surface) is turned down and the radius and ulna are slightly crossed.
elevators or **levators**	muscles which raise or lift a part; the levator scapulae raises the scapula
depressors	pull down or lower as in the case of the jaw muscles which open the mouth ("depressor mandibulae")
constrictor	rings of muscle fibers which close openings or decrease diameters as in the case of the sphincter muscles of the gut or the constrictor colli, a dermal muscle of the neck

The comparative anatomy of shoulder muscles

As an example of comparative myology the muscles of the shoulder region of the mammal can be compared with those of a reptile and an amphibian.

Reptile The musculature of *Iguana* is much like that of *Sphenodon, Lacerta,* or *Alligator.* In *Iguana* (Figure 14-13) the dorsal extrinsics consist of a **trapezius,** which has an anterior **pars clavotrapezius** (including the **sternomastoideus**) and a posterior **pars spinotrapezius,** and a **latissimus dorsi.** Beneath this layer is a large **levator scapulae** and a two-parted **sternohyoideus** (including the **sternothyroideus**). A **serratus** muscle, attached to the suprascapular cartilage, draws the girdle backward, while three slips of muscle, the **rhomboideus** (whose fibers extend from the body wall upward and posterolaterally to the inner surface of the suprascapula), draws it forward and down. Ventrally the pectoralis has an anterior and a main division.

On the shoulder, as viewed laterally, are the **clavicular** and **scapular** divisions of the **deltoid.** With this layer reflexed (Figure 14-14) the **teres minor** (proscapulohumeralis anterior) and **supracoracoideus** are revealed. From the posterior and inner margin of the suprascapula and scapula arises a **teres major.**

As viewed ventrally (Figure 14-15), with the **pectoralis** reflexed, the supracoracoideus is seen to arise from much of the coracoid. A part of it is covered by an insertion tendon of the sternomastoid part of the trapezius. Behind and partly

TABLE 14-2 EMBRYOLOGICAL DEVELOPMENT OF THE PROXIMAL MUSCLES OF THE FORELIMB

dorsal premuscular anlage	deltoid division	deltoideus
		teres minor
	subscapular division	subscapularis
		teres major
	latissimus dorsi division	latissimus dorsi
		extensor antibrachialis
	triceps division	three heads of triceps
ventral premuscular anlage	supracoracoid division	supraspinatus
		infraspinatus
	ventral brachial division	coracobrachialis
		biceps
		brachialis
	pectoral division	pectoralis
		pectoantibrachialis

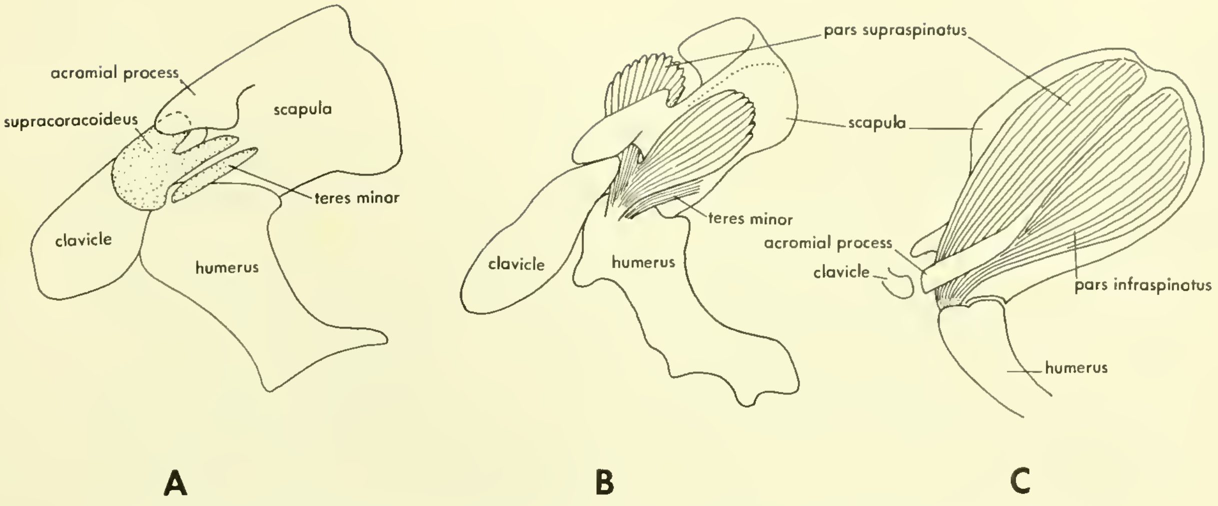


Figure 14-11. Three stages in the development of the supracaracoideus of the opossum. (After Cheng, 1955)

concealed by the supracoracoideus are the two heads of the **biceps** muscle and the fleshy belly of the **coracobrachialis brevis.** The **coracobrachialis longus** arises from the inner surface of the coracoid, behind the level of the glenoid fossa (socket for humerus). The coracobrachialis longus inserts with the biceps and on the proximal end of the humerus adjacent to its origin. On the inner aspect of the pectoral girdle is a large **subscapularis** which is joined with the teres major (Figure 14-14).

The upper arm muscles consist of the **brachialis,** biceps, and **triceps.** The latter has three heads: **lateralis, longum,** and **medialis.**

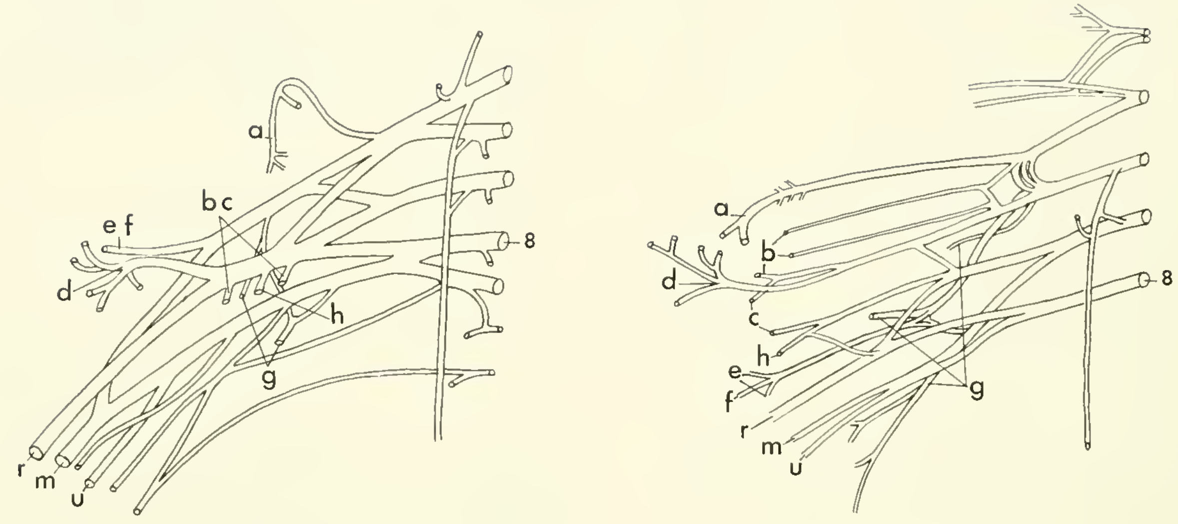
The forearm muscles are simpler than those of the mammal (Figure 14-13). The dorsal layer consists of an anterior, two-parted **extensor carpi radialis,** a middle (and superficial) **extensor digitorum,** and a posterior **extensor carpi ulnaris.** The extensor carpi radialis, which includes the **supinator,** inserts along the length of the radius. Below the extensor digitorum is the **abductor and extensor pollicis brevis,** which inserts both at the base and further out on the first digit. Associated with this muscle, and arising from the region of the ulnare, are **short extensors** (and **interosseus muscles**) of the digits II to V.

On the ventral aspect of the forearm (Figure 14-15), from front to back margin, are a **flexor carpi radialis,** a **palmaris longus,** one or more heads of a **flexor digitorum,** and a **flexor carpi ulnaris.** The flexor radialis (includes the **pronator teres**) inserts distally on the radius and on the radiale. The flexor ulnaris is bound to the extensor ulnaris and inserts on the pisiforme bone and through this movable element on the rear margin of the hand. The palmar fascia is thick and covered externally with distinct short flexors for the digits. With the exception of that of the fifth digit, these radiate from the region of the pisiform.

With the palmaris reflexed and the palmar sheet opened, the three heads of the **flexor digitorum profundus** and its tendon are seen. Involved in the origin of the heads are the bellies of the palmaris and flexor ulnaris, which arise from the inner condyle of the humerus, and a strip along the ulna anterior to the ulnar origin of the flexor ulnaris. From the palmar part of the tendon of the flexor digitorum profundus, branches extend to all five digits. On the palmar expansion of the tendon are seen thin muscle bellies collectively identified as the **lumbricales.** Below the flexor digitorum is a strongly developed pronator layer, on which is seen a separate division of the profundus which inserts on the radiale along with the flexor carpi radialis. The proximal part of the pronator layer, is semiseparate, while the distal part is a typical **pronator quadratus.**

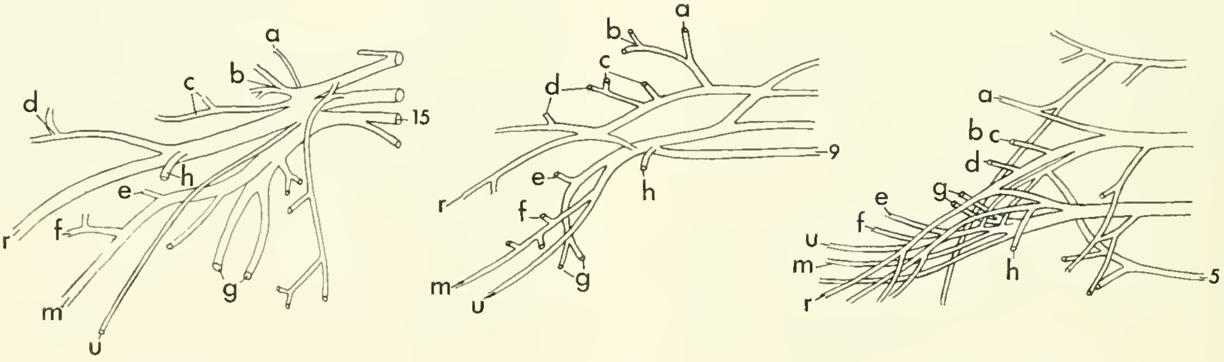
Amphibian The muscles of the amphibian are more difficult to separate from the enclosing connective tissue than those of the higher forms. Among the salamanders there is much variation in the details of the musculature and some variation in the presence and absence of particular muscles, just as among reptiles or mammals. As a large and easily dissected type, *Cryptobranchus* will be described.

The dorsal extrinsics (Figure 14-16) are the **trapezius** and **latissimus.** The former has two parts whose fibers tend to cross in reaching their insertion on the base of the scapula and the coracoid. The bellies of both the trapezius and latissimus begin some distance from the midline where the segmental myotomes are well marked. The insertion of the latissimus is along an arched line across the belly of the triceps and extending to the margin of the deltoid insertion. Below this superficial layer of muscles is an anterior **levator scapulae** and a posterior **serratus.**



A HUMAN

B RABBIT



C BIRD

D LIZARD

E SALAMANDER

Figure 14-12. Brachial plexus and its branches. A, man; B, rabbit; C, bird (*Buteo*); D, lizard (*Lacerta*); E, salamander (*Salamandra*). Nerves serving the different muscles are identified as follows: a, supracoracoideus; b, subscapularis; c, teres major; d, deltoideus and teres minor; e coracobrachialis; f, biceps brachii; g, pectoralis; h, latissimus dorsi. The number is that of the last cervical nerve root. (D after Romer, 1944; E after Hoffman, 1873–78).

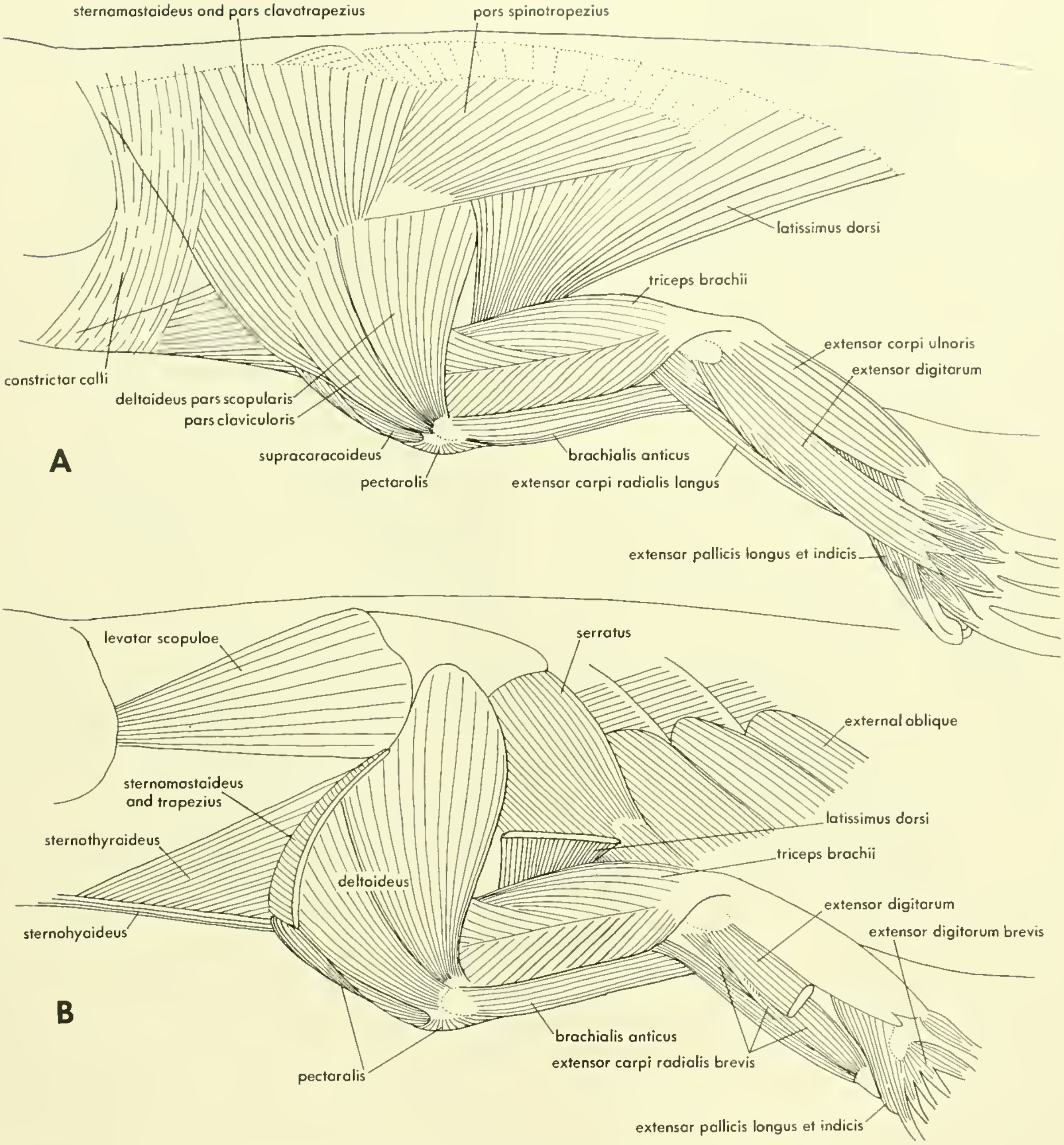


Figure 14-13. Dorsal musculature of the shoulder and arm of *Iguana*. A, superficial muscles; B, same as A but with trapezius, latissimus, and superficial layer of forearm removed.

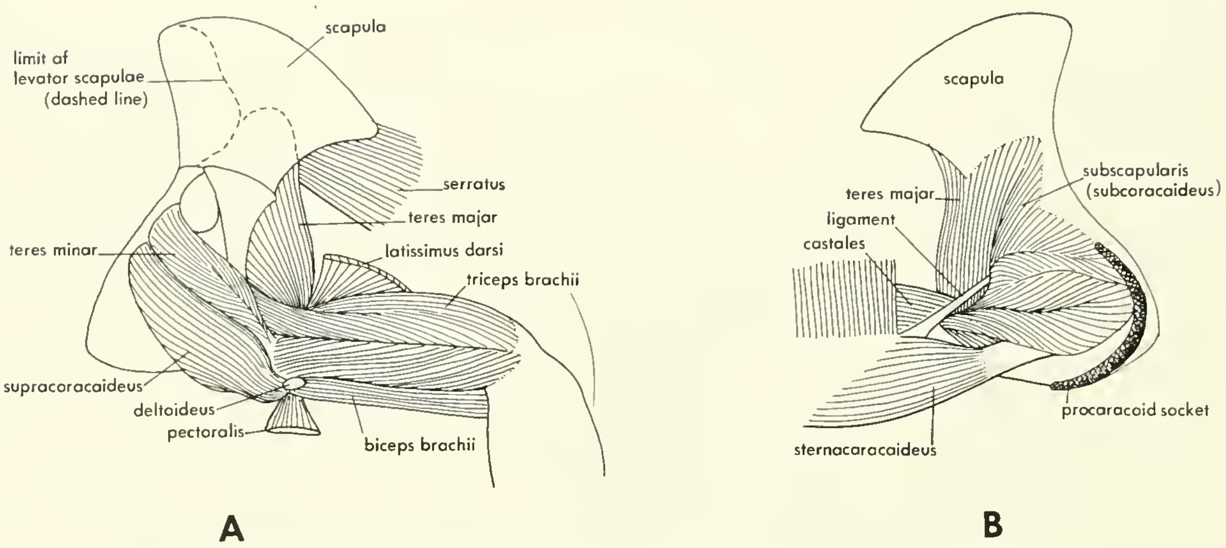


Figure 14-14. Muscles of the shoulder joint of *Iguana*. A, deep muscles on outer aspect of girdle; B, muscles of inner surface of girdle.

Ventrally (Figure 14-17) the **pectoralis** is a single mass; the muscles of the two sides meet along the midline separated only by a line of connective tissue. The **sternohyoideus** layer does not attach directly to the girdle; it is only an anterior continuation of the segmental ventral body-wall muscles. A lateral division of this series attaches to the inner surface of the scapula; this is the **rhomboideus.**

The **deltoid** has both **scapular** and **clavicular** heads; the latter is very large and joined marginally with the **teres minor.** Section of the teres minor reveals a deeper layer composed of a fan-shaped **supracoracoideus,** a thin proximal head of the **biceps** and a **coracobrachialis brevis.** Lateral to the brevis is the **coracobrachialis longus,** which arises from the margin of the coracoid and inserts along the length of the humerus and along the biceps tendon and, therefore, on the radius and ulna along with the brachialis.

The upper arm muscles are similar to those of the other groups except that the biceps is reduced to a tendon. The **triceps** has a single head. What appears to be a medial head arises from the margin of the coracoid rather than from along the humerus as in the reptile and the mammal. From its origin, this head is part of the coracobrachialis longus. Viewing the medial aspect of the girdle, a small **subcoracoideus** inserts below the **triceps head** of the coracobrachialis longus.

The forearm musculature is simpler than that of the reptile. Dorsally (Figure 14-15) there is an **extensor carpi radialis,** which includes the **supinator,** a broad **extensor digitorum,** and a thick **extensor carpi ulnaris,** joined for much of its length with the extensor digitorum. The extensor carpi radialis inserts along the radius and on the radiale. With the extensor digitorum reflexed, the deeper layer of muscles is exposed. There is an **abductor and extensor pollicis brevis,** whose belly arises off the end of the ulna. Distally this belly joins a slip of the short extensor of the first digit. The **extensor digiti brevis,** the short extensor series, arises from the proximal carpals and sends slips to all five digits.

The ventral musculature (Figure 14-17) consists of a **flexor carpi radialis,** a **palmaris longus,** and a **flexor carpi ulnaris.** Beneath the palmaris is a **flexor digitorum profundus** of two parts, one inserting on the radiale and first digit, the other on the remaining three digits. The origin of the profundus is along the ulna. Beneath the profundus is a **pronator quadratus,** which lacks a proximal division.

General observations The musculature of the amphibian suggests the embryological stages of the higher forms in the incomplete separation of some of the muscles, particularly those of the forearm. It also suggests specialization in the reduction of the main biceps belly to a tendon. The idea that there is an evolutionary sequence beginning with the amphibian and leading through the reptile to the mammal must be replaced by the view that these classes are separate lines developed from a common ancestral form. If one defines the amphibian as the ancestor of the reptiles and the mammals, then what should living amphibians be called? Each of these living groups has features which represent specializations and each retains primitive features.

The homologizing of muscles in these three classes appears relatively easy. The differences also suggest the types of problems encountered, such as the fusion of two muscles, as in the case of the mammalian **digastricus**—a jaw muscle; the separation of one muscle into two, the supracoracoideus; or the loss of a muscle sometimes accompanied by occupation of its region by another. In the course of sub-

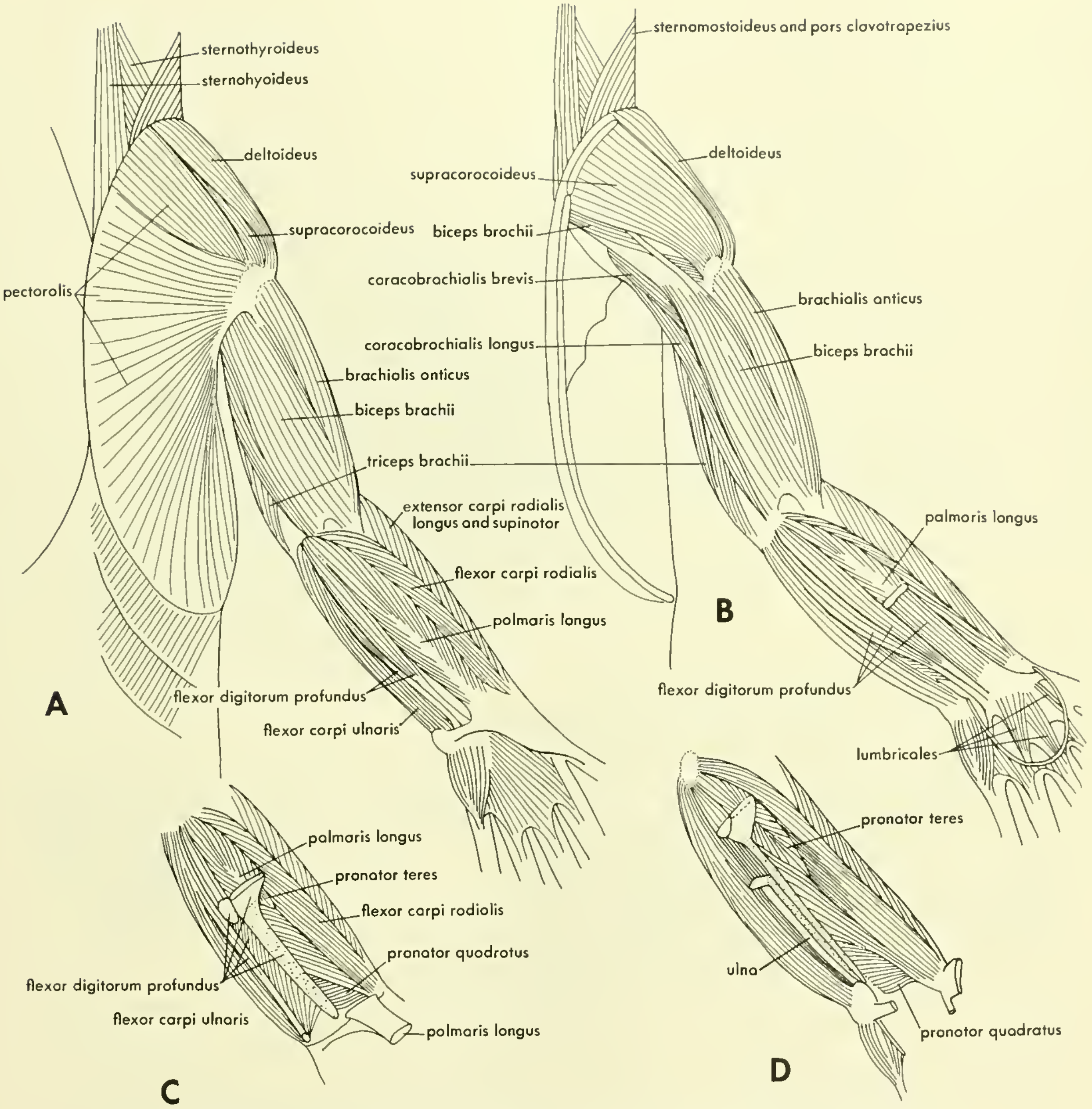


Figure 14-15. Ventral view of body and arm. A, superficial muscles; B, deeper muscles as seen with pectoralis, and with palmaris removed; C, next deeper layer of forearm muscles; D, deepest layer.

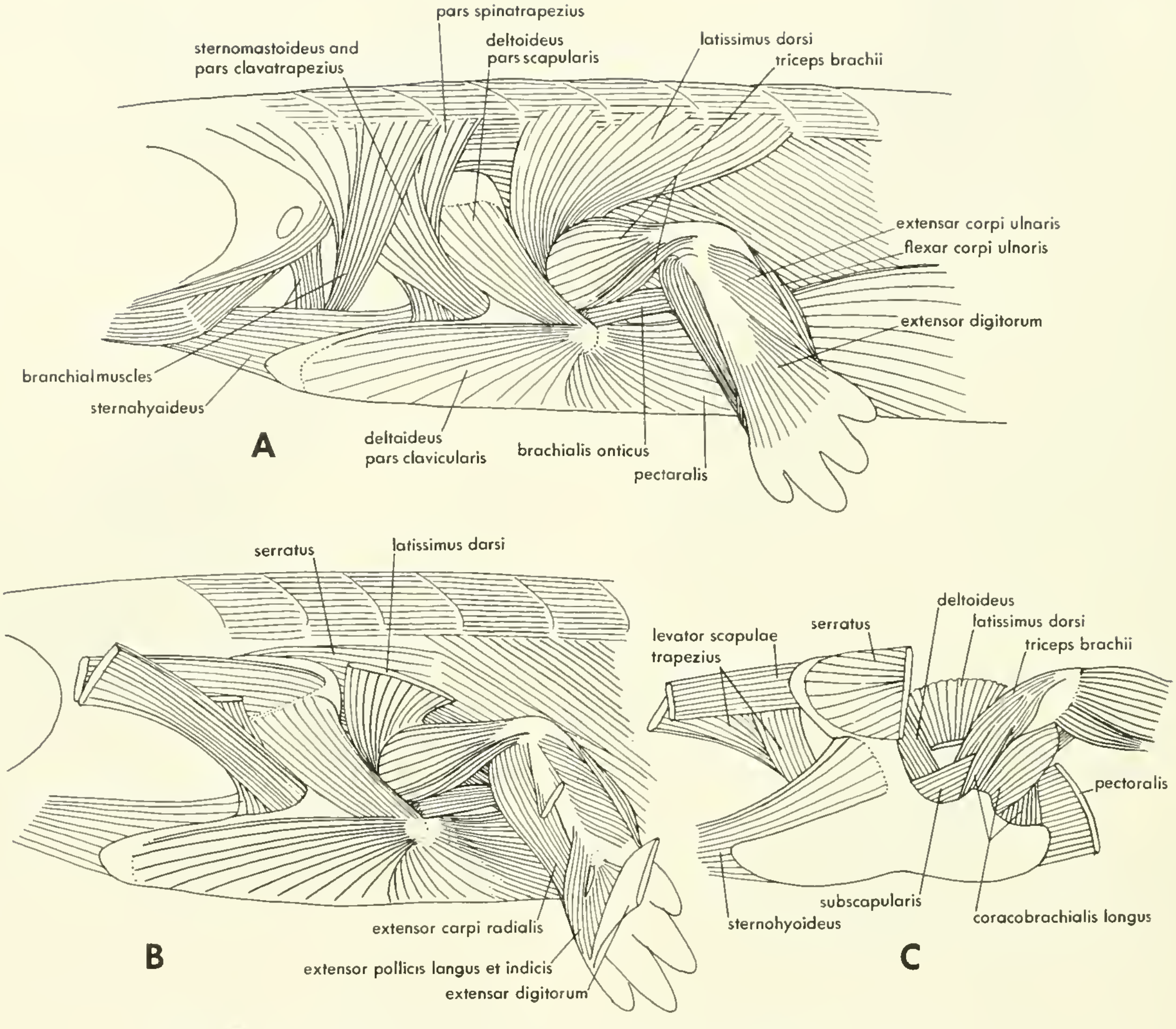


Figure 14-16. Lateral and medial view of bady and arm of *Cryptobranchus*. A, lateral view of superficial muscles; B, lateral view of deeper layer; C, inner view of shaulder region.

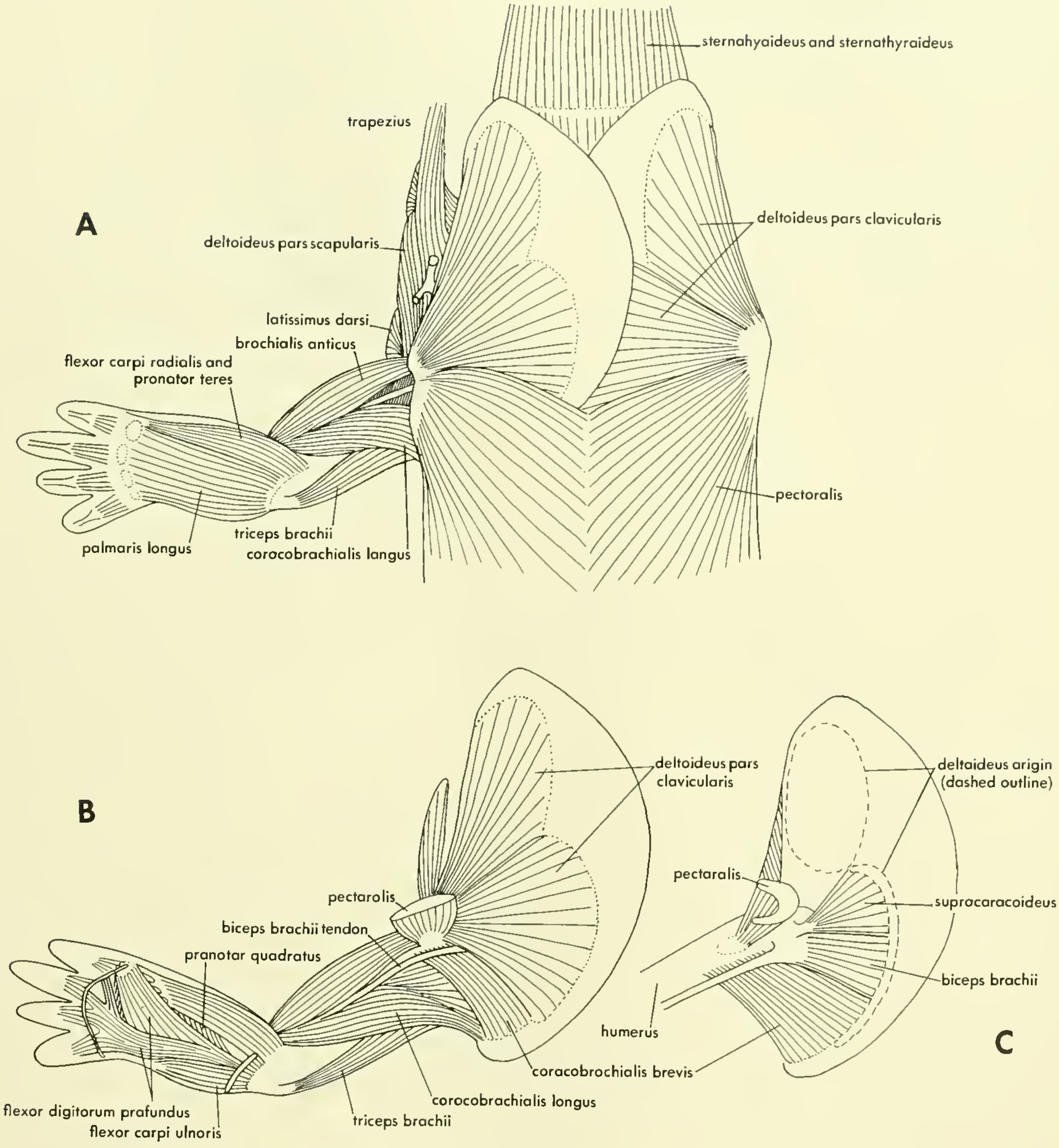


Figure 14-17. Ventral view of body and arm of *Cryptobranchus*. A, superficial muscles; B, deeper layer with pectoralis removed; C, same with clavicular deltoid removed.

TABLE 14-3 HOMOLOGY OF MUSCLES IN THREE GROUPS OF MAMMALS COMPARED WITH OTHER TETRAPODS

Placental	Marsupial	Monotreme	Reptile	Bird	Urodele
latissimus dorsi	latissimus dorsi	latissimus dorsi	latissimus dorsi	latissimus dorsi	latissimus dorsi
extensor antibrachialis	omoanconeus	dermoepitrochlearis	(lacking)	(lacking)	(lacking)
subscapularis	subscapularis	subscapularis	subscapularis	subcoracoscapularis	subscapularis
teres major	teres major	teres major	scapulohumeralis posterior	scapulohumeralis posterior (or dorsalis scapulae)	subscapularis
deltoideus scapularis clavicularis	deltoideus scapularis clavicularis	scapulodeltoideus coracohumeralis	deltoideus scapularis clavicularis	deltoideus tensor patagii	dorsalis scapulae procoracohumeralis longus
teres minor	teres minor	teres minor; proscapulohumeralis	scapulohumeralis anterior	(pro) scapulohumeralis anterior	procoracohumeralis brevis
triceps	triceps	triceps	triceps	triceps	triceps
pectoralis	pectoralis	pectoralis	pectoralis	pectoralis	pectoralis
panniculus carnosus	dermobrachialis	panniculus carnosus	(lacking)	(lacking)	(lacking)
supraspinatus* infraspinatus*	supraspinatus infraspinatus	supracoracoideus	supracoracoideus	pectoralis secundus	supracoracoideus
coracobrachialis	coracobrachialis	coracobrachialis superficialis coracobrachialis profundus	coracobrachialis longus coracobrachialis brevis	coracobrachialis posterior coracobrachialis anterior	coracobrachialis longus coracobrachialis brevis
biceps	biceps	biceps	biceps	biceps	biceps
brachialis brachioradialis	brachialis	brachialis	brachialis inferior humeroradialis (Sphenodon and crocodiles)	(tensor patagii brevis tendon) (tensor patagii longus tendon)	brachialis inferior (lacking)

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* Identified in text as parts of the supracoracoideus.

division and rearrangement of the parts of the primitive muscle sheets, there have resulted, without doubt, muscles which represent functional parallelisms, i.e. analogs. Where homologies begin or end must be arbitarily decided in each case.

Table 14-3 serves to show the homologies of the muscles discussed in the several groups, and in additional groups, and also indicates the nature of muscle synonymies, i.e. a listing of the names applied by different authors to a muscle of a particular organism or to the same muscle in different animals. For example, the pars scapularis of the deltoid is called the dorsalis scapulae in the Urodele, while in the bird the term dorsalis scapulae has been applied to the teres major. Synonymies are a usual feature of comparative studies since through time more accurate and thorough studies have lead to refinements of knowledge. Each step in this process has been marked by changes in nomenclature. The process is still going on.

General observations on muscles

On the basis of the eye muscles, the agnath is distinct from the gnathostome, if one assumes that the lamprey is representative. The weight of evidence supports such an assumption and there is no reason why one should suspect that the lamprey's eye musculature is anything but unmodified. The several groups of tetrapods show similar and perhaps parallel variations in their eye musculature.

Demonstration of a common pattern of tetrapod limb musculature has the value of focusing attention on the many adaptational changes observed in the several groups. One can observe muscles in every stage of multiplication, change of relationship, or loss. This variation suggests that musculature is of limited value in terms of broad phylogenies either because of the difficulties of analyzing the many details of structure involved in such a complex system or the ready response of this system to adaptive modification.

15

A Summation of Chordate Morphology

One of the desired goals of this text is to stimulate the student to make independent formulations about chordate morphology from his own summation of the facts and concepts presented. There are, however, still many aspects of such a summation which might be commented on before any arrangement of vertebrate types is attempted. These last comments are offered with the hope that they will inspire further adventures into chordate morphology.

It should be stated first of all that one can devise a phylogenetic classification of the chordates, based on their apparent morphological evolution, from the materials of this survey, for similar surveys have been the source of our current classifications. Although the materials now available to the student are certainly not complete, they are as adequate as those available to many students in the past. The student should approach the formulation of a phylogeny (or classification) as a reasearch effort at the border of our knowledge, not as a sterile exercise. This experience in systematics involves not only information on structure but also ways in which structure can be interpreted and utilized in a classification. An understanding of vertebrate systematics also includes a realization of the limitations of any classification. At this point the student should be aware that although the evolutionary process is strongly indicated, the pattern of phylogeny is quite hazy, but worthy of consideration.

TERMINOLOGY AND DEFINITION

Throughout this survey the problem of the definition of terms has been encountered again and again: terms applied to anatomical details or complexes, terms used at every level of description or discussion. The vagaries of terminology may leave the impression that comparative morphology is plagued more than other areas of science. This of course is not the case; semantics and definition are constant problems for every scientific field. One has only to penetrate the superficial aspects of any subject to encounter them.

Terms of special interest in the formulation of a phylogeny are primitive and advanced (or specialized), as they are applied in an evolutionary sense. A primitive feature is one presumed to be present in the common ancestor of any taxonomic grade or level. From this ancestral condition by specialization (radiation) modifications are produced and these adaptive changes are considered advanced features. A primitive feature of a particular group (genus, family, order, etc.) may be so identified because all, or most, species show it, because it is shared with other similar groups, or because it is the simplest condition known. These criteria do not always succeed in identifying the starting point of an anatomical sequence. For example, most fishes, fossil and living, have some sort of an operculum. Was this the primitive stage or did the pharyngeal slits open separately to the outside as in the sharks and some agnaths? The operculate condition may have stemmed from one in which the slits opened into bilateral atrial pouches or it may represent a specialization achieved separately in each of the several lines of fishes. In the case of lungs there is a very real question whether lungs were present in the primitive vertebrate and lost in a few of its derivative lines. There is also the problem whether all lungs (primitively present or achieved in some fishes) opened at first ventrally, laterally, or dorsally. Usually the first view is maintained.

In approaching a morphological definition of groups, one can be impressed more by differences than by similarities. These terms involve opposite approaches to comparisons and each can produce a different end product. On the one hand, the mammals might be viewed as constituting a well-defined and homogeneous group, while, on the other hand, their blending with the therapsids through several lines of descent could be considered as evidence against recognition of such a group. In systematics, one works with terms which come to be defined in a manner that fits the materials in a way that is thoroughly understood only by the person who knows the materials. Even observations tend to differ in terms of the background of the observer and the emphasis he places on differences or similarities. An understanding of the characteristics or features on which a phylogeny is based is difficult to transmit from one person to another; the shades of meaning and significance involved are open to many interpretations.

One of the great problems of systematics concerns the equating of living forms with primitive types. We are all inclined to represent the modern amphibians, reptiles, and mammals as progressively more complex stages. This type of staging is, however, extremely artificial and inaccurate. One must necessarily move back in time and carefully follow structural changes in each of these groups until a concept of the actual or hypothetical ancestral type is achieved. The ancestral tetrapod is *not* like a living amphibian. One may then ask whether the use of "amphibian" to identify the primitive tetrapod is proper. If the basis for defining an amphibian is only its habit of laying eggs in water, eggs which develop to a larval form which metamorphoses to an adult, then perhaps the original tetrapod was an amphibian. Again, the question of definition arises in the use of the term **metamorphosis.** In the case of the salamander this term infers only that the early stages have gills, while the adult utilizes lungs, without undergoing any sudden or drastic change in its way of life. In terms of the structure of the adult modern amphibian, the primitive tetrapod was as distinct from it as is the reptile or the mammal.

Let us consider specific cases in which problems of definition or interpretation crop up.

INTERRELATIONSHIPS OF AGNATHS AND GNATHOSTOMES

Perhaps the best marked division we have observed is that between agnath and gnathostome. In spite of the apparent difference of these two categories, there is considerable doubt as to how they should be identified. Generally speaking, it is assumed that the agnaths preceded in time, and represented a structural stage leading to, the gnathostomes. If it is assumed that some sort of skeleton was characteristic of the ancestral vertebrate, whether or not this is of a procartilaginous material, cartilage or bone, then this general type of skeleton should be common to these two groups. The skeleton observed in the agnath should be of a more primitive (or simpler) type than that of the gnathostome and the skeleton of the latter should show evidence of having been derived from the former. Looking at the cranial structure of these two groups, one cannot visualize such an interrelationship. It might be assumed that these two lines became distinct before the development of the complex skeletal system and, therefore, that the cranial skeleton cannot be utilized for comparison in this respect. Such a negative approach merely shifts the burden of proof to some other area of information.

Attempts to compare the various cartilaginous rods observed in the living agnaths with the various arches of the gnathostome suggest that, in fact, the gnathostome type is the less modified and, in some ways, the more primitive. However, the lack of articulation in the agnath branchial rods would seem to be a less modified condition than the articulated rods observed in the gnathostomes, although this form could also be achieved by carrying over the embryonic form into the adult (paedomorphosis or neoteny). This conflict of interpretations is not in itself a strange situation, but rather is typical of what one encounters in trying to analyze the features of living forms in terms of ancestral or primitive types.

Regarding the separation of the agnath and gnathostome lines, one can search for evidence from other areas. The lack of a premandibular aortic arch and the breaking up of the mandibular arch in both gnathostome and agnath, or the complexity of the cranial nerves, suggest that a complex mouth, like that of the gnathostome, was a basic vertebrate feature and that the first radiation of the vertebrates involved loss of this type of mouth by the agnaths. Such a feeding adaptation is matched by the several basic changes in the jaws of the gnathostomes in the course of their evolution.

In terms of the various systems of soft parts, there is nothing striking to support the direct derivation of the agnath from the gnathostome, or the reverse. However, from analyzing these systems, one does arrive at an image of the primitive vertebrate, an organism from which both agnath and gnathostome lines might have been derived with a minimum of change (this ancestral type was partly described at the end of Chapter 2). In comparisons with this hypothetical primitive type the agnath may appear to be more markedly specialized and modified than the gnathostome. For example, in their venous systems the lamprey and hagfish appear to have diverged from the basic vertebrate pattern further than the gnathostome. The same might be said of the digestive tract (loss of pancreas) and the excretory system (development of a peculiar type of holonephros).

In viewing the agnath-gnathostome dichotomy, one is impressed not by the positive nature of the evidence, but rather by the number of individually inconclusive clews on which one sort of interrelationship or another might be founded. No feature positively delimits these two groups. Each bit of evidence when added to others becomes more convincing but only in terms of probability or possibility. This taxonomic division, like most others, must be based on a number of characteristics, some of which may be true only of the majority of members. These features cannot generally be identified as primitive or advanced.

The theory of the agnath to gnathostome sequence is founded in part on the observation that the agnaths occur earlier in the fossil record. However, the first agnath fishes were already a rather heterogeneous array when first encountered. It is certainly true that we do not know a great deal about the structure of the first fishes, but there is sufficient evidence to support the view that at least three distinct types were present. These types differed in such fundamental features as the histology of their bones; that is, osteostracans had bone cells as opposed to the heterostracans which had acellular, aspidin bones. These three distinct types indicate that a great deal of vertebrate evolution had already occurred. When first encountered, at a somewhat later time, the gnathostomes also are highly diversified as to form.

The fossil evidence can be interpreted as indicating that the development of a bony armor occurred first among the agnaths and that this group was more widespread in distribution and its individuals were more numerous than the gnathostomes. The large gaps in the fossil record can only be interpreted as failures to record vertebrates rather than as evidence of their nonexistence. The nature of the fossil record does not support the view that the vertebrates arose only shortly before the first fossils, of Lower Ordovician age, were entrapped. It is quite possible that vertebrates, or protovertebrates, were present in the Cambrian along with representatives of other phyla. They may have been very few in numbers, local in occurrence, and limited to habitats in which fossilization was difficult or impossible.

The fossil record suggests that the earliest vertebrates were naked and that one of the first evolutionary trends among vertebrates was an increase in size and the development of some kind of support mechanism (skeleton), either internal or external. The fossil record does not reveal much as to the marine or fresh-water origin of these organisms. The fact that the earliest fossils occur in marine or brackish water deposits says little since these were already widespread, highly developed, and diversified creatures.

THE SHARK AS A PRIMITIVE VERTEBRATE

As a second question, let us consider the generally held view that the shark is a primitive vertebrate and is representative of a type from which the higher forms have stemmed. The general statements of this view vary somewhat. Some believe that *Squalus* is like the type, while others are less positive and suggest that it is the most direct derivative of the common ancestor, many of whose features it retains. The idea of the shark being like the ancestral vertebrate is reflected by the palaeontologists continual references to sharks, or shark-like vertebrates, in the early fossil record. As we have come to know more about the structure of vertebrates, and sharks, it is evident that the shark, as it is now defined, was not present until the late Devonian and was then quite distinct from the modern forms. The Devonian sharks are of several diverse kinds and these may not be closely interrelated.

The earliest gnathostomes (Upper Silurian, or if the *Palaeodus* and *Archodus* denticles are teeth, the Lower Ordovician) are described as acanthodians, and these are sometimes identified as sharks; however, the anatomy of an acanthodian, as least as far as it is known, is quite different from that of a shark. The general idea one can draw from the fossil record is that the shark is only one of several kinds of vertebrates produced by the first radiation; it is not the ancestral type nor necessarily more similar to the ancestral type than the others.

Yet the value of the shark to comparative anatomy is still rather high, since it does retain many features of the early vertebrate. What are some of these primitive features? One cannot say that the amphistylic or hyostylic jaw suspension of the shark is any more primitive than the kinds of jaw suspensions observed in palaeoniscoid or primitive choanates. In fact, it is doubtful that the palatoquadrate of the shark includes the autopalatine portion observed in the osteichthian. The orbital process of the shark palatoquadrate is perhaps a parallel development comparable to the epipterygoid. The solidly roofed chondrocranium may be somewhat more primitive than the more open roof observed in other groups, but this solid roof might also be a modification reflecting the simple observation that the shark did not develop a dermal roof of bones. The variations in chondrocrania observed in the shark, acanthodians, and arthrodires suggest an early period of experimentation. The type observed in the palaeoniscoid fishes and choanates may represent an independent development.

The circulatory system, the digestive system, the excretory system of the shark seem to retain many, if not most, of the ancestral features, and it is in this area of soft anatomy that the shark is most revealing. However, the development of a pronephric Müllerian duct in the shark and the peculiar holonephric kidney may be specializations peculiar to this group. The rectal gland of the shark, although it may be homologous to the bladder or allantois of higher forms, is unique in terms of its detailed structure. In terms of the finfold theory, it has already been pointed out that the fin of the shark may be primitive only for a part of the vertebrate array; it is not primitive for all kinds of gnathostomes and probably not for the Osteichthyes.

THE ORIGIN OF THE TETRAPODS

A third area of interest concerns the origin of the tetrapods. It is generally believed (Barrell, 1916) that the Devonian was a dry period, during which many ponds and streams tended to dry up seasonally, and that certain crossopterygian fishes were better able to move from drying pools to those of a less transitory nature. This thesis accounts for the development of the limb of the amphibian through the necessity of periodic escapes from drying pools. Although this view is generally accepted, it is now under attack. The attack is based on the observation that escape from drying pools would occur at a time when the moist skin of the fish would suffer most from drying. Movement over land by fishes is best done under moist conditions, not dry conditions. Further, movement over land can be accomplished by the use of fins, not necessarily by the use of limbs. It would seem more probable that the fin would be of more use to an aquatic form and would be as usable as a limb for short periodic escape jaunts over dry land. The idea that this periodic escape led directly to terrestrial habitation by these vertebrates was rejected by Romer (1958), for he finds it is fairly evident from the fossil record that amphibians and early reptiles were water inhabitants until the Pennsylvanian, and perhaps the late Pennsylvanian at that.

The problem of the origin of the limb does not seem to be resolvable in terms of periodic drought. It is not likely that a limb would be developed for periodic escape in a population many of whose members inhabited permanent waters. The fact that permanent waters existed, and on a widespread scale, is indicated by the occurrence and wide distribution of crossopterygians and early actinopterygians.

The origin of the limb must be sought in some other direction. It is more likely that amphibians developed in an aquatic habitat where the limb was advantageous, not for short periods but throughout the entire life of the organism. The nature of the waters in which the amphibian developed would be different from that in which crossopterygians and dipnoans lived. This is necessarily the case simply on the basis of the observation that limbs did not develop in these groups or that, at least, these groups remained fishes.

It might be assumed that the limb developed as a means for progression through vegetation-choked waters. Such waters around the margins of ponds or along stream courses were areas into which food organisms could escape from the open-water predators. Such food reservoirs would be attractive to an organism which could crawl through, around, over, and under various obstacles. At this time, aquatic and terrestrial vegetation was beginning to develop; certainly vegetation-choked waters were common during the carboniferous. Such waters, because of rotting, would require an air-breathing type of animal. Invasion of this kind of habitat could explain the development of limbs and air breathing structures much better than the theory of movement over dry land. The limb, as developed for the invasion of such waters, would also serve for escape during periods of drying. It was perhaps a more effective or preadapted device for progression over the land than the fin.

The exact ancestry of the amphibian is open to question. The general view is that an osteolepid crossopterygian was the ancestral type since there is best agreement in terms of the cranial roof. However, as is evident from our review, this supposition is not particularly well founded. There appear to be striking resemblances between many features of the amphibians and the dipnoans. These features are, perhaps, just as important as the agreement in cranial plates. The differences in the snout region between the amphibian and any choanate fish would suggest that this is a separate line of evolution, which arose at the same time as the other choanate lines. The common ancestor of all these choanate organisms might have been somewhat closer to the osteolepiform than to the dipnoan in some features, but it would seem to be somewhere in between these two extremes in an over-all evaluation.

As far as specific details are concerned, one might say that the palatoquadrate of the ancestral tetrapod was closely articulated with the endocranium, that the hyomandibula was greatly reduced, and the pharyngohyal portion well developed. The symplectic disappeared along with the reduction of the hyomandibula, and the ceratohyal became attached primarily to the palatoquadrate area. In this way the many intermediate features of the hypothetical amphibian ancestor could be described in detail, but this seems unnecessary.

The view, then, that the amphibian is an osteolepid or "crossopterygian" must be rejected on the grounds that, as defined, the amphibian and crossopterygian represent parallel, or largely contemporaneous, developments. The general supposition that the crossopterygian, dipnoan, and amphibian all had a three-chambered heart at the time of their separation, suggests that in some ways the amphibian was the least modified of the three main groups and thus was closer to the ancestral form. The crossopterygian, the actinistian, and the dipnoan may represent modifications away from the amphibian toward a more aquatic way of life.

These three examples are typical of the questions that arise in systematics. In discussing them the nature of the fossil record has been stressed, as well as the general role of anatomical detail. Next, the place of embryology in a phylogeny should be mentioned.

THE BIOGENETIC LAW

The so-called biogenetic law, that ontogeny recapitulates phylogeny, can now be reconsidered with more understanding. As a generality, one can say that ontogeny supplies little information on phylogeny. If we consider the early stages of development as described in Chapter 7, it is apparent that a general pattern of cleavage, blastulation, gastrulation, and organogenesis occurs in each of the vertebrates but each of these stages in this sequence of events varies in each of the types described. The developmental stages appear to be the most direct way by which a unicellular egg can reach a multicellular, complex organisms. The similarities of developmental stages reflect the similarities of starting point and end product.

From the many styles of development observed, it would be difficult to say which is the more primitive and which the more advanced. The development of the lamprey, for example, is probably primitive in the form of the egg, its cleavage, and gastrulation. The development of the nerve tube from a solid neural keel may be either primitive or advanced; the latter view is generally held. A similar type of neural keel is observed in the actinopterygian fishes and probably represents a parallel modification. It can be assumed that an egg with a small amount of yolk is primitive, and therefore that the lamprey is, perhaps, the most primitive of the vertebrates in this respect; but in contrast to the lamprey, the hagfish represents a highly modified form. Thus, within the agnath fishes one sees both extremes, not only in terms of the egg but also in terms of the neural tube.

The variations of development as described indicate rather clearly that each kind of vertebrate has modified different stages of the developmental sequence to fit its own individual adaptive adjustment. The return to a relatively yolk-free egg in the mammals is a reflection of the development of a placenta, a new way of supplying nutritive materials to the developing embryo and foetus. Nutritive needs have called forth a variety of kinds of placentation in several kinds of animals.

Ontogeny may occasionally give clews to phylogeny; for example, the appearance of a dorsal diverticulum in some sharks suggests a rudimentary lung. In birds the pterygoid bone is primitively a single unit which, in many species, later becomes divided into two articulating parts, the more anterior one of which fuses with the palatine. This assumed phylogenetic sequence is revealed by the development of the bone. The appearance of rudimentary structures, some of which later degenerate and disappear, suggests retention of phylogenetically revealing pathways of development.

On the basis of this review of morphological problems and theories, the actual structuring of a phylogeny can now be approached.

VERTEBRATE PHYLOGENIES

The delineation of phylogenies has occupied the attention of many comparative morphologists working on the theory that an understanding of the actual pathways followed in evolution will contribute to our understanding of the evolutionary process. The student will find many diagrams and discussions of this matter in the literature of morphology. Table 15-1 is a summary of opinions held up to about 1930. This pattern does not represent any individual's opinion, but rather is a composite or average view. The position of the ostracoderms is peculiar, but it was not until this time that it was realized that they were agnath fishes. A more recent tree of the vertebrates, Table 15-2 (Romer, 1955) shows a slight modification of earlier views, a replacement of the idea that the dipnoans are along the line of decent of the tetrapod organisms. Here the dipnoans become a side issue, and the osteolepiforms lie on the main line of descent. In this scheme the actinopterygian evolved through two series, the chondrosteans and holosteans.

Table 15-3 is a current European view which is peculiar only in that the coelacanths are removed from the choanates, and the Dipnoi are set aside as a dead-end group distinct from the choanates. The term choanate is here restricted to crossopterygian fishes and their derivatives, the various kinds of tetrapods. This particular scheme is somewhat unique in that it derives the urodeles from the porolepiforms and the labyrinthodonts from the osteolepiforms. Further, the sauropsid and therapsid, the reptiles, are derived directly from osteolepiforms rather than indirectly through a common ancestor as the Anura also are.

Table 15-4 is a summary of the basic views presented in this book. It varies from the others in that the holocephalans and sharks are not placed together any more closely than either is to the arthrodires and acanthodians. This phylogeny does not include primitive groups which have not been discussed; there are other branches, then, among those shown. The branch of the gnathostomes which leads to the Osteichthyes produced two main lines, the actinopterygians and the choanates. The actinopterygian line gave rise

TABLE 15-1 A DEPICTION OF THE VIEWS, GENERALLY HELD PRIOR TO 1930, OF THE PHYLOGENY OF THE VERTEBRATES (AFTER JARVIK, 1960)

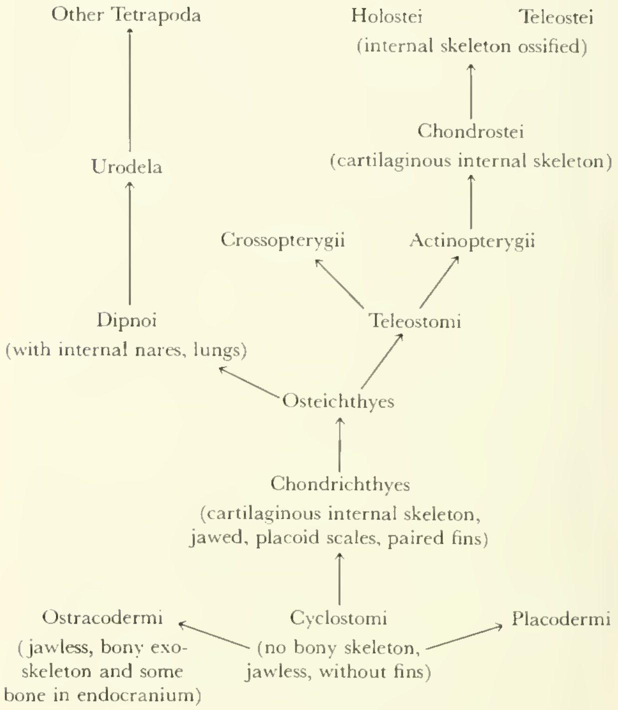


TABLE 15-2 THE BASIC PHYLOGENY OF THE VERTEBRATES AS CONCEIVED BY ROMER (1955)

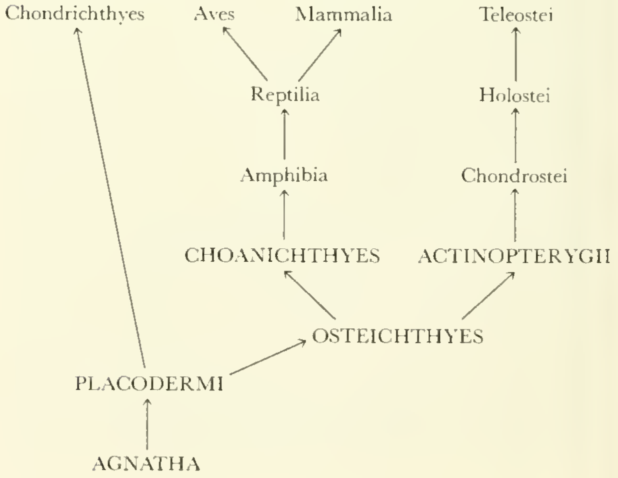
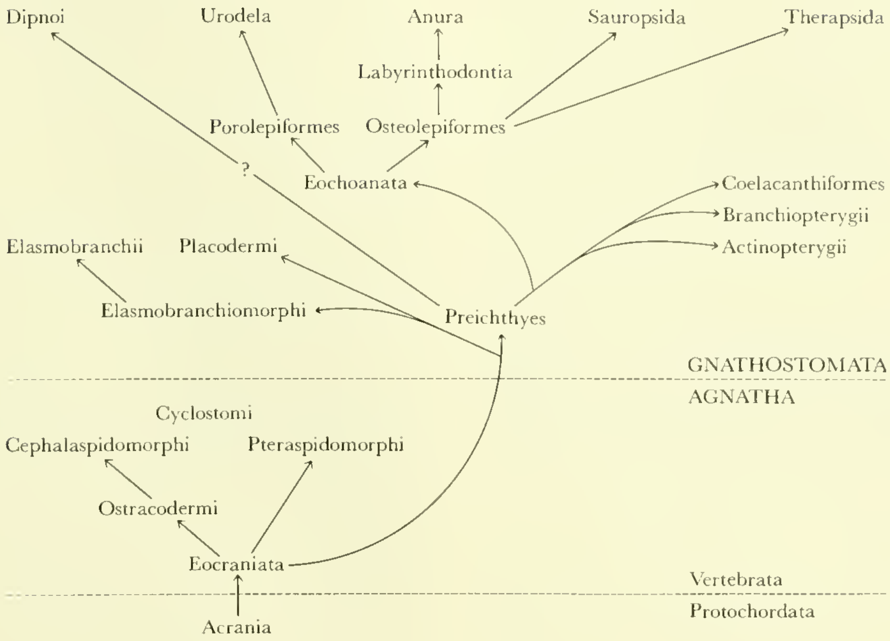


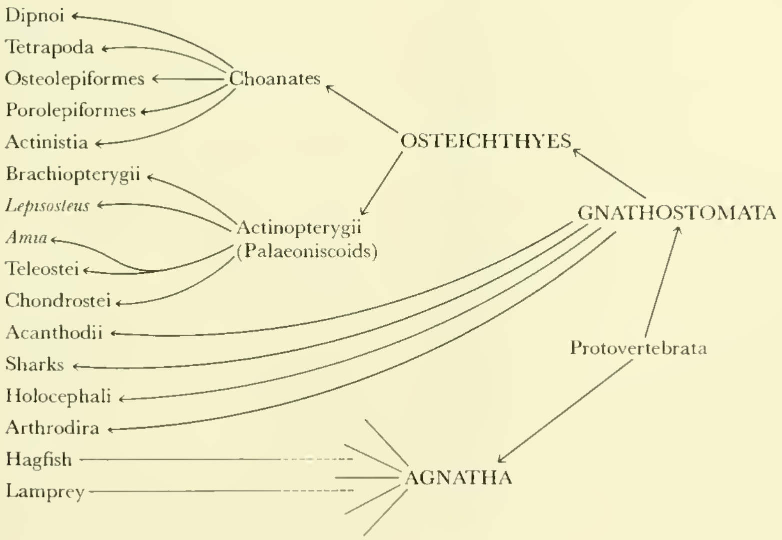
TABLE 15-3 THE PHYLOGENY OF THE VERTEBRATES ACCORDING TO JARVIK (1960)



periodically to radiating sidelines; some of these became extinct and a few survived. An early branch gave rise to the brachiopterygian type, while later ones gave rise to the sturgeons and *Lepisosteus*.

The living holosteans present a special problem. The differences between *Amia* and *Lepisosteus* have long been known (Hay, 1898), but these two kinds of fishes are still placed together, and the inference is that they are closely related. Our examination suggests that although they do agree in having lepidosteid tubes in their cranial bones, they disagree in many features. The presence of lepidosteid tubes is suggestive only of a functional parallelism in bone development; it is not indicative of close common ancestry. Like the brachiopterygian, *Lepisosteus* appears to be a relatively

TABLE 15-4 BASIC PHYLOGENY OF THE VERTEBRATES AS SUGGESTED IN THIS TEXT



direct derivative of a primitive palaeoniscoid type, whereas *Amia* appears to be a highly modified actinopterygian more closely related to the teleost.

In some ways, as in its scale structure, *Amia* appears to be as advanced as the teleost, but in other features it is more primitive, as in the less ossified endocranium, the retention of supramaxillae, and in the heavier bones throughout the body. *Amia* agrees with the teleost in having an interopercle and apparently is a derivative of one of the early lines in which this bone appeared. The interopercle may be a parallel development in several lines or it may indicate common ancestry, having been developed only once, early in the evolution of the actinopterygians.

The evolution of the choanates suggests that primitively the lungs were highly developed, aerial respiration was well established, and a three-chambered heart was present. This line underwent a period of radiation which produced several kinds of fishes and the ancestral tetrapod. The tetrapods have been placed between the osteolepids and the dipnoans to indicate that structurally they are somewhere in between these two groups. The tetrapod line is not identified as amphibian for the simple reason that when it first appeared, it was already a complex array of types, rather than a single simple line. Furthermore, the pelycosaur and sauropsid reptiles appeared almost as early in the record as the amphibians. The Amphibia then may be only an array of types paralleling in some respects the two early lines of reptiles. As the two lines of reptiles developed, one gave rise to the mammals and the other to the living reptiles and birds.

These superficial remarks leave many possibilities for interpretation and documentation to the student, who may evaluate them and form his own conclusions. This review of phylogenetic concepts and facts should at least strengthen the impression that the classifications of vertebrates are open to refinement and that there is much yet to be learned about the chordates and their evolutionary history.

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A list of references in a text is sometimes viewed as superfluous since many, or most, students do not use it; however, those who do will find the experience informative and stimulating. Comparative morphology has perhaps the most extensive literature of any of the areas of biological study and among its sources are some of the first works in science (see Cole, F. J., "A History of Comparative Anatomy from Aristotle to the Eighteenth Century," London, The Macmillan Co., 1944; or Nordenskiöld, E., "The History of Biology: A Survey," New York, Tudor Publishing Co., (1928). One might wonder which is the more interesting: a study of the literature regarding the chordates, or the direct study of the materials. Certainly the student should not separate these two aspects of his study.

References fall into a number of categories: basic reference works, texts, and articles in periodicals. As sources for any particular subject the student should go to *Biological Abstracts,* which lists short summaries according to author and subject, and *Zoological Record* (London), which lists an even greater number of authors and titles in different subject areas, but without abstracts. Some groups of vertebrates have special bibliographies which are quite complete (up to the date of their publication), such as Strong's "Bibliography of Birds" (Chicago Museum) and Dean's "Bibliography of Fishes" (American Museum).

Because of the large number of references involved in almost any investigation, the most direct method is to look for a recent paper in the area of interest, or a basic reference, and then explore the cited literature and the lists of references given by these. Working back in this way to the earliest papers gives a good cross-section, but not necessarily a complete one, of what has been written. Many papers are in obscure periodicals, which are seldom available and thus generally overlooked. Further, the most recent papers will have to be found by search of the periodicals themselves, because the indexing services are a year or two behind the actual publishing dates.

Journals giving much space or attention to subjects of morphological interest include the following: *Acta Zoologica* (Stockholm), *American Journal of Anatomy, American Journal of Microscopy, Anatomical Record, Anatomische Hefte* (*Abt.* 2, *Ergebnisse der Anatomie und Entwicklungsgeschichte*), *Anatomische Anzeiger, Arkiv für Anatomie* und *Physiologie* (*Anatomische Abt.*), *Archives de Biologie, Arkiv för Zoologi, Jahrbuch für Morphologie und Microscopische Anatomie, Journal of Anatomy* (London), *Journal of Morphology, Journal of Comparative Neurology, Philosophical Transactions of the Royal Society of London, Proceedings of the Zoological Society of London, Quarterly Review of Biology, Quarterly Revues, Quarterly Journal of Microscopical Science, Transactions of the Royal Society of Edinburgh, Transactions of the Zoological Society of London, Zeitshrift für Anatomie und Entwicklungsgeschichte, Zeitschrift für Morphologie und Ökologie der Tiere* (*Abt. A of Zeitschrift für Wissenschaftliche Biologie*), *and Zoologische Jahrbücher* (*Abt. für Anatomie und Ontogenie der Thiere*). This list is only a partial one; it does not include the irregular publications (Bulletins, Festschriften, Memoires, Monographs, Occasional Papers, etc.) of many museums, institutes, universities, or academies. Other periodicals are indicated below in the chapter references.

There are several basic reference works in this field, most of which are multivolumed. Currently being produced is the "Traité de Zoologie," edited by Pierre-P. Grassé, Paris, Masson et Cie, (Vols. XI, XII, XIII, XV and XVII are complete). This series of volumes represents a summary of our knowledge of the morphology, physiology, behavior, and systematics—each chapter by an expert in the particular area under discussion. Of particular interest is Volume XII, "Vertébrés: Généralités, Embryologie Topographique, Anatomie Comparée, Caracteristiques Biochimique." Of a similar nature is the "Handbuch der Zoologie," edited by W. Kukenthal and T. Krumbach (Berlin, W. deGruyter). Started in 1923, it is still incomplete. Bronn's "Klassen und Ordnungen des Thier-reichs" Leipzig, C. F. Wintersche, 1874–1938 preceded the Handbuch, but is still incomplete. A thorough summary of vertebrate (and cephalochordate) morphology is given by the six volumes of Bolk, Göppert, Kallius, and Lubosch's "Handbuch der vergleichenden Anatomie der Wirbeltiere" (Berlin und Wein, Urban und Schwarzenberg, 1931–1938). The various chapters, again written by experts in the area discussed, present many and often divergent views. Many areas of information are discussed at great length while others are scarcely mentioned. These volumes certainly are a starting point for any serious morphological investigation, both for the facts presented and for the references to the literature.

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More restricted references of interest include "Traité de Paleontologie," edited by Jean Piveteau. Volumes V (1955) and VI (1961) are completed, and cover the tetrapods from the Amphibia to the Mammalia. Many details of anatomy are discussed; those affecting or marking the skeletal system. G. Kingsley Noble's "The Biology of the Amphibia" (New York, McGraw-Hill Book Co., Inc., 1931; New York, Dover Publications, Inc., 1954) is a fine general account for amphibians, with an excellent reference section. "The Physiology of Fishes" (in two volumes) ed. by M. E. Brown (New York, Academic Press, 1957) and "The Biology Comparative Physiology of Birds" (in two volumes, ed. by A. J. Marshall (New York, Academic Press, 1960–1961)) supply many useful notes and citations. J. F. Daniel's "The Elasmobranch Fishes," 3rd ed. (Berkeley, University of California Press, 1934) is a rather detailed but incomplete account of the anatomy of sharks and includes extensive lists of the literature regarding the various structural systems. G. R. De Beer's "The Vertebrate Skull" (Oxford, Clarendon Press, 1937) brought together most of what was known of and believed about the vertebrate head skeleton. A. S. Romer, "Osteology of the Reptiles," (Chicago, Univ. of Chicago Press, 1956) contains a wealth of information on the bony structure and fossil history of the reptiles. Mammalian Anatomy is well covered in the two volumes of "Die Saugetiere" by M. Weber, H. M. de Burlet, and O. Abel (Jena, Gustav Fischer, 1927–28). Histology texts such as Maximow and Bloom's "Textbook of Histology," 6th ed. (Philadelphia, W. B. Saunders Co., 1957), Ham's "Histology," 3rd ed. (Philadelphia, J. B. Lippincott Co., 1957) and LeGros Clark's "The Tissues of the Body," 2nd ed. (London and New York, Oxford University Press, 1945) tell much about the fine structure of the mammal. There are several comparative histologies, but Krause's "Mikroskopische Anatomie der Wirbeltiere" (Berlin and Leipzig, 1923) remains the standard. Comparative Embryology began with O. Hertwig's "Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere" (Jena, 1901–1906), the three volumes of which still remain interesting and useful, particularly as sources for the early literature. O. E. Nelsen's "Comparative Embryology of the Vertebrates" (New York, McGraw-Hill Book Co., Inc., 1953) and A. F. Huettner's "Fundamentals of Comparative Embryology of the Vertebrates," 2nd ed. (New York, The Macmillan Co., 1949) bring this area up to the present. The fundamentals of the developmental processes and the details of human embryology are discussed by many modern texts.

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Index

Capitalized entries are author's names; italicized page numbers refer to illustrations.